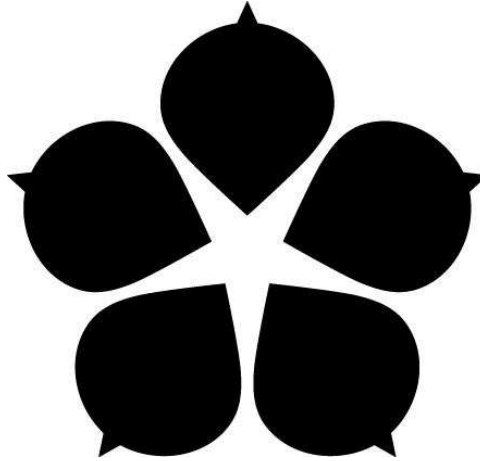


University of South Bohemia in České Budějovice  
Faculty of Science



**How universal are reserve design rules? A test using  
butterflies and their life history traits**

RNDr. Thesis

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### **Annotation**

This thesis uses butterfly species lists for 125 Czech National Nature Reserves and Monuments to test the validity of generally agreed 'reserve design rules' using multivariate ordination analyses. We used analyses of butterfly life history traits to seek for biological mechanisms responsible for butterfly community responses to geometric and heterogeneity characteristics of the reserves. We found that different design characteristics are important for individual species, depending on their life histories.

### **Declaration [in Czech]**

Prohlašuji, že svoji rigorózní práci jsem vypracovala samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

Prohlašuji, že v souladu s § 47b zákona č. 111/1998 Sb. v platném znění souhlasím se zveřejněním své rigorózní práce, a to v nezkrácené podobě elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejích internetových stránkách, a to se zachováním mého autorského práva k odevzdanému textu této kvalifikační práce. Souhlasím dále s tím, aby toutéž elektronickou cestou byly v souladu s uvedeným ustanovením zákona č. 111/1998 Sb. zveřejněny posudky školitele a oponentů práce i záznam o průběhu a výsledku obhajoby kvalifikační práce. Rovněž souhlasím s porovnáním textu mé kvalifikační práce s databází kvalifikačních prací Theses.cz provozovanou Národním registrem vysokoškolských kvalifikačních prací a systémem na odhalování plagiátů.

České Budějovice, 1. 9. 2017

Mgr. Alena Bartoňová

### **Contribution of the candidate**

This thesis is based on the following publication:

Bartoňová A., Beneš J., Fric Z., Chobot K., Konvička M. (2016) How universal are reserve design rules? A test using butterflies and their life history traits. *Ecography* 39: 456-464.

Alena Bartoňová is the first and corresponding author of the paper based on her Master thesis. Alena processed data collected by many lepidopterologists and data provided by Nature Conservation Agency of the Czech Republic, and did the statistical analyses. She wrote the manuscript together with M. Konvička.

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## How universal are reserve design rules? A test using butterflies and their life history traits

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We used butterfly species lists available for a set of 125 Czech Republic National Nature Reserves and Monuments, the highest small-sized conservation category in the country encompassing practically all biotope types existing in central Europe, to test the validity of generally agreed ‘reserve design rules’ using multivariate ordination analyses. Further, we used ordination analysis of butterfly life history traits to seek for biological mechanisms responsible for butterfly community responses to essentially geometric reserves characteristics. Reserve area, relative perimeter, within reserve habitat heterogeneity, and surrounding landscape compositional and configurational heterogeneity all affected the composition of butterfly assemblages after controlling for effects of geographical position and prevailing biotope type. Species inclining towards large reserves displayed low mobility and high local population density, probably because they require large habitat areas to maintain self-sustaining populations; such species tend to have restricted distribution in the country and threatened status. Reserves with relatively long boundaries hosted species with high mobility, broad trophic range and long adult period; faunas of such reserves contain high proportions of widespread generalists. Species with narrow trophic ranges inclined towards reserves containing diverse habitats, probably due to requirements for high floristic diversity. Species with short adult flight, low generations number and overwintering in early stages inclined towards reserves situated amidst diverse landscapes, perhaps because such species require finely-grained mosaics for metapopulation dynamics. Commonly agreed reserve design rules thus hold for Central European butterflies, but different design characteristics are important for individual species, depending on their life histories.

Protected areas are indispensable for biodiversity conservation. Aside from large areas such as national parks – aiming to maintain evolutionary and ecological processes on large scales – there exist small reserves around the world, conserving regionally important natural values providing biodiversity refuges and dispersal stepping stones in human-altered landscapes (Thomas et al. 2012). Over the course of years, conservation biologists have agreed upon several ‘rules’ concerning optimal reserve design (Diamond 1975, Soule and Simberloff 1986), mirroring the progress of ecological theory (e.g. island biogeography theory: MacArthur 1967; metapopulation theory: Hanski 1999) and much debated such issues as whether large isolated reserves are better than clusters of several small ones (SLOSS debate: Lomolino 1994, Kunin 1997, Pysek et al. 2002). Because reserves rarely exist in isolation (Laurance 2008) and species occurring in reserves may also utilise the surrounding non-protected ‘matrix’ (Ricketts 2001), the habitats and landscape heterogeneity structure surrounding individual reserves affect the species richness and composition within the reserves (Dennis 2004, Slancarova et al. 2014). This applies, in particular, for overexploited human-dominated landscapes, in which

surrounding landscape heterogeneity affects populations’ stability (Oliver et al. 2010) and accessibility of a reserve for migrating animals (Duflot et al. 2014). Because ecosystems are naturally patchy (Vera 2000) and because species tend to utilise varying resources in specific stages of life or for specific activities, reserves should also harbour internal heterogeneity of conditions (Dennis et al. 2003). To reiterate, a high quality reserve should be large, with a relatively short perimeter, located in a diverse landscape, and containing high internal habitat diversity.

For a long time, the reserve design debates had been restricted to maximising species richness (Soule and Simberloff 1986). However, species are not equal, and their requirements for site conditions may vary with trophic levels, degrees of specialisation or taxonomic group (McCarthy et al. 2006, Robinson et al. 2014). Even closely related species may differ in the degree of their association with the reserve-protected habitats – from species entirely depending on the reserve-protected habitats to those utilising the non-protected matrix and occurring in a reserve only by chance. Limiting the focus to threatened species numbers does not help much either, because the causes of threats may

vary among species, including closely related ones (Slancarova et al. 2012) and because threatened species may vary in their perceptions of habitats (e.g. forest interior vs edge specialists) (Tingley et al. 2013, Jeppsson and Forslund 2014).

The above problems are surmountable using multivariate statistical techniques, or ordinations, which analyse effects of external predictors on the species composition of natural communities, retaining species identities (Ter Braak and Smilauer 2012). Furthermore, ordination results can be attributed to life histories of constituent species (traits analysis: Boerschig et al. 2013, Carboni et al. 2014). In the context of reserve design rules, this approach promises linking such essentially geometric reserve attributes as area or boundary shape with individual species life histories, disclosing the general biological mechanisms structuring reserve faunas, and providing advice for practical conservation.

Butterflies are a popular model group, both in studies of reserve faunas (Koh and Sodhi 2004, Wenzel et al. 2006, Jarosik et al. 2011, Slancarova et al. 2014) and life history traits analyses (Barbaro and van Halder 2009, Boerschig et al. 2013, Carnicer et al. 2013). In temperate regions, butterfly life histories are believed to form a generalist–specialist continuum, loosely linked to distribution and conservation status (Menendez et al. 2007). Generalists, in contrast to specialists, tend to be wide-ranging, mobile, large-bodied, occurring in low densities, forming multiple generations per year, overwintering in later stages and utilising broad trophic ranges (Bartonova et al. 2014); they also tend to display high genetic diversity and low differentiation (Habel and Schmitt 2012). Specialists, often closely connected with certain habitat conditions, are more prone to habitat loss or fragmentation (Menendez et al. 2007). Recent findings, however, are challenging the conjecture that strict specialists should be the most threatened group (Habel and Schmitt 2012, Dapporto and Dennis 2013, Habel et al. 2013), as well as the oversimplified view that butterfly life histories form just a single dominant gradient (Bartonova et al. 2014), or that this continuum remains the same under changing habitat conditions (Carnicer et al. 2013).

Here, we analyse species lists of butterflies recorded in 125 nature reserves in the Czech Republic (Fig. 1), none of them established explicitly for butterfly or even insect conservation, relating the reserve geometry to the butterfly life history traits. The lists were compiled during a short three-year period following the same field protocol. The reserves, on the other hand, encompassed a great variety of reserve sizes, altitudes, surrounding landscape types and reserve-protected biotopes. They included practically all natural habitats existing in central Europe, from lowland dry grasslands and floodplains to mountain woodlands and subalpine habitats. This diversity of surveyed reserves allows testing the generality of reserve design rules for a well-studied animal model group (Boggs et al. 2003).

Specifically, we first asked if the reserve attributes routinely believed to influence reserve quality affect butterfly assemblages inhabiting the reserves, after statistically controlling for site-specific conditions. Second, we analysed the species responses to reserve attributes on the level of species life histories, asking which traits are in fact linked to reserve quality criteria.

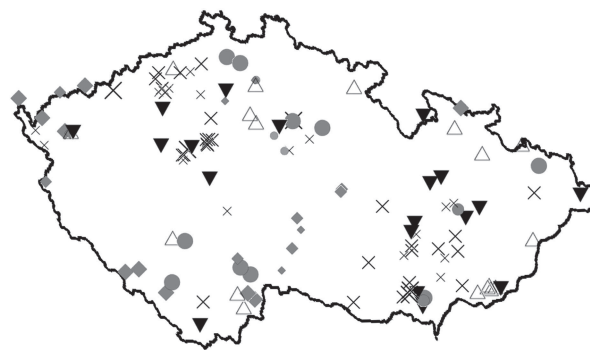


Figure 1. Positions of 125 National Nature Reserves/Monuments used for study on butterfly life history traits composition in the Czech Republic. Prevailing biotope types and ranked reserve sizes are symbolized. Black triangle: forest, cross: steppe, white triangle: meadow, grey diamond: peat bog, grey circle: wetland; symbol size: small (< 10 ha), medium (10–100 ha), and large (> 100 ha) reserves.

## Methods

### Butterfly survey in National Nature Reserves

Butterfly data for this study originated from a survey of 125 National Nature Reserves and National Natural Monuments, commissioned by the Nature Conservation Agency of the Czech Republic, and carried out in 2004–2006 (Benes and Konvicka 2006, Cizek et al. 2013). Czech National Nature Reserves/Monuments (NNR, herein ‘reserves’, total  $n = 221$ ) are typically smaller localities, believed to cover most valuable nature sites in the country and administered by the central government; in addition to them, the Czech protected areas system includes four large-sized National Parks, 25 large-sized Protected Landscape Areas, and about 1800 small-sized Regional Reserves. The 125 National Reserves analysed here are scattered across the whole country (Fig. 1) and cover a wide distribution of area sizes (mean = 166.4 ha, median = 55.8 ha, range 0.3–2050.3 ha; 43 of them > 100 ha, 31 of them < 10 ha), altitudes (mean = 435.2 m, median = 375 m, range 160–1195 m); and protected biotopes.

Butterfly surveys were carried out by 38 experienced lepidopterists, contracted for the work. Each reserve was visited by a lepidopterist five times, always under weather suitable for butterfly activity, once per month between May and September, to cover all seasonal aspects. Butterflies were recorded by the timed survey method (Kadlec et al. 2012). Visit durations scaled with reserve area (< 25 ha: 1 h, < 50 ha: 1.5 h, < 100 ha: 3 h, < 200: 4 h, > 200 ha: 5 h). (See Supplementary material Appendix 1 for the list of species recorded in each reserve.)

For each reserve, we considered the following characteristics presumably influencing the composition of butterfly assemblages (Storch et al. 2003, Cizek et al. 2013): area; latitude (lat); longitude (long), average altitude (alt), and prevailing biotope type (simplified categories, distinguishing steppe grassland, meadow, wetland, peat bog, forest).

GIS processing (ArcGIS 10; ESRI 2011) was used to describe the reserve heterogeneity and geometry. Shapefiles

of all reserve boundaries and extensions as 2000 m buffers around the boundaries were created. Next, we merged the shapefiles with the layer of 'habitats', created by mapping the entire Czech territory land covers and distinguishing 172 types of natural and human-altered habitat types obtained from the database of the Nature Conservation Agency of the Czech Republic and defined by Chytrý et al. (2011).

Using these two layers, the following characteristics were extracted: 1) the reserve area; 2) relative perimeter, expressed as perimeter:area ratio, reflecting the influence of reserve surrounding on the communities within the reserve (cf. Farhat et al. 2014); 3) the number of habitat types within the reserve (habitats within); 4) the number of habitat patches within the reserve (patches within); 5) the number of habitat types in the 2000 m buffer around the reserve (habitats outside); and 6) the number of habitat patches in the 2000 m buffer (patches outside). Numbers of habitat types (3, 5) represent compositional heterogeneity of reserves and their surroundings, i.e. the diversity of habitats within the area considered, whereas the number of habitat patches (4, 6) represent configurational heterogeneity, i.e. into how many separate patches are the habitats divided (Gustafson 1998, Slancarova et al. 2014). The 2000 m buffer was selected as a workable compromise between studies that detected landscape effects on butterflies at much smaller (i.e. 500 m: Flick et al. 2012, Slancarova et al. 2014) and larger (5 km: Bergman et al. 2004, 2008) buffers. (See Supplementary material Appendix 2 for each reserve's characteristics.)

### Butterfly life histories and phylogeny

For all butterflies recorded, we coded ten life history traits referring to their dispersal and survival abilities (cf. Bartonova et al. 2014) and two additional attributes describing their distribution extent and conservation status. Traits linked to dispersal were 1) body size, approximated as forewing length (from Higgins and Riley 1970); 2) mobility, or the propensity to disperse (ranked 1–9 scale, from extremely sedentary to extremely mobile; Reinhardt et al. 2007); 3) density, the number of individuals which can occur per unit area of habitat (ranked 1–9 scale, sparse to dense, adapted from area demand in Reinhardt et al. 2007); 4) voltinism, or the average number of generations per year in the Czech Republic (Benes et al. 2002); 5) flight period length, number of months of summed adult flight, excluding months of hibernation (Benes et al. 2002), 6) range size, the total geographical range (ranked 1–4 scale, from the size of Europe to larger than Palearctic realm, adopted from Tolman and Lewington 2008). Traits related to landscape scale survival were 7) fertility, defined as number of eggs for a female at eclosion (ranked 1–9 scale, from few to many, Reinhardt et al. 2007); 8) overwintering stage, as a proxy for development speed (ranked 1–5 scale, from egg to migrating adult, from Tolman and Lewington 2008); 9) trophic range, expressed as an index that weights the number of consumed host plant families (F) and genera (G):  $I = (G \times F^a)^{1/2}$ , where  $a = F/2G$  (data obtained from Ebert and Rennwald 1991; index modified after Garcia-Barros 2000); and 10) host plant form, expressing prevailing host plant apparancy (ranked 1–4, from small forbs to trees). The additional

two attributes were 11) distribution, the number of Czech Republic atlas grid squares with positive records for a given species in 2002–2013 (obtained from Czech Butterflies and Moths Recording [CBMR]); and 12) Red list, the species status in the national Red list (Benes et al. 2005).

In the cases of mobility, density and fertility, there were missing values for 30 species (Reinhardt et al. 2007). The missing density and fertility values were replaced by means for the respective traits; whereas for mobility, we used the expert assessment of the authors.

Additionally to analysing the above traits separately, we computed a principal component analysis (PCA), an unconstrained ordination technique, relating all the butterflies to their traits. The first ordination axis from this analysis, explaining the highest amount of variation in the data and roughly distinguishing specialists from generalists, is herein coined the S–G continuum (see also Bartonova et al. 2014). (See Supplementary material Appendix 3, Table A3-1 for detailed traits scaling, and Table A3-2 for individual species' values.)

Because life histories tend to covary with phylogeny, a phylogenetic tree of all recorded species was constructed, based on published phylogenies, supplemented by formal classification into genera and subgenera. (See Supplementary material Appendix 4 for the obtained tree and list of compiled literature.)

### Statistics

To evaluate the relations between reserve heterogeneity and butterfly life histories, we generated three data matrices: 1) environmental (geography and geometry characteristics of all reserves; Supplementary material Appendix 1); 2) species (species presence/absence in all reserves; Supplementary material Appendix 2); 3) traits (life history traits of all species; Supplementary material Appendix 3). A patristic distance matrix (the distance of any pair of taxa measured along the branches of the phylogenetic tree) was used as a supplementary table to filter out the possible influence of phylogeny in life histories (Supplementary material Appendix 4).

Relations between geography and geometric characteristics influencing the composition of butterfly faunas and life histories displayed by the faunas were analysed using the fourth-corner method (Legendre et al. 1997), which detects the relationships between the supplementary variables associated with the rows and columns of a binary (presence or absence) data table. We used the procedure contained in the multivariate statistical package CANOCO 5 (Ter Braak and Smilauer 2012), which first ordines species responses to environmental variables, and then interprets the results according to life history traits. For constrained ordinations, significances were evaluated by the Monte Carlo tests (999 permutations).

We first computed an unconstrained (DCA) ordination to inspect the mutual positions of the reserves solely according to their butterfly assemblages (species matrix). Next, to filter out rather trivial effects of geography and prevailing biotope type on the mutual positions of reserves, we used a constrained ordination method, canonical correspondence



analysis (CCA), to define a combination of geographical coordinates, altitude and prevailing biotope type that explained highest possible variation in the composition of butterfly assemblages. This was done using forward selection from all variables including their second degree polynomials and interactions. Resulting combination of variables was used as covariates in a partial DCA model, showing the mutual positions of the reserves independent of geography and biotope type effects.

Third, separate partial CCAs, containing the combination of covariates as in the partial DCA above, plus the individually entered predictors area, relative perimeter, habitats within, patches within, habitats outside and patches outside, tested the effects of the predictors on residuals of the constrained models. In analyses with numbers of patches and habitats within and outside the reserve, the relevant area (reserve or buffer) was added as additional covariate, to filter out its effect.

The partial CCA models formed the basis for life history traits analyses, asking how the reserve geometry influenced constituent species traits, plus the composite variable S–G continuum, while controlling for the effects of phylogeny. The phylogenetic tree was turned into a patristic distance matrix using principal coordinate analysis (PCO). These centred and standardized PCO scores were used as explanatory variables against the partial CCA responses; only significant ( $p < 0.04$ ) PCO scores were selected as influencing the partial CCA results. Finally, the partial CCA responses were explained by functional traits, with the partial PCO scores (i.e. phylogeny effects) used as covariates.

All the above analyses were computed twice, first for all butterflies detected, and second, after excluding species ( $n = 10$ ) which were detected in one reserve only, to see to what extent these ‘singletons’ affected analyses’ results.

## Results

In total, 128 butterfly species were recorded, which is approximately 94% of current Czech fauna (from 136 species according to CBMR, excluding reintroduced species and species of uncertain status). The mean number of species in a reserve was 33 (median: 32, min = 6; max = 72).

DCA ordinating the reserves according to their butterflies species lists explained 21.7% (23.1% excluding singletons) of the data variability (Fig. 2, top). Visually, the first axis reflected a gradient of humidity, from wetlands and forests in negative values to dry grasslands in positive values. The second axis is interpretable by reserves’ longitudinal positions, with reserves in the eastern part of the country in positive axis values and reserves in the western part of the country in negative axis values. The forward selection of reserve covariates returned the following model:  $y \sim \text{lat} + \text{long} + \text{alt} + \text{biotope type} + \text{lat}^2 + \text{long}^2 + \text{alt}^2 + \text{lat} \times \text{long} + \text{lat} \times \text{alt} + \text{long} \times \text{alt}$  (CCA, eigenvalues: 0.233, 0.120, 0.100, 0.071; explained variability 28.8%; Monte Carlo F (all axes) = 3.3,  $p = 0.001$ ). Excluding singletons, the model retained the same predictors structure (CCA, eigenvalues: 0.228, 0.118, 0.097, 0.061; explained variation 30.5%; F (all axes) = 3.7,  $p = 0.001$ ). The partial DCA explained 18.0% (16.5%

excluding singletons) of the data variation, dissolving the obvious biotopes and geography pattern (Fig. 2, bottom).

Partial CCAs, computed separately for each of the reserve design predictors, detected significant effects of area, relative perimeter, and both compositional and configurational habitat heterogeneity within and outside the reserves on the butterfly assemblages composition (Table 1).

Only a few individual traits correlated significantly with the reserve design predictors (Table 2). With all species included, host plant form, mobility and distribution correlated negatively with area, while density and Red list displayed positive correlations. Therefore, larger reserves hosted more species which feed on unapparent plants, are sedentary, live in high densities, inhabit fewer grid squares in the country and are endangered. Positive correlations with relative perimeter revealed that reserves with notched borders hosted larger-bodied, highly mobile species with long adult flight periods, broad trophic ranges and wide distributions; such species are rarely endangered, as shown by the negative correlation with Red list status. No trait correlated with heterogeneity within reserve (i.e. habitats within, patches within). Red list correlated positively with both habitats outside and patches outside, suggesting that more heterogeneous landscapes host more endangered species.

After excluding singletons from the species data, the traits’ correlations retained the same directions, but more relationships with traits became statistically significant (Table 2). Reserves with more habitats within supported more Red list species, species with narrow trophic range and restricted distribution. Reserves surrounded by more patches outside supported species with low numbers of generations and shorter flight periods. Reserves surrounded by more habitats outside supported species forming few generations and overwintering in early stages.

Finally, S–G continuum correlated negatively with area and positively with relative perimeter in the analysis with all species, revealing that specialists tended to prevail in large reserves and generalists in reserves with relatively long perimeters. It also correlated positively with relative perimeter and negatively with habitats within in analyses without singletons (Table 2).

## Discussion

Areas and relative perimeters of nature reserves, as well as the number and heterogeneity of habitats within and around the reserves, affect reserves-inhabiting butterfly assemblages in a consistent way, reflected in the representation of the butterflies’ life history traits. Some traits commonly associated with specialism (low mobility, high density, small distribution range) were overrepresented in large reserves, whereas in reserves with high perimeter:area ratio, traits associated with generalism (large body size, high mobility, large range size, long flight period, wide trophic range) prevailed. Other traits associated with specialism, but describing species development (low number of generations, short flight period, overwintering in early stages) were overrepresented in reserves situated amidst heterogeneous landscapes.

The positive effects of area, internal habitat diversity and surrounding landscape heterogeneity are well known



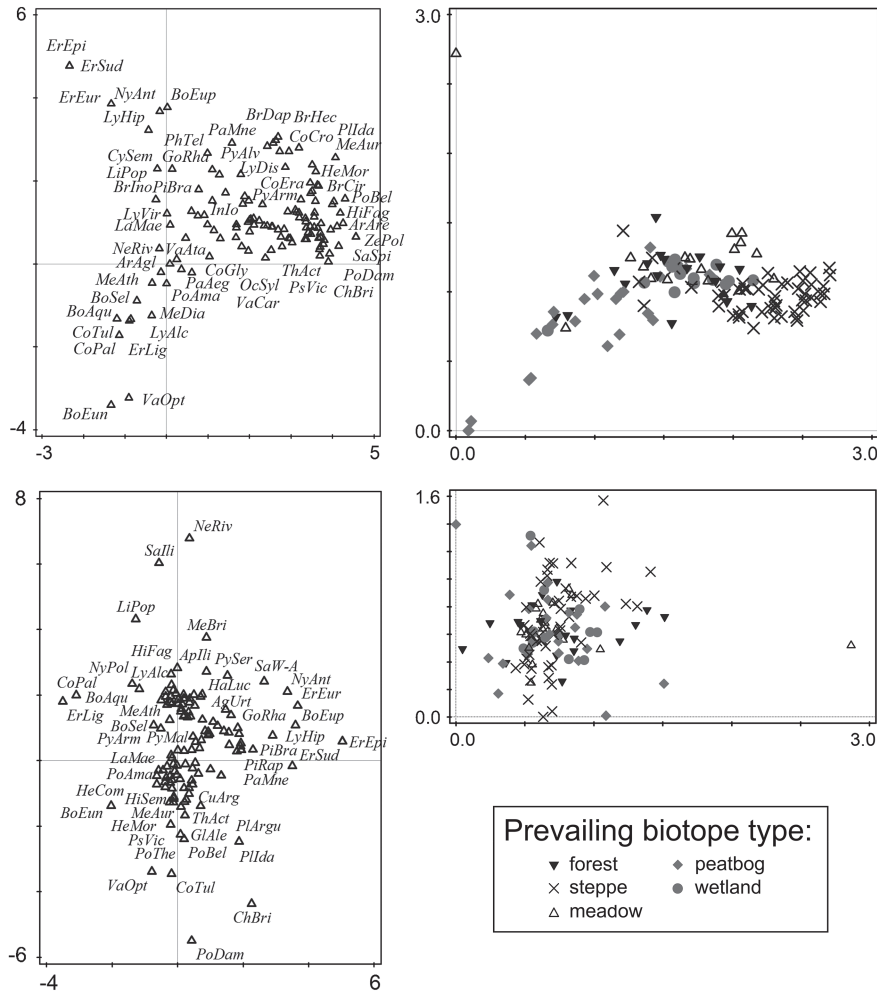


Figure 2. DCA diagrams (axes 1 and 2) of 125 Czech reserves according to their butterfly species. Upper row: ordination of species and reserves. Lower row: partial DCA of species and reserves after correlation for latitude, longitude, altitude and prevailing biotope types. Prevailing biotope type of each reserve is symbolised in the figure. Positions of all species are visualised, but only selected species are named. Species abbreviations: AgUrt – *Aglais urticae*, ApHyp – *Aphantopus hyperantus*, ApIli – *Apatura ilia*, ApIri – *A. iris*, ArAgl – *Argynnis aglaja*, ArAre – *Arethusana arethusa*, BoAqu – *Boloria aquilonaris*, BoEun – *B. eunomia*, BoEup – *B. euphrosyne*, BoSel – *B. selene*, BrCir – *Brintesia circe*, BrDap – *Brenthis daphne*, BrHec – *B. hecate*, BrIno – *B. ino*, CaPal – *Carterocephalus palaemon*, CaRub – *Callophrys rubi*, ChBri – *Chazara briseis*, CoCro – *Colias crocea*, CoEra – *C. erate*, CoGly – *Coenonympha glycerion*, CoPal – *Colias palaeno*, CoTul – *Coenonympha tullia*, CuArg – *Cupido argiades*, CuDec – *C. decoloratus*, CySem – *Cyaniris semiargus*, ErEpi – *Erebia epiphron*, ErEur – *E. euryale*, ErLig – *E. ligea*, ErSud – *E. sudetica*, GlAle – *Glaucopsyche alexis*, GoRha – *Gonepteryx rhamni*, HaLuc – *Hamaeris lucina*, HeCom – *Hesperia comma*, HeMor – *Heteropterus morpheus*, HiFag – *Hipparchia fagi*, HiSem – *Hipparchia semele*, InIo – *Inachis io*, LaMae – *Lassiomata maera*, LiPop – *Limenitis populi*, LyAlc – *Lycaena alciphron*, LyDis – *L. dispar*, LyHip – *L. hippothoe*, LyTit – *L. tityrus*, LyVir – *L. virgaureae*, MeAth – *Melitaea athalia*, MeAur – *M. aurelia*, MeBri – *M. britomartis*, MeDia – *M. diamina*, NeRiv – *Neptis rivularis*, NyAnt – *Nymphalis antiopa*, NyPol – *N. polychloros*, PaAeg – *Pararge aegeria*, PaMne – *Parnassius mnemosyne*, PhTel – *Phengaris teleius*, PiBra – *Pieris brassicae*, PiRap – *P. rapae*, PlArgu – *Plebejus argus*, PlIda – *P. idas*, PoAma – *Polyommatus amandus*, PoBel – *P. bellargus*, PoDam – *P. damon*, PoThe – *P. thersites*, PsVic – *Pseudophilotes vicrama*, PyAlv – *Pyrgus alveus*, PyArm – *P. armoricus*, PyMal – *P. malvae*, PySer – *P. serratulae*, Salli – *Satyrus ilicis*, SaSpi – *S. spini*, SaW-A – *S. w-album*, ThAct – *Thymelicus acteon*, VaAta – *Vanessa atalanta*, VaOpt – *Vacciniina optilete*, ZePol – *Zerynthia polyxena*.

determinants of reserve species richness, commonly evoked in reserve design literature targeting diverse groups of organisms (e.g. plants: Kivinen et al. 2006; birds: Morelli et al. 2013; bees: Fabian et al. 2013). In butterfly studies, these determinants often perform better at predicting the richness of specialist than generalist species (based on varying definitions, e.g. the degree of association with focal habitat: Krauss et al. 2003, Zulka et al. 2014; or the number of habitats occupied, Menendez et al. 2007), or the species composition of faunas (Slancarova et al. 2014). Typically, researchers

of the phenomena restricted themselves to rather uniform systems consisting of either a single habitat type (cultural grasslands: Boerschig et al. 2013; dry grassland patches: Slancarova et al. 2014, Zulka et al. 2014; wetlands: Cozzi et al. 2008), assumingly surrounded by non-habitat, or to sets of localities within a single landscape (urban reserves: Jarosik et al. 2011, Lizee et al. 2012). Our results, based on analyses of a high number of reserves protecting a broad range of habitats scattered across a middle-sized European country, are unique in demonstrating the general validity of

Table 1. Results of (partial canonical correspondence analyses), testing the effects of geometric and surrounding landscape characteristics of 125 National Nature Reserves/Monuments in the Czech Republic on the composition of butterfly assemblages inhabiting the reserves. Each line represents the test of a single predictor on residual variation from a covariate model, controlled for geographic position and prevailing biotope type in the reserves (see Results for details). F and p refer to Monte-Carlo tests ( $p < 0.05$  <sup>\*</sup>,  $p < 0.01$  <sup>\*\*</sup>).

	All species		Excluding singletons	
	Var [%]	F, p	Var [%]	F, p
Area	1.34	1.5*	1.11	1.2, $P > 0.05$
Relative perimeter	1.41	1.6*	1.52	1.7**
Patches within	1.33	1.5*	1.26	1.4*
Habitats within	1.35	1.5*	1.41	1.6**
Patches outside	1.52	1.7*	1.43	1.6**
Habitats outside	1.39	1.5**	1.40	1.6**

area, habitat diversity and landscape heterogeneity effects on reserve faunas on a relatively large scale and regardless of the type of reserve-protected biotope.

Comparison of the unconstrained and partial DCA ordinations of reserves and their butterflies (the latter controlled for geography and habitat types) illustrates this point. While unconstrained ordination clustered the reserves according to geography and protected biotope, agreeing with earlier studies carried out on this spatial scale (Storch et al. 2003), control for covariates disrupted these straightforward patterns. Subsequent analyses revealed effects of reserves and surrounding landscapes geometry on residuals from the geography and biotopes ordination.

Ockinger et al. (2010), in a meta-analysis of multiple studies from two continents, demonstrated the generality of area and isolation effects on butterfly and moth species richness. Our study differs both in focus (geometric reserve attributes) and in the analysed response (community composition and underlying species life history traits). Earlier studies working with butterfly life history traits focused on particular biotope types (Barbaro and van Halder 2009, Lizee et al. 2011, 2012, Leingartner et al. 2014, Robinson et al. 2014), whereas we showed how life histories respond to reserves' general geometry, after statistically controlling for variation due to protected biotope types and geography.

In analyses with all species, large reserves hosted poorly mobile butterflies occurring in high densities. Assuming that poor dispersers depend on reserve territory for their entire life cycles (James et al. 2003, Cozzi et al. 2008) and butterfly population densities tend to be inverse to mobility (Baguette and Schtickzelle 2006, Konvicka et al. 2012, Bartonova et al. 2014), a reserve must be large to contain viable populations of specialists. The negative relationship between area and distribution, and the positive relationship between area and status, only corroborate that poorly mobile species with high local densities tend to inhabit small ranges and often are threatened (cf. Cowley et al. 2001).

Reserves with long relative perimeter hosted butterflies with traits associated with generalism. Some of the traits were opposites of those associated with large reserve areas (high mobility, wide distribution, low threat levels). Additional traits responding positively to long reserve boundaries were broad trophic range and long flight period. Butterflies scoring highly in these traits include such widely distributed

Table 2. Associations between reserve-inhabiting butterflies' life history traits and characteristics of 125 National Nature Reserves/Monuments in the Czech Republic. The partial CCAs from Table 1 attributed to phylogeny-controlled PCO scores of individual traits. Only statistically significant and marginally significant responses and correlation directions are displayed.  $p = 0.05$  <sup>\*</sup>,  $p < 0.05$  <sup>\*\*</sup>,  $p < 0.01$  <sup>\*\*\*</sup>.

All species	Body size	Host plant form	Voltinism	Fertility	Mobility	Range size	Density	Flight period	Overwintering	Feeding index	Distribution	Red list	S-C continuum
Area		(-) <sup>*</sup>			(-) <sup>*</sup>		(+) <sup>*</sup>			(+) <sup>*</sup>	(-) <sup>**</sup>	(+) <sup>**</sup>	(-) <sup>**</sup>
Relative perimeter	(+) <sup>*</sup>				(+) <sup>**</sup>			(+) <sup>*</sup>		(+) <sup>*</sup>	(+) <sup>**</sup>	(-) <sup>**</sup>	(+) <sup>**</sup>
Patches within													
Habitats within													
Patches outside												(+) <sup>*</sup>	
Habitats outside												(+) <sup>**</sup>	
Excluding singletons													
Relative perimeter								(+) <sup>*</sup>		(+) <sup>**</sup>	(+) <sup>**</sup>	(-) <sup>**</sup>	(+) <sup>**</sup>
Patches within												(+) <sup>**</sup>	
Habitats within												(+) <sup>**</sup>	
Patches outside			(-) <sup>**</sup>					(-) <sup>*</sup>		(-) <sup>**</sup>	(-) <sup>*</sup>	(+) <sup>**</sup>	(-) <sup>*</sup>
Habitats outside		(-) <sup>*</sup>							(-) <sup>*</sup>		(-) <sup>*</sup>		

generalists as the swallowtail *Papilio machaon*, the pierids *Pieris brassicae* and *P. napi*, the nymphalids *Vanessa cardui* and *Polygonia c-album*, and the lycaenid *Celastrina argiolus* (cf. Benes et al. 2002, Bartonova et al. 2014). Long perimeters, or notched boundaries, expose reserve interiors to influences from outside landscapes (Farhat et al. 2014). In this study, the reserves with the longest relative perimeters were either very small (<1 ha) patches of rare habitats (e.g. Seminsky presyp: aeolic sands, Radouc: limestone grassland) or geological phenomena (e.g. Kank, Ruzickuv lom). They were typically situated in settings not allowing establishment of more generous reserves. As it is unlikely they host self-sustaining butterfly populations, their butterfly faunas were dominated by species penetrating the reserves from outside. The representation of generalists mirrored the pauperised fauna of common European farmlands (cf. Ekroos et al. 2013).

Exclusion of singletons diluted the previously significant effect of area, possibly because several such species inhabited some of the largest reserves in our sample, e.g. Praded (2050 ha): *Erebia sudetica*, *E. epiphron*; Koda (512 ha): *Pyrgus armoricanus*; Devin (379 ha): *Zerynthia polyxena*, *Polyommatus dorylas*; Mrtyv luh (331 ha): *Coenonympha tullia*. Detection of a species in a single reserve might have several reasons. Once widely distributed species may be surviving at a last locality due to human pressures; such cases exist in the Czech Republic (Cizek and Konvicka 2005, Konvicka et al. 2008), but were not represented in our data (Benes and Konvicka 2006). Other species may be quite common, but require conditions under-represented in the reserve system (e.g. humid ruderals: *Zerynthia polyxena*, submountain pastures: *Pyrgus armoricanus*) (Spitzer et al. 2009). Finally, a naturally rare relic may be genuinely restricted to a single site (e.g. the mountain relics *Erebia epiphron* and *E. sudetica*) (Kuras et al. 2003).

Surrounding landscape heterogeneity related to species traits only in analyses excluding singletons. Narrow trophic ranges were associated with reserves containing multiple habitats, arguably because more habitat types imply more diverse flora, including host plants of trophic specialists (Jarosik et al. 2011). Diverse landscape composition and configuration were further associated with species forming few generations per year, having short flight periods and overwintering in early stages. In temperate butterflies, such a combination of traits restricts the time window available for adult dispersal (cf. Boerschig et al. 2013). This combination of traits applied, e.g. to Lycaenidae: Theclinae, or hairstreaks, who often inhabit shrubby mantels and hedgerows – features quite common in diverse landscapes but rare in homogeneous ones (Sklenicka et al. 2009). Incidentally, hairstreaks also display restricted mobility, cf. a study on *Satyrium ilicis* (Maes et al. 2014), and hence require landscapes with a high density of edges. Other butterflies from this category include univoltine Nymphalidae: Argynini, or fritillaries, such as *Argynnis niobe*, developing on decrepit violets growing on disturbed grounds (Salz and Fartmann 2009) and hence rarely found in great abundances, or some late-seasonal Nymphalidae: Satyrinae, such as *Erebia aethiops*, utilising finely-grained patchworks of shady woodlands and open grasslands (Slamova et al. 2013).

The specialist–generalist continuum, as a composite variable based on all the species traits considered, responded

to area, relative perimeter and habitats within, but not to surrounding landscape heterogeneity. Although much used in conservation literature, the division of species into generalist based on their life histories only poorly predicts the conservation fates of individual species (Dapporto and Dennis 2013, Bartonova et al. 2014). The variation of particular traits according to particular landscape conditions may partly explain this.

The role of landscape heterogeneity for reserves-inhabiting biota is sometimes obscured by conceptual ambiguity between heterogeneity, viewed positively in conservation literature, and habitat fragmentation, viewed negatively. Earlier demonstrations of negative fragmentation effects on butterflies typically asked how dissection of a habitat would affect species depending on that habitat (Steffan-Dewenter and Tschardt 2000, Ockinger and Smith 2006). Much of this ambiguity probably stems from a misunderstanding of what constitutes a habitat for an animal species – it is rarely a distinct patch of land or a specific plant community, but rather a conjunction of its vital resources (Dennis 2010, Dennis et al. 2013). Temperate ecosystems would naturally be patchy (Vera 2000), and traditional landscapes, consisting of diverse mosaics of varying land uses, would contain multiple resources in close proximities. Remnants of such mosaics represent some of the most species rich sites of temperate Europe (Spitzer et al. 2009, Cizek et al. 2013, Loos et al. 2014). Bearing this in mind, fragmentation, rather than being defined as dissecting uniform land covers into smaller patches, should be understood as separating diverse biotope mosaics by large stretches of uniform land covers, such as intensively farmed fields, improved grasslands, or plantation forests (cf. Tryjanowski et al. 2011).

Our test using butterfly faunas of nature reserves in a European country corroborated that across all possible biotopes, the ideal reserve for conserving specialised butterflies should be large, with low perimeter:area ratio, containing multiple habitats within its boundaries, and embedded within a heterogeneous landscape. Mechanistically, reserve area and within-reserve habitat diversity appear to be particularly important for poorly mobile specialists forming dense populations. Habitat diversity within reserves seems important for species with narrow trophic niches, plus perhaps other specific resource requirements (cf. Dennis 2010). Finally, diverse surrounding landscape is important for species with a short adult flight period, which limits their ability to disperse through homogenised landscapes.

Czech Republic ‘National Nature Reserves/Monuments’ are considered the most precious conservation sites in the country. Recall that the reserves analysed were not established explicitly for butterfly conservation, but rather for entire habitats, plant communities, rare plants, birds, or geology (Jarosik et al. 2011). This history explains why the national reserves do not include localities of some of the rarest Czech butterflies (mostly protected by lower conservation categories). It also explains a discrepancy between plants and butterflies, pointed to in an earlier analysis by Cizek et al. (2013), who compared the same reserves with 41 similarly-sized military training areas: the reserves represented superior sites for plants, but not for butterflies, arguably due to the requirements of many butterflies for biotope and vegetation

heterogeneity. To further increase reserves efficacy for insect conservation, the message is quite straightforward: wherever a reserve covers a single habitat type, it should be enlarged to include parts of adjoining habitats; if this is not possible, the vegetation inside the reserve should be managed in a more diverse way; and wherever it is politically and financially feasible, the management of close reserve environs should be as diverse as possible, to enhance landscape heterogeneity.

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Supplementary material (Appendix ECOG-01642 at <[www.ecography.org/appendix/ecog-01642](http://www.ecography.org/appendix/ecog-01642)>). Appendix 1–4.