

Distribution patterns in butterflies and birds of the Czech Republic: separating effects of habitat and geographical position

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Abstract

Aim To evaluate the relative role of environmental factors and geographical position (latitude and longitude) in determining species distribution and composition of local assemblages of butterflies and birds.

Location Czech Republic, central Europe.

Methods Canonical correspondence analysis that ordines species and samples (grid cells in distribution atlases) such that interspecific and intersample differences attributable to environmental factors are maximized. The technique allowed us to test the significance of individual factors, including the geographical ones, by controlling the other factors and accounting for spatial autocorrelation.

Results Altitude and climate (temperature and precipitation) accounted for most variance in the interspecific differences in distribution of both butterflies and birds. The distribution of birds was also strongly affected by the area of water bodies, and less strongly, but still significantly, by the area of meadows and mountain open habitats. Habitat types important for the differences in butterfly distribution were deciduous forests, meadows, swamps and mountain open habitats. Some less common habitat types were important only because of the presence of rare species. Latitude and longitude invariably accounted for a large proportion of total variance, and their effect was highly significant even after controlling for the effect of all other environmental factors.

Main conclusions Although environmental factors, especially those related to elevation and climate, represent the main determinants of species distribution and composition of local assemblages, the geographical position is very important on this scale of resolution. Understanding distribution patterns, thus, must include not only an understanding of species ecological requirements, but also an understanding of geographical context, which affects structure and dynamics of species' geographical ranges.

Keywords

Biogeography, Canoco, communities, habitat models, macroecology, ordination, spatial distribution.

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INTRODUCTION

There are principally two necessary conditions for species occurrence at any place: suitable habitat and means of getting there. The spatial distribution of any species is thus affected by the spatial distribution of appropriate habitat patches, as well as by a large-scale spatial context that can affect dynamics of dispersal and local colonization and extinction (Hanski, 1999). Generally, all distribution patterns can be related either to the spatial structure of the environment and the habitat requirements of species, or to spatial aspects of population dynamics. Indeed, most macroecological hypotheses concerning patterns in diversity and distribution are based on one of these two groups of factors. The positive relationship between species' abundance and distribution (Gaston *et al.*, 1997), for example, has commonly been explained in terms of the relative width of ecological niches of species and consequent habitat suitability (Brown, 1984), or alternatively in terms of meta-population dynamics and a positive feedback between abundance and occupancy (Hanski & Gyllenberg, 1993). Similarly, the species–area relationship has been attributed either to habitat heterogeneity (Rosenzweig, 1995) or to the dynamics of local colonization and extinction (Hanski & Gyllenberg, 1997). The relative importance of habitat factors on the one hand, and factors related to the spatial dynamics of species' ranges on the other hand, are thus essential for understanding the causes of macroscopic distribution patterns.

It is not difficult to show that both environmental and geographical factors affect the distribution of species in a particular case (e.g. Dennis *et al.*, 1998, 2000). It is more difficult, however, to assess which factors are essential for generating contemporary distribution patterns within a whole species assemblage. One possibility is to generate 'null' hypotheses that account for only particular processes and test them against observed patterns (e.g. Storch & Šizling, 2002; Storch *et al.*, 2003). The second option is to decompose the variability in species distributions and the composition of local assemblages to assess to what extent this is attributable to environmental variables, and whether any portion of the variability can be attributed to variables reflecting geographical position. The approach relies on two assumptions. The first is that variation in 'habitats', i.e. conditions suitable for individual species, can be approximated by variation in climate, elevation and land cover types, and the second is that the effect of geography, after controlling for habitat, implies the role of spatial dynamics and colonization/extinction history. Whereas a similar type of decomposition of geographical and environmental factors has been commonly applied to variables such as species richness or total abundance (e.g. Koehler & Williams, 2000), to our knowledge it has never been applied for multivariate data of local species composition and spatial distribution for faunas of large geographical units, to assess whether interspecific differences in distribution can be related to environmental or geographical factors.

We attempted to estimate the relative role of environmental factors and geographical position on the distribution of Czech butterflies and birds. The Czech Republic constitutes an appropriate area for such a study, because it is very heterogeneous in terms of altitudinal extent and land cover, and at the same time is located at the crossroads of several biogeographical zones (Culek *et al.*, 1996). Therefore, both purely ecological factors and geographical ones – especially spreading of a faunistic element from adjacent biogeographical provinces – could potentially play a role in species distribution. Butterflies and birds are especially suitable for this type of analysis, because owing to their popularity, they are amongst the best-studied groups of animals in terms of habitat requirements and distribution (e.g. Gibbons *et al.*, 1993; Hagemeyer & Blair, 1997; Asher *et al.*, 2001; Kudrna, 2002).

Discerning between environmental and geographical factors is always complicated, as the spatial distribution of any environmental variable has its own geographical dimension. Spatial autocorrelation in distribution data not only precludes using common statistical procedures (Lennon, 2000), but also does not enable direct inference of the role of spatial dynamics and history of dispersal simply from the fact that species distribution is biased towards some geographical directions, because geographical trends in species distributions could be due to the spatial distribution of their habitats as well. However, using sophisticated methods of multivariate statistics, we were able to test the effects of individual factors separately, controlling for the other factors, and for spatial autocorrelation. Although it is not possible directly to infer processes responsible for a pattern just from the pattern, we were able to demonstrate the importance of factors that affect the spatial distribution of butterflies and birds and are not directly related to contemporary habitat distribution revealed by remote sensing. Our analyses thus represent the first attempt to separate the effects of habitat and geographical factors for the entire fauna of a country in two unrelated groups of animals.

DATA

Data on the distribution of bird and butterfly species were extracted from two distribution atlases, on birds by Št'astný *et al.* (1996) and on butterflies by Beneš *et al.* (2002). Both atlases are based on a grid of 624 rectangles (hereafter grid cells), each of them spanning 10' of longitude and 6' of latitude, which represents *c.* 11.1 × 12 km in the Czech Republic. The atlases differed in methods of data collection. The data on birds were collected by 750 recorders from 1985 to 1989. The recorders worked in pre-assigned grid cells and visited these repeatedly, spending time in different habitats types proportionally to their representation in each quadrat. Besides this regular mapping, they were also allowed to submit their casual observation records from other quadrats, which were then added to the regular record sheets thereof. We considered all records of probable or confirmed breeding. On the contrary, the butterfly data were obtained by a questionnaire-like method. As there were less recorders (176 in

total), they were not asked to survey a particular grid cell, but instead to submit their records from all localities they had ever visited, including those visited prior to the mapping project. All distribution data retrievable from regional natural history literature and from about a half of public collections were also retrieved. The butterfly atlas thus contains records from the entire twentieth century, but we considered only those data from 1981 to 2002 in the analyses.

Owing to the survey methodology, the bird atlas achieved 100% coverage of the country and relatively even coverage across the grid cells. The butterfly data, on the contrary, suffered multiple biases. The most apparent bias was under-recording of some areas. This is reflected in a skewed distribution of both numbers of records (mean = 143.8, SE = 10.06, median = 61.5, range = 0–2051) and numbers of species (mean = 38.1, SE = 1.14, median = 41.0, range = 0–111) per grid cell, and, more importantly, in the presence of empty cells in the data set (535 cells contained records of a species presence). As the under-recorded areas tended to be those with few rare habitats/species, the likely effect of the bias was relative under-representation of common species in the data. However, the data set was large, containing 89,186 records of species in particular grid cells. As there were no guidelines for recorders in terms of which sites to visit, and the recorders worked independently of one another, we assume that any biases in the data were averaged out, and that interspecific differences in distribution should not be affected by it.

All grid cells were characterized by minimum and maximum altitude (i.e. MINALT and MAXALT in Table 1) and the relative proportion of individual habitat types (all listed in Table 1). The original thirty-seven land cover types recognized in the CORINE Land Cover Database (based on

remote sensing with basic spatial units of 100 × 100 m) were amalgamated in such a way that the resulting sixteen classes represented habitats potentially relevant for birds and butterflies. All grid cells were also characterized by one variable (CLIMATE) that subsumes temperature and precipitation. These two climatic parameters are closely negatively correlated in central Europe, and thus we combined them by the principal component analysis into one variable (the first principal component) with arbitrary units (the higher the value of CLIMATE, the higher mean annual temperatures and lower annual precipitation is within a grid cell). The grid cells were also characterized by longitude (EASTING), and latitude counted from the north to the south (SOUTHING).

For the purposes of testing the effect of individual variables by accounting for possible spatial autocorrelation (see below) we delineated two rectangles within the area of the Czech Republic within which the data were permuted by toroidal shifts. Rectangle A was elongated in a north–south direction, and rectangle B in a west–east direction (Fig. 1). As these rectangles also contained some grid cells with no butterfly records, which is not appropriate for this type of analysis, all the grid cells were considered as occupied by the five most widely distributed butterfly species (*Pieris napi*, *Inachis io*, *Gonepteryx rhamni*, *Pieris rapae* and *Aglais urticae*). All these species are actually ubiquitous within the area of central Europe (Beneš *et al.*, 2003) and their absence in some grid cells was due only to sampling bias. Although the rectangles partially overlapped, they differed as to the composition of major landscape types. Rectangle A was located in the western part of the Czech Republic (i.e. Bohemia) and contained mostly heterogeneous hilly landscape consisting of fine-grained mosaics of fields, villages, water bodies and smaller or larger forests, and the largest mountains

Table 1 Characterization of environmental variables used for the analyses

Name	Description	Range or area (%)
MAXALT	Maximum altitude (m.a.s.l.)	100–1602
CLIMATE	Composite variable of temperature and precipitation (arbitrary units)	1–13
MINALT	Minimum altitude (m.a.s.l.)	100–950
CONIFEROUS	Area of coniferous forests	21.33
DECIDUOUS	Area of deciduous forest	2.48
MIXED FOREST	Area of mixed forest	7.08
WATER	Total area of water bodies	0.62
MEADOWS	Area of meadows and pastures	2.99
SWAMPS	Area of swamps and peat bogs	0.10
HEATHLANDS	Area of heathlands and low dense vegetation including scrub <i>Pinus mugo</i>	0.05
ORCHARDS	Area of orchards and vineyards	0.60
FIELDS	Area of fields	47.18
SUBURBAN	Area of village or town human settlements including gardens	4.42
URBAN	Area of compact human settlement in city centres	0.02
BAREGROUNDS	Total area of building sites, mines, etc.	0.94
ROCKS	Area of rocks and debris, associated with steep slopes	0.01
SHRUB	Area of shrub including young forest regrowth	3.02
OPEN MOSAICS	Total area of heterogeneous vegetation types including sparse shrub, parks, etc.	9.09
RIVERS	Area of large rivers	0.06
EASTING	Longitude	1–40
SOUTHING	Latitude counted from north to south	1–24

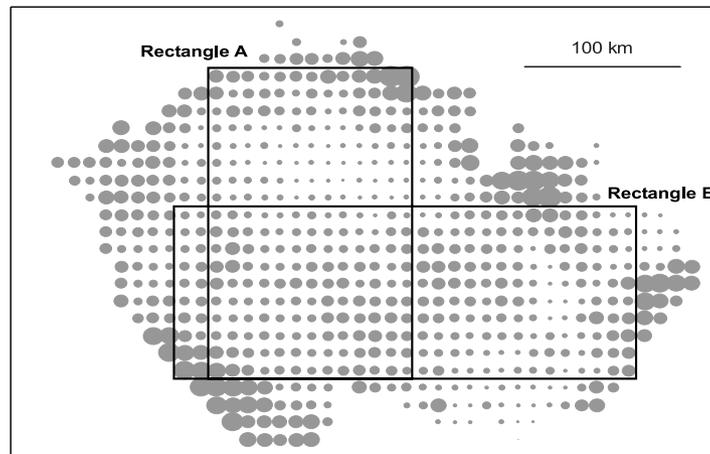


Figure 1 Position of rectangles A and B within the area of the Czech Republic. Individual grid cells are represented by circles, whose size is related to maximum altitude within a cell.

(Krkonoše and Šumava) including the mountaintops above the treeline. Rectangle B contained the typical heterogeneous landscape as well, but also large almost unforested lowlands in the eastern part of the Czech Republic (Moravia). The rarer habitat types, such as swamps and heathlands, were sparsely distributed throughout both rectangles.

ANALYSES

The multivariate data of species composition of the grid cells were analyzed by correspondence analysis (CA), which ordinated individual samples (grid cells) in a space such that the differences among them were maximized (ter Braak & Šmilauer, 1998). Each ordination axis represents a gradient along which the centroids of individual variables and/or samples are distributed so as to maximize the distances between them. The first axis represents the gradient explaining most of the variability, the second axis represents an orthogonal gradient explaining most of the variability that is not accounted for by the first axis and so on.

For estimating the effect of individual environmental parameters, we used the canonical version of the correspondence analysis (CCA). This method ordines species and samples such that the ordination axes represent the maximum variability that is attributable to the environmental parameters; the ordination is in this case constrained by the environmental parameters to maximize variability accountable by them. Relative effects of individual environmental parameters are then visualized by the relative length of the respective vectors in the ordination space.

Statistical testing of significance of the effects of individual environmental variables for the interspecific distributional differences is complicated for two reasons. First, individual variables are often strongly intercorrelated, and thus it is not easy (or even possible) to decide which factors are actually responsible for the patterns. Although there is no definite solution to this problem, it is possible to test the significance

of the effects of individual variables by Monte Carlo simulation, using the Forward selection option of the program Canoco (ter Braak & Šmilauer, 1998). This procedure randomly permutes values of the variable in question, keeping the values of all other variables that have been included in the model, and calculates the *F*-ratio that evaluates the strength of the relationship between this particular variable and species composition in each permutation step. The level of significance is then represented by the percentage of these randomly generated *F*-ratios that are equal or higher than the observed value of *F*-ratio. The ordering of variables that are subsequently included in the model is important, however, as including a variable that is strongly correlated to some other variable precludes revealing any significant effect of this other variable, because of low residual variability of it. Thus, we used manual Forward selection that allowed subsequent inclusion of individual variables according not only to their general importance, but also our expectation (see Table 2). We first included the most important variables, whose importance was revealed by the ordination, i.e. elevation and climate. Then followed other variables whose effect was expected (area of forests, water bodies, etc.), followed by the rarer habitat types whose effect was not expected, and finally, after controlling for all other factors, we tested the effect of longitude and latitude. This ensured that the significance of less obvious habitat factors was not because of their correlation with the obvious ones. We also performed the same tests with reversed ordering of explanatory variables, to check whether the significance of the most obvious variables was not only due to their correlation with those that had appeared less obvious.

A second problem in testing spatially structured data is that individual samples (grid cells) are not independent, as sites that are close to each other share both environmental conditions and species. Some apparent associations can potentially be only due to the accidental co-occurrence of species and particular environments on adjacent sites, the risk of

false association being higher in variables that are more spatially autocorrelated (Lennon, 2000). Our Monte Carlo permutations were for this reason performed by toroidal shifts that kept the spatial structure of the data (ter Braak & Šmilauer, 1998). As the toroidal shifts could be performed only within a rectangular area, all the testing was based on the two such areas selected within the Czech Republic (see Data and Fig. 1). In each randomization step, the coordinates of all values of the tested variable moved by a common random number in both geographical directions and the F -ratio was calculated from that new, randomly generated species-environment association. The rectangles were taken as toroids, i.e. the cells with the newly generated coordinates that shifted to the right from the range of real coordinates were considered as moving to the left part of the range, and a similar procedure was performed for those grid cells that occurred above the range of real coordinates. This procedure accounted for the autocorrelation except for that in the general spatial trends, which was directly tested using the environmental variables, i.e. SOUTHING and EASTING.

We performed all the analyses both without and with downweighting of rare species to estimate the role of rare species in the overall distribution patterns.

RESULTS

Unconstrained correspondence analysis

The differences in species composition of individual sites (grid cells) maximized by the unconstrained (indirect) CA were most strongly related to altitude, as revealed by the maps of sample scores of first ordination axes for both birds and butterflies (Fig. 2; see Fig. 1 for comparison). These scores correlated most closely to MAXALT in the case of birds ($r = -0.741$), and MINALT for butterflies ($r = 0.646$). In both cases, CLIMATE was the second strongest correlate of the first axis. Sample scores for the second axis were not so strongly related to any environmental parameter, but they revealed strong geographical pattern. Although the closest (negative) correlate of this axis was MINALT in birds

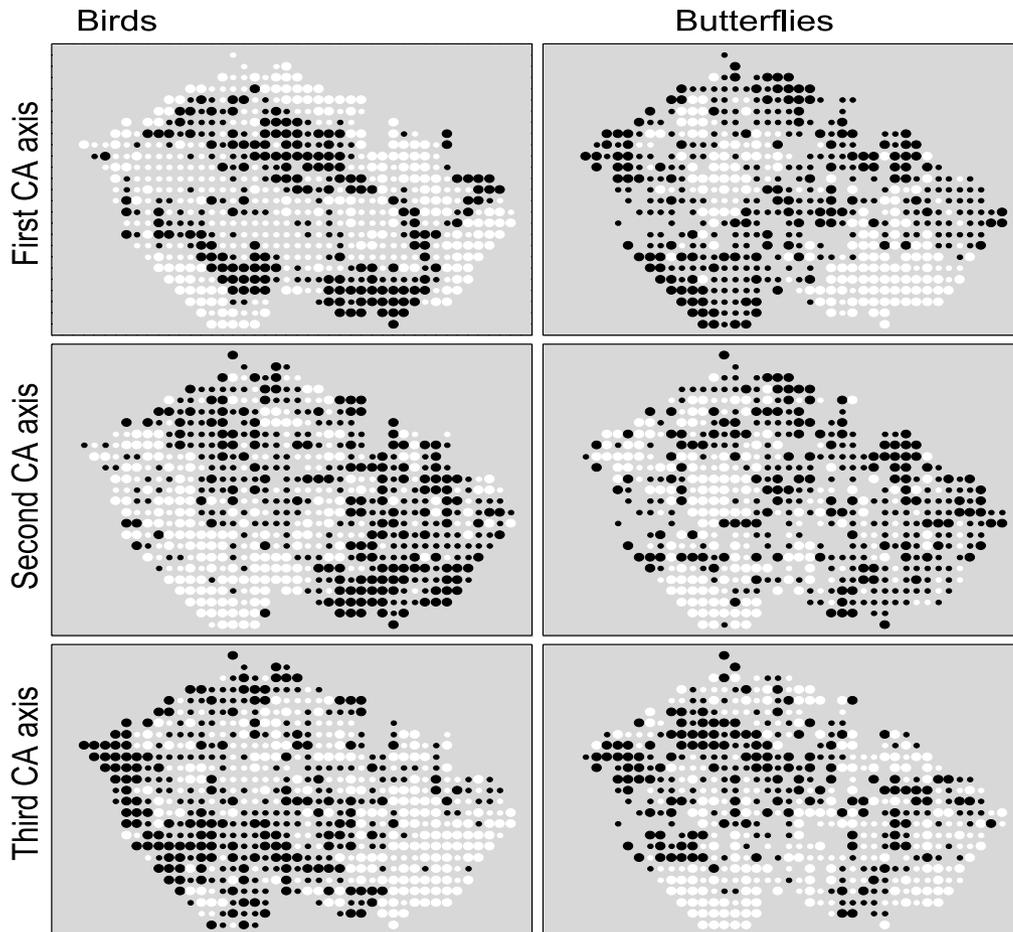


Figure 2 Maps of scores of unconstrained correspondence analysis for the three first ordination axes. White circles represent values < 0 , whereas black ones represent values > 0 . Large circles represent values from the upper and lower quartile of the distribution of values, respectively. Note that the sign of values is arbitrary, so the fact that in birds high values of the first axis are related to high altitude, but in butterflies to low altitude, is due to chance.

($r = -0.440$), the highest values were confined mostly to the south-eastern part of the Czech Republic, whereas the lowest values were confined mainly to the south-west. In the case of butterflies, the grid cells with lowest values of the second axis scores were located mainly in the western part of the Czech Republic, and indeed, EASTING was the strongest correlate of this axis ($r = 0.368$). This was also the case for the third axis in birds, where ordination scores were strongly related to the east-west gradient, and EASTING was the strongest correlate from all the environmental variables ($r = -0.490$). In butterflies the third axis was related to the north-south gradient, and SOUTHING was the strongest correlate ($r = -0.238$). Therefore, although altitude was most important, both latitude and longitude were strongly related to the differences in species composition on grid cells. As this could arise because of a strong geographical pattern of environmental variables as well as because of patterns in spatial distribution independent of ecology, it was then

necessary to apply the constrained ordination analysis that is able to separate the effects of individual factors.

CCA: relating species distribution to environmental factors

When we used CCA, i.e. the ordination constrained by the environmental parameters, we obtained similar results as in the case of unconstrained ordination (Fig. 3). In both birds and butterflies, the first axis was strongly related to altitude and other environmental variables correlating with it (CLIMATE and FIELDS, ORCHARDS and DECIDUOUS were negatively correlated with altitude, whereas CONIFEROUS was positively related). The second canonical axis was related most strongly to EASTING in the case of birds, but – in the opposite direction – also to MINALT and WATER. The third axis was apparently related mostly to SOUTHING in birds. In butterflies, both second and third

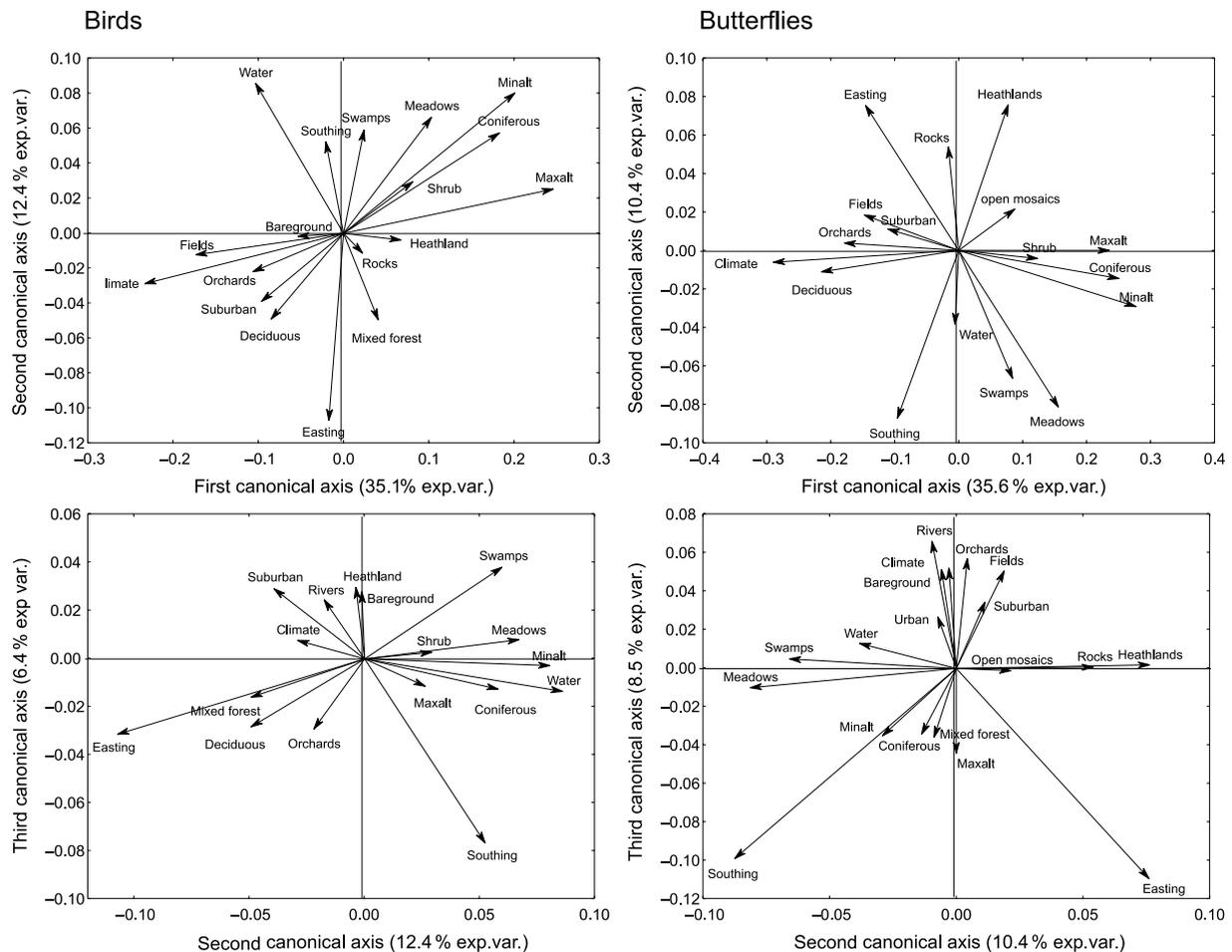


Figure 3 Results of canonical correspondence analysis – relative importance of individual environmental variables revealed by the length of respective vectors in the ordination biplots (biplots of first vs. second, and second vs. third axes are shown). For clarity, the variables that were unimportant, i.e. their vectors were too close to zero in individual biplots, are not shown. Percentage of variance explained by individual canonical axes is given in parentheses.

Table 2 Results of manual forward selection analysis that tested significance of individual environmental variables by Monte Carlo permutation, using toroidal shifts that kept spatial structure of the data. Values of *F* statistics are given after accounting for the effect of variables that are above the respective variable in the table (**P* < 0.05; ***P* < 0.01; ****P* < 0.005). In bold are values that remained significant (*P* < 0.05) even after reversing the ordering of explanatory variables included in the model; DW = downweighting of rare species

Environ. variable	Birds				Butterflies			
	Rect. A	DW	Rect. B	DW	Rect. A	DW	Rect. B	DW
Maxalt	12.09***	11.69***	11.29***	12.58***	8.51***	7.34***	8.58***	8.40***
Climate	2.68**	2.91**	2.76**	3.13*	4.49**	4.65**	4.32***	4.95***
Minalt	5.47*	5.64*	8.33**	10.25***	2.37*	2.29*	2.94**	2.85*
Coniferous	2.28*	2.28*	1.92*	1.94**	2.14*	1.72	1.78	1.51
Deciduous	1.42	1.84	2.51*	2.81**	1.55	1.70	3.91**	2.77**
Mixed forest	1.84*	2.29***	1.87*	2.24**	1.47	1.47	1.70	1.76
Water	10.25***	5.77***	12.02***	6.11***	2.10*	1.64	1.68	1.60
Meadows	2.96**	2.07**	3.05***	2.52**	3.51**	2.01*	2.87	2.05
Swamps	2.59**	1.29	3.60***	1.37	2.98***	1.20	3.62***	1.65
Heathlands	9.75**	3.67***	1.49	1.35	8.17**	2.75*	1.73	1.42
Orchards	1.54	1.42	2.00*	1.29	1.51	1.23	1.52	1.05
Fields	0.97	1.05	1.39	1.15	1.70	1.48	1.62	1.40
Suburban	1.11	1.25	1.40	1.40	1.56	1.35	2.07*	1.66
Urban	1.06	1.04	1.14	0.62	1.08	1.05	1.14	0.96
Bare grounds	0.76	0.95	1.16	1.12	1.94*	1.61	1.03	0.91
Rocks	2.54***	0.65	0.99	1.10	0.56	0.56	1.62	1.24
Shrub	1.19	1.26	1.03	1.12	1.09	0.79	0.97	0.86
Open mosaics	1.53	1.92**	2.47*	1.68*	1.69	1.45	1.64	1.20
Rivers	0.89	1.06	0.64	0.72	1.32	1.04	0.99	0.99
Easting	1.75**	1.74**	3.22**	4.14***	2.47*	2.18	3.15***	3.21*
Southing	2.00***	2.05***	1.56**	1.57*	2.51***	2.11*	3.00***	3.19***

axes were related to EASTING and SOUTHING as well, but the second axis correlated most closely to MEADOWS and SWAMPS on one side, and ROCKS and HEATHLANDS on the other side. However, it is not possible on the basis of these ordination plots to discern which relations are only correlative, and which represent real biologically meaningful relationships. It is also not possible to discern which of the relationships are statistically significant, although the significance of all environmental factors together was very high (*P* < 0.002 in all cases, Monte Carlo permutation test). Significance of individual parameters was thus estimated using Monte Carlo tests based on toroidal shifts of values of respective variables, controlling for the other variables.

Testing significance of individual environmental variables

For birds, the only parameters that were highly statistically significant in all cases (i.e. for each sampled rectangle and also for the ordinations in which rare species were downweighted) were WATER and MAXALT, although MAXALT was not so important when MINALT had been included in the model, i.e. in the reversed sequence of variable inclusion (Table 2). CLIMATE was also generally significant (mostly even after controlling for altitude), although not so strongly in rectangle B if the rare species were downweighted. In rectangle A, a generally highly significant variable was HEATHLANDS (note that this variable includes also mountain shrub, especially in rectangle A). The

significance of different types of forests was generally higher when rare species had been downweighted, which was also the case for OPEN MOSAICS, whose significance, however, diminished when the ordering of variables had been reversed (indicating an effect of correlation with SOUTHING or EASTING). Thus, downweighting of rare species generally increases the importance of more common habitat types, whereas the opposite is true for less common habitat types: SWAMPS and ROCKS in rectangle A were apparently significant only because of the presence of rarer species. MEADOWS were significant in all cases, but the significance diminished when the ordering of variables in the model had been reversed, indicating correlation with some variables at the bottom of Table 2 (probably SOUTHING or EASTING). Both EASTING and SOUTHING were statistically significant even after all other variables were controlled for. Interestingly, their effect was stronger in this case than if tested without controlling for other variables, apparently because geographical position is more important for the residual variability in species distribution, whose major driver is altitude and related factors.

In butterflies, the only generally significant environmental parameter was altitude, although the significance of MAXALT diminished if MINALT had been added into the model and vice versa. CLIMATE was significant only when MINALT (and following variables) had not been included in the model. DECIDUOUS was significant only in rectangle B, whereas CONIFEROUS was marginally significant in rectangle A, but this diminished when rare species had been

downweighted, and was not supported when the ordering of variables included in the model had changed. SWAMPS was significant in both rectangles, but also only without downweighting of rare species, indicating the role of this relatively uncommon habitat type for rarer species. In rectangle A, MEADOWS and HEATHLANDS (including mountain shrub) were also significant, although downweighting of rare species lowered their significance level. Three other environmental variables were slightly significant (BAREGROUND and WATER in rectangle A and SUBURBAN in rectangle B), but also only without downweighting of rare species, and in the case of BAREGROUND and WATER the significance was not confirmed by reversing the ordering of explanatory variables. On the contrary, SOUTHING was significant in all cases (although slightly less in rectangle A with downweighting of rare species), whereas EASTING was highly significant only in rectangle B. This is not surprising, considering that rectangle A is quite narrow on the east–west axis, and the potential variability in this direction is consequently low.

DISCUSSION

Habitat effects in birds and butterflies

Altitude and climate, which are closely correlated, represent the most important factors affecting the interspecific differences in distribution of birds and butterflies in the Czech Republic. This is not very surprising – both these environmental parameters are related to many features of habitat and can affect animal ecology in many ways. As they remained significant even after controlling for all other habitat factors, their correlation with habitat composition of grid cells was apparently not responsible for the pattern, although the role of correlation with the presence of some habitat types that could not be recognized using the CORINE database (based on remote sensing) cannot be excluded. It is, however, very probable that the effect of climate is more or less direct, because climate can affect many population parameters by influencing metabolic rate, timing of reproduction, etc. The effect is more obvious in butterflies, which as heliophilous ectothermous organisms are strongly associated with warmer climate in central/northern Europe (Turner *et al.*, 1987) and many of them depend on warm refugia (Thomas, 1993; Bourn & Thomas, 2002). The direct role of climate for birds is generally less clear, although temperature, for example, has been revealed as the most important correlate of bird species richness in Great Britain (Lennon *et al.*, 2000), and the effect of weather on reproductive parameters of bird populations is obvious (e.g. Sillett *et al.*, 2000). In birds the effect of each of the variables, MAXALT, MINALT and CLIMATE was significant even if the other two were controlled for, which was not the case in butterflies. This follows because there are groups of bird species associated with mountains as well as groups associated with lowlands, but only three species of butterflies are truly alpine in the Czech Republic (i.e. reside in habitats above the treeline and are restricted to them) and no species

is associated with closed-canopy mountain coniferous forests (Beneš *et al.* 2002). Thus, for butterflies minimum altitude is much more important than maximum altitude, but for birds either parameter can play a role for some groups of species.

Amongst habitat factors, the area of forest generally affected the differences in species distribution, although this was not the case for all types of forest, and for butterflies the only case of a strong correlate was the area of deciduous forest in rectangle B. In birds, many species are strongly associated with different types of forest, but in our data set these effects are weakened by the fact that different types of forest are rather widespread and occur in most grid cells. The effect is even weaker in butterflies, as very few butterflies in temperate Europe inhabit closed-canopy woodlands, and these species (e.g. speckled wood *Pararge aegeria*) tend to be omnipresent almost irrespective of woodland type. Moreover, it has repeatedly been shown that the butterflies that are found in woodland regions have exacting habitat requirements and tend to be restricted to edges, ecotones and early successional sites (Warren & Key, 1991; Warren, 1995; Konvička & Kuras, 1999). Even those that feed on woody host plants may require such specialized conditions as young trees or branches exposed to direct sun (e.g. Boehm & Kostler, 1996; Fuldner, 1997). The effect of deciduous forest for the differences in butterfly distribution in rectangle B is therefore probably due to the association of this type of forest with particular habitats within the forests and on their edges.

The most important difference between birds and butterflies was in the effect of water bodies, which was substantial for birds but unimportant for butterflies. In fact, one-third of all bird species breeding in the Czech Republic are associated with wetlands (Sádlo & Storch, 2000), and bird communities occupying wetland habitats strongly differ in species composition from communities of all other habitat types (Storch & Kotecký, 1999). On the contrary, there are no butterfly species associated with water bodies, and this huge difference is probably the main reason why hot spots of different taxa within Europe often do not coincide (Prendergast *et al.*, 1993; Gaston & David, 1994): presence of wetlands overwhelms all other habitat factors in birds. This also shows the potential danger of generalizing across different taxa, including closely related ones; among moths, the closest relatives of butterflies, there are distinct and species-rich assemblages inhabiting waterlogged reeds in central Europe (e.g. Marek, 1977).

In both birds and butterflies there are specialized species that depend on swamps and peat bogs (Mikkola & Spitzer, 1983; Št'astný *et al.*, 1996), which is reflected in the significant effect of these habitats for the rarer species. The same holds for meadows, at least in rectangle A, where the effect remained significant even when longitude and latitude had been controlled for. The problem with this habitat type, as with HEATHLANDS that were significant for both birds and butterflies in rectangle A, is that they are not actually homogeneous and consist of different types that could not be distinguished from the CORINE satellite database. Meadows can be 'improved' ones that are intensively utilized by agriculture and do not support any butterfly species

(cf. Asher *et al.*, 2001), or may represent the natural or seminatural 'steppes' that belong among the most species-rich habitats in Europe (Van Swaay, 2002). HEATHLANDS comprise both true heathlands and dense shrubby vegetation in mountains, including cover of *Pinus mugo*. As HEATHLANDS had a strong effect for both birds and butterflies only in rectangle A, which comprises high mountains in the north and south-west (Krkonosé and Šumava mountains), and does not comprise any extensive areas of true heathlands, this effect is due to the species associated with mountain vegetation above the treeline. These habitat types, which appeared generally more important for rare species, show the limits of our methodology: species often perceive habitats on finer scales than revealed by remote sensing. This is more pronounced in butterflies, which perceive their habitats on considerably finer scales than birds, and often exhibit highly exacting habitat requirements (Thomas, 1995).

Geography vs. ecology

Both latitude and longitude appear as very important factors affecting species distribution even after controlling for all environmental factors including climate, and accounting for spatial autocorrelation. This implies a role of spatial dynamics and history in producing distributional patterns, although it can be partially related also to the fact that some habitat types unrecognized by the remote sensing are themselves related to latitude and longitude. This latter effect could be potentially strong in butterflies that depend on a particular host plant species, whose distribution itself can be affected by geographical context and history.

The strong effect of geographical position on bird and butterfly occurrence agrees well with knowledge of the biogeographical position of the Czech Republic within Europe. The Czech Republic lies just on the 'ecotone' (if the term can be used in this large-scale sense) between regions with Atlantic and continental climate, in the area that was not glaciated during Quaternary ice-ages, and thus represented the ice-free band connecting south-eastern and south-western glacial refugia (Hewitt, 2000). Several species reach their distributional limits here, both in north-south and west-east directions, and many of them have colonized northern parts of Europe in relatively recent post-glacial periods (Schmitt & Seitz, 2001). The role of historical patterns of dispersal for contemporary distributional patterns is also supported by the existence of hybrid zones, which are concentrated mainly just within central Europe (Hewitt, 2000). These have been documented primarily for plants, amphibians and mammals (Taberlet *et al.*, 1998), but there are also examples in birds and butterflies. Ranges of two species or subspecies of crows *Corvus corone corone* and *C. corone cornix* overlap just in this area forming the hybrid zone between the eastern and western populations. Ranges of 'southern' collared flycatcher *Ficedula albicollis* and 'northern' pied flycatcher *Ficedula hypoleuca* also overlap just in central Europe, and they occasionally interbreed within the area of the Czech Republic (Saetre *et al.*, 1997). Hybrid zones might also occur between

western and eastern populations of the butterflies *Erebia medusa* and *Polyommatus coridon* (Schmitt & Seitz, 2001).

Of course, all these patterns can at least be reinforced by contemporary environmental settings, and thus may not be attributable solely to the dynamics of dispersal and history of local colonization and extinction. The exact role of dynamics can be proven only by comparing distributional patterns from different periods, or by ascertaining that species range boundaries do not copy environmental conditions, but are maintained by migration from adjacent areas (Holt & Keitt, 2000). In that case geography rather than ecology affects the shape and structure of geographical ranges. Although we do not have any detailed knowledge about processes that maintain species distribution in the study area, some indirect observations demonstrate the role of the spatial population dynamics for at least the rarer species. Storch & Šizling (2002) showed for the same bird data that rare species of birds did not occupy all patches of suitable habitat, and this 'unsaturation' was related to a strong geographical distributional trend within Europe, and was more pronounced in species whose population trend was either increasing or decreasing, indicating the role of colonization and extinction dynamics. As these rare species actually represent the majority of all species, processes related to the dynamics of population colonization and extinction may importantly affect major distributional patterns of Czech avifauna. This is in good agreement with our evidence for the importance of both latitude and longitude for the differences in local species composition.

Our results stress the importance of factors that are not directly related to contemporary ecological conditions in explaining distributional patterns of even such mobile groups as are birds and butterflies. The importance of historical dispersal, migration routes and isolation has, of course, been recognized from the beginning of biogeography. However, it has largely been neglected when dealing with patterns based on atlas works within individual countries (e.g. Pasinelli *et al.*, 2001, but see Dennis *et al.*, 2002). We show that even at this relatively small scale it is necessary to consider these effects on distribution patterns, as even if these patterns were apparently related to habitat factors, it could be only a by-product of similar geographical structure of habitat and species data. Our results also demonstrate that although the remote sensing data can reveal some important associations between species distribution and habitats, they are not appropriate for revealing all the important ecological factors that can affect the distribution of species perceiving habitats on finer scales. On smaller scales these methods cannot replace – at least as far as conservation is concerned – the painstaking studying of the habitat requirements of individual species in the field, and the no-less painstaking distribution mapping.

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