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RESEARCH PAPER

Relationships between bird species richness and different facets of landscape heterogeneity – insights from a military area

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Abstract. Military areas often host extraordinary biodiversity compared to the typical agricultural landscape in Europe. It has been suggested that this is due to the high landscape heterogeneity caused by disturbances from military training. This study aimed to test this hypothesis using data from the military area Hradiště and nearby farmland in the Czech Republic (Central Europe). Here, we measured two facets of landscape heterogeneity – the number of woody vegetation patches and habitat diversity – and supplemented these measures with previously published data from bird point counts performed on the same sites. The number of woody vegetation patches was higher in the military area than in the farmland and was positively related to the species richness of birds of conservation concern. Habitat diversity did not differ between both regions. It showed, however, a hump-shaped relationship with total bird species richness. Our results indicate that open landscapes of military areas host a higher number of birds of conservation concern than the farmland due to a finer grain of woodland-grassland mosaic. To support more bird species, it is essential to keep habitat diversity high in open landscapes but at a level that does not harm bird populations by area limitation.

Key words: biodiversity conservation, habitat diversity, woodland mosaic, disturbance, anthropogenic habitats, farmland

Introduction

European biodiversity has declined sharply over the last few decades (Stoate et al. 2009). This decline has become a problem not only for nature conservation but also more broadly, as biodiversity is closely linked to the sustainability of agricultural production and food security (Hautier et al. 2015). In a European environmental context, farmland currently accounts for about half of the area of the continent (FAO 2014), and more than half of European species are associated with it (Sutcliffe et al. 2015). The main driver of biodiversity loss is the intensification of agriculture, with habitat diversity loss and landscape homogenisation as a result (Stoate et al. 2009).

Some modern anthropogenic habitats, such as unreclaimed post-mining sites (Šálek 2012), brownfields

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(Meffert & Dziock 2012) or military areas (Warren et al. 2007), have been recognised as refuges of biodiversity, as they may offer conditions that have disappeared from the intensified agricultural landscape. Military areas represent a huge potential for nature conservation, as they are present in all major global ecosystems, and their estimated total area is up to 5-6% of the Earth's surface (Zentelis & Lindenmayer 2014). They host unusually high numbers of plant species (Čížek et al. 2013), insects (Warren & Büttner 2008, Čížek et al. 2013, Harabiš & Dolný 2018) and birds (Reif et al. 2011, Bušek & Reif 2017, Culmsee et al. 2021) with disproportionately large numbers of threatened and endangered species (Warren et al. 2007). The uniqueness of military areas lies in the absence of intensive agriculture, urbanisation, and military activities. The effect of military training activities on species and ecosystems have been examined in various studies (e.g. Milchunas et al. 2000, Lindenmayer et al. 2016, Fish et al. 2019), which mostly recognised their contribution to the maintenance of early successional habitats and to reducing competitive pressure in favour of less competitive species (Leis et al. 2005, Warren & Büttner 2008, Jentsch et al. 2009, Aunins & Avotins 2018).

On the other hand, surprisingly little attention is paid to the question of what environmental conditions of military areas are behind such enormous species biodiversity. The answer to this question is vital for the guidance of management in active military areas (Woodcock et al. 2005) as well as in those that have already been abandoned by the army and gained the status of a protected area (Hagen & Evju 2013, Ellwanger & Reiter 2019). Following the middle disturbance hypothesis (Connell 1978), Warren et al. (2007) suggested that biodiversity in military areas is high due to the high heterogeneity of disturbances causing high landscape heterogeneity. However, as far as we are aware, there is no study which would test this suggestion. In this article, we aim to fill this knowledge gap, test the difference in landscape heterogeneity inside and outside the military area, and test the importance of landscape heterogeneity for biodiversity. We use birds as model organisms since they often serve as state-of-nature indicators reflecting conditions at large spatial scales and higher trophic levels (Fraixedas et al. 2020). In addition, we focus specifically on open areas because the high conservation values of European military areas for birds are mainly due to their open (i.e. non-forest) habitats (Reif et al. 2013, Bušek & Reif 2017, Aunins & Avotins 2018, Culmsee et al. 2021, Šálek et al. 2022).

We express landscape heterogeneity using two measures: the number of woody vegetation patches and habitat diversity. They represent two complementary factors reflecting different mechanisms of how landscape heterogeneity might affect bird species richness. While the number of woody vegetation patches increases the availability of ecological space for bird species adapted to mosaic habitats and the landscape connectivity for bird species using woody vegetation (Pustkowiak et al. 2021), high habitat diversity provides different kinds of habitats facilitating the coexistence of species with different habitat requirements (Evans et al. 2005).

Our study uses data from a large military area and its surroundings in the Czech Republic (Central Europe) to test the following hypotheses. First, we hypothesise that landscape heterogeneity (i.e. the number of woody vegetation patches and habitat diversity) is higher in an open landscape of the military training area than in the nearby typical farmland landscape. Second, we predict that this difference accounts for a higher bird species richness recorded in the military area by Bušek & Reif (2017).

Material and Methods

Study area and selection of study plots

Our research occurred in the Hradiště military area and its nearby landscape in western Bohemia, the Czech Republic, Central Europe. The Hradiště military area is the largest military area in the Czech Republic, covering an area of about 300 km^2, with a cold climate and hilly relief from 334 to 933 m a.s.l. The open landscape with woodland-grassland mosaic is the area's dominant land cover type (Skokanová et al. 2017). From the management perspective, about one-third of the area is used by the army, which creates disturbances resulting in heterogeneous early succession habitats; the other parts are left with no disturbance or just extensive management (grazing or mowing), resulting in a higher proportion of shrub and tree enclaves (Vojta et al. 2010, Skokanová et al. 2017). Only a minor part of the military area is covered by commercially managed forests (Matějů 2010). The nearby landscape mainly consists of commercial forests (approximately 30%), pastures (25%) and arable land (20%), as well as other various agricultural habitats (18%). Unlike the military area, there are human settlements, industrial areas and water bodies; on the other hand, natural grasslands and scattered woody vegetation are found here sporadically.

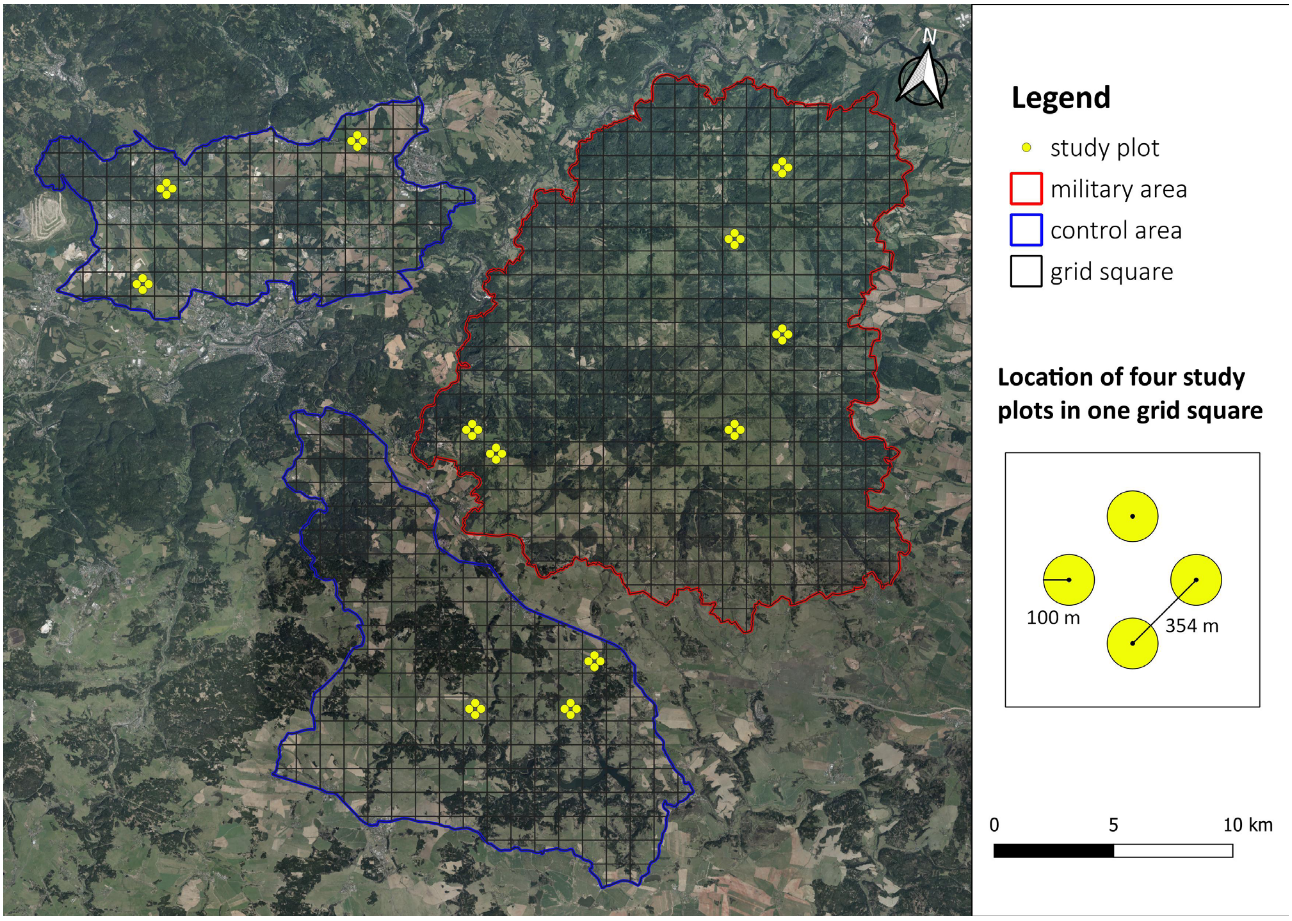

Fig. 1. Map of the study area overlapped by a grid of 1 × 1 km squares used to select study plots. Four study plots were located in each of the squares selected by stratified random approach. The aerial photograph is from 2018.

For this study, we used bird data from Bušek & Reif (2017), who studied birds in the Hradiště military area and nearby landscape as a control area and provided full details on the study design. In brief, Bušek & Reif (2017) sampled the military and control areas. As a control area, they selected a nearby agricultural landscape holding similar proportions of the main land cover types to the military training area (Bušek & Reif 2017). To establish the study plots, Bušek & Reif (2017) applied a stratified random approach using a grid with cells of 1 × 1 km randomly selecting six grid cells in the military area and six in the nearby control area from the pool of the open-habitat cells in respective areas. Open-habitat cells were considered those with more than 50% of the area covered by open habitats (Bušek & Reif 2017). Each cell contained four study plots with a radius of 100 m established in a regular design with the centres of the nearby plots being 354 m apart (see Bušek & Reif 2017, their Fig. 3). In total, the number of study plots was 24 in the military area and 24 in the control area. Habitat mapping and bird census were performed on these circular plots (Fig. 1).

Data collection

We extracted data on bird species richness on individual study plots from Bušek & Reif (2017). They performed point counts in the spring of 2014 at the points located at the centres of respective study plots. Each study plot was surveyed twice per the breeding season in the early morning hours under favourable weather conditions within a fix-radius distance of 100 m around each point (Bibby et al. 2000). See Bušek & Reif (2017) for more details on bird counts.

For each study plot, Bušek & Reif (2017) expressed the total bird species richness and the species richness of birds of conservation concern (CC). As species of conservation concern, Bušek & Reif (2017) considered species deserving special protection by national legislation (Act No. 114/1992 Coll. on Nature Conservation and Landscape Protection 1992, https://www.zakonyprolidi.cz/cs/1992-114) and species listed in the Czech national bird Red List (Šťastný & Bejček 2003). Therefore, we used these two measures of bird species richness for further analysis.

Table 1. Characteristics of linear mixed models testing difference in A) the number of woody vegetation patches and B) the habitat diversity between military area and nearby farmland (expressed as a variable "region").

A) Model	AIC	Deviance	df	*P*
log (patches) ~ 1	177.99	171.99		
log (patches) ~ region	164.10	156.10	1	0.00007
B) Model	**AIC**	**Deviance**	**df**	***P***
diversity ~ 1	66.58	60.58		
diversity ~ region	65.90	57.90	1	0.10130

In 2018, we collected data on landscape heterogeneity on each study plot. Landscape heterogeneity was expressed by two measures: the number of woody vegetation patches and habitat diversity. The number of woody vegetation patches was counted for each study plot using detailed aerial photographs in ArcGIS (ESRI 2013) with a 1 m resolution. The single patch of woody vegetation was defined as a single shrub/tree or cluster of shrubs/trees covering at least 1 m^2 and being isolated by at least a 1 m large gap from another woody vegetation. We set these rules assuming that 1) shrubs/trees smaller than 1 m^2 have a limited ecological function for birds and 2) shrubs/trees located closer than 1 m to each other ecologically function as a continuous block of vegetation and do not increase the landscape heterogeneity.

To measure habitat diversity, we mapped the areas of 14 habitat types (listed below) in the field from April to June. Coniferous or deciduous forests were considered as stands formed solely by coniferous or deciduous tree species. Mixed forest was represented by stands containing a mixture of deciduous and coniferous trees. Non-native forest was represented by stands of exotic trees (irrespective of whether coniferous or deciduous), usually the horse chestnut *Aesculus hippocastanum* and the northern red oak *Quercus rubra*. Forest clearing was a patch of short vegetation (up to 2 m in height) in a forest created by natural or human disturbance. Shrubs were any woody vegetation outside the forest. Grasslands were classified as either managed (represented by regularly cut meadows or active pastures) or unmanaged. As wetland vegetation, we considered all humid areas covered by herbs. Gardens and orchards were woody vegetation patches with human cultivation, typically containing fruit trees. As human settlements, we considered any buildings recorded at study plots. Note that gardens, orchards and human settlements had only marginal representation in the study plots because Bušek & Reif (2017) avoided these habitat types for sampling birds. Streams and ponds were running and still water bodies, respectively, both natural and man-made. Paved and unpaved roads were at least two meters wide, permitting the movement of cars and similar vehicles; we did not recognise footpaths. The area of individual habitat types was calculated using ArcGIS (ESRI 2013). Subsequently, habitat diversity expressed as the Shannon diversity index was calculated across these areas for each study plot.

Statistical analyses

We used linear and generalised linear mixed models (R package "lme4"; Bates et al. 2015), where the identity of the grid cell (each containing four study plots, see Study area and selection of study plots) always acted as a random effect. If the random effect

Table 2. Characteristics of the generalised linear models testing the effects of the number of woody vegetation patches (in Model terms referred to as "patches") and the habitat diversity (in Model terms referred to as "diversity") on total bird species richness and conservation concern (CC) bird species richness. AIC value and deviance of the most supported models are in bold.

		Total bird species richness		CC bird species richness	
Model terms	df	AIC	Deviance	AIC	Deviance
diversity + log (patches)	2	253.733	56.916	**114.607**	**42.738**
diversity + diversity^2 + log (patches)	3	**242.383**	**43.566**	116.439	42.570
diversity + log (patches) + diversity × log (patches)	3	248.761	49.945	116.302	42.434
diversity + diversity^2 + log (patches) + diversity × log (patches) + diversity^2 × log (patches)	5	244.144	41.328	119.941	42.072

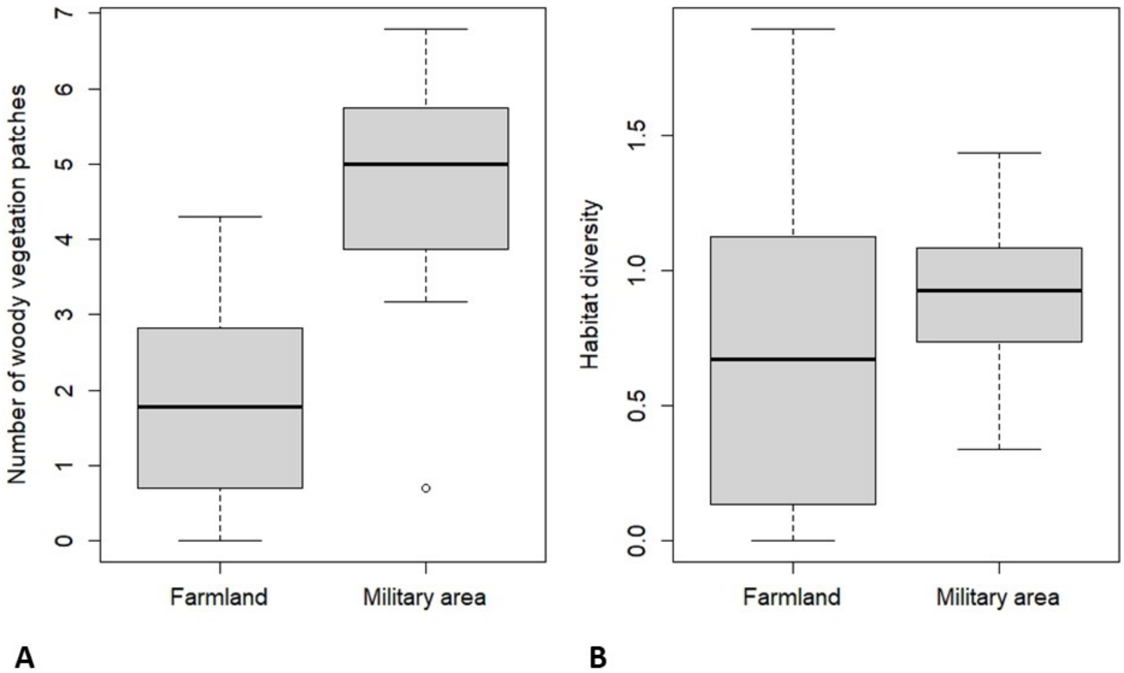

Fig. 2. Boxplot comparing A) the number of woody vegetation patches (log-transformed) and B) habitat diversity between the military area and nearby farmland. The median is the bold line, the box is the interquartile range (IQR), and the whiskers are 1.5 the IQR.

showed zero variance, we used a linear model instead. To achieve the goals of our study, we performed two sets of analyses.

First, we tested hypotheses that the military area and the farmland, expressed as a two-level explanatory categorical variable called "region", differ in the number of woody vegetation patches or habitat diversity. These latter two variables were used as respective response variables. We constructed two linear mixed models (LMMs) for each response variable with a normal distribution – a model containing the region as the explanatory variable and a null model (containing only the random effect; see Table 1). The hypothesis was not supported if the model with the explanatory variable did not have a lower AIC value (delta AIC ≤ 2) than the null model.

Second, we tested hypotheses that the total bird species richness and the CC bird species richness were related to habitat diversity or the number of woody vegetation patches on study plots. The study design intended to include cluster as a random effect. However, due to its zero variance when fitting generalised linear mixed models (GLMMs), we excluded it and used generalised linear models (GLMs) instead. For each of the response variables, i.e. the total bird species richness and the CC bird species richness, we constructed four generalised linear models explaining their variability by the number of vegetation patches and habitat diversity in different combinations: 1) linear main effects of both explanatory variables, 2) linear main effects of both explanatory variables + quadratic term of habitat diversity, 3) linear main effects of both explanatory variables and their interaction, and 4) linear main effects of both explanatory variables + quadratic term of habitat diversity and the interactions between the linear term of the number of woody vegetation patches and both linear and quadratic term of habitat diversity (see Table 2). Based on comparing AIC values of respective models, we chose the best model for each response variable and used that model for inference. The Poisson distribution with log link function was used for all those models because none showed significant overdispersion.

As diagnostic graphs of tested models recommended a logarithmic transformation of the number of vegetation patches, this variable was logarithmic in all models described above. The variables used in the models showed no signs of collinearity according to the variance inflation factor (VIF; the R package "usdm"; Naimi et al. 2014). After log transformation, the number of woody vegetation patches was weakly correlated with the habitat diversity according to Pearson's correlation coefficient, but the correlation ($r = 0.43$) was considerably lower than the value of $r = 0.7$ suggested as a threshold for the collinearity becoming an issue (Dormann et al. 2013). For all models described above, we checked for the possible presence of spatial autocorrelation in residuals using smoothed

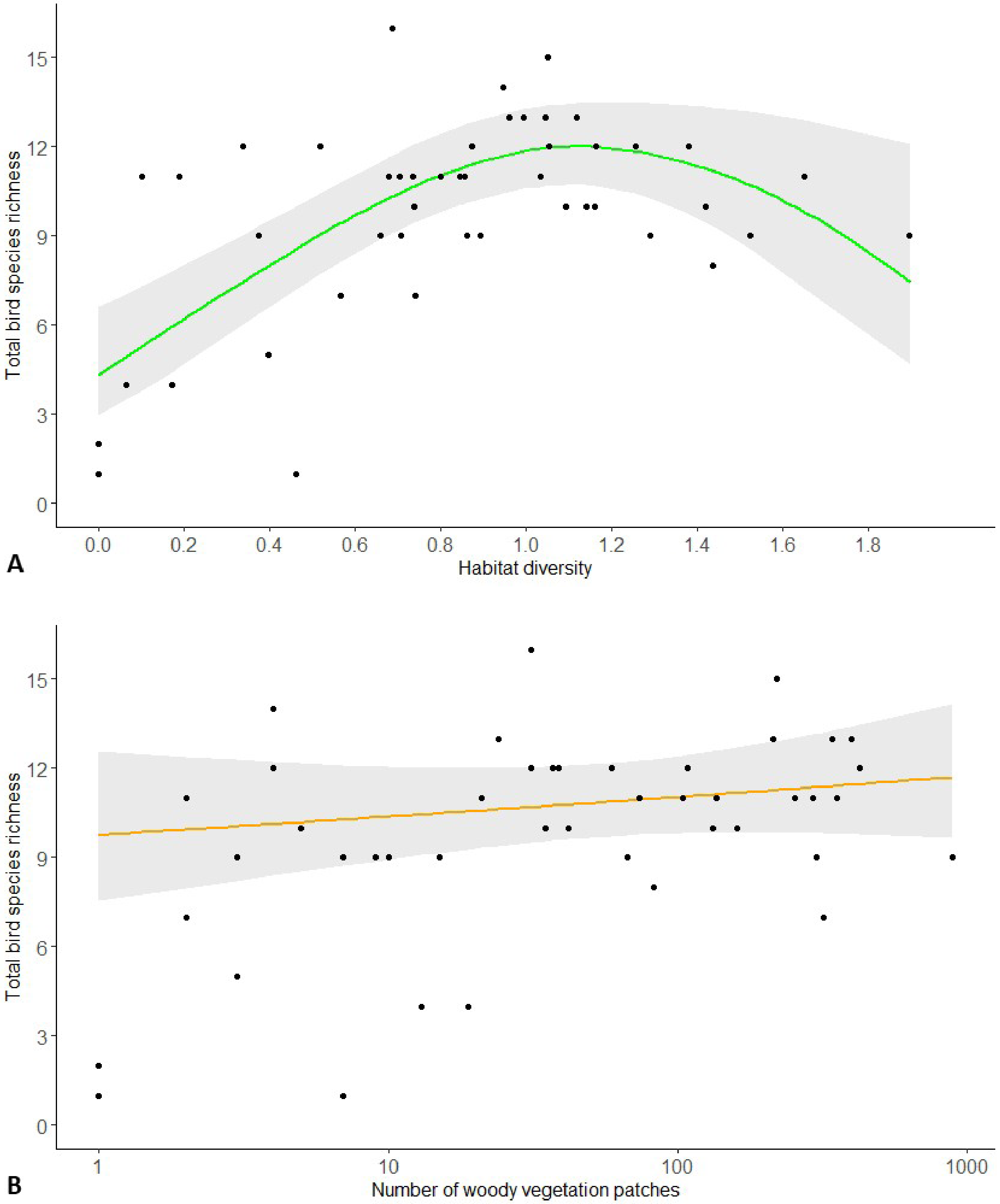

Fig. 3. Visualisation of the relationships between total bird species richness and A) habitat diversity, resp. B) the number of woody vegetation patches according to the best-supported generalised linear model. Shaded areas correspond to 95% confidence intervals. In addition, the estimates from the best model for each response variable are shown.

nonparametric functions (spline.correlog function from the R package "ncf"; Bjornstad 2019) with 95% confidence intervals computed using a bootstrap with 1,000 replications. No significant autocorrelation was indicated in any model. All analyses were performed in software R (version 4.1.0; R Core Team 2021).

Results

Landscape heterogeneity

The median number of woody vegetation patches for study plots in the military area was 147 patches (mean = 206, SD = 37, range 1-892). In nearby

Table 3. Coefficients of the explanatory variables in the model that best explains variation in total bird species richness (see Table 2).

	Coefficient	SE	*P*
diversity	1.76924	0.42161	0.00003
diversity^2	–0.78521	0.22586	0.00051
log (patches)	0.02669	0.02881	0.35421

farmland (the control area), the median was five patches (mean = 13, SD = 20, range 0-73; see Fig. 2A). Statistical models supported the hypothesis that there is a higher number of woody vegetation patches in the military area. Specifically, the deviance of the model explaining the number of woody vegetation patches by the variable region was significantly lower than the deviance of the null model, and the models also differed in AIC when the model with the variable region showed a considerably lower value (delta AIC = 5.71; see Table 1A).

At study plots in the military area, habitat diversity (expressed as Shannon diversity index, see Material and Methods) varied from 0.337 to 1.436, with a mean = 0.926 (SD = 0.266). In nearby farmland (the control area), it varied from 0 to 1.898, with a mean = 0.681 (SD = 0.584; see Fig. 2B). For habitat diversity, a comparison of the null model and the model with the region as an explanatory variable did not support the hypothesis that there is higher habitat diversity in the military area. The models did not differ significantly in deviance and had similar AIC values (delta AIC = 0.68; see Table 1B).

Bird species richness

According to the data of Bušek & Reif (2017), the bird population showed higher species richness in the military area compared to the surrounding agricultural landscape, both for all species and for CC birds. Specifically, the average number of species in military plots was 11.2 (SD = 1.8), and in control plots 7.8 (SD = 4.2). On the other hand, the average number of CC species in military plots was 1.3 (SD = 1.1) and in control plots 0.6 (SD = 0.8). For the list of recorded species, see Table S1.

Testing four models representing different combinations of the effects of the number of woody vegetation patches and habitat diversity on the total bird species richness partly confirmed our hypothesis that landscape heterogeneity affects total bird species richness. The best model with the lowest AIC contained a linear effect of the number of woody vegetation patches and a quadratic effect of habitat diversity without interactions (Table 2). According to this model, the relationship between habitat diversity and total bird species richness was hump-shaped (Table 3, Fig. 3). The other models had considerably worse performance (Table 2): two models had much higher AIC values (delta AIC > 6), and one model had a similar AIC value but a higher number of parameters, so it must be considered as less competitive.

The four models aiming to explain variation in the CC bird species richness by landscape heterogeneity partly confirmed our hypothesis. The best model with the lowest AIC value was the simplest one containing only linear main effects of habitat diversity and the number of woody vegetation patches (Table 2). According to this model, CC bird species richness significantly increased with an increasing number of woody vegetation patches but not with habitat diversity (Table 4, Fig. 4). The other models had higher or similar AIC values but contained a higher number of parameters (Table 2).

Discussion

Military areas have been recognised as biodiversity refuges with an unusually high proportion of protected species (Warren et al. 2007). Bušek & Reif (2017) confirmed this pattern specifically for birds and showed a higher species richness of CC birds in the military area compared to the nearby landscape. Warren et al. (2007) suggested that the reason for such an unusually high conservation value of military areas is the higher landscape heterogeneity due to the specific disturbance regime underpinned by the army's activities. To test this idea, our study has linked two measures of landscape heterogeneity with bird species richness data collected by Bušek & Reif (2017). Our results showed that the species richness of CC birds was greater with an increasing number of woody vegetation patches. At the same time, this aspect of landscape heterogeneity was higher in the military area than in nearby farmland. Interestingly, the second aspect of landscape heterogeneity, habitat diversity, was unrelated to CC bird species richness and did not differ between the military area and nearby farmland. Nevertheless, it showed a hump-shaped relationship with total bird species richness. Below we discuss these findings.

Birds of conservation concern benefit from woody vegetation patches

The number of patches of woody vegetation was significantly higher in the open landscape of the

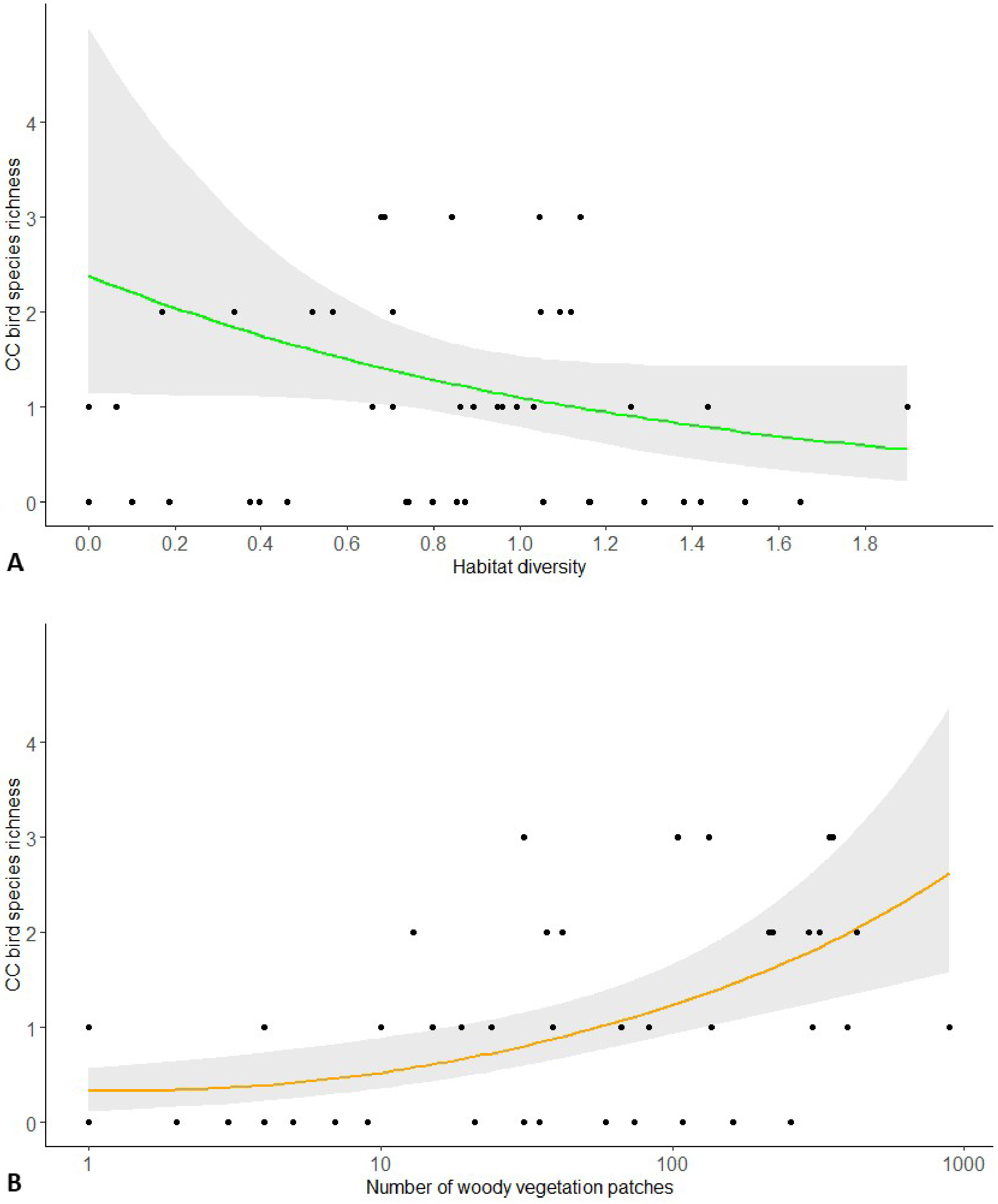

Fig. 4. Visualisation of the relationships between conservation concern (CC) bird species richness and A) habitat diversity, resp. B) the number of woody vegetation patches according to the best-supported generalised linear model. Shaded areas correspond to 95% confidence intervals. The estimates from the best model for each response variable are shown.

military area compared to the nearby farmland. This military area and farmland do not differ in their land cover composition from other such areas in the Czech Republic (Bušek & Reif 2017), so we can reasonably assume that the observed difference is a general feature characterising these kinds of landscapes, and some specific conditions in our study region were not responsible. The number of woody vegetation patches indicates how the woody vegetation is fragmented into a woodland-grassland matrix (Marcolin et al. 2021). Our findings, therefore, indicate that military areas have a finer-grained landscape mosaic in their

Table 4. Coefficients of the explanatory variables in the model that best explains conservation concerns for bird species richness (see Table 2).

	Coefficient	SE	*P*
diversity	–0.76832	0.42460	0.07040
log (patches)	0.34216	0.08769	0.00010

non-forest parts than agricultural landscapes. This phenomenon is most likely caused by military training disturbances and their high spatial heterogeneity (Warren et al. 2007). In contrast, in an intensively used agricultural landscape, a fine-grained mosaic of open and woodland habitats is undesirable, as it complicates the mechanised cultivation of soil blocks and reduces their profitability (Huth & Possingham 2007). Therefore, this mosaic has been significantly suppressed with increasing intensification in recent decades (Stoate et al. 2009).

The number of woody vegetation patches was positively related to the CC bird species richness, which explains the high number of CC bird species in the military area found by Bušek & Reif (2017). The reason why CC birds prefer environments with many woody vegetation patches can probably be attributed to their habitat preferences. CC bird species found in the open landscape of Central Europe (where our data were collected) are mostly the species adapted to the traditional extensive farmland. Many of these species need a combination of trees and shrubs with open habitats for nesting, foraging, defending territory or protecting against predators – whether in the form of individual trees (Pustkowiak et al. 2021), smaller or larger shrub patches (Tryjanowski et al. 2014), hedgerows (Morelli 2013) or woodlots (Dvořáková et al. 2022). With the advancing intensification of agriculture, these non-productive landscape elements were largely removed. Therefore, military areas with many woody vegetation patches represent a much-needed living space for these bird species, to which they do not typically have access in the current intensive agricultural landscape (Culmsee et al. 2021, Šálek et al. 2022). Indeed, CC birds recorded in the military area were mainly associated with a mosaic of woody vegetation and grasslands (e.g. corn bunting *Emberiza calandra*, red-backed shrike *Lanius collurio*, barred warbler *Sylvia nisoria*, Eurasian wryneck *Jynx torquilla*). This reasoning is confirmed by Reif et al. (2011), who showed that military areas are critical refuges for the species of early succession stages.

The positive relationship between the number of woody vegetation patches and the CC bird species richness was linear. However, it is worth mentioning that the number of patches was logarithmically transformed for the analysis. Therefore, the CC bird species richness increases with the non-transformed number of woody vegetation patches following a logarithmic function. It means that in homogeneous open landscapes, where no or only a few woody vegetation patches are present, even a small increase in their number may benefit CC birds. At the same time, in areas where the landscape mosaic is already relatively fine-grained, a further increase in the number of woody vegetation patches would not have such a strong effect. Similar patterns were found in birds' relationships to other types of woody vegetation elements in open landscapes, such as the number of solitary trees (Fischer et al. 2010, Carrasco et al. 2018) and the number of hedgerows or isolated bushes (Ceresa et al. 2012).

Total bird species richness is hump-shaped related to habitat diversity

Habitat diversity was the only factor (from those that we considered in our models) which affected the total bird species richness. This relationship was hump-shaped: habitat diversity increased the total bird species richness, but the number of bird species decreased above a particular habitat diversity value. This finding is not surprising in the context of recent research, which has revised the view on habitat diversity-species richness relationships: although originally these relationships were considered positive (Tews et al. 2004, McMahon et al. 2008), they may be absent (Hortal et al. 2009, Šálek et al. 2018) or negative under some circumstances (Chocron et al. 2015, Carrasco et al. 2018, Heidrich et al. 2020).

Increasing species richness with increasing habitat diversity is a well-known pattern in community ecology: multiple habitats represent different niches that different species can occupy. Increased niche availability reduces interspecies competition and thus allows the coexistence of more species in the same area. However, the existence of a quadratic relationship between species richness and habitat diversity is supported by the theory of Kadmon & Allouche (2007), who combined niche theory and island biogeography into one model. According to them, niche theory predicts a positive relationship between species richness and habitat diversity following the reasoning explained above, but area and dispersion limitations may create this relationship unimodal and even negative. Under these conditions, further diversification of habitats lowers their carrying capacity because their limited areas are too small to provide enough habitat for species (the "area-heterogeneity trade-off"; Allouche et al. 2012).

Consistent with this theoretical background, it can be assumed that in a relatively homogeneous landscape, increasing habitat diversity allows more bird species to coexist, but too high habitat diversity reduces the effective area available per species, leading to the absence or stochastic extinction of some species. Indeed, in recorded total bird species richness prevailed non-CC species with diverse requirements on specific (even though not rare) habitats — e.g. black woodpecker *Dryocopus martius*, mistle thrush *Turdus viscivorus*, and red crossbill *Loxia curvirostra*, which need non-fragmented forests or Eurasian skylark *Alauda arvensis* and meadow pipit *Anthus pratensis* which need large open space with fields and grasslands. To some extent of habitat diversity, these species can coexist, but the overall small area of their habitats can limit their co-occurrence.

Interestingly, we did not find a higher habitat diversity in the military area compared to the nearby agricultural landscape indicating that habitat diversity is not the factor responsible for high bird biodiversity in military areas. The absence of difference between the habitat diversity of the military area and the nearby landscape also informs about the environmental consequences of the disturbance regime associated with military activity. Although this regime increases landscape heterogeneity in terms of the number of woody vegetation patches (this study) and some other landscape elements such as ponds or surface heterogeneity (Aunins & Avotins 2018, Harabiš & Dolný 2018), it does not increase the number of different habitats, at least in categories we recognised here. Instead, habitat diversity seems to result from other kinds of human activities, such as different land uses and settlements.

Caveats

Two caveats can be identified concerning the data we used in this study. First, the data were collected in a single military area and nearby farmland. Therefore, the patterns we report here may be confined to the specific conditions in the study region and not valid for the other areas in Central Europe. Although we cannot exclude this possibility given our data, we consider it improbable. The land cover composition of the Hradiště military area corresponds well to the composition of the other large military areas in the Czech Republic (Bušek & Reif 2017), and the military training activities creating the landscape heterogeneity are similar to those performed elsewhere (Skokanová et al. 2017). Therefore, we suggest that the environmental conditions and biota observed in the Hradiště military area represent similar areas, at least in the Czech Republic.

Second, a time lag exists between the year of bird data collection (2014) and the year of data collection on landscape heterogeneity (2018). If the landscape heterogeneity experienced major changes, its measures might not correspond to the bird data. This caveat is highly unlikely because no such changes were observed on the study plots (O. Bušek, J. Hernová, pers. observ.). Theoretically, vegetation succession could slightly alter the number of woody vegetation patches. Some previously isolated patches might become connected, while some new patches could arise due to the growth of shrubs or trees that were previously not detectable. However, the four-year period was relatively short regarding the successional changes that would be important for birds. Significant changes in bird species richness in response to vegetation succession are reported at the time scale of tens of years in the Northern temperate zone (Wesołowski & Tomiałojć 1997, Holmes & Sherry 2001), while the time lag is only four years in our case. Therefore, although we cannot exclude subtle changes in patch numbers due to vegetation succession on the study plots, these changes are unlikely to alter the patterns in our data.

Conclusions and conservation implications

The results show that different aspects of landscape heterogeneity affected the total bird species richness and CC bird species richness of our studied open landscapes. Specifically, CC bird species richness was related to the number of woody vegetation patches but not habitat diversity. This finding is probably because the CC bird species richness was represented by a specific subset of species with similar habitat preferences to a woodland-grassland mosaic (as described above). Thus, it was related to the amount of one specific habitat (scattered woody vegetation patches), and other habitats probably did not matter for those species. On the contrary, the total bird species richness was related to habitat diversity but not to a higher number of woody vegetation patches, which means that the preference of the CC bird subset was not reflected in the preference of the whole bird community. Indeed, it has been reported that the spatial patterns of species richness are driven mainly by common generalist species rather than by rare ones (Lennon et al. 2004, Dvořáková et al. 2022), which may also explain the differences between the total species richness and the CC bird species richness patterns because the CC birds are typically rare.

Our study shows that open landscapes of military areas may host an exceptionally high number of birds of conservation concern compared to the typical agricultural landscape due to fine-grained woodland-grassland mosaic with patchy or singular point woody vegetation. As this fine-grained mosaic is a by-product of the disturbances caused by military training, it is therefore beneficial from the conservation perspective to maintain the continuity of these training activities or, in the case of military areas that have already been abandoned, to replace the activities of the army with conservation management, which will have a similar ecological impact. To this end, the established conservation management should be adequately heterogeneous in the intensity, time and space to achieve grain fineness and effective in maintaining early succession habitats to ensure the persistence of an open matrix.

Our study also provides general recommendations for protecting biodiversity in military areas and the typical agricultural landscape. Although environmental heterogeneity is generally considered desirable in nature conservation, it should be remembered that heterogeneity has several facets, each of which can affect the community differently. For example, to promote birds of conservation concern in a landscape with an open character, providing a fine-grained landscape mosaic with a high number of shrub and tree patches in an open matrix is beneficial. Especially in the homogenous open landscape, such as intensively managed farmland, adding even a small amount of these woody patches can have a tremendous impact. On the other hand, to enhance total bird species richness, the habitat diversity should be increased, but just to a particular value which does not harm populations by area limitation. Further research is needed to specify what rate of habitat diversity is still beneficial for what taxa and how it is affected by the spatial arrangement of habitats in the landscape.

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Author Contributions

J. Reif conceived the idea, J. Reif with O. Bušek and J. Hernová designed the study, O. Bušek and J. Hernová carried out the fieldwork for bird and landscape data, respectively. L. Dvořáková analysed the data and led writing with inputs from J. Reif.

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Supplementary online material

Table S1. List of recorded species (https://www.ivb.cz/wp-content/uploads/JVB-vol.-72-2023-Dvorakova-et-al.-Table-S1.xlsx).