Increased landscape heterogeneity supports the conservation of European rollers (*Coracias garrulus*) in southern Hungary

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Abstract European rollers (*Coracias garrulus)* were almost extinct from large parts of Hungary in the 1970-1980s. However up till now their population size increased considerably, mainly due to a nature conservation campaign, supplying artificial nest-boxes for breeding. We studied which factors affected rollers' occurrences at the landscape scale in southern Hungary, under natural circumstances and when artificial nest-boxes were supplied. We analysed the composition and the configuration of the landscape at two spatial scales. We found that beside the presence of natural grassland, heterogeneous landscape provided high quality breeding and hunting sites was favourable for rollers. Even though habitat characteristics of roller territories with natural holes or nest-boxes were similar, but breeding sites without artificial nest-boxes harboured higher coverage of forest and heterogeneous agricultural areas. Sites with occupied and unoccupied nest-boxes considerably overlapped, suggesting that the available habitats were not saturated. Nest-box supplementation proved to be an effective tool for rollers' conservation in areas where natural nesting sites were limited, but feeding resources were available. Consequently, the preservation of landscape heterogeneity is a key factor which should take into consideration in the conservation management of roller populations.

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1. Introduction

Understanding bird-habitat relationships is important for developing an effective management plan for avian conservation. Territory selection of birds is a hierarchical process, proceeding from assessment of landscape heterogeneity characteristics through the local scale selection of suitable habitat patches to the fine-scale selection of nest-sites (Wiens, 1989). Birds are selective to the vegetation types in which they breed, but may use patches of several different habitat types within their home-ranges (Virkkala et al., 2004). Consequently, the distribution pattern of a bird population can be explained both by the local characteristics of the nesting sites and the whole landscape structure. Habitat selection is often studied at the local scale, using measures such as food availability and abundance (Hart et al., 2006) or nest site characteristics (Golawksi & Golawska, 2008; Goławski & Meissner, 2008; Pasinelli, 2007). Large scale landscape data may also be used effectively to predict the distribution and abundance of species (Jansson & Angelstam, 1999; Bennett et al., 2006).

Habitat characteristics may affect survival rate of the populations, their breeding success, population growth rate, and predation risk (Cody, 1985; Wiens, 1989; Martin, 1995). At larger scales, landscape composition influence movement patterns and reproductive performance of birds (Bruun & Smith, 2003; Hakkaraainen et al., 2003; Bionda & Brambilla, 2012). Habitat fragmentation may increase predation rate and results in a variety of edge effects (Chalfoun et al., 2002; Bayne & Hobson, 1997).

Habitat mapping projects such as national land-use databases (Sanchez-Zapata & Calvo, 1999) and the Pan-European Corine Land Cover (CLC) project have already been used to understand bird distribution patterns and their responses to landscapes changes (e,g. Radovic et al., 2009). For example, analysing the effects of landscape composition proved to be useful for detecting changes in the size of farmland bird populations (Fuller et al., 2006;

Batáry et al., 2007). In order to develop and implement appropriate measures for conserving bird populations we need the knowledge on habitat requirements of the endangered bird species and the landscape factors affecting the occurrence of these species (Virkkala et al., 2004; Morales et. al., 2005; Warren et al., 2005; Lopez-Iborra et al., 2011; Moreira et al., 2012).

The European roller (*Coracias garrulus*) is a threatened bird species in Europe (its IUCN status is "near threatened, NT", see birdlife database at http://www.birdlife.org/datazone/species/factsheet/22682860). European population of rollers declined considerably in the 1970s, disappearing as a breeding species from Finland, Denmark, Germany and the Czech Republic (Cramp et al., 1993). The Hungarian population also suffered a serious decline from the 1980s: European rollers completely disappeared from western Hungary, and the stronger populations of the eastern and southern regions also declined (Magyar et al., 1998). The reasons for this decrease have not been completely revealed. The main causes could be the loss of suitable habitats due to changing in agricultural practices and the loss of proper nesting hollows (Kovács et al., 2008). In Hungary the lack of nesting hollows seems to be the main limiting factor, since nest-box programmes successfully increased the breeding population in different habitats (Molnár, 1998; Kiss et al., 2014). Whilst in 1994 the estimated population size of rollers was about 600 pairs in Hungary, nowadays it is about 1100 pairs (Kiss et al., 2014) and the majority of rollers breed in artificial nest-boxes. As European rollers are migratory birds, unfavourable changes on their migration routes and wintering areas could probably contribute to this process, including the use of pesticides and illegal hunting (Kovács et al., 2008). Unfortunately, exact data about the migration routes and the location of their wintering areas are only available for the Western European population (Emmenegger et al., 2014; Rodríguez-Ruiz et al., 2014).

The European roller is a secondary cavity-nesting species, consequently, rollers in Hungary naturally nest in the abandoned nest cavities of larger-sized woodpeckers such as the green woodpecker (*Picus viridis*) and the black woodpecker (*Dryocopus martius*) (Szijj, 1958). Occasionally rollers also breed in sand cliffs and buildings (Cramp et al., 1993), however it was not detected in our study area (Southern-Hungary; Molnár, 1998). The most typical feeding habitats are pastures and meadows or agricultural fields where rollers consume large insects, although they occasionally eat small vertebrates (Kiss et al., 2014).

Although several studies have targeted the small-scale habitat characteristics that affect rollers' nest-site selection (Avilés et al., 2000a,b; Rodriguez et al., 2011) and their conservation (Avilés & Parejo, 2004), rollers’ environmental requirements at large geographical scales are still poorly understood. Agricultural intensification affected roller populations negatively in Spain; it reduced roller abundance at their natural breeding sites (Avilés et al., 2000a), as well as their breeding success and clutch sizes (Avilés & Parejo, 2004). Just a few studies investigated characteristics of natural nesting sites such as hollows or human structures (Catry et al., 2011; Václav et al., 2011; Bouvier et al., 2014).

The objectives of the present study were:

(i) To compare the density and distribution of rollers in sites with artificial nest-boxes and in natural breeding sites in southern Hungary.

(ii) We also aimed to determine factors affecting the occurrence of European rollers in landscapes without artificial nest-boxes at large spatial scales. We hypothesized that the effects of agricultural intensification on rollers would be detected at the landscape scale. Rollers' presence/absence data without artificial nest-box supply were used at different spatial scales for detecting what factors affect rollers' occurrences under natural circumstances. We predicted that landscapes with high frequencies of natural breeding sites are favourable for rollers, but the elevated level of intensive agricultural fields would cause an opposite effect.

(iii) Finally, we analysed the factors which affected rollers' presence at the individual-territory level. A successful nest-box program for roller conservation in this area (Molnár, 1998; Kiss et al., 2014) allowed us to also compare the effects of habitat characteristics at the individual (territory) level. We predicted that high quality feeding sites, such as natural or semi-natural grassland habitats over intensively farmed fields, are favourable for rollers when nest-boxes are offered to occupy.

2. Methods

2.1. Study species and census methods

The European roller is a medium-sized, colourful, insectivorous bird species. Rollers are typical sit-and-wait predators, utilizing perch sites as vantage points when they look for prey. Perch sites used by rollers include fences, pylons and power lines, solitary trees, dead tree branches, sticks or any other vantage point from which they can detect prey on the ground (e.g., we have observed rollers perched on haystacks). Our study took place in Csongrád (N46° 25' 35.25''; E20° 14' 05.75'') and Bács-Kiskun counties (N46° 34' 01. 59''; E19° 22' 42.17'') in southern Hungary, a region characterised by a matrix of intensively and extensively managed agricultural fields, sandy and alkaline grasslands (Fig. 1). The distribution of rollers in this region was surveyed at the landscape-scale in 2010. Rollers' occurrence was surveyed by territory mapping based on two visits. The first was in the early breeding season (between May 10-20) and the second one in the middle of the breeding season (between June 10-20) before nestlings fledged. The observers used binoculars and scopes to survey the whole area. We also checked for the occupancy of the nest-boxes at least twice during the breeding season (between May 20– June 10, and June 20 – July 20).

Rollers' breeding density varies by region in Europe. Václav et al. (2011) found mean density of 0.63 pairs/100 m in human buildings (e.g. bridges) in Spain; however, such a high breeding density has not been reported yet from Hungary. In the latter area rollers rarely use buildings and sand cliff, which can provide relatively aggregated potential nest sites, but they rather prefer to use new and abundant feeding sites such as freshly mowed grasslands (our pers. obs.). Rollers typically defend a 50-100 m radius circular area around the nest (Cramp et al., 1993), but published studies reported a high variation in distances between foraging sites and nesting holes. Avilés and Parejo (2004) reported ca. 170 m as a mean value, but Cramp et al. (1993) mentioned longer distances (0.5-1 km, or exceptionally even more). An earlier study in our study site found the average territory size ca. 4.8 ha (cc. 125 m; Molnár, 1988). We determined the number of roller pairs in our study area based on the maps of observations and occupied nest boxes. Following the published records (see above), in this study we assumed that rollers typically use about an area with 1 km radius. For this reason we considered rollers as potential breeders in natural hollows if they were observed further than 1.5 km from any occupied nest-boxes. To avoid the overestimation of the number of breeding pairs, in cases when two birds were detected within 500 m and out of 1.5 km radius zone of an occupied nest-box, we considered them as the same breeding pair, except for cases when nearby nest-boxes were occupied by different pairs.

2.2. Environmental data

Geographic coordinates where rollers were observed, as well as the geographic coordinates of the occupied and unoccupied nest-boxes, were fed into a Geographic Information System (Quantum GIS 1.8.0). We analysed habitat composition of roller territories (natural territories: 22, occupied boxes: 27, empty boxes: 16) and evaluated, which factors affected rollers' occurrences. We measured habitat composition on rollers' occurrence within a 1 km radius buffer area around occupied and unoccupied nest-boxes and at the locations where rollers were observed (each sampling plots covered 3.14 km^2 area). The overlapping occupied and unoccupied nest-boxes were excluded from the analysis. Data on habitat composition were obtained from the maps of the CORINE 50 Land Cover 2006 program using Quantum GIS 1.8.0. We selected 14 land cover classes which potentially affected rollers' habitat occupancy (Table 1). Usage of multispatial scales for study bird distribution may lead to different results or favour to fit better models (Morelli et al., 2013; Sánchez-Zapata & Calvo, 1999; Schindler et al., 2013). For detecting factors that influence rollers' occurrence under natural circumstances we used presence/absence data without artificial nest-box supply at different spatial scales. Two spatial scales were considered for the analysis of environmental variables and rollers' occupancy pattern (5×5 km and 10×10 km UTM grids). We used classes of land cover data from CORINE 50 Land Cover maps, such as arable land, grasslands, heterogeneous agricultural areas, permanent crops, broadleaved forests (Table 2). Different landscape metrics such as diversity indices (Shannon, Simpson, evenness, dominance), fragmentation metrics (degree of landscape division, effective mesh size, splitting index), edge and form analysis were calculated by using a vector-based landscape analysis tool (V-late 1, extension for ArcGis 9, ESRI, Redlands, USA) (Table 2). The number of occupied/unoccupied artificial nest-boxes and also the number of roller' observations were determined for each cell based on nest-box occupancy and territory mapping data. At the lower (5×5 km) spatial scale, besides the 68 cells contained roller observations, 70 empty cells were randomly selected for the analyses. At the larger spatial scale (10×10 km) all of the surveyed cells were used for the analysis (occupied: n = 33; empty: n = 46) (Fig. 1).

2.3. Data analysis

We analysed the effects of landscape composition on territory occupancy of rollers using canonical correspondence analysis (CCA) using CANOCO 4.5 (Lepš & Šmilauer 2003). We included the occupied artificial nest-boxes, unoccupied artificial nest-boxes and natural breeding holes in the analyses and used the CLC coverage data for characterizing land cover types. Shannon and Simpson diversity scores together with the Mean Shape Index of the patches were used as environmental variables.

At the smaller and larger spatial scales, the presence or absence of rollers outside the 1.5 km zone of occupied nest-boxes was used as the binary response variable in the analyses of rollers occurrence. We used autologistic regression analysis (Augustin et al., 1996) to select the landscape variables important for roller occurrence (Table 2). After a preliminary evaluation of the Pearson's correlation matrix including all variables, we selected only one variable from the set of inter-correlated variables ($r > 0.5$) for model building (see for actual variables in the full and best-fit models in Tables 3 and 4.). However, alternative data-sets were also considered if biologically relevant variables (e.g. diversity) were dropped by this preliminary variable selection (c.f. Tables 3a and 3b, and Tables 4a, 4b and 4c). These variables were used as independent variables for linear modelling, and the presence or absence of rollers in a grid cell was used as the binary dependent variable. We performed autologistic regression analysis using the SAM version 4.0 program package (Rangel et al., 2010). In this spatial version of the binary logistic regression analysis the term 'autocovariate' was added to the list of the independent variables (see list of variables in Table 2). Rollers' occurrence in any of the UTM grid systems was used as the binary dependent variable (see the list of independent variables in Table 2). The Akaike information criteria were used to rank models and to select the 'best approximating' models for both spatial scales (Burnham & Anderson, 2002).

3. Results

3.1. Rollers' density

At the larger 10×10 km spatial scale we detected either roller territories or occupied nest-boxes in 70.5% of the UTM cells. Rollers bred in natural holes in 41% of these cells. The mean density of roller pairs breeding in natural holes was 1.55/100 km^2 ± 2.8 S.E., and the maximum number of breeding pairs in a cell was 13. Artificial nest-boxes were present in 79 UTM cells (39.7%) and at least one occupied box was found in 33.3% of the cells. Mean density of breeding pairs in artificial nest-boxes was 2.07 pairs/100 km^2 ± 6.61 S.E., with the maximum of 52 pairs in a cell. The average distance between the closest neighbouring occupied nest-box was 1487 m, but 69.01% of the occupied nest-boxes were closer than 1 km to each other. Our study plots for nest-box supply and natural cavity breeding area without nest boxes separated well, only 3 UTM cells contained breeding both in nest-boxes and natural holes. At the smaller 5×5 km spatial scale rollers bred in 55.6% of the cells, either in natural holes (47.4% of cells) or in artificial nest-boxes (9% of the cells), and only one cell contained both types of breeding.

3.2. Environmental characteristics

The most typical land cover type in the studied breeding territories were arable lands (ARA1 and ARA2), which covered about 50% of the total area. Pastures, natural grasslands and heterogeneous agricultural habitats (COMP, HET1 and HET2; see for codes in Tables 1) all had mean coverage higher than 10%.

CCA ordination (cumulative percentage variance of species-environment relation for the first two axes was 95.5, eigenvalues for the first and second axes were 0.273 and 0.182, respectively; total inertia: 2.193; Fig. 2) showed that territories with natural breeding were characterized by higher habitat diversity (SH) and more irregular shape (MSI) (Fig. 2). CCA also revealed that the territories with natural breeding were predominantly characterised by some kind of woody vegetation, e.g. grasslands with trees (GRA1) and forested areas, such as broadleaved forest (FOR1), mixed forest (FOR2) or even woodland-shrubs (FOR3). We found that farmsteads (FARM) and heterogeneous agricultural areas (COMP) were typical in the territories of the rollers in case of the natural breeding. Grasslands without trees (GRA2) and arable lands with small fields (ARA2) were typical both for natural breeding territories and the surroundings of the nest-boxes as well. Large arable fields (ARA1), marshes (MARS), sparse vegetation on saline areas (ALKA) and HET1 were typical only for the environment of the nest-boxes.

CCA revealed only slight differences between the environment of the occupied and empty nest-boxes (Fig. 2).

3.3. Effects of landscape structure on the occurrence of rollers at different spatial scales

The best-fit linear model (Table 3) revealed a significant spatial effect on rollers occurrence (the tag "autocovariate"). At the 5×5 km spatial scale, the landscape variables CLCTYPE, NARABLE and MSI positively and PERM negatively affected rollers' occupancy pattern. The variables NARABL and MSI also were included in the model with positive coefficients, however, MSI was not significant. The model showed a good fit to the data (McFadden Rho^2 = 0.284; classification accuracy 63%; Table 3), as McFadden Rho^2 (ϱ^2) between 0.2 and 0.4 is known to indicate a good fit (McFadden 1973). At this spatial level Shannon's diversity (SH) had positive, but Simpson's diversity had negative effect on rollers' occurrence (McFadden Rho^2 = 0.282; classification accuracy: 65%; Table 3). At the larger 10×10 km spatial scale, we found the same effect of Shannon's diversity (SH) (McFadden Rho^2 = 0.598; classification accuracy: 82%; Table 4/b). High fragmentation (DIVISION) was also favourable (McFadden

Rho^2 = 0.583; classification accuracy: 81%; Table 4/c). NATGRAS positively MPS and MARSH negatively influenced rollers' occurrence (McFadden $\varrho^2 = 0.598$; classification accuracy: 82%; Table 4./b). The spatial autocovariate also showed a high ($p <= 0.002$) spatial relatedness (Table 4).

4. Discussion

European rollers were abundant in our study area: roller presence was detected in more than half of the cells in the 10×10 km UTM grid. Although rollers breeding in natural hollows and artificial nest-boxes were spatially separated in our study area, we found high similarity in the landscape composition of sites with nest-box supplementation and natural breeding sites (Figure 1). We think that the most important difference between these two groups of sites is the lack of natural breeding hollows in sites where nest-boxes were provided for rollers, supporting the importance of the conservation programs for rollers.

We also performed territory-level analysis comparing the artificial nest-box and natural breeding sites of European rollers in our study area. Previous work showed that providing nest-boxes promotes roller conservation in Hungary when high quality feeding habitat is available (Kiss et al., 2014). In the present study habitat composition of the natural breeding sites was similar to nest-box breeding sites, but contained higher coverage of forest and heterogeneous agricultural areas (complex cultivation pattern) and farms. Installation of nest-boxes in habitats where the natural nesting holes are missing, such as in treeless grassland and arable land, may help to extend rollers' distribution area. The implementation of nest-boxes, in general, needs some caution to maximize the rate of their occupancy (avoiding unfavourable habitats), and also to avoid their potential negative consequences on reproductive success. For example, nest-boxes became ecological traps in Spain due to the high rate of snake predation (Rodriguez et al., 2011), but snake predation was absent from our site, where the most abundant predator was the beech marten (*Martes foina*). A previous study in Spain has shown that nest-boxes located near motorways or in areas with high densities of almond groves and pine plantations were not favoured by rollers (Rodriguez et al., 2011). In natural territories rollers more frequently chose woodpecker holes in more natural patches of landscapes, rather than habitat patches with high intensity of land use (Bouvier et al., 2014). The landscape composition of sites with empty nest-boxes did not differ from either the sites with occupied natural holes or the ones with occupied nest-boxes. This suggests that, even though the unoccupied nest-boxes were installed in sites with proper landscape composition, further factors, such as orientation, may limit nest-box occupancy (Rodriguez et al., 2011; Bouvier et al., 2014). However, the presence of conspecifics (Václav et al., 2011) or heterospecific habitat copying, when animals may use public information from other species with similar ecological requirements (Parejo et al., 2005), may also influence nest-box occupancy. For example, kestrels (*Falco tinnunculus*) might occupy rollers' nest-boxes, but in our nest-boxes the low entrance size prevented kestrels from using them.

Several studies have investigated the relationship between occupancy rate, breeding parameters and breeding site characteristic in rollers at the level of individual territories (Avilés et al., 2000a,b; Avilés & Parejo; 2004; Parejo et al., 2004; Rodriguez et al., 2011). In homogenous habitats in Spain rollers showed a clear preference for breeding near irrigated crops, olive groves and holm-oaks, but avoided breeding near areas of cereal cultivation (Avilés et al., 2000a). Agricultural intensification negatively affected rollers' densities and reproductive success (Avilés & Parejo, 2004). However, the effects of landscape characteristics on territory establishment in rollers have rarely been examined. In France lower land use intensity such as higher proportion of meadows and fallows were favorable for rollers (Bouvier et al., 2014). Catry et al. (2011) also found preference for fallow lands and avoidance of irrigated cultures, vineyards, olive plantations and orchards. In accordance with these results we found negative effect of permanent crops on rollers’ occurrence at the 5×5 km scale.

Although anthropogenic changes of landscapes may negatively affect bird populations, several bird species show preference for heterogeneous agricultural landscapes; some bird populations may benefit from habitat heterogeneity of farmlands (Benton et al., 2003; Fahrig et al. 2011; Morelli et al. 2012; Stirnemann et al. 2014). However, at larger scales in Europe, heterogeneity may affect species richness and abundance of grassland birds either positively or negatively (Báldi & Batáry 2011a,b). Our results on landscape composition at different spatial scales highlighted the importance of heterogeneous landscapes for roller populations. We also found a degree of division higher, which indicates higher fragmentation, where rollers were present at the 10×10 km scale. Even though, European rollers use open farmland areas as foraging sites, but the presence of forest edges, old trees or treelines as nesting places are also required. Therefore both the composition and the configuration of the landscape are crucial for the long time existence of the species. We found different effects of diversity measured by the Shannon's or Simpson's indices: Shannon’s diversity promoted rollers occurrence at 5×5 km scale but Simpson’s diversity had negative effect on it (c.f. Morris et al., 2014; Nagendra, 2002). As Shannon’ diversity is more sensitive for rare types and

Simpson’s diversity is more responsive for the dominant cover types, our result may indicate that scarce habitats (e.g. forests, tree, treelines) of nesting sites or high-quality feeding grounds are crucial for rollers.

The local-scale heterogeneity was also found favourable for birds in Hungary by Báldi & Batáry (2011a,b). In our study the territory-level analysis showed that besides rollers prefer nesting in deciduous woodlands, rollers use heterogeneous farmland patches as foraging sites. Furthermore, we found that more irregular patch shape favours roller occurrence (MSI at territory and 5×5 km level). In case of forest birds diversity Gil-Tena et al. (2008) found that shape irregularity, measured by the mean circumscribing circle index, may also positively affect species richness.

Natural grasslands (NATGRAS) also facilitated rollers' occurrence at the larger scale, indicating that the presence of these patches as high-quality feeding sites is an important factor in territory establishment (c.f. Kiss et al., 2014). Mosaic grasslands in agricultural environments are also important for the conservation of lesser grey shrikes (*Lanius minor*), which utilize similar prey resources (Lovászi et al., 2000; Giralt et al., 2008). Small farms and neighbouring agricultural fields are typically connected by dirt roads. These roads are preferred hunting sites for birds, offering high visibility of crossing ground arthropods (Tagmann-Ioset et al., 2012).

The distribution of potential natural breeders seems to be clustered in space. It might be explained by historical landscape changes of our study area. In this region human activities resulted in highly fragmented landscape, the reduction of grasslands and their transformation into arable lands and vineyards were typical (Biro et al. 2013). However, according to our results small extensive arable lands and the great variety of different habitats (CLCTYPE and SH) at 5×5 km level might ensure suitable foraging places for rollers. Afforestation with non-native tree species was frequent as well, but a significant area of poplar-juniper and partly poplar-hawthorn scrubs still have remained which can provide nesting places for rollers (Biro et al. 2013). However, our analyses also revealed negative effects of landscape structure on roller occurrence. Permanent crops (PERM, typically vineyards) at the smaller spatial scale and proportion of marshes (MARSH) at the larger scale seem to be unfavourable habitats for rollers.

Concerning the effect of different agricultural practices, Catry et al. (2011) found that extensive cereal cultivation is favourable for rollers. Avilés et al. (2000a) revealed the opposite effect of cereals for rollers' breeding performance as a consequence of the decrease in available food. The presence of high-quality food supply seems to be one of the key factors if intensive farming is acceptable for rollers, or has a negative impact on the roller population (Kiss et al., 2014). In our study, among the CLC categories, the heterogeneous agricultural areas contained these kinds of habitats, and this variable (CLCTYPE) positively affected rollers' territory establishment. Báldi et al. (2005) found that rollers were abundant in mosaic-complex of different grasslands in the northern parts of the Hungarian Great Plain, about 150 km north from our study sites, where they preferred grazed pastures.

5**. Conclusions**

Intensification of agricultural practices is the most serious threat for farmland birds throughout Europe including the disappearance of natural habitats with a landscape scale homogenisation (increasing proportion of agricultural monoculture) which have negative impacts on bird populations (O'Connor & Shrubb, 1990). Rollers are also sensitive to agricultural intensification, which might have detrimental effects on their populations (Avilés et al., 2000a; Avilés & Parejo, 2004; Donald *et al*. 2006).

Our results from southern Hungary suggest that the preservation of landscape heterogeneity in agricultural landscapes play a key role in the long-term conservation of rollers. In our study area preservation of habitat heterogeneity and patches of natural vegetation may provide suitable habitats for rollers in an agricultural environment, and nest-box supplementation successfully compensates the decrease in the availability of nesting holes.

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Table 1. Variables used in the CCA analysis.

Variable	**Description (CORINE codes)**	**Mean (range)**
ARA1	Arable land with large fields (2111)	20.4 (0-96)
ARA2	Arable land with small fields (2112)	31.2 (0-79)
VINE	Vineyards (221)	1.02 (0-38.3)
FARM	Farmsteads (24222)	4.2 (0-21.6)
COMP	Complex cultivation patterns (242)	2.6 (0-40.7)
HET1	Agricultural areas with significant share of natural vegetation, and with prevalence of arable land (2431)	0.19 (0-3.17)
HET2	Agricultural areas with significant share of natural vegetation, and with prevalence of grasslands or scattered natural vegetation (2432,2433,2435)	0.35 (0-7.2)
FOR1	Broad-leaved forest (311)	3.1 (0-24.4)
FOR2	Mixed forests (313)	0.7 (0-12.8)
FOR3	Transitional woodland-shrub (324)	1.6 (0-21.3)
MARS	Marshes (411)	4.3 (0-26.2)
GRA1	Grasslands with trees and shrubs (2311, 3211)	1.5 (0-12.4)
GRA2	Grasslands without trees and shrubs (2312, 3212)	21.3 (0-87.7)
ALKA	Sparse vegetation on saline areas (3333)	0.41 (0-8.6)
MSI	Mean Shape Index	8.27 (1.32-39.6)
SH	Habitat diversity measured using Shannon diversity index	1.25 (019-2)
SIMPS	Habitat diversity measured using Simpson diversity index	0.63 (0.08-1.4)

Table 2. Description and descriptive statistics (mean and range) of each explanatory variable used in logistic regression analysis.

Variable (short name)	**Description (CORINE code)**	**Mean (range)**	
Landscape structure:		**5 × 5 km**	**10 × 10 km**
ARABLE	Proportion of arable land (211)	50.4 (0-100)	54 (11-97)
GRASS	Proportion of pastures and natural grasslands (231,321)	13.3 (0-92.3)	14.4 (0-41)
HETER	Proportion of complex cultivation patterns and of agricultural land, with significant natural vegetation (242, 243)	7.1 (0-38.3)	6.2 (0-36)
FOREST	Proportion of broad-leaved forest (311)	10.2 (0-55)	7.4(0-50)
FEDGE	Total edge of broad-leaved forest	17975 (0-63168)	47855 (0-174493m)
HETPATCH	Number of heterogeneous agricultural patches (242,243)	4.29 (0-17)	10.2 (0-39)
NARABL	Number of arable patches	4.38 (0-20)	7.34 (1-26)
NGRAS	Number of grassland patches	5.07 (0-16)	12.8 (0-26)
NP	Number of patches	21.9 (1-46)	59.9 (6-129)
CLCTYPE	Number of different land cover classes	8.33 (1-14)	11.3 (3-17)
MARSH	Proportion of marshes (411)	1.2 (0-31.8)	1.29 (0-29)
PERM	Proportion of permanent crops (vineyards, fruit trees and berry plantations) (222)	3.55 (0-48)	4.18 (0-52)
NATGRAS	Proportion of natural grassland (321)	3.24 (0-61)	4.39 (0-29)
MPS	Mean patch size	2041284 (521399-24594093)	2987068 (775530-16680260)
MSI	Mean Shape Index	1.84 (1.3-1.35)	1.93 (1.43-2.25)
MFRACT	Mean Fractal Dimension	1.29 (1.16-1.35)	1.29 (1.24-1.35)
MPAR	Mean Area-Perimeter Ratio	0.13 (0.001-0.09)	0.3 (0.005-0.78)
ED	Edge Density (m/ha)	53.8 (8.07-91.6)	45.4 (8.1-77.9)
TE	Total Edge length (m)	131854 (19838-219614)	454146 (81001-779975)
DIVISION	Degree of Landscape Division	66.8 (0-96)	67.8 (5.9-98)
SPLIT	Splitting Index	5.66 (1-25)	8.85 (1.06-51.6)
MESH	Effective Mesh Size (ha)	813.4 (95.9-2459.4)	3221 (193.9-9418.9)

SH	Habitat diversity measured using Shannon diversity index	1.32 (0-2)	1.37 (0.15-2.29)
SIMP	Habitat diversity measured using Simpson diversity index	0.4 (0-0.87)	0.58 (0.06-0.88)
D	Dominance	0.4 (0.13-1)	0.41 (0.12-0.94)
EVEN	Evenness Index	0.53 (0.19-1)	0.44 (0.19-0.77)

Table 3. (a) Autologistic regression analysis of rollers occurrence in a 5×5 km UTM grid system (dependent binary variable), and the best fit model, including the number of Corine Land Cover categories (CLCTYPE), permanent crops (PERM), number of arable patches (NARABLE), and shape-index (MSI), as well as the spatial autocovariate as independent variates. (b) The second best fit model with the independent variates of permanent crops (PERM), number of arable patches (NARABLE), shape-index (MSI), Shannon's diversity (SHANNON), Simpson index of diversity (SIMPSON) and the spatial autocovariate (Autocovariate).

(a)

5×5 km scale					
Spatial logistic regression					
Variables	Coeff.	Stand. Coeff.	SE	*t*	*p*
Intercept	-8.279	0	1.867	-4.435	**<0.001**
CLCTYPE	0.285	1.584	0.116	2.453	**0.014**
PERM	-0.095	-1.476	0.036	-2.609	**0.009**
NARABL	0.181	1.130	0.082	2.215	**0.027**
MSI	<0.001	0.720	<0.001	1.645	0.100
Autocovariate	8.522	2.005	2.980	2.86	**0.005**

McFadden $\varrho^2 = 0.2835$; $\chi^2 = 54.224$, $p < 0.0001$; AIC = 149.055; $\Delta\text{AIC}_{1\text{-BEST}} = 0$; classification accuracy: 63%; variables not included in the best model: BROAD, GRASS, NGRASS, HETER, MPS, TE, ED, NP, MPAR, MFRACT, DIVISON, SPLIT, MESH, EVEN, D

(b)

5×5 km scale					
Spatial logistic regression					
Variables	Coeff.	Stand. Coeff.	SE	*t*	*p*
Intercept	-7.194	0	1.688	-4.262	**<0.001**
PERM	-0.092	-1.437	0.037	-2.490	**0.013**
NARABL	0.160	0.995	0.087	1.831	0.067

MSI	<0.001	0.934	<0.001	2.000	**0.046**
SHANNON	5.152	5.616	2.300	2.240	**0.025**
SIMPSON	-10.702	-4.884	5.448	-1.964	**0.049**
Autocovariate	10.003	2.353	3.249	3.079	**0.002**

McFadden $\varrho^2 = 0.282$; $\chi^2 = 53.853$, $p < 0.0001$; AIC = 151.427; $\Delta AIC_{2\text{-BEST}} = 2.372$; classification accuracy: 65%; variables not included in the best model: BROAD, GRASS, NGRASS, HETER, MPS, TE, ED, NP, MPAR, MFRACT, DIVISON, SPLIT, MESH, EVEN, D

Table 4. (a) Autologistic regression analysis of rollers occurrence in a 10x10 km UTM grid system (dependent binary variable), and the best fit models, including the proportion of marshes (MARSH), proportion of natural grasslands (NATGRAS), Shannon's diversity index (SHANNON) as independent variates. In the 2nd best fit model (b) SHANNON was replaced by mean patch size (MEANPATCHSIZE), and by degree of landscape division (DIVISION) in the 3rd best fit model.

(a)

10×10 km scale					
Spatial logistic regression					
Variable	Coeff.	Stand. Coeff.	SE	*t*	*p*
Intercept	-14.324	0	4.221	-3.393	**<0.001**
MARSH	-0.582	-2.741	0.228	-2.552	**0.011**
NATGRAS	0.100	1.456	0.062	1.615	0.106
SH	2.601	3.114	1.344	1.935	0.053
Autocovariate	21.214	5.541	6.250	3.394	**<0.001**

McFadden $\varrho^2 = 0.598$; $\chi^2 = 64.294$, $p < 0.001$; AIC = 53.074; $\Delta\mathrm{AIC}_{1\text{-BEST}} = 0$; classification accuracy: 80% variables not included in the best model: HETPATCH, BROAD, NGRAS, PERM, MPS, TE, ED, NP, MSI, MPAR, MFRACT, DIVISION, SPLIT, MESH, SIMPS, EVEN, D

(b)

10×10 km scale					
Spatial logistic regression					
Variable	Coeff.	Stand. Coeff.	SE	*t*	*p*
Intercept	-7.551	0	3.500	-2.157	**0.031**
MARSH	-0.580	-2.730	0.238	-2.433	**0.015**
NATGRAS	0.149	2.156	0.070	2.119	**0.034**
MPS	<0.001	-9.976	<0.001	-1.855	0.064
Autocovariate	20.118	5.255	6.445	3.122	**0.002**

McFadden $\varrho^2 = 0.598$; $\chi^2 = 68.162$, $p < 0.001$; AIC = 53.206; $\Delta\mathrm{AIC}_{2\text{-BEST}} = 0.132$; classification accuracy: 82%

variables not included in the best model: HETPATCH, BROAD, NGRAS, PERM, TE, ED, NP, MSI, MPAR, MFRACT, DIVISION, SPLIT, MESH, SH, SIMPSON, EVEN, D

(c)

10×10 km scale					
Spatial logistic regression					
Variable	Coeff.	Stand. Coeff.	SE	*t*	*p*
Intercept	-14.482	0	4.442	-3.260	**0.001**
MARSH	-0.484	-2.279	0.210	-2.298	**0.022**
NATGRAS	0.114	2.655	0.064	1.770	**0.077**
DIVISION	0.044	2.494	0.027	1.601	0.109
Autocovariate	22.423	5.857	6.265	3.579	**<0.001**

McFadden $\varrho^2 = 0.583$; $\chi^2 = 62.548$, $p < 0.001$; AIC = 54.820; $\Delta\text{AIC}_{3\text{-BEST}} = 1.746$; classification accuracy: 81%
variables not included in the best model: HETPATCH, BROAD, NGRAS, PERM, MPS, TE, ED, NP, MSI, MPAR, MFRACT, SPLIT, MESH, SH, SIMPSON, EVEN, D

Legend to figures

Figure 1 Geographic location of the study area with the distribution of the rollers' occurrences and the nest-boxes. The 10×10 km grid and the selected 5×5 km UTM cells are also presented

Figure 2 CCA ordination of landscape composition of roller' territories. (Eigenvalues: 1st axis – 0.273; 2nd axis – 0.182. Total inertia: 2.193. Cumulative percentage variance of species data: 1st axis – 12.4%; 1st+ 2nd axis – 20.7 %. Cumulative percentage variance of species-environment relation: 1st axis – 57.2 %; 1st+ 2nd axis 95.5%) Notations: □ breeding in natural holes, ○ empty artificial nest-boxes, ◊ occupied artificial nest-boxes. Refer to Table 1 for definitions of habitat variable codes.

744 Figure 1

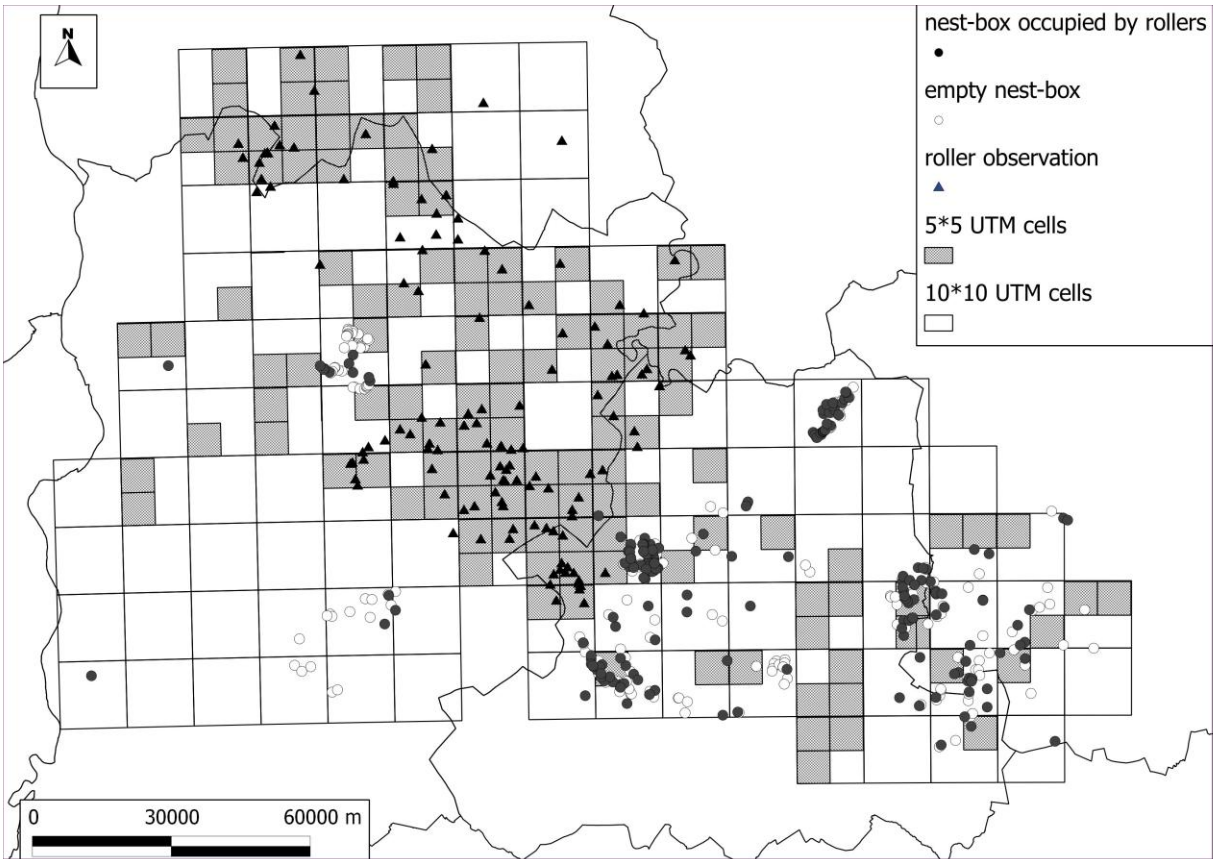

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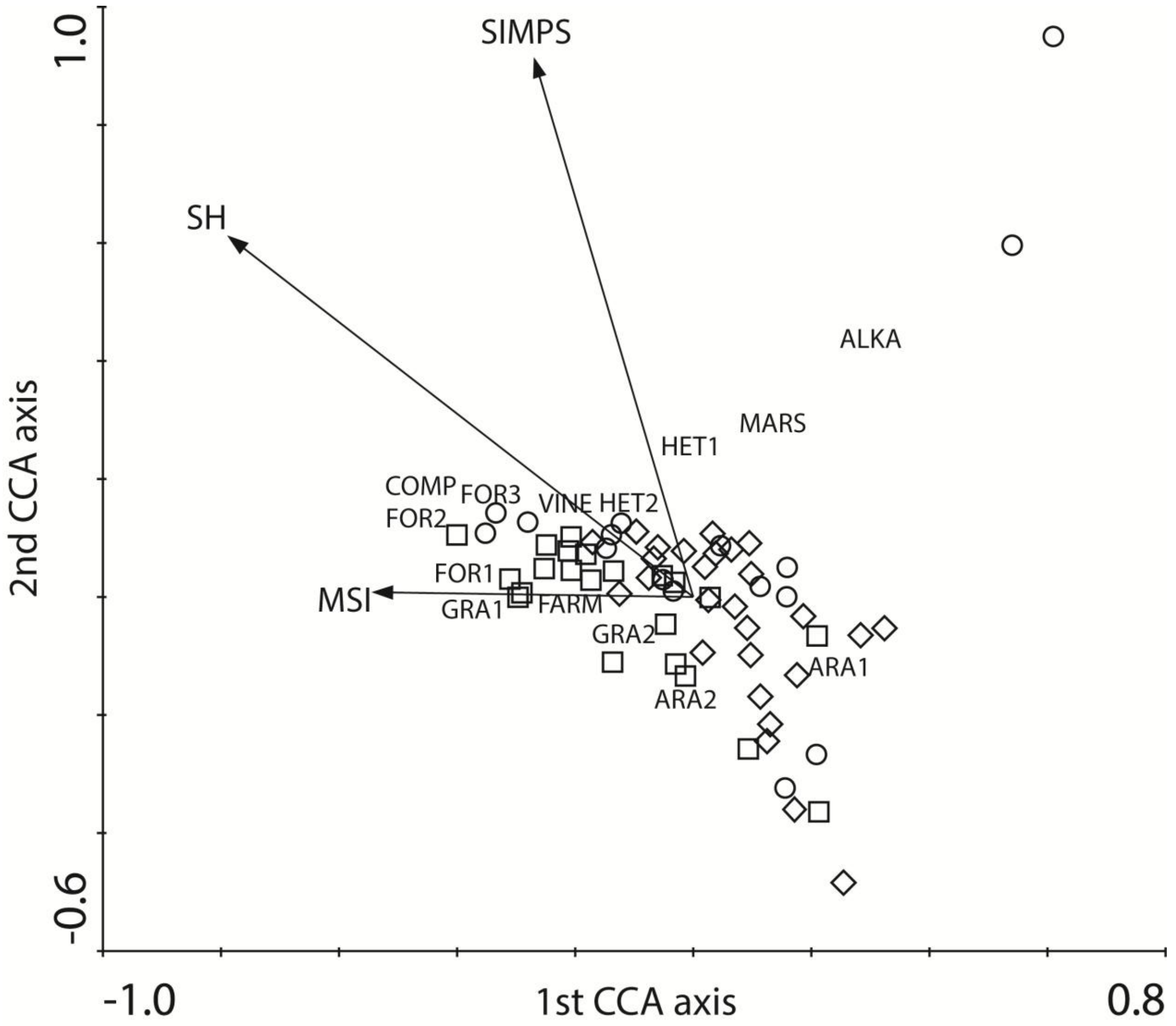
Figure 2


1.0
SIMPS
SH
ALKA
MARS
HET1
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FOR3
VINE
HET2
FOR2
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GRA1
FARM
GRA2
ARA1
ARA2
2nd CCA axis
-0.6
-1.0
1st CCA axis
0.8