Both landscape heterogeneity and configuration determine woodlarks (*Lullula arborea*) breeding territories in Austria

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Farmland birds have declined in the last decades mostly due to agriculture intensification. The Woodlark *Lullula arborea*, a farmland species of conservation concern and protected by the European Bird Directive, occurs in a variety of habitats across its geographic range. Although habitat heterogeneity has been recognized key, the preference or avoidance to certain habitat attributes might differ across its range as different localities may have distinct conditions, thus challenging conservation efforts at the local level. Our aim was to assess habitat associations of Woodlarks and determine whether the habitat attributes identified as important in other habitats across its range could be generalised and applied to Austrian populations. In addition, we examined changes in land use from 2007 to 2016 in areas previously occupied. We mapped the territories of 18 singing males and quantified the composition and configuration of the local landscape. We found that the probability of Woodlarks' territories increased with landscape heterogeneity above 50 %, raised with disaggregated bare soil patches, decreased with patch density and where at least 40 m away from dirt roads. In contrast to previous studies, vegetation height, the presence and proximity to woodland were not identified as important habitat characteristics. Thus, some conservation recommendations can be derived from other localities; for example, maintaining or enhancing landscape heterogeneity; but others should be adapted to the local conditions. In Austria, conservation efforts should focus on including disaggregated patches of bare soil and having dirt roads nearby, besides promoting a heterogeneous landscape.

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Abstract

Farmland birds have declined in the last decades mostly due to agriculture intensification. The Woodlark *Lullula arborea*, a farmland species of conservation concern and protected by the European Bird Directive, occurs in a variety of habitats across its geographic range. Although habitat heterogeneity has been recognized key, the preference or avoidance to certain habitat attributes might differ across its range as different localities may have distinct conditions, thus challenging conservation efforts at the local level. Our aim was to assess habitat associations of Woodlarks and determine whether the habitat attributes identified as important in other habitats across its range could be generalised and applied to Austrian populations. In addition, we examined changes in land use from 2007 to 2016 in areas previously occupied. We mapped the territories of 18 singing males and quantified the composition and configuration of the local landscape. We found that the probability of Woodlarks' territories increased with landscape heterogeneity above 50 %, raised with disaggregated bare soil patches, decreased with patch density and where at least 40 m away from dirt roads. In contrast to previous studies, vegetation height, the presence and proximity to woodland were not identified as important habitat characteristics. Thus, some conservation recommendations can be derived from other localities; for example, maintaining or enhancing landscape heterogeneity; but others should be adapted to the local conditions. In Austria, conservation efforts should focus on including disaggregated patches of bare soil and having dirt roads nearby, besides promoting a heterogeneous landscape.

Introduction

Farmland birds are declining at unprecedented rates in Europe and although a steepest decline occurred between 1980–1995, the decline nonetheless continues (e.g., Donald et al. 2006; Gregory et al. 2019). A driver for this decline is agricultural intensification (Chamberlain et al. 2000; Jerrentrup et al. 2017), which comprises changing crop management including type and relative abundance of different crops, shifting the timing for certain agricultural management activities and increasing the use of artificially produced fertilizers and herbicides (Chamberlain et al. 2000; Donald et al. 2001; Stanton et al. 2018). In addition, habitat homogenisation through the loss or reduction of important landscape elements like hedgerows and wetlands have also contributed to the decline of farmland birds in the last decades (Benton et al. 2003; Stanton et al. 2018). Intense farming modifies the preferred farmland bird habitats which not only affect the required conditions for breeding but also affect their food resources (Gil-Tena et al. 2015). For protecting farmland birds, therefore, detailed knowledge about the habitat requirements of each farmland bird species is key for augmenting their populations (Whittingham et al. 2005).

One of the farmland birds susceptible by habitat modification caused by agricultural intensification is the Woodlark (*Lullula arborea*). Woodlarks are insectivorous and ground-nesting birds, which occupy different kinds of habitats across its geographical range, from Christmas-tree plantations (Fartmann et al. 2018), forest clear cuts and reforestation (Wright et al. 2007) to vineyards (Arlettaz et al. 2012; Bosco et al. 2019; Buehler et al. 2017) and heathlands (Mallord et al. 2007). Woodlarks are listed on the Annex I of the European Bird Directive (79/409/EEC of 2 April 1979) and although there is a recent tendency of an overall moderate increase (EBCC 2021), the population size has shown a high level of fluctuation in Europe in recent years mainly due to habitat changes in their breeding grounds (Takacs et al.

2020). In Austria, Woodlarks are classified as vulnerable in the Austrian Red List (Dvorak et al. 2017) and few populations occur in Upper Austria (Uhl and Wichmann 2013), Lower Austria (Straka 2008) and Lake Neusiedl (Dvorak et al. 2009). In Upper Austria, the Woodlark population has decreased from 38-42 breeding territories in 2007 to 16-18 breeding territories in 2017 (Uhl and Wichmann 2018). Thus, it is of great importance identifying habitat associations at the local landscape and understanding the role of local land-use change in altering their habitats.

Habitat heterogeneity at multiple scales has been identified as a key factor for farmland birds in general (Benton et al. 2003) and Woodlarks in particular (Sirami et al. 2011). At the microhabitat scale (~5 m around the nest), Woodlarks are associated with areas with tall and dense vegetation (Buehler et al. 2017; Mallord et al. 2007) and with a mosaic of grass, herbs and bare soil (Arlettaz et al. 2012; Schaub et al. 2010). At the mesohabitat scale (~50 m) besides bare soil, open grassland and sparse cover of bushes and trees are favoured (Sirami et al. 2011; Sitters et al. 1996). At the macrohabitat scale (~100 m), an interplay between habitat amount and habitat fragmentation emerge (Bosco et al. 2021). If habitat amount is below 20 % Woodlarks avoid fragmented areas, but if habitat amount exceeds 20 % then there is a preference for fragmented areas. In addition, the degree of connectivity is also relevant at the macrohabitat scale (Campedelli et al. 2015).

The preference or avoidance to certain habitat attributes, however, might change across the Woodlark's geographical range as different areas may exhibit different limiting factors or abiotic conditions, thus habitat associations depend on the context (Whittingham et al. 2007). Indeed, effective conservation measures are likely influenced on detailed knowledge about the variation in response across the species' range, hence targeting management strategies at the local level is needed (Whittingham et al. 2007). In addition, changes in land use occur at the local level as they are not only influenced by policies but also by farmers' personal perspectives (Kristensen et al. 2016). For example, farmers can change the area of land, the intensity of management, or the focus of produced goods (van Vliet et al. 2015). All this might have an impact on Woodlarks' habitat associations that ultimately will affect conservation efforts.

The aim of this study was to assess habitat associations of Woodlarks at the macrohabitat scale (i.e. local landscape *sensu* Fahrig 2013) and determine whether the habitat characteristics identified as important in other habitats across its range (e.g. vineyards) were also important or have similar ranking of importance in a cropland-grassland-forest habitat mosaic. We evaluated both habitat amount and the spatial arrangement of habitat elements and human features (i.e. configuration) to better understand whether previous conservation recommendations can be translated to other regions or should be adapted for effective conservation measures. In addition, we examined changes in land use from 2007 to 2016 as an ongoing agriculture intensification has been documented in Upper Austria (van der Sluis et al. 2016). Altogether, this knowledge can be used to provide adequate support to this vulnerable species.

Materials & Methods

Study area

The study was conducted in the region Mühlviertel located in the north-eastern part of Upper Austria, Austria (Fig. 1). It covers an area of 3090 km² and has around 270 000 inhabitants. Within the Mühlviertel region, we focused on the Nature Park (Rechberg 48°19′ N, 14°42′ E), in the eastern part, and Neumarkt (Neumarkt im Mühlkreis 48°25′ N, 14°29′ E), in the north of the Mühlviertel region located approximately 20 km apart. We selected these areas as the main population of Woodlarks in Upper Austria occur in this region (Uhl 2009; Uhl and Wichmann 2013).

The region has continental climate and the mean annual temperature is between 5-9 °C. The area is characterized by hills and a mixture of forest, grassland and cropland. In some parts, the region is rich on landscape elements, like groves, trees and hedgerows, and in other parts these elements are scarce. Around a quarter of the agricultural area is cultivated organically and the average farm size is around 30 ha (BMLFUW 2017).

Territory mapping

Based on previous sightings and territories (Uhl 2009; Uhl and Wichmann 2013), we mapped territories of 18 singing males and randomly selected 16 non-territories in the breeding season of 2017 (Fig. 1). The territory mapping was performed following Südbeck et al. (2005). The area was surveyed systematically from 13 March to 19 May between sunrise and 10:00 h during days without rain or strong winds (Beaufort wind force < 4). During each survey, we recorded Woodlark's location using a global positioning system, behaviour (singing or foraging) and position (e.g., on the ground, on top of tree). Observations of individuals singing in flight were excluded for territory mapping as they could not be associated with any habitat use. The territory centre either corresponded to the centre of the Woodlark territory or to the nest, in few instances, where we were able to find the nest. The 16 non-territories were randomly placed within the mapped study area where no Woodlarks were recorded and corresponded to pseudo-absence (hereafter referred as "absence"). The minimum distance between Woodlark territories and absence areas was 266 m.

Habitat characteristics

We established a 150 m radius around the centre of the territories and absence areas, which equals approximately to 7 ha in total. We selected this size to capture the range size of Woodlarks' territories through their different life phases (Harrison and Forster 1959) and also correspond to the average territory size of Woodlarks in this region (Uhl 2009). For characterizing the macrohabitat within the study plots of 7 ha between April and May 2017, we identified the type of vegetation (grassland, cropland, rough pastures i.e. non-intensive grazing pastures, forest and groves), estimated the area covered and the height, and measured the diameter at breast height (DBH) for forest and groves. We randomly allocated the amount of measuring points in each vegetation patch based on its size (e.g., from 2 measuring points in patches of < 0.7 ha until 20 measuring points for patches of > 6.4 ha). Vegetation patches smaller than 15 m² were not characterized and the minimum distance between measuring points was 10 m. In addition, we measured the length on linear elements such as dirt roads, asphalt roads, and electricity lines, counted isolated trees and estimated the area of residential areas. We estimated the distance from the centre of the territory to all mentioned elements and to vegetation patches.

We used ArcGIS v. 10.5.1 (ESRI 2017) to digitalize the collected field data and used FRAGSTATS v 4.2 (McGarigal et al. 2012) to describe the arrangement of the different vegetation patches in the sampling plots (i.e. spatial configuration). We calculated patch density (PD, number of patches per 100 ha) as it is a useful metric of landscape configuration in which it indicates whether patches were small and numerously distributed in the landscape or if they were few or mainly large patches. Landscape shape index (LSI) measures the landscape disaggregation – the greater the value of LSI, the more dispersed are the patch types. Mean proximity index (PROX_MN) calculates the degree of patch isolation. Contagion index

(CONTAG) quantifies the degree of habitat aggregation and compaction of patch types and Simpson diversity index (SIDI) calculates the heterogeneity of the landscape (McGarigal et al. 2012). A higher value of Simpson's diversity index means greater compositional heterogeneity.

Land-use change

We used agricultural land-use data of the area of Mühlviertel from the years 2007, 2012 and 2016 provided by the Federal Ministry of Agriculture, Forestry, Environment and Water Management to identify land-use changes. The focus of this analysis was on the 15 municipalities where Woodlarks were recorded from 2007 until 2016 (BirdLife Austria 2017). For these 15 municipalities, four land-use types were analysed: Grassland referred to wild flower strips, permanent pasture, managed meadows (cut once to thrice per year) and seeded pastures. Cropland included different types of legumes, field forage, summer grain, winter grain, potato, corn and other field crops. Woody vegetation referred to Christmas trees, energy forests, tree nurseries, and different types of fruit trees. Other comprised protected arable land ('*Landschaftselement Acker*'), protected grassland ('*Landschaftselement Grünland*'), natural monuments and areas with good agricultural and environmental conditions (GAECs).

Data analysis

We performed a conditional Random forest algorithm (Breiman 2001; Hothorn et al. 2006) to rank the 56 explanatory variables according to their importance. The magnitude importance of the predictors was compared using the Conditional Variable Importance values from the random forest approach. Conditional Variable Importance calculates the mean decrease of prediction accuracy of the response variable devoted to an explanatory variable after permuting it over all data and avoids overestimating the importance of correlated predictor variables (Strobl et al.

2008). We used the cforest function from the R package "partykit" (Hothorn and Zeileis 2015) with 5000 bootstrap samples and mtry=p/3 variables at each split.

We checked for multicollinearity of the most important variables identified by the conditional Random forest algorithm using variance inflation factor (VIF) with the R-package "usdm" (Naimi 2015). Those variables with VIF>2 were excluded from further analysis. To determine which habitat characteristics were the most important for the Woodlarks in the Mühlviertel, a Generalized Estimating Equations (GEE) was performed with the response variable absence (0) and presence (1) of Woodlarks in the study plots and the remaining five explanatory variables. These variables were landscape heterogeneity, patch density, landscape shape index of bare soil, percentage of dirt roads, and distance from dirt roads. We included the region as a random factor and the AR-1 correlation structure to account for the spatial correlation of the data (package "geepack"; Højsgaard et al. 2006). Model selection was completed via model averaging (package "MuMIn"; Barton 2020) to show the influence of all variables where QIC (Quasi Information Criteria) change was smaller than two (Zuur et al. 2009).

We performed a compositional data analysis to test whether land-use types (i.e., grassland, cropland, woody vegetation and other) changed in the 15 municipalities where Woodlarks occurred from 2007 to 2016. The response variable was the land-use type and represents compositional data because scores for each class are proportions of the total area covered and therefore are interdependent (Aitchison 1982). The explanatory variable was years (2007, 2012 and 2016). We performed an analysis of variance (ANOVA) adjusted to compositions (van den Boogaart and Tolosana-Delgado 2013) as this technique accounts for the dependence of the compositions and inspected the residuals and checked for symmetry and normality within the package "compositions" (van den Boogaart et al. 2021). All the statistical analysis were done with R v. 4.0.3 (R Core Team 2020).

Results

The proportions of land-use types (grassland, cropland, woody vegetation, other) did not differed among years ($F_{2,21}$ = 0.8108, df = 2, p = 0.458; Fig. 2), thus there was no indication of land-use change from 2007, 2012 and 2016. The area was mainly covered by cropland (65.1%). Grassland covered 33.8 % and woody vegetation and other covered 1.1% of the area. Some fluctuation in area covered occurred, but they were less than 5% being those non-significant.

The most important variables for the occurrence of Woodlarks' territories were landscape heterogeneity, length of dirt road, proportion of dirt roads, patch density of the landscape, landscape shape index of bare soil, patch density of grassland, proportion of bare soil, distance from dirt roads, and contagion index (Fig. 3). The variance inflation factor (VIF) of the most important variables showed that length of dirt road, patch density of grassland, proportion of bare soil, and contagion index had a VIF >2, thus were excluded from further analysis.

The Generalized Estimated Equations (GEE) showed that the strongest predictors on the occurrence of Woodlarks' territories were landscape heterogeneity, distance from dirt roads, patch density and landscape shape index of bare soil (Table 1). All of Woodlarks' territories occurred in areas with a mixture of grasslands (average 25 %), croplands with short (< 20 cm) and tall (20-150 cm) vegetation (12 % and 21 %, respectively), forest (23 %) and bare soil (10 %). The probability of the occurrence of Woodlarks territory increased rapidly with landscape heterogeneity above 50 %, raised with disaggregated bare soil patches, decreased with patch density and where at least 40 m away from dirt roads (Fig. 4).

Discussion

Our results show that Woodlarks were associated with landscape heterogeneity (quantified as Simpson diversity index), patch density, landscape shape index of bare soil and distance from dirt roads. Landscape heterogeneity has been previously identified as a key characteristic in other habitats across the Woodlark's range such as in Christmas-tree plantations (Fartmann et al. 2018), Mediterranean landscapes (Sirami et al. 2011), low-intensity agricultural systems (Brambilla et al. 2012) and vegetated vineyards (Bosco et al. 2019). Heterogeneous landscapes provide a mixture of resources to meet vital needs as has been postulated in the complementation hypothesis (Dunning et al. 1992). In our study, all of Woodlarks' territories where in areas with a mixture of grasslands, croplands with short and tall vegetation, forest and bare soil. This intermix of short and tall vegetation and bare soil might contribute to the patchiness in accessibility of potential prey and avoidance of potential predators important for Woodlarks (Lima and Dill 1990; Schaub et al. 2010).

Besides landscape composition, the configuration was also relevant for the occurrence of Woodlarks' territories. Territories were established in areas with lower patch density suggesting that aggregated patches were more attractive than highly fragmented disaggregated patches in the local landscapes. Similarly, aggregated vegetated fields in vineyards are preferred when the amount of habitat was less than 20 % (Bosco et al. 2021). However, at the broad scale (1 km^2) Woodlarks were more abundant in fragmented steppe habitats (Campedelli et al. 2015).

Woodlarks were also associated with disaggregated bare soil patches. Although the disaggregation of patches of bare soil in particular was not evaluated in previous studies, it has been recognized that few patches of bare soil offer attractive conditions for breeding Woodlarks in vineyards (Schaub et al. 2010). Accessibility of invertebrate prey rather than abundance and avoidance of predation risk are two reasons that have explained the relevance of bare soil in Woodlarks' territories (Schaub et al. 2010).

The importance of disaggregated patches of bare soil was also supported by Woodlarks' attraction of having dirt roads in proximity to their territories. In our study area, dirt roads consisted mostly of bare soil with a vegetated strip between the track lanes. Some were completely covered with short and sparse vegetation or had no vegetation at all. During the study period, Woodlarks were seen dust bathing in the sand of dirt roads, which might be one reason for the significant positive effect of dirt roads in Woodlarks' territories. Another possible reason why dirt roads were important could be the accessibility of food resources on the bare soil or in the short and sparse vegetation (Harrison and Forster 1959; Schaub et al. 2010). In vineyards, Woodlarks prefer strips with a vegetation cover as these provide high abundance of invertebrate prey (Bosco et al. 2019; Rösch et al. 2021).

In contrast to previous studies (Buehler et al. 2017; Harrison and Forster 1959; Mallord et al. 2007), vegetation height was not identified as an important habitat characteristic. This could be related to within-season variability, in which Woodlarks' habitat association change early and late in the breading season (Brambilla and Rubolini 2009). In our study, we focused on the first clutch, so assessment on whether vegetation height becomes an important predictor late in the breeding season requires further study. Another reason might be the scale of analysis considered. Here, we focused on the local landscape, whereas those studies were at the microhabitat scale (immediate surroundings around the nest). Other studies have found that Woodlarks were associated with the presence and proximity to woodland in steppes landscapes (Campedelli et al. 2015; Schaefer and Vogel 2000) which was not the case in our study. Although the proportion of woodland was a habitat element in our study area, it was not relevant by itself but contributed to the overall heterogeneity of the landscape. Thus, habitat associations vary across the Woodlark's geographical range as these are context-dependent (Whittingham et al. 2007), but landscape heterogeneity was the ubiquitous attribute at multiple spatial scales and across its range.

Interestingly, we did not detect any significant land-use changes from 2007 to 2016. The proportion of land-use types considered was similar during this period, which could be attributed to the 'stabilisation of intensification' that happen in most regions in Europe from 2001 to 2011 (van der Sluis et al. 2016). However, it is important to note that we evaluated these changes at the local level in which farmers' personal perspectives play a greater role that policies (Kristensen et al. 2016). In addition, we only evaluated changes in area of land, but other forms of intensification like increasing fertilizer application may be more relevant (Kirchner et al. 2016).

In conclusion, landscape heterogeneity was a key habitat characteristic for Woodlarks as was previously identified across its range. In addition, the configuration of habitat elements should be considered when assessing habitat associations. Even though there was no evidence of changes in land use until 2016, further monitoring is recommended to mitigate potential effects it might have on Woodlarks' habitats. Although some conservation recommendations can be derived from other regions; for example, maintaining or enhancing landscape heterogeneity (e.g., Bosco et al. 2019; Fartmann et al. 2018; Sirami et al. 2011); others should be adapted as important habitat characteristics vary across its range. In Upper Austria, management and conservation efforts should focus on maintaining or enhancing a mixed-habitat landscape of grassland, cropland, forest, and bare soil (i.e. landscape heterogeneity as was previously shown). These elements should be aggregated except for bare soil which should be disaggregated.

Finally, dirt roads should be at least 40 m away from Woodlarks' territories. Together, these measures will benefit Woodlarks and likely also other farmland birds occurring in the area.

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Table 1 (on next page)

(on next page)

Result of the GEE showing the estimate, standard error, Wald value and p-value (P).

Significant results are in bold.

	Estimate	Std. error	Wald	P
(Intercept)	-0.416	0.061	46.9	**<0.001**
Landscape heterogeneity	1.988	0.287	47.9	**<0.001**
Distance from dirt roads	0.870	0.136	41.6	**<0.001**
Landscape shape index of bare soil	0.438	0.076	33.5	**<0.001**
Patch density	-0.354	0.043	69.2	**<0.001**

Figure 1

Location of the study areas in Upper Austria.

Occupied Woodlark territories (presence) plots and non-territories ('absence') plots.

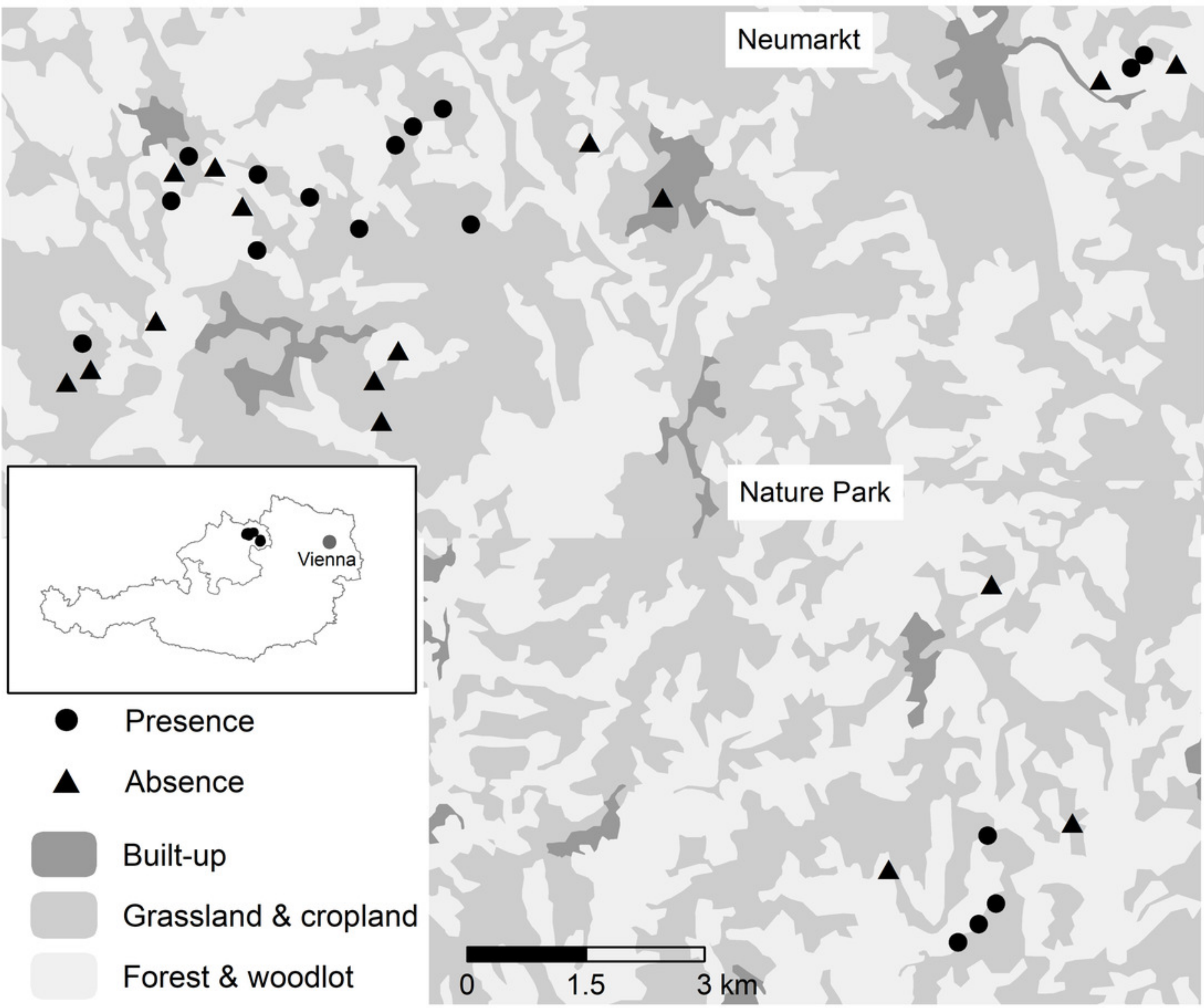


Figure 2

Bar chart representing the parameters of a linear model with compositional response and year as main effect.

Colours depict the associated land-use type.

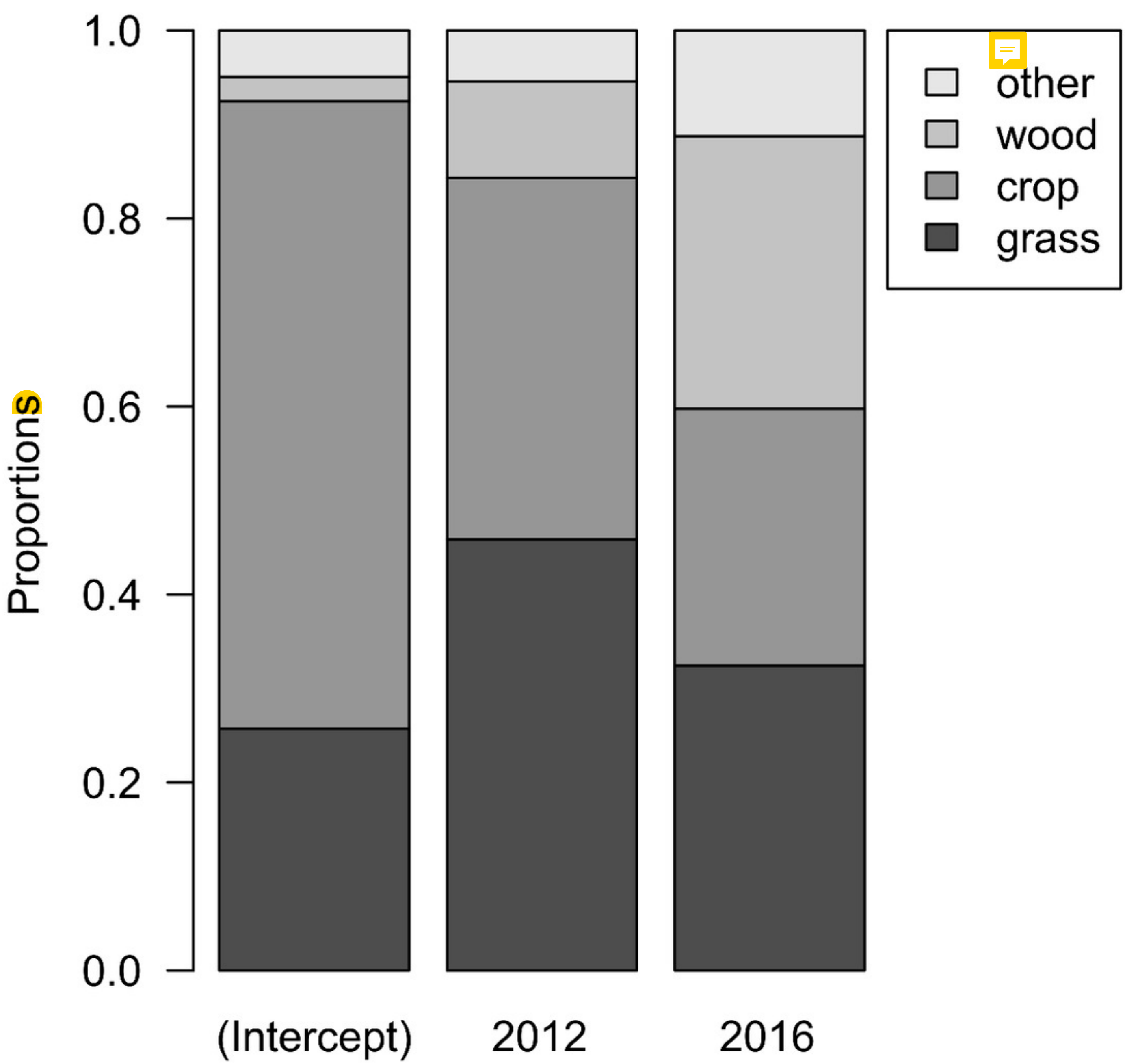


Figure 3

Most important variables based on the conditional random forest analysis.

Landscape heterogeneity (SIDI), length of dirt road (len_dirt_rd), proportion of dirt roads (PLAND_ dirt_rd), patch density of the landscape (PD), landscape shape index of bare soil (LSI_soil_A), patch density of grassland (PD_grassland), proportion of bare soil (PLAND_soil_A), distance from dirt roads (dis_ dirt_rd), and contagion index (CONTAG).

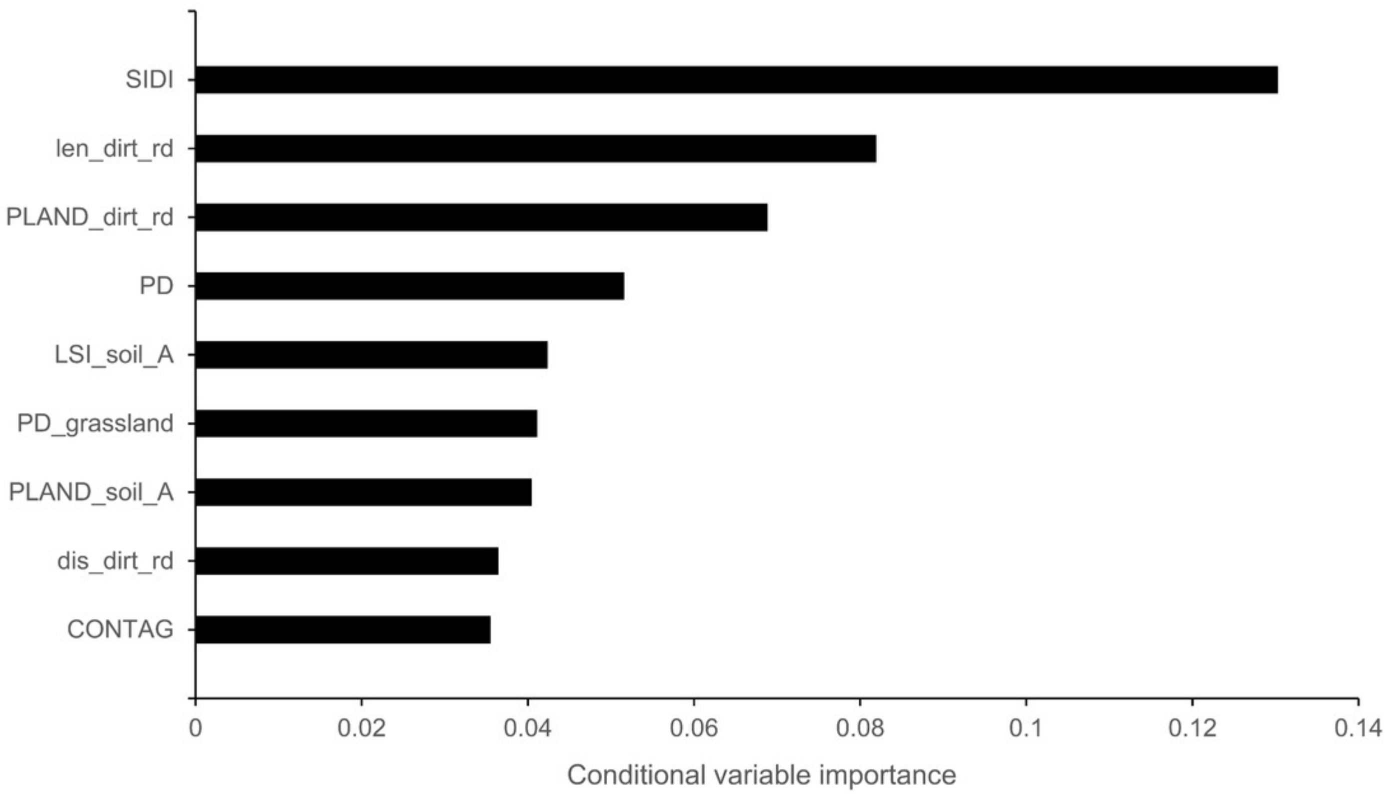
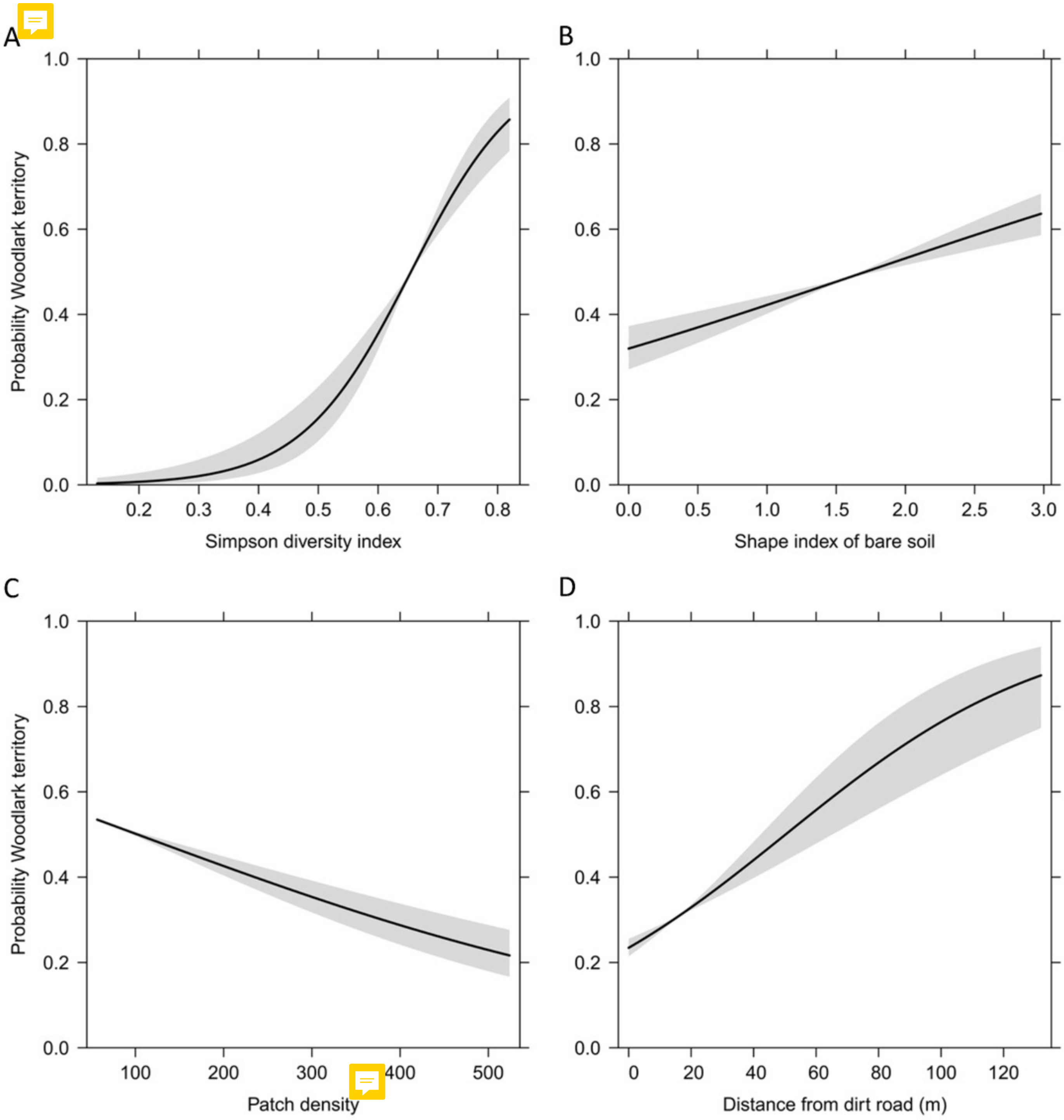


Figure 4

Fitted values (line) and confidence intervals (gray) obtained by the GEE depicting the probability of the occurrence of Woodlarks' territory and significant predictors.

(A) landscape heterogeneity represented by the Simpson diversity index, (B) landscape shape index of bare soil, (C) patch density, and (D) distance from dirt roads.


A
B
C
D
Probability Woodlark territory
Simpson diversity index
Shape index of bare soil
Patch density
Distance from dirt road (m)