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ORIGINAL ARTICLE

Common pastures are important refuges for a declining passerine bird in a pre-alpine agricultural landscape

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Abstract

Agricultural landscapes play an important role in biodiversity conservation. The Tree Pipit (*Anthus trivialis*) was once a widespread breeding bird in European farmlands. Today, however, its numbers are sharply declining in most European countries. The aim of our study was to compare territory densities of Tree Pipits in common pastures and control plots in the surrounding pre-alpine agricultural landscape in southern Bavaria (Germany). Additionally, we determined the drivers of territory and home-range establishment in Tree Pipits. Habitat composition in common pastures and control plots reflected distinct differences in land-use intensity. Common pastures had larger areas of nutrient-poor habitats and higher landscape diversity compared to control plots. In line with this, we detected a clear response of Tree Pipits to differences in habitat composition. Territories were nearly exclusively found in common pastures. Within the common pastures, Tree Pipits preferred those parts that had higher landscape diversity and, additionally, at the territory scale, larger areas of groups of trees. The common pastures are important refuges for the threatened Tree Pipit in the pre-alpine agricultural landscape of the study area. In contrast to the control plots, the common pastures provided (i) sufficient suitable song posts and (ii) heterogeneous vegetation with appropriate nesting sites and a high availability of arthropod food resources. Our study corroborates findings from other studies across Europe highlighting the prime importance of traditionally used wood pastures for the Tree Pipit, and for biodiversity in general.

Keywords Landscape heterogeneity · Land-use change · Farmland bird · Habitat structure · Traditional land use · Tree Pipit (*Anthus trivialis*)

Zusammenfassung

Allmendweiden sind wichtige Refugien für eine gefährdete Singvogelart in der prä-alpinen Agrarlandschaff.

Agrarlandschaften spielen eine wichtige Rolle für den Schutz der Biodiversität. Der Baumpieper (*Anthus trivialis*) war früher ein häufiger Brutvogel in europäischen Agrarlandschaften. Das Ziel unserer Studie war der Vergleich der Revierdichte des Baumpiepers in Allmendweiden und in Kontrollflächen der umgebenden prä-alpinen Agrarlandschaft in Südbayern (Deutschland). Zudem haben wir die Umweltfaktoren ermittelt, die für die Reviergründung und die Nutzung des Aktionsraums entscheidend waren. Die Habitattypenzusammensetzung in den Allmendweiden und Kontrollflächen spiegelt deutliche Unterschiede in der Landnutzungsintensität wider. Allmendweiden wiesen größere Flächen an nährstoffarmen Habitaten und eine höhere Landschaftsdiversität als die Kontrollflächen auf. Baumpieper zeigten eine deutliche Reaktion auf diese Unterschiede in der Habitattypenzusammensetzung. Reviere wurden nahezu ausschließlich in den Allmendweiden festgestellt. Innerhalb der Allmendweiden wurden die Teile präferiert, die eine hohe Landschaftsdiversität aufwiesen und auf der Revierebene zusätzlich durch eine größere Fläche an Baumgruppen gekennzeichnet waren. Allmendweiden sind wichtige Refugien für den gefährdeten Baumpieper in der prä-alpinen Agrarlandschaft des Untersuchungsgebiets. Im Gegensatz zu den Kontrollflächen wiesen Allmendweiden erstens ausreichend geeignete Singwarten und zweitens eine heterogene Vegetation mit Nistplätzen und einer hohen Verfügbarkeit an Arthropoden als Nahrung auf. Unsere Studie bestätigt die Befunde anderer

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Arbeiten aus Europa, die traditionell genutzten Waldweiden eine herausragende Bedeutung für den Baumpieper und für den Erhalt der Biodiversität generell zusprechen.

Introduction

Over the past 200 years, humankind has altered the physical environment of the earth at an unprecedented rate (Rockström et al. 2009), resulting in a dramatic loss of biodiversity (Sala et al. 2000; Foley et al. 2005). Current extinction rates are 1000 times the natural background rate (De Vos et al. 2014). Consequently, Barnosky et al. (2011) suggest that we are heading for a sixth global mass extinction. For terrestrial biomes, land-use change is assumed to be the main driver of this biodiversity crisis (Sala et al. 2000; Foley et al. 2005).

A large part of Europe's biodiversity is associated with agricultural land (Donald et al. 2006; Henle et al. 2008; Kleijn et al. 2009). Farmland constitutes the single largest habitat in Europe; more than 40% of European (EU-27) (Eurostat 2016) and 54% of German (BMU 2007) terrestrial land surfaces are used for agriculture. Consequently, agricultural landscapes play an important role in biodiversity conservation (BMU 2007; Henle et al. 2008). Nevertheless, across different taxa such as plants, insects, and birds, farmlands exhibit the largest decrease in biodiversity (Vickery et al. 2001; Donald et al. 2006; Flohre et al. 2011). The two main drivers of current losses in farmland biodiversity are (i) land-use intensification at productive soils and (ii) abandonment of marginal land (Foley et al. 2005; Henle et al. 2008; Kleijn et al. 2009). Both lead to homogenisation at the landscape and habitat scale with severe negative effects on biodiversity. Bird assemblages have been shown to be very good indicators of overall habitat and, in particular, farmland biodiversity (Donald et al. 2001; Gregory et al. 2004; Graham et al. 2017; Newton 2017). Land-use change affects birds mainly due to the alteration of food supply and its influence on the breeding habitat (Vickery et al. 2001; Benton et al. 2002; Newton 2004).

The Tree Pipit (*Anthus trivialis*) was once a widespread breeding bird in European farmlands (Hagemeijer and Blair 1997; Bauer et al. 2012). However, especially since the 1980s, its numbers are sharply declining in most European countries (Sanderson et al. 2006; Gregory et al. 2007). For example, for the English population, a decline of 82% was recorded between 1981 and 2006 (Baillie et al. 2014). Comparable declines have been observed in our study area at the northern foothills of the Alps in southern Bavaria (Bauer et al. 2012). As a consequence, the Tree Pipit is today considered threatened in Bavaria (Fünfstück et al. 2004) and Germany (Grüneberg et al. 2015). Our study area is one of the last regions in central Europe where large common pastures of high conservation value have remained (Pille et al. 2002; Lederbogen et al. 2004; Helbing et al. 2014). Within these common pastures, the Tree Pipit is a regular breeding bird (Lederbogen et al. 2004).

The aim of our study was to compare territory densities of Tree Pipits in common pastures and control plots in the surrounding pre-alpine agricultural landscape. Additionally, we gathered environmental parameters at the plots, as well as at the Tree Pipit territories and home ranges, and their randomly selected controls. These data were used to determine the drivers of territory and home-range establishment of Tree Pipits. Based on the results, we discuss the relevance of common pastures for the survival of Tree Pipits in modern agricultural landscapes.

Materials and methods

Study area

The study area is located at the northern foothills of the Alps in southern Bavaria, Germany (750–900 m a.s.l.) (Fig. 1). It is characterised by a rather cool and wet climate (mean annual temperature: 6.0–7.0 °C, mean annual precipitation: 1300–1500 mm; German Weather Service, pers. comm.). The dominant form of land use in the hilly and heterogeneous young moraine landscape is dairy farming on mostly small grasslands (BfN 2017). Within the glacially formed hollows and valleys, different mire types have evolved (Succow and Jeschke 1990). The end moraines are usually covered by woodland (BfN 2017).

In contrast to many other parts of Europe, several common pastures have remained in the study area (Lederbogen et al. 2004). Brown dairy cows with a low stocking capacity of 0.5–2.0 livestock units per hectare typically graze there from May to October. The dominant habitat types within the common pastures are grasslands, followed by groups of trees, forests, and fens (cf. Table 1). Common pastures have never been fertilised, except for very small areas of grasslands on mineral soils where manure application had taken place (Lederbogen et al. 2004).

Study species

The Tree Pipit (*Anthus trivialis* L., 1758) is an insectivorous passerine bird with a Palearctic breeding range (BirdLife International 2004; Bauer et al. 2012). The wintering

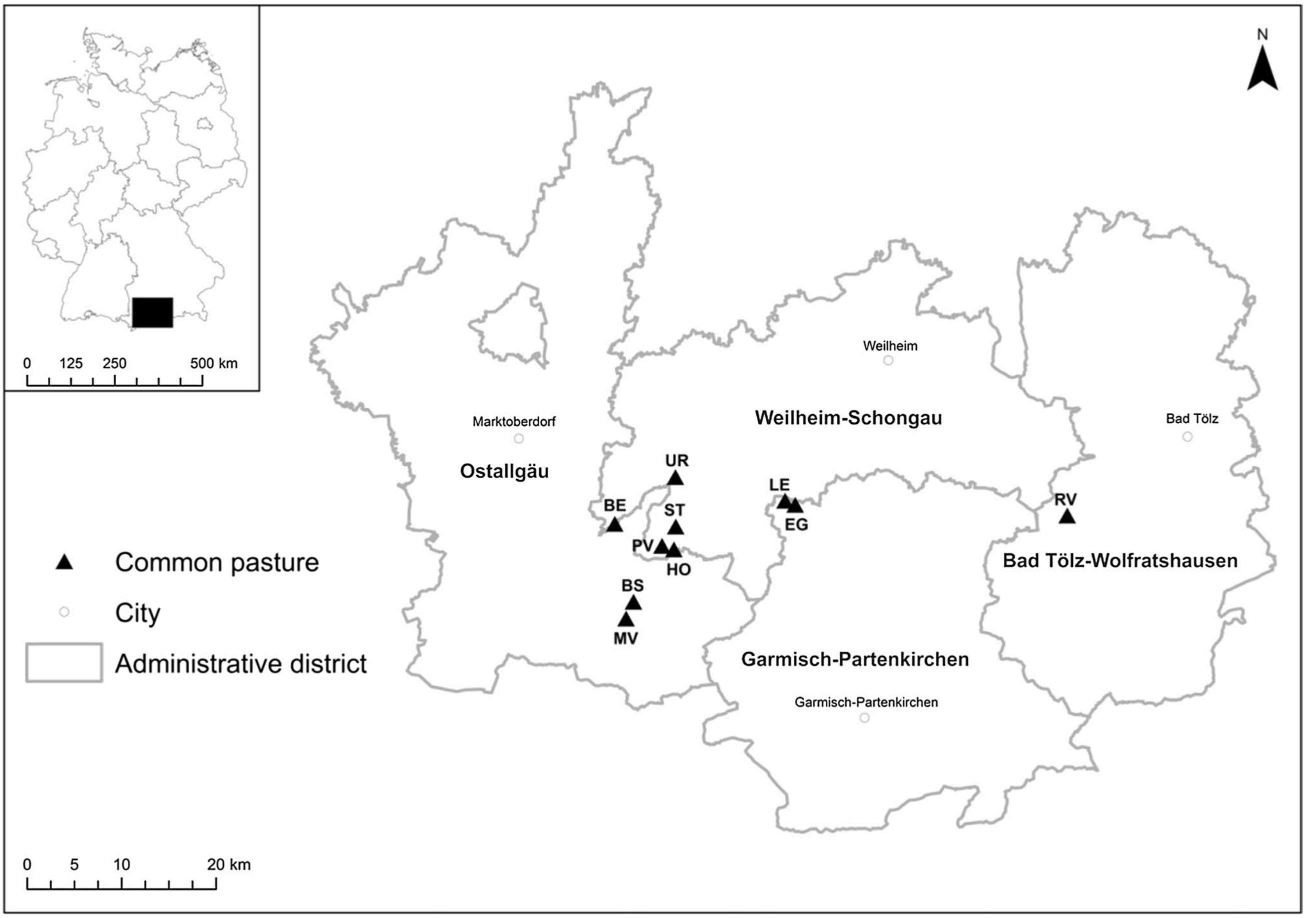


Fig. 1 Location of the study area and common pastures in southern Bavaria (Southern Germany). Common pasture: *BE* Bernbeuren, *BS* Berghofer Söldner, *EG* Echelsbach Gschwend, *HO* Holzer Viehweide, *MV* Mühlenberger Viehweide, *PV* Premer Viehweide, *RV* Rieder Viehweide, *SG* Steingädele, *UR* Urspringer Viehweide

grounds of the European breeding population of this long-distance migrant are the sub-Saharan savannahs in Africa. The Tree Pipit is a characteristic breeding bird of semi-open and open landscapes, if sufficient song posts are available (Loske 1987b; Pätzold 1990; Burton 2007; Petrusková et al. 2008; Moga et al. 2009). Territories are typically located at forest edges or where solitary trees occur in clearings, young afforestations, heathlands, grasslands, and mires (Loske 1987a; Moga et al. 2009; Bauer et al. 2012). The nests are built in sheltered depressions on the ground (Loske 1987a).

Experimental design

Plots

Field studies were conducted in the ten largest common pastures within the study area (Fig. 1). The mean size (±SE) of the commons was 58.6±8.7 ha. We randomly selected one quadratic study plot (25 ha) per common pasture. To compare data from common pastures with those of the surrounding agricultural landscape, control plots of the same size were established. The western edge of the control plots was located 500 m eastwards to the fence of the common pasture. If the cover of water bodies or human settlements exceeded 25%, the control plot was placed 500 m southwards.

Habitat mapping and bird surveys

For each plot, the habitat composition was mapped according to Riecken et al. (2006) (Table 1). Additionally, the number of solitary trees was counted (used variable solitary-tree density), and the borderline length (edge length between open and woodland habitats within each plot) was measured. The landscape diversity (H') of each plot was calculated using the Shannon Index (O'Neill et al. 1988):

$$H' = \sum_i p_i \cdot \ln p_i \text{ with } p_i = \frac{n_i}{N},$$

Table 1 Mean values (± SE) of environmental parameters in common pastures ($N = 10$) and control plots ($N = 10$)

Parameter	Common pasture	Control plot	*P*
Large-scale habitat type (ha)			
Traffic area/settlement	0.1 ± 0.1	0.3 ± 0.1	n.s.
Grassland	11.9 ± 1.7	20.3 ± 1.2	**
Transition bog	0.6 ± 0.3	0.0 ± 0.0	*
Fen	2.2 ± 0.6	0.0 ± 0.0	**
Reed	0.3 ± 0.2	0.0 ± 0.0	n.s.
Group of trees	5.3 ± 1.5	1.5 ± 0.5	n.s.
Forest	3.9 ± 1.9	2.5 ± 1.3	n.s.
Small-scale habitat type (m^2)			
Peat bog	559 ± 258	0 ± 0	*
Stream	91 ± 63	287 ± 115	n.s.
Pioneer forest	1337 ± 967	378 ± 237	n.s.
Derived parameters			
Borderline density (km/km^2)	19.0 ± 15.1	7.2 ± 1.0	***
Solitary-tree density (no./km^2)	63.0 ± 13.7	22.0 ± 6.5	*
Landscape diversity (H')	1.7 ± 0.2	0.8 ± 0.1	**

For data with normal distribution and homogeneous variances, differences were tested using paired *t* tests; otherwise Wilcoxon tests were performed

n.s. not significant

*$P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

where N is the number of habitat types per plot, and n_i is the area of each habitat type in the plot. All spatial analyses were conducted using ArcGIS 10.2 (ESRI Inc.).

Mapping of Tree Pipit territories was performed in all plots from the end of April to June 2014 at early morning (Fischer et al. 2005). Altogether, five surveys were conducted, with an interval of at least 10 days between each visit. During each visit, we noted all observations of territorial behaviour, such as singing, according to Bibby et al. (2000), in a map (scale 1:1500) by following a non-linear transect covering the entire study area. According to the guidelines described by Fischer et al. (2005), establishment of a territory was assumed if a bird showed territorial behaviour at least twice within a span of 10 days between each survey. One of these observations had to belong to the period between mid-May and early June.

The size of Tree Pipit territories can vary greatly (Kumstátová et al. 2004). Usually, they range from 0.5 to 1.6 ha (Loske 1987b; Meury 1989). In addition, Tree Pipits often use habitats adjacent to their defended territories for foraging (Kumstátová et al. 2004). Denerley (2009) reported a mean foraging distance of 36 m and a maximum of 110 m from the nest. Consequently, we analysed habitat composition within a radius of 50 m (0.8 ha; hereafter referred to as ‘territory’) and 100 m (3.1 ha; hereafter referred to as ‘home range’) around the centre of each cluster of observations belonging to one Tree Pipit territory (cf. Berg 2008) using the buffer tool in ArcGIS. To compare habitat composition within Tree Pipit territories and home ranges in common pastures with available habitat structures, 30 random points (three per common pasture; hereafter referred to as ‘control’) were created using the data management toolbox in ArcGIS and the same radii as previously described.

Statistical analysis

At the landscape level, differences in habitat composition and territory densities between common pastures and control plots were analysed using paired *t* tests for data with normal distribution and homogeneous variances; otherwise Wilcoxon tests were performed. At the habitat level in common pastures, differences in habitat composition of territories and home ranges, respectively, and control were analysed using *t* tests if data had a normal distribution and homogeneous variances; otherwise Mann–Whitney *U* tests were conducted.

In order to detect habitat-quality parameters that explain the selection of territories and home ranges in common pastures in comparison to control, binomial generalised linear mixed-effects models (GLMM) were calculated with ‘plot’ as a random factor and several environmental parameters as predictors. To increase model robustness and identify the most important environmental parameters, we conducted model averaging based on an information-theoretic approach (Burnham and Anderson 2002; Grueber et al. 2011). Model averaging was conducted using the ‘dredge’ function (R package ‘MuMIn’, Bartón 2016), and only included top-ranked models within $\Delta\mathrm{AIC}_\mathrm{C}$ (corrected Akaike information criterion) < 3 (cf. Grueber et al. 2011).

To avoid multi-collinearity in the GLMM (cf. Dormann et al. 2013; Löffler and Fartmann 2017), Spearman rank correlations (r_s) were conducted to exclude variables with strong inter-correlations ($|r_s| \geq 0.5$) (cf. Table 3). All statistical analyses were performed using R 2.15.0 (R Development Core Team 2017).

Results

Landscape level

Grassland, groups of trees, and forest were the dominant habitat types in common pastures and control plots (Table 1). However, habitat composition in the two plot types reflected distinct differences in land-use intensity. Common pastures were characterised by significantly larger areas of nutrient-poor habitat types (fen, transition, and peat bogs) and significantly higher habitat heterogeneity indicated by higher landscape diversity, as well as higher borderline length and higher solitary-tree density, than control plots. In contrast, grassland had a significantly greater extent in control plots. All other parameters did not differ between plot types.

Altogether, 35 Tree Pipit territories were detected at the 20 plots. However, all but two territories were found in the common pastures. Consequently, mean Tree Pipit abundance was significantly higher at common pastures than at control plots (Fig. 2). All territorial males used groups of trees as song posts. In contrast, songs were never displayed at forest edges.

Habitat level

According to their area, the most important habitat types within the Tree Pipit territories and home ranges were grassland, forest, groups of trees, and fen (Table 2). Within common pastures, the environmental conditions differed strongly between territories and home ranges, and control plots. Territories and home ranges were characterised by significantly larger areas of fens and groups of trees, as well as significantly higher landscape diversity, than control plots. Additionally, territories had a significantly higher borderline density and home ranges a significantly higher cover of reed. All other parameters did not differ.

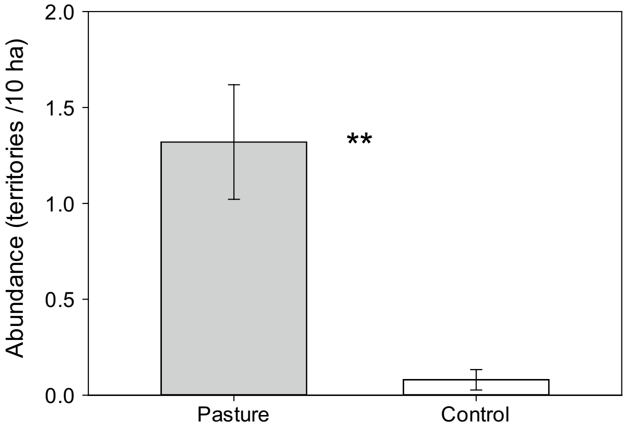


Fig. 2 Mean abundance (±SE) of Tree Pipit territories in common pastures ($N=10$) and control plots ($N=10$). Differences were tested using Wilcoxon test: $Z=-2.809$, $^{**}P<0.01$

According to the GLMM, the likelihood of both territory and home-range establishment in common pastures increased with landscape diversity (Table 3, Fig. 3). Additionally, the cover of groups of trees had a positive influence on territory establishment. Model accuracy was up to twice as high for the territory scale as for the home-range scale (maximum pseudo R^2 [Nagelkerke]: 0.33).

Discussion

In our study, both common pastures and control plots in the pre-alpine agricultural landscape of southern Bavaria were dominated by grassland, groups of trees, and forest. Nevertheless, habitat composition in the two plot types reflected distinct differences in land-use intensity. Common pastures had larger areas of nutrient-poor habitats and higher landscape diversity compared to control plots. In line with this, we detected a clear response of Tree Pipits to differences in habitat composition. Territories were nearly exclusively found in common pastures. Within the common pastures, Tree Pipits preferred areas with higher landscape diversity

Table 2 Mean value (±SE) of environmental parameters in Tree Pipit ($N=33$) territories (50 m radius) and home ranges (100 m radius), respectively, and control ($N=30$). For data with normal distribution and homogeneous variances, differences were tested using *t* tests; otherwise Mann–Whitney *U* tests were performed

Parameter	Territory	Control	*P*	Home range	Control	*P*
Large-scale habitat type (ha)						
Grassland	0.22 ± 0.04	0.32 ± 0.05	n.s.	0.92 ± 0.14	1.15 ± 0.16	n.s.
Fen	0.13 ± 0.03	0.06 ± 0.03	**	0.42 ± 0.08	0.15 ± 0.05	**
Group of trees	0.15 ± 0.03	0.06 ± 0.02	**	0.46 ± 0.06	0.27 ± 0.07	*
Forest	0.16 ± 0.04	0.20 ± 0.05	n.s.	0.75 ± 0.14	0.92 ± 0.17	n.s.
Small-scale habitat type (m^2)						
Traffic area/settlement	123 ± 43	372 ± 261	n.s.	403 ± 100	315 ± 81	n.s.
Peat bog	14 ± 14	34 ± 34	n.s.	72 ± 68	121 ± 111	n.s.
Stream	13 ± 13	48 ± 31	n.s.	620 ± 553	146 ± 74	n.s.
Reed	191 ± 97	106 ± 80	n.s.	729 ± 396	308 ± 207	*
Transition bog	511 ± 233	191 ± 189	n.s.	1404 ± 602	494 ± 429	n.s.
Derived parameters						
Borderline density (km/km^2)	26.8 ± 2.8	17.4 ± 3.1	*	27.1 ± 5.8	18.3 ± 2.1	n.s.
Solitary-tree density (no./km^2)	109 ± 28	102 ± 46	n.s.	68 ± 15	66 ± 16	n.s.
Landscape diversity (H')	1.3 ± 0.1	0.9 ± 0.1	**	1.6 ± 0.1	1.2 ± 0.1	**

n.s. not significant

$^{*}P<0.05$, $^{**}P<0.01$, $^{***}P<0.001$

Table 3 Model-averaging results (GLMM): relationship between the territory occupancy of Tree Pipits ($N_{\mathrm{territories}} = 33$, $N_{\mathrm{control}} = 30$; binomial response variable) and environmental parameters at the territory (a) and home-range scale (b)

Parameter	Estimate	SE	*Z*	*P*
(a) Territory (50 m radius)[a]				
(intercept)	$-1.463\mathrm{e}^{+00}$	$7.201\mathrm{e}^{-01}$	2.032	*
Group of trees	$4.533\mathrm{e}^{-04}$	$2.288\mathrm{e}^{-04}$	1.982	*
Landscape diversity (*H′*)	$1.108\mathrm{e}^{+00}$	$5.624\mathrm{e}^{-01}$	1.970	*
Not significant: fen, forest, grassland, peat bog, reed, solitary-tree density, stream, traffic area/settlement, transition bog				
Range of pseudo R^2 (Nagelkerke) = 0.15–0.33				
(b) Home range (100 m radius)[b]				
(intercept)	$-1.815\mathrm{e}^{+00}$	$8.007\mathrm{e}^{-01}$	2.267	*
Landscape diversity (*H′*)	$1.347\mathrm{e}^{+00}$	$5.292\mathrm{e}^{-01}$	2.545	*
Not significant: borderline density, grassland, group of trees, peat bog, solitary-tree density, stream, traffic area/settlement, transition bog				
Range of pseudo R^2 (Nagelkerke) = 0.17–0.19				

Model-averaged coefficients (full average) were derived from the top-ranked models ($\Delta\mathrm{AIC}_{\mathrm{C}} < 3$) (cf. Table 4). The explanatory power of the models is shown by the range of pseudo R^2 values (Nagelkerke) of the top-ranked models ($\Delta\mathrm{AIC}_{\mathrm{C}} < 3$).

n.s. not significant, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

[a] Borderline length was excluded from the GLMM because it was inter-correlated with landscape diversity (*H′*) ($r_s = 0.62$, $P < 0.001$)

[b] Reed was excluded from the GLMM because it was inter-correlated with fen ($r_s = 0.51$, $P < 0.001$) and landscape diversity (*H′*) ($r_s = 0.56$, $P < 0.001$); fen was excluded from the GLMM because it was additionally inter-correlated with landscape diversity (*H′*) ($r_s = 0.68$, $P < 0.001$); forest was excluded from the GLMM because it was inter-correlated with grassland ($r_s = -0.59$, $P < 0.001$)

and, additionally, at the territory scale, larger areas of groups of trees.

Based on the results of our study, we assume that the high land-use intensity and the low habitat heterogeneity are the main reasons for the virtual absence of Tree Pipit territories in the control plots. Song posts, such as trees at forest edges, groups of trees or solitary trees in semi-open and open habitats are one of the key resources in Tree Pipit breeding habitats (Loske 1987a; Pätzold 1990; Burton 2007; Moga et al. 2009; Bauer et al. 2012). Although these habitat structures were less widespread in the control plots, they were still common and can hardly explain the almost complete lack of colonisation by the Tree Pipit.

Besides sufficient song posts, suitable nesting sites and foraging habitats are of prime importance for successful breeding of the Tree Pipit. Nesting sites are usually characterised by heterogeneous vegetation with high field-layer cover and low to medium vegetation height (e.g., Loske 1985, 1987a; Burton 2007). In contrast, for foraging, the Tree Pipit mainly depends on short and sparsely vegetated habitats rich in small, soft-skinned arthropods (Loske 1985). However, today, such habitats are rare in the agricultural landscape of the study area. Natural environmental gradients have largely been destroyed by drainage, flattening, and intensive fertilisation, resulting in a homogeneous and intensively used landscape with improved grasslands characterised by high amounts of fertiliser application and high stocking rates or many mowings per year (Konold 1996; Ringler and Grabherr 2017). Consequently, the proportion of high-nature-value grassland in the study area is 5–13%, which is below the generally low German average of 17% (Matzdorf et al. 2010), and would be even lower when excluding the common pastures. Even if Tree Pipits established territories in these uniform grasslands, their breeding success would be low due to current grassland management (high stocking rates or early and frequent cutting) (cf. Gatter 2000; Wilson et al. 2009; Newton 2017).

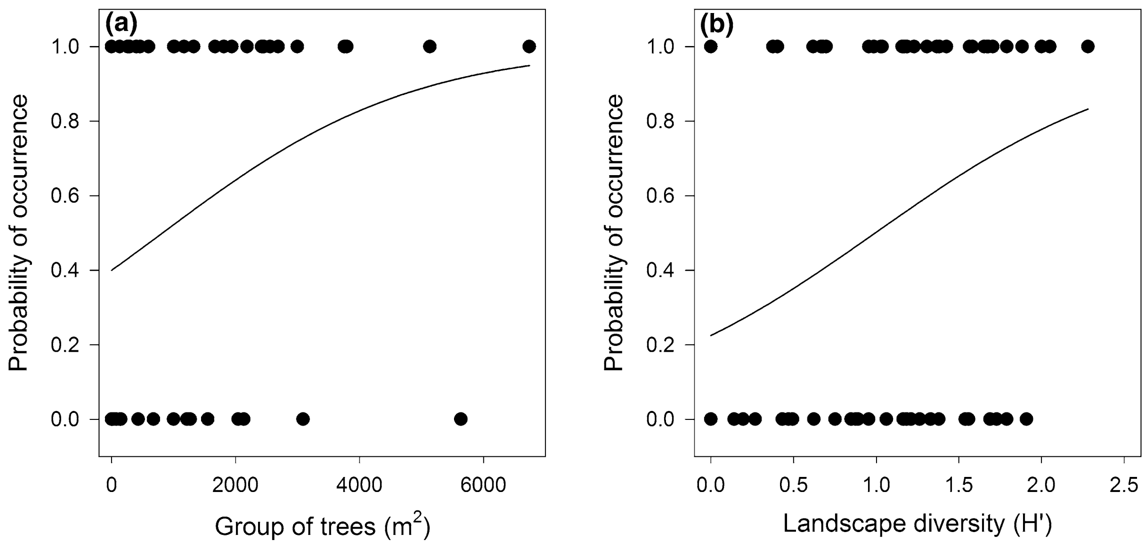
In contrast, the common pastures of the study area were characterised by nutrient-poor conditions and diverse mosaics of different open, semi-open, and woodland habitats (this study; Lederbogen et al. 2004). Consequently, they offered sufficient suitable song posts and microhabitats with the preferred habitat structure for nesting and foraging as described above. Current stocking rates are low, with 0.5–2.0 livestock units per hectare (Lederbogen et al. 2004) resulting in a low likelihood of nest loss by trampling (cf. Pavel 2004) and, additionally, favouring high arthropod densities (Vickery et al. 2001; van Klink et al. 2015).

The demands regarding the territories of Tree Pipits are more complex than those concerning the home ranges as they include, in addition to foraging habitats, song posts, and nesting sites (Kumstátová et al. 2004). In line with this, territory establishment was driven by landscape diversity and the area of groups of trees. In contrast, the only predictor at the home-range scale was landscape diversity. As a result of the complexity of the requirements Tree-Pipit territories have to fulfil, model accuracy was up to twice as high at the territory scale compared to that of the home-range scale.

Although nesting and foraging sites of Tree Pipits differ in vegetation structure, both have a heterogeneous vegetation (see above), explaining the positive effect of landscape diversity on territory and home-range establishment. At the home-range scale, landscape diversity was correlated with the area of fens. The fens in the common pastures had a lower grazing pressure than the grasslands resulting in a more heterogeneous vegetation structure and high arthropod densities (Lederbogen et al. 2004) and, therefore, conditions that should favour foraging and net food intake of the Tree Pipit.

High visibility of the males during song flights, good sound propagation, and an all-round view are important attributes for attracting females and for territory selection. Hence, all else equal, males should prefer small groups of trees or solitary trees over forest edges as song posts. In

Territory



Home range

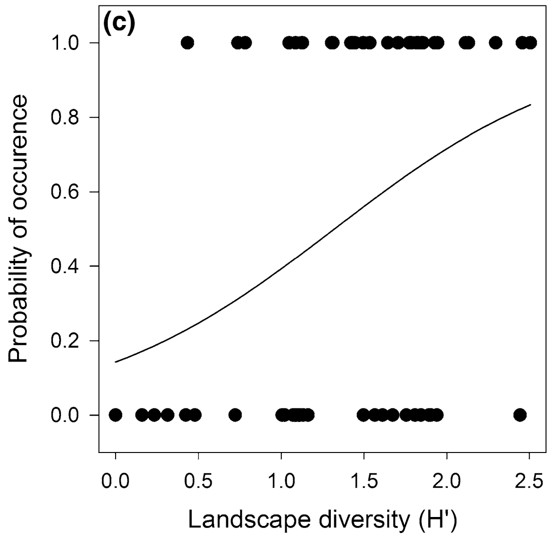


Fig. 3 Results of the model-averaging (GLMM) analyses: relationship between the probability of occurrence of Tree Pipit territories and the significant predictor variables at the territory (**a**, **b**) and home-range scale (**c**) (see Table 3). The regression slopes were fitted using univariate GLM with binomial error structure

line with this, in Romanian wood pastures Tree Pipits use tall, mature trees as song posts, and not widely available forest edges (Moga et al. 2009). Consequently, we associate the preference for larger areas of groups of trees in the territories with better visibility, sound propagation, and an all-round view. In contrast, we attribute the insignificance of solitary trees as song posts in our study to the almost complete lack of tall solitary trees in common pastures (own observation). However, due to the described adaptability in song post selection and the nearly complete lack of colonisation of the control plots, although song posts were largely available, we assume that the occurrence of the Tree Pipit in most parts of central Europe is usually limited by suitable habitat structures for breeding and foraging and not by song post availability.

Conclusions

Summing up, the common pastures are important refuges for the threatened Tree Pipit in the pre-alpine agricultural landscape of the study area. In contrast to the control plots, the common pastures were characterised by nutrient-poor conditions, low land-use intensity (grazing with low stocking rates), and diverse mosaics of different open, semi-open and woodland habitats providing (i) sufficient suitable song posts (groups of trees) and (ii) heterogeneous vegetation with appropriate nesting sites and a high availability of arthropod food resources. Our study corroborates findings from other studies across Europe highlighting the prime importance of traditionally used wood pastures for the Tree Pipit (Moga et al. 2009) and biodiversity in general (e.g., Diaz et al. 1997; Pinto-Correia and Mascarenhas 1999; Lederbogen et al. 2004; Streitberger et al. 2012; Hartel and Plieninger 2014; Helbing et al. 2014).

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Appendix

See Table 4.

Table 4 Top-ranked models (GLMM): relationship between the territory occupancy of Tree Pipits ($N_{\text{territories}} = 33$, $N_{\text{Control}} = 30$; binomial response variable) and environmental parameters at the territory (a) and home-range scale (b)

Parameters	AIC$_C$	ΔAIC$_C$	AIC weights	R^2
(a) Territory (50 m radius)				
Fen + group of trees + H′ + stream	83.4	0.0	0.18	0.32
Fen + group of trees + H′	83.9	0.5	0.14	0.27
Fen + group of trees	84.5	1.1	0.11	0.22
Fen + group of trees + stream	85.1	1.7	0.08	0.25
H′ + stream	85.2	1.8	0.08	0.21
Fen + group of trees + H′ + peat bog + stream	85.3	1.8	0.07	0.33
Fen + forest + group of trees + H′ + stream	85.4	2.0	0.07	0.33
Fen + H′ + stream	85.4	2.0	0.07	0.25
Fen + group of trees + H′ + peat bog	85.9	2.5	0.05	0.28
Fen + forest + group of trees + H′	85.9	2.5	0.05	0.28
H′	85.9	2.5	0.05	0.15
Fen + H′	86.0	2.5	0.05	0.19
(b) Home range (100 m radius)				
H′	85.1	0.0	0.22	0.17
H′ + peat bog	86.4	1.3	0.12	0.19
Group of trees + H′	86.4	1.4	0.11	0.19
H′ + stream	86.8	1.8	0.09	0.18
Traffic area/settlement + H′	87.0	1.9	0.09	0.18
Borderline density + H′	87.1	2.0	0.08	0.17
H′ + transition bog	87.2	2.1	0.08	0.17
H′ + solitary-tree density	87.3	2.2	0.07	0.17
Grassland + H′	87.3	2.3	0.07	0.17

Only models with ΔAIC$_C < 3$ were presented. R^2 = pseudo R^2 values (Nagelkerke)

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