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RESEARCH ARTICLE

Untangling the role of a novel agroecosystem as a habitat for declining farmland birds

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Abstract

As a result of agricultural industrialisation, traditionally managed habitats have dramatically declined throughout Europe. As a result, farmland specialists across several taxa have become increasingly threatened. Concurrently, altered farming practices have also contributed to the emergence of novel agricultural habitats, such as Christmas tree plantations, but knowledge of their impact on biodiversity is still scarce. In the following study, we analysed the drivers behind the territory selection of four declining farmland birds—Common linnet (*Linaria cannabina*), Tree pipit (*Anthus trivialis*), Woodlark (*Lullula arborea*) and Yellowhammer (*Emberiza citrinella*)—in a landscape dominated by Christmas tree plantations. Our study suggests that Christmas tree plantations provide well-suited breeding conditions for the species and thus may represent important refuges in human-modified landscapes. We found that all four species favoured young Christmas tree plantations (<6 years) for territory establishment. In particular, the territories of Tree pipit and Woodlark were characterised by a high proportion of young plantations, which provide open habitat structures rich in bare ground. However, older plantations (>6 years) were also of high importance for some of the model organisms, especially for Common linnet and Yellowhammer. The territory establishment of Yellowhammer was additionally favoured by brushwood plantations, clear-cut/fringe vegetation and low-growing shrubland. We attribute the high value of Christmas tree plantations mainly to the coexistence of open habitat structures rich in bare ground and less intensively managed stands, which both represent important foraging sites for the model organisms. At least in intensively used agricultural areas, Christmas tree plantations may represent important refuges for declining farmland birds. Therefore, further measures aiming to promote habitat quality while reducing the use of herbicides in the plantations should be addressed.

KEYWORDS
agroecology, bird conservation, Christmas tree plantation, habitat management, land-use change, short-rotation forestry

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1 | INTRODUCTION

Farmland biodiversity is strongly driven by land-use intensity and habitat heterogeneity (Benton et al., 2003; Reif & Hanzelka, 2020; Vickery et al., 2001). Especially low-intensity farming promotes species richness and has an outstanding importance for biodiversity conservation (Halada et al., 2011; Reif et al., 2008; Veen, et al., 2009). However, as a result of agricultural industrialisation, the area of traditionally managed grasslands and arable fields has dramatically declined throughout Europe during the last century (e.g., Firbank, 2005; Löffler et al., 2020; Stoate et al., 2001). Consequently, farmland specialists across several taxa have become increasingly threatened (e.g., Donald et al., 2006; Flohre et al., 2011; Reif & Hanzelka, 2020). At the same time, altered farming practices have contributed to the emergence of novel agricultural ecosystems that are characterised by new species communities and may also represent valuable habitats for biodiversity conservation (Hobbs et al., 2009; Sambell et al. 2019).

The relationship between farmland management and the biodiversity of traditional agricultural habitats (e.g., arable fields, semi-natural grasslands or vineyards) has been studied intensively (e.g., Happe et al., 2018; Puig-Montserrat et al., 2017; Reif et al., 2008; Vickery et al., 2001). By contrast, knowledge of the impact of novel agricultural systems, such as Christmas tree plantations, on biotic communities is still scarce. With sales of more than 50 million trees per year, Christmas tree farming is a growing agricultural sector in the EU representing the largest market worldwide. Germany is the most important producer of Christmas trees in Europe, and within Germany, the study area—the 'Upper Sauerland' low-mountain range in western Germany—plays a particularly large role (Rüther, 1990).

The cultivation of Christmas trees is generally associated with intensive management. The plantations are usually characterised by short-rotation cycles, a moderate input of fertiliser and the application of herbicides, especially during the first growing years of the trees (for details see Section 2.2.2; Maurer, 2014). However, they provide open to semi-open and heterogeneous habitat structures, which are known to be beneficial for the majority of farmland specialists (Fartmann et al., 2018; Newton, 2017; Ram et al. 2020). Accordingly, recent studies found that Christmas tree plantations can harbour rich biodiversity, regardless of the rather intensive farming practice (e.g., Bagge et al., 2012; Fartmann et al., 2018; Gailly et al., 2017; Hagge et al., 2019; Streitberger & Fartmann, 2020, 2021). This especially applies to farmland birds (e.g., Fartmann et al., 2018; Gailly et al., 2020; Gailly et al., 2017), which rank among the most severely threatened species throughout Europe (BirdLife International, 2017; Reif et al., 2008).

Birds are known to be good indicators of overall farmland biodiversity (Morelli & Tryjanowski, 2017; Newton, 2017). Especially insectivorous and granivorous birds have suffered strong declines across European agricultural landscapes (BirdLife International, 2017; Reif & Hanzelka, 2020). Agricultural land use affects birds mainly by its impact on food supply and the availability of potential nesting sites (Benton et al., 2002; Holland et al., 2012; Vickery et al., 2001). Despite growing evidence that the cultivation of Christmas trees has recently contributed to a regional increase of threatened farmland birds (e.g., Gailly et al., 2020; Grüneberg et al., 2013), their value for biodiversity conservation is still under debate. Nevertheless, there are clear indications that Christmas tree plantations can provide suitable breeding habitats and thus might represent important refuges for some declining farmland birds in human-modified landscapes (Fartmann et al., 2018; Gailly et al., 2020, 2017). Fartmann et al. (2018) showed strong landscape-scale associations of four declining bird species with Christmas tree plantations: (a) Common linnet (*Linaria cannabina*), (b) Tree pipit (*Anthus trivialis*), (c) Woodlark (*Lullula arborea*) and (d) Yellowhammer (*Emberiza citrinella*) (BirdLife International, 2017, 2021). However, still little is known about the environmental conditions driving the territory occupancy of these species in Christmas tree plantations.

In the following study, we investigated the environmental drivers of breeding-territory selection of the four abovementioned species within a landscape dominated by Christmas tree plantations with special consideration for young (<6 years) and old (>6 years) plantations. Based on these findings, we discuss the role of different plantation types and stages for the occurrence of the model organisms and derive recommendations for plantation management promoting the long-term habitat suitability for farmland birds.

2 | MATERIALS AND METHODS

2.1 | Model organisms

Common linnet, Tree pipit, Woodlark and Yellowhammer have been identified as indicator species of central European Christmas tree plantations in a previous study (Fartmann et al., 2018). Hence, they are well-suited to evaluate the effects of cultivation practices on breeding habitat selection within landscapes dominated by Christmas tree plantations. All four species prefer open or semi-open habitats for breeding and are largely associated with agricultural habitats, but they differ in their ecological traits, such as food preferences, nest-site selection and migration strategies (Table 1, Bauer et al., 2012; Glutz von Blotzheim, 2004). They have all suffered strong long-term population declines (BirdLife International, 2017). Furthermore, they are of European conservation concern (SPEC 2 = European species with global population concentrated in Europe, but with unfavourable conservation status in Europe): Common linnet, Woodlark and Yellowhammer; (SPEC 3 = species not concentrated in Europe, but with unfavourable conservation status in Europe): Tree pipit and are threatened in Germany (BirdLife International, 2017; Ryslavy et al., 2020). Woodlark is additionally listed as a species of Annex I of the European Birds Directive (European Commission, 2009).

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TABLE 1 Species traits, home-range size and corresponding territory radius, European population status and threat status (NT, near threatened; VU, vulnerable; LC, least concern) of the four model organisms derived from BirdLife International (2021), Glutz von Blotzheim (2004), Bauer et al. (2012), Ryslavy et al. (2020)

Parameter	Common linnet (*Linaria cannabina*)	Tree pipit (*Anthus trivialis*)	Woodlark (*Lullula arborea*)	Yellowhammer (*Emberiza citrinella*)
Habitat	Semi-open landscape/ shrubland	Semi-open landscape	Semi-open landscape rich in bare soil	Semi-open landscape
Diet	Granivorous	Insectivorous	Insectivorous	Granivorous/insectivorous
Migration	Partial migrant	Long-distance	Short-distance	Short-distance
Nest-site	Shrub-nesting	Ground-nesting	Ground-nesting	Ground- or shrub-nesting
European population status	SPEC 2	SPEC 3	SPEC 2	SPEC 2
German threat status	VU	NT	NT	LC
Home range (ha)	0.95	0.80	2.50	0.40
Considered territory buffer (m)	55	50	90	36

Abbreviations: SPEC 2, European species with global population concentrated in Europe, but with unfavourable conservation status in Europe; SPEC 3, species not concentrated in Europe, but with unfavourable conservation status in Europe.

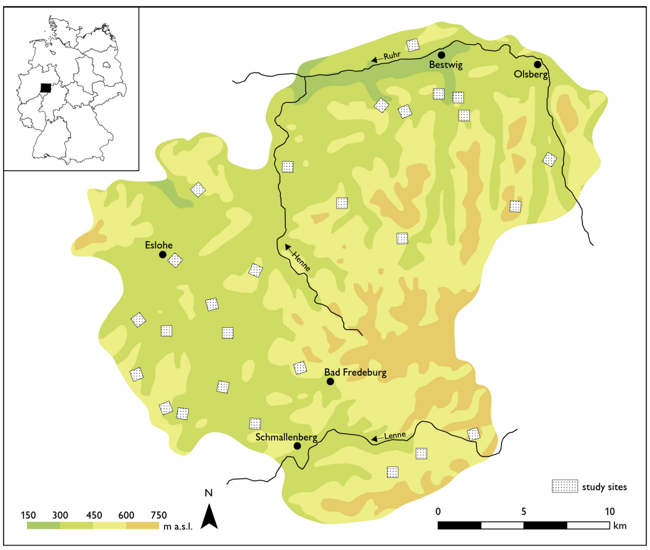

FIGURE 1 Location of the study area and study plots in Germany

2.2 | Study area

2.2.1 | General characteristics

The study area has a size of 541 km^2 and is located in the north-western part of the 'Upper Sauerland' (51°6′N/8°5′E and 51°22′N/8°33′E, 250–650 m a.s.l.), a low-mountain range in western Germany (Figure 1). It is characterised by a rather cool and wet climate (mean annual temperature: 8.0°C; mean annual precipitation: 1,184 mm; meteorological station Eslohe [351 m a.s.l]; reference period: 1981–2010, DWD, 2019). The study area is dominated by nutrient-poor soils on acidic bedrock (Geological Federal Agency NRW, 1998). The rural landscape is largely shaped by intensive forestry and agriculture. Forests, covering almost 50% of the study area, are largely dominated by nonnative Norway Spruce (*Picea abies*) stands. Improved grassland (23%), arable land (11%) and Christmas tree plantations (7%) account for the dominant habitat types in the agricultural landscape. With a total area of 18,000 ha, the 'Upper Sauerland' is a hotspot of Christmas tree cultivation in central Europe (Fartmann et al., 2018).

2.2.2 | Christmas tree production

The large-scale cultivation of Christmas tree plantations in the study area started in the 1980s as a consequence of the introduction of the milk quota by the Common Agricultural Policy of the EU following agricultural overproduction (Rüther, 1990). Since then, the area of Christmas tree plantations on former pastureland has increased steadily and experienced an additional boost because of the expansion of the plantations on windthrows following the European storm 'Kyrill' in 2007 (Kranz, 2014). The vast majority of these plantations are used to grow the Caucasian Fir (*Abies nordmanniana*). Apart from the large-scale cultivation of classical Christmas trees, the plantations often include smaller areas which are used for the production of brushwood (cutting of twigs and small branches), for example, Noble fir (*Abies procera*), Oriental Arborvitae (*Thuja orientalis*) or Western Redcedar (*Thuja plicata*). All cultivated species are nonnative to the study area.

The cultivation of Christmas trees requires intensive management, which differs depending on the cultivation type (classical Christmas tree vs. brushwood production) and the age of the plantations. While classical Christmas tree plantations are characterised by short-rotation cycles of 8–12 years, brushwood plantations have a rotation cycle of up to 25 years. To meet the required quality of the customers, the cultivation of Christmas trees is usually associated with the regular application of fertiliser and herbicides. By contrast, the use

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of insecticides is only carried out in the case of pest infestation (Maurer, 2014).

For weed control, herbicides are especially applied during the first years of cultivation (≤6 years hereinafter considered as young Christmas tree plantations) always at the beginning of the growing season in spring and after the lignification of the tree shoots in autumn (Matschke, 2005; Maurer, 2014). In addition, the herb layer between the tree rows is often mulched in late summer (Matschke, 2005; Maurer, 2014). While weed control by herbicides becomes less important with increasing tree age, the annual input of fertiliser steadily increases from less than 50 kg N/ha in young plantations up to 150 kg N/ha until the harvest (>6 years hereinafter considered as old Christmas tree plantations) (Maurer, 2014). However, fertilisation is usually restricted to a moderate level as it leads to rapid height growth of the trees with negative effects on sales opportunities (Matschke, 2005; Maurer, 2014). In contrast to classical Christmas tree plantations, brushwood plantations are generally characterised by taller woody vegetation with low-intensity management with negligible fertilisation and herb regulation, except for the period after the planting of young brushwood trees. All brushwood plantations within the plots were older than 10 years.

As a result, the rows between the Christmas trees are usually covered by heterogeneous mosaics of bare ground (∼5–10% cover), stones/gravel (∼5–10%) and weeds (∼40–45%) in summer (Fartmann et al., 2018; Streitberger & Fartmann, 2020). To avoid browsing the shoot tips by deer, the plantations are always fenced. Consequently, there is no public access and little disturbance by humans and domestic dogs, while predators like foxes are not restricted by the used game fences due to their large mesh size.

2.3 | Sampling design

2.3.1 | Study plots

The study was carried out on 27 plots (each 40 ha; 632.5 × 632.5 m), which were randomly selected from landscape sections of the study area that were dominated by Christmas tree plantations. At least 40% of each plot was covered by Christmas tree plantations (cf. Fartmann et al., 2018; Streitberger & Fartmann, 2020). Within the plots, habitat composition in the territories of the four model organisms was compared against those in randomly selected control samples (for more details see Sections 2.3.2–2.3.4; Figure S1).

2.3.2 | Breeding-bird surveys

We surveyed birds using standardised territory mapping, which is among the most accurate methods to detect breeding birds (Bibby et al. 2000). Territory mapping of the four model organisms was performed in all plots covering the total plot area from the end of March to June 2016 (Fischer et al. 2005). In total, six early morning surveys were carried out, with an interval of at least 10 days between the visits. All observations of territorial behaviour, such as singing or alarming birds, were plotted on field maps according to Bibby et al. (2000). Following the guidelines of the German breeding-bird census, we additionally used playbacks of its song to detect Woodlark (Fischer et al., 2005). After the completion of the field surveys, clustered records of a species were used to define its breeding territories. Breeding was assumed if a bird showed territorial behaviour on at least three occasions with a distance of 10 days between the registrations or if a bird showed behaviour that strongly suggested breeding like distraction behaviour or feeding adults (Fischer et al., 2005). Special attention was paid to simultaneous observations of singing males for separating different territories situated close to each other.

2.3.3 | Environmental parameters

For each plot, we mapped the habitat types in the field according to the German habitat classification scheme on a scale of 1:5,000 (Riecken et al., 2003). For further analysis, the habitat types were classified into the following 10 main types: arable land, semi-natural grassland, improved grassland, clear-cut/fringe vegetation, ruderal vegetation, Christmas tree plantation, low-growing shrubland, high-growing shrubland, deciduous woodland, coniferous woodland and built-up area. As previous studies have shown that densities of open habitat birds in plantations peaked up to an age of 6 years (Burton, 2007; Takacs et al., 2020), we additionally distinguished between young (≤6 years old) and old (>6 years old) Christmas tree plantations as well as brushwood plantations (see Section 2.2.2; Table 2).

Furthermore, we measured the elevation (m a.s.l.) at the centre of all territories and controls using a digital elevation model in ArcGIS 10.2.

2.3.4 | Habitat composition in territories and controls

We calculated the area of each habitat type within a species-specific buffer around the centre of the territories of the model organisms in ArcGIS 10.2 (cf. Berg, 2008). The radii of the buffers around territory centres and the corresponding control samples were derived from the average home-range sizes of the model organisms according to Bauer et al. (2012) and Glutz von Blotzheim (2004) (cf. Table 1). To compare the habitat composition in the territories with that of the surrounding landscape, we randomly selected control samples using the '*create random points*' tool in ArcGIS 10.2 throughout all plots (Figure S1). The number of control samples was adjusted to the frequency of the model organisms and corresponded to the half of the number of territories of each species: Common linnet ($N_{\text{territories}} = 78$ vs. $N_{\text{control}} = 39$), Tree pipit ($N_{\text{territories}} = 46$ vs. $N_{\text{control}} = 23$), Woodlark ($N_{\text{territories}} = 66$ vs. $N_{\text{control}} = 33$), Yellowhammer ($N_{\text{territories}} = 252$ vs. $N_{\text{control}} = 126$).

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TABLE 2 Differences in habitat composition of territories and controls of the four model organisms (mean ± *SE*): (a) Common linnet, (b) Tree pipit, (c) Woodlark, (d) Yellowhammer

Parameter	(a) Common linnet (*Linaria cannabina*) Territory (*N* = 78)	Control (*N* = 39)	*p*	(b) Tree pipit (*Anthus trivialis*) Territory (*N* = 46)	Control (*N* = 23)	*p*	(c) Woodlark (*Lullula arborea*) Territory (*N* = 66)	Control (*N* = 33)	*p*	(d) Yellowhammer (*Emberiza citrinella*) Territory (*N* = 252)	Control (*N* = 126)	*p*
Habitat type (×1,000 m^2)												
Arable land	0.0 ± 0.0	0.3 ± 0.2	n.s.	0.2 ± 0.2	0.7 ± 0.3	n.s.	0.6 ± 0.3	2.0 ± 0.9	n.s.	0.1 ± 0.0	0.2 ± 0.1	n.s.
Semi-natural grassland	0.1 ± 0.0	0.0 ± 0.0	n.s.	0.0 ± 0.0	0.0 ± 0.0	n.s.	0.1 ± 0.1	0.1 ± 0.1	n.s.	0.0 ± 0.0	0.1 ± 0.0	n.s.
Improved grassland	0.3 ± 0.1	0.7 ± 0.3	n.s.	**0.1 ± 0.1**	**1.7 ± 0.6**	*	0.1 ± 0.3	0.2 ± 0.8	n.s.	**0.2 ± 0.0**	**0.5 ± 0.1**	***
Ruderal vegetation	0.0 ± 0.0	0.1 ± 0.1	n.s.	0.3 ± 0.2	0.4 ± 0.3	n.s.	0.1 ± 0.1	0.2 ± 0.1	n.s.	0.0 ± 0.0	0.1 ± 0.0	n.s.
Christmas-tree plantation	**7.2 ± 0.1**	**4.3 ± 0.5**	***	**7.2 ± 0.4**	**4.7 ± 0.8**	***	**21.1 ± 0.6**	**15.0 ± 1.4**	***	**3.2 ± 0.1**	**2.1 ± 0.2**	***
Young (<6 a)	2.0 ± 0.3	2.7 ± 0.5	n.s.	**5.6 ± 0.5**	**1.4 ± 0.6**	***	**14.8 ± 1.0**	**7.8 ± 1.4**	***	1.1 ± 0.1	1.3 ± 0.1	n.s.
Old (>6 a)	**5.1 ± 0.3**	**1.5 ± 0.4**	***	**0.1 ± 0.3**	**2.7 ± 0.7**	*	5.9 ± 0.9	5.0 ± 1.1	n.s.	**2.0 ± 0.1**	**0.8 ± 0.1**	***
Brushwood plantation	0.2 ± 0.1	0.1 ± 0.1	n.s.	0.5 ± 0.2	0.6 ± 0.3	n.s.	0.4 ± 0.2	2.0 ± 0.7	n.s.	0.1 ± 0.0	0.2 ± 0.0	n.s.
Clear-cut/fringe vegetation	0.0 ± 0.0	0.2 ± 0.1	n.s.	0.3 ± 0.2	0.2 ± 0.2	n.s.	**0.1 ± 0.1**	**1.5 ± 0.5**	*	0.1 ± 0.0	0.1 ± 0.0	n.s.
Low-growing shrubland	0.1 ± 0.0	0.2 ± 0.1	n.s.	0.3 ± 0.2	0.4 ± 0.3	n.s.	0.4 ± 0.3	0.5 ± 0.2	n.s.	0.1 ± 0.0	0.1 ± 0.1	n.s.
High-growing shrubland	0.0 ± 0.0	0.0 ± 0.0	n.s.	0.3 ± 0.2	0.0 ± 0.0	n.s.	0.1 ± 0.0	0.2 ± 0.1	n.s.	**0.0 ± 0.0**	**0.1 ± 0.0**	*
Deciduous woodland	**0.1 ± 0.0**	**1.1 ± 0.4**	*	0.2 ± 0.1	0.7 ± 0.4	n.s.	0.4 ± 0.1	1.1 ± 0.5	n.s.	**0.1 ± 0.0**	**0.2 ± 0.1**	**
Coniferous woodland	**0.1 ± 0.0**	**0.9 ± 0.3**	*	0.3 ± 0.1	0.7 ± 0.4	n.s.	0.5 ± 0.2	1.7 ± 0.7	n.s.	**0.1 ± 0.0**	**0.3 ± 0.1**	**
Built-up area	0.2 ± 0.0	0.3 ± 0.0	n.s.	0.2 ± 0.2	0.7 ± 0.3	n.s.	0.6 ± 0.1	0.7 ± 0.1	n.s.	0.1 ± 0.0	0.1 ± 0.0	n.s.
Habitat diversity (*H′*)	0.5 ± 0.1	0.6 ± 0.1	n.s.	0.6 ± 0.1	0.7 ± 0.1	n.s.	**0.7 ± 0.1**	**1.0 ± 0.1**	**	0.5 ± 0.1	0.5 ± 0.1	n.s.
Elevation (m a.s.l.)	468 ± 9	471 ± 14	n.s.	450 ± 10	451 ± 18	n.s.	469 ± 10	458 ± 13	n.s.	438 ± 4	454 ± 7	n.s.

Note: Statistical significances were assessed using separate univariable general linear mixed-effect models (GLMM) with binomial response variable (territories vs. controls) and different habitat categories as predictor. 'Plot' was set as a random factor in all models. Significance levels are indicated as follows: n.s. $p > .05$, *$p \le .05$, **$p \le .01$, ***$p \le .001$.

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TABLE 3 Results of the synthesis model showing the relationship between territory occupancy (territory vs. control) of the four model organisms: (a) Common linnet, (b) Tree pipit, (c) Woodlark, (d) Yellowhammer and environmental parameters analysed using general linear mixed-effect models (GLMM) with a binomial error structure

Parameter	Est.	*SE*	*Z*	*p*	Variable	Est.	*SE*	*Z*	*p*
(a) Common linnet (*Linaria cannabina*) AUC = 0.83					(b) Tree pipit (*Anthus trivialis*) AUC = 0.84				
Intercept	−2.01	0.65	−3.09	**	Intercept	−0.64	0.40	−1.61	n.s.
Young CTP	5.91	1.14	5.18	***	Young CTP	4.28	1.15	3.73	***
Old CTP	3.01	1.07	2.81	**					
(c) Woodlark (*Lullula arborea*) AUC = 0.81					(d) Yellowhammer (*Emberiza citrinella*) AUC = 0.81				
Intercept	−2.42	1.12	2.13	*	Intercept	−1.31	0.35	−3.7	***
Young CTP	1.97	0.57	3.41	***	Young CTP	4.33	1.07	4.06	***
Old CTP	1.54	0.51	2.97	**	Old CTP	8.6	1.17	7.35	***
					Brushwood plantation	7.37	2.72	2.71	**
					Clear-cut/fringe vegetation	6.39	2.39	2.68	**
					Low-growing shrubland	4.82	2.32	2.08	*

Note: 'Plot' was set as a random factor in all models. Since in all cases only the full model containing all variables met the $\Delta AIC_C < 2$ criterion, coefficients were derived from each full model. Model performance based on area under the curve (AUC). Only significant variables are shown. CTP, Christmas-tree plantation. Significance levels are indicated as follows: $p > .05$, *$p \le .05$, **$p \le .01$, ***$p \le .001$.

Moreover, we calculated habitat diversity (H') for each territory and control using the Shannon index (cf. Fartmann et al., 2018; Schwarz et al., 2018):

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

where N is the total area of the species-specific buffers and n_i is the area of each habitat type in the buffers around territories and control samples.

2.4 | Statistical analysis

All statistical analyses were performed using R 3.6.2 (R Development Core Team, 2019). Differences in the habitat composition of territories and controls were tested for each species by univariable binomial generalised linear mixed-effect models (GLMM) with territories and controls as binary response variables (R package *lmer*, Bates, et al., 2015; Table 2). To assess the impact of the environmental predictors on the territory selection of the model organisms, we conducted multivariable binomial GLMMs. The variable 'plot' was used as a random intercept (factor) in both types of GLMMs (cf. Crawley, 2012). To avoid overfitting, the impact of the predictors was first determined in three submodels for each species: (a) a habitat-type model including the cover of the different habitat types as predictors, (b) a Christmas tree plantation-type model including the cover of the different plantation types and (c) a model with further predictors (i.e., habitat diversity and elevation) (for details see Table S1). Only significant predictors of the three submodels were included in the final synthesis model (Table 3). To account for multicollinearity within the models, all variables were checked for intercorrelations before the analyses (Spearman's rank correlation, $|r_S| > .7$; Dormann et al., 2013).

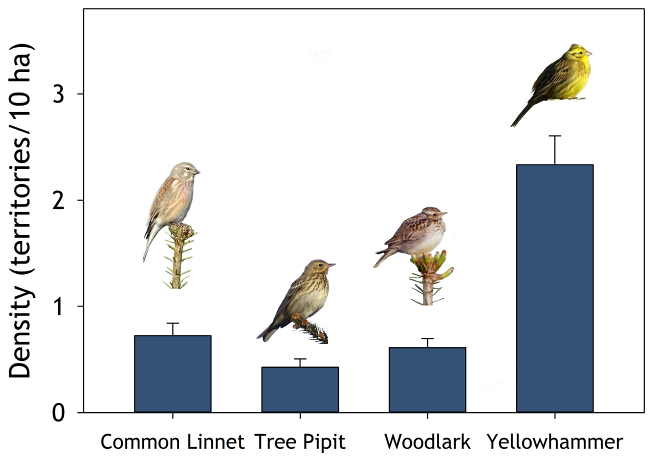

FIGURE 2 Mean density (±*SE*) of the studied threatened breeding bird species

To increase model robustness and identify the most important environmental parameters, we conducted model averaging based on an information-theoretic approach (Burnham & Anderson, 2002; Grueber et al., 2011). Model averaging was conducted using the '*dredge*' function (R package *MuMIn*, Bartón, 2019) and only included top-ranked models within $\Delta AIC_C < 2$ (cf. Grueber et al., 2011). Model performance was assessed by calculating the area under the curve (AUC).

3 | RESULTS

3.1 | Environmental conditions in the plots

The plots were situated at an elevation of 362–647 m above sea level (a.s.l.) (mean ± *SE*: 453.3 ± 2.6 m). Christmas tree plantations

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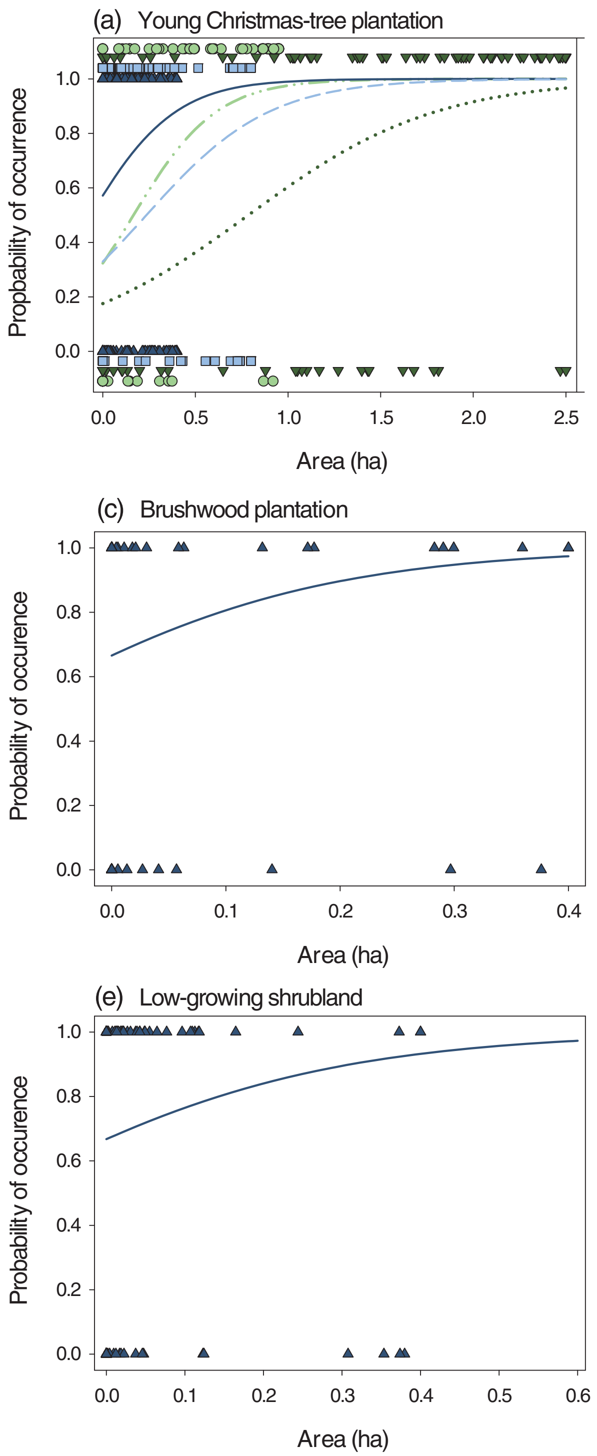

FIGURE 3 Results of the GLMM analyses: relationship between presence/absence of studied species and the significant environmental parameters area of (a) young Christmas-tree plantation, (b) old Christmas-tree plantation, (c) brushwood plantation, (d) clear-cut/fringe vegetation, (e) low-growing shrubland (cf. Table 3). GLMM, general linear mixed-effect model

altogether covered 55% of the plots. They were largely dominated by classical Christmas tree plantations including young (30%) and old stands (20%). A minor part of them was covered by brushwood plantations (5%). The remaining area of the plots was covered by improved grassland (12%), coniferous woodland (7%), deciduous woodland (6%), arable land (6%), clear-cut/fringe vegetation (4%), low-growing shrubland (3%), built-up area (3%), semi-natural grassland (2%), high-growing shrubland (1%) and ruderal vegetation (1%). The habitat diversity within the plots ranged from 1.14 to 2.18 (Shannon index [mean ± *SE*]: 1.77 ± 0.05).

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3.2 | Differences between territories and controls

All model organisms occurred in a high frequency throughout the plots. In total, we detected 252 Yellowhammer, 78 Common linnet, 66 Woodlark and 46 Tree pipit territories within the 27 plots. Accordingly, territory density (territories/10 ha; mean ± *SE*) varied between the species and was 0.72 ± 0.12 for Common linnet, 0.43 ± 0.08 for Tree pipit, 0.61 ± 0.09 for Woodlark and 2.33 ± 0.27 for Yellowhammer (Figure 2).

Territories were characterised by a higher cover of Christmas tree plantations compared to controls in all model organisms (Table 2). We found distinct preferences of the studied species associated with the different types of Christmas tree plantations. While Tree pipit and Woodlark especially preferred young Christmas tree plantations, the territory establishment of Common linnet and Yellowhammer was favoured by a higher cover of old Christmas tree plantations. In the case of Woodlark, the area of young Christmas tree plantations within the territories was twice as high, and for Tree pipit even four times higher than in the controls. The area of old Christmas tree plantations within Yellowhammer territories was more than two times higher and in those of Common linnet more than three times higher than in the controls. By contrast, territories occupied by Tree pipit were characterised by a lower cover of old Christmas tree plantations. In addition, we found a lower area of improved grassland in territories occupied by Tree pipit and Yellowhammer. Moreover, Common linnet and Yellowhammer preferred territories with a lower cover of coniferous and deciduous woodland. In the case of Woodlark, the territories were also characterised by a lower cover of clear-cut/fringe vegetation and generally a lower habitat diversity (Table 2).

3.3 | Key factors of territory selection

The multivariable GLMM analyses revealed that the likelihood of territory occupancy increased with the area of young Christmas tree plantations in all four investigated species (Figure 3). However, the territory's establishment of Common linnet, Woodlark and Yellowhammer was favoured by the area of old Christmas tree plantations as well. Territory selection of Yellowhammer was additionally promoted by an increased area of low-growing shrubland, clear-cut/fringe vegetation and brushwood plantations. Generally, model performance was high, with AUC values of 0.73–0.84.

4 | DISCUSSION

While altered farming practices have contributed to a steep decline of several bird species associated with agricultural landscapes (BirdLife International, 2017; Reif & Hanzelka, 2020), recent studies have found high frequencies of threatened farmland birds within Christmas tree plantations (Fartmann et al., 2018; Gailly et al., 2017). However, until now, knowledge about the factors driving the occurrence of these species within the plantations was largely lacking. Our study revealed that the habitat composition within the territories of the four studied species (Common linnet, Tree pipit, Woodlark and Yellowhammer) differed from those in controls. Occupied territories contained higher shares of young Christmas tree plantations in all four species. In particular, the territories of Tree pipit and Woodlark were characterised by a high proportion of young plantations. However, older plantations were also of high importance for some of the model organisms, especially for Common linnet and Yellowhammer. The territory establishment of Yellowhammer was additionally favoured by the area of brushwood plantations, clear-cut/fringe vegetation and low-growing shrubland.

Christmas tree plantations are characterised by open to semi-open habitat structures, which are beneficial to the majority of farmland birds (Newton, 2017; Ram et al., 2020). Within the studied plantations, Christmas trees covered almost half of the cultivated area (Streitberger & Fartmann, 2020). In particular, through intensive weed control (e.g., by herbicide application and mulching, see Section 2.2.2), Christmas tree plantations are generally rich in the bare ground (Streitberger & Fartmann, 2020), which especially facilitates the accessibility of prey and is, therefore, a key factor for the occurrence of ground-foraging insectivorous bird species (Schaub et al., 2010; Vickery et al., 2001). Moreover, there is evidence that the Christmas tree plantations in the study area provide high arthropod densities (Freienstein et al., 2018; Höppner, 2014). Although herbicides are regularly applied at the beginning of each growing season (cf. Maurer, 2014, also see Section 2.2.2), the herb layer usually covers approximately 40% of the area at the end of the breeding season in June (cf. Streitberger & Fartmann, 2020). Because the vegetation was typically dominated by annual ruderals (cf. Streitberger & Fartmann, 2020), it can be assumed that there is also a sufficient supply of seeds. For these reasons, the availability and accessibility of food for both the insectivorous and granivorous model organisms are generally high. Furthermore, the habitat structures within Christmas tree plantations provide suitable nesting sites for the species studied. However, the importance of the different plantation types differs between the species owing to different management within the plantations.

Although the likelihood of territory occupancy increased with the area of young Christmas tree plantations in all model organisms, Tree pipit and Woodlark showed the strongest dependency on this plantation type, with an area twice as high in Woodlark territories and even four times higher in Tree pipit territories compared to the controls (Table 2). Both species are insectivorous, preferring bare ground or low-growing vegetation for foraging (Bosco et al., 2019; Burton, 2007). They build their nests under sheltered conditions on the ground (Bauer et al., 2012), in the case of Woodlark often directly under Christmas trees (Höppner, 2014). Due to a lower tree cover and regular weed control (see Section 2.2.2), young Christmas tree plantations are characterised by open habitat structures with a heterogeneous mosaic of bare ground and herbaceous vegetation between the tree rows (cf. Streitberger & Fartmann, 2020). On the one hand, these conditions ensure high availability and accessibility of invertebrate prey (i.e., ground-dwelling arthropods, such as carabids

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and spiders, cf. Borchard et al., 2014; Cameron & Leather, 2012; Hagge et al., 2019) for the insectivorous model organisms (cf. Holland et al., 2006; Mackowicz, 1970; Schaub et al., 2010). On the other hand, they also provide suitable nesting sites and sufficient shelter against predators for ground-nesting species.

Previous studies from Southern Britain revealed similar patterns in young conifer plantations: Langston et al. (2007) found that the recent increase of the British Woodlark population has been closely associated with the colonisation of habitats rich in the bare ground in forest clearings and restocked conifer plantations. Furthermore, Burton (2007) showed that the population density of Tree pipit peaked in young pine plantations up to an age of 6 years. There is clear evidence that both species are favoured by ground disturbance and/or regular management, for example, by forestry activities (Takacs et al., 2020) or rough grazing (Hawkes et al., 2019; Schwarz et al., 2018). While the original habitats of these species (e.g., heathlands and nutrient-poor grasslands) have become frequently unsuitable for breeding as a result of management changes and increased nitrogen input across European landscapes (Fartmann et al., 2015; Langston et al., 2007), the young plantations rich in the bare ground usually meet the habitat requirements of both species. The high value of Christmas tree plantations for these species is underlined by the fact that the territory densities of Woodlark (0.61 territories/10 ha) in our study even exceeded those of the originally preferred habitats, the heathlands in the North German Plain (0.49 territories/10 ha, Flade, 1994). In Tree pipit, most territories in our study were situated adjacent to forest margins, which represent suitable song posts for this species (Fonderflick et al., 2013). Therefore, it is very likely that a lack of suitable song posts (e.g., solitary trees) within the centre of young Christmas tree plantations may have limited even higher territory densities of Tree pipit in the plantations (cf. Schwarz et al., 2018).

By contrast, old Christmas tree plantations were more important for territory occupancy of Common linnet and Yellowhammer. In our study, the territory densities of both species were higher compared to other agricultural habitats across central and northern Germany (cf. Flade, 1994). Both species prefer later seral stages for territory establishment but also require stands with low-growing vegetation for foraging (McHugh et al., 2016; Moorcroft et al., 2010; Whittingham et al., 2005). Adults of both species are mainly granivorous (Glutz von Blotzheim, 2004; Holland et al., 2006), but invertebrates play an important role in the diet of Yellowhammer chicks (Bauer et al., 2012). Moreover, the availability of foraging sites is of crucial importance in the territory selection of Yellowhammers (McHugh et al., 2016). As herbicide application plays a minor role in the older stands (Maurer, 2014), it is likely that old Christmas tree plantations generally provide higher seed densities and might also increase the availability of herbivorous arthropods, such as grasshoppers, which represent an important food resource for Yellowhammer chicks (Glutz von Blotzheim, 2004). Furthermore, the higher cover of trees probably increases the availability of suitable nesting sites for the shrub-breeding Common linnet.

Although brushwood plantations only covered a minor part of the plots, this plantation type favoured the territory establishment of Yellowhammer. Brushwood plantations are generally characterised by taller trees and less-intensive management with negligible fertilisation and herb regulation (Maurer, 2014), which seems to correspond to the habitat requirements of the species. This is in line with the findings of previous studies from British farmlands showing that Yellowhammer depends on patchy mosaics of woody landscape elements, such as hedgerows and trees, and only marginally cultivated habitats that provide essential food resources (Bradbury et al., 2000; Whittingham et al., 2005). Furthermore, the likelihood of territory occupancy of Yellowhammer increased with the area of clear-cut/fringe vegetation and low-growing shrubland, which typically occurred on windthrows within the plots. This corresponds to the study of Bakx et al. (2020), which revealed the high importance of such habitats for Yellowhammer population in Sweden.

Windthrows can regularly be found in the study area as a result of the storm Kyrill in 2007 (cf. Fartmann et al., 2018). For a while, they have had high importance for threatened songbirds of open habitats (e.g., Tree pipit, Willow warbler, Yellowhammer) (e.g., Fartmann et al., 2018; Zmihorski, 2010). However, after afforestation or with ongoing succession they rapidly lose their value for the species (Wesołowski et al., 2018). By contrast, the short-rotation cultivation of Christmas trees maintains open habitat structures in the long run.

Our study showed that Christmas tree plantations provide suitable breeding habitats for the four model organisms, while both improved grassland (Tree pipit, Yellowhammer) and intensively used forests (Common linnet, Yellowhammer) were usually avoided (cf. Fartmann et al., 2018). These findings support the hypothesis that Christmas tree plantations represent important refuges for declining farmland birds in the intensively used landscape of the study area. Due to the open habitat structures, Tree pipit and Woodlark were most strongly associated with young Christmas tree plantations. By contrast, the later successional stages of Christmas tree plantations (old Christmas tree and brushwood plantations) were more important for Common linnet and Yellowhammer. Despite their current value as a habitat for breeding birds, there are still many ecological concerns about the intensive management of Christmas tree plantations. Although evidence on the detrimental effects of Christmas tree plantations on biodiversity is largely lacking so far, it should be noted that Christmas tree production as well as another short-rotation forestry could at least reduce habitat quality for some farmland inhabitants in agricultural landscapes with low land-use intensity. To address these challenges, future studies should also seek to evaluate the impact of alternative management practices in Christmas tree plantations and similar short-rotation forestry on farmland birds and other taxonomic groups.

5 | IMPLICATIONS FOR MANAGEMENT

The high value of Christmas tree plantations, especially young stands, is mainly attributed to the existence of open habitat structures rich in the bare ground that ensure high food accessibility for the

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insectivorous and ground-foraging model organisms (Tree pipit and Woodlark). However, the presence of these structures in the plantations is mainly a result of regular herbicide use, which is also known to cause detrimental effects on biodiversity and ecosystem services (e.g., Winter et al., 2018). Alternative methods for weed control in Christmas tree plantations comprise (a) grazing by Shropshire sheep (Maurer, 2014) and (b) mechanical weed removal by milling, mowing or mulching (Matschke, 2005; Sæbø et al., 2009). Plantations grazed by sheep are usually dominated by homogenous grassland-like vegetation lacking bare ground (Streitberger & Fartmann, 2020). Due to continuous grazing, the plants in the herb layer rarely flower and hence, rarely produce seeds (own observation). We, therefore, assume that these measures usually restrict the food availability for both insectivorous and granivorous farmland birds in the plantations. Milling, mowing or mulching may increase the risk of nest loss in ground-nesting species (Fartmann et al., 2018). Therefore, it must be assumed that the habitat suitability of the plantations for the studied species depends to a large extent on the use of herbicides. Nonetheless, herbicide use should be carefully applied and restricted to the absolute minimum necessary rate. In particular, we suggest restricting herbicide use to inter-rows between the trees while avoiding it along with uncultivated areas, such as fences and tramlines, of all types of Christmas tree plantations (Fartmann et al., 2018; Streitberger & Fartmann, 2020). Both old Christmas tree plantations and brushwood plantations are mostly characterised by less intensive management (cf. Section 2.2.2; Maurer, 2014). Due to the annual demand for Christmas trees, the plantations mostly exhibit mosaics of parcels with different tree ages and management (Fartmann et al., 2018). Because the importance of young and old Christmas tree plantations, as well as brushwood plantations, varied between the model organisms, the small-scale mosaic of different plantation types and ages, should be preserved. Although the plantations already have a high value as a refuge for declining farmland birds as well as birds of semi-open woodlands, further measures aiming to increase habitat heterogeneity should be addressed. For instance, promoting solitary trees and hedgerows, as well as flower-rich fringes and tolerating temporary fallows after harvesting may further foster bird biodiversity within the plantations.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author.

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