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# Landscape-scale effects of Christmas-tree plantations in an intensively used low-mountain landscape – Applying breeding bird assemblages as indicators

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ABSTRACT

Novel ecosystems are characterised by recent establishment due to human activities and new species combinations. A characteristic example in farmlands are Christmas-tree plantations. The aim of this study is to evaluate the landscape-scale effects of the novel ecosystem Christmas-tree plantation on breeding bird assemblages in an important European stronghold of Christmas-tree production, the intensively used low-mountain landscape of the Hochsauerland (Central Europe), in comparison with currently competing land-use types.

The study revealed that the five studied landscape types differed in habitat composition and landscape diversity. Landscape diversity was significantly highest in the two types of Christmas-tree plantation landscapes and windthrow landscapes, differing from grassland and forest landscapes. Bird species assemblages clearly responded to the differences in habitat composition. This was especially true for threatened species having a peak of species richness and breeding-pair density in the two types of Christmas-tree plantation landscapes and slightly weakened at windthrow landscapes.

The high species richness of threatened breeding bird species in Christmas-tree plantation landscapes was driven mainly by high landscape heterogeneity. Densities of the threatened indicator species of the Christmas-tree plantation landscapes were probably promoted by (i) high availability of suitable food (arthropods, seeds) and (ii) high accessibility to the food resources due to bare ground (tree pipit [*Anthus trivialis*], woodlark [*Lullula arborea*]) or low-growing vegetation (linnet [*Carduelis cannabina*], yellowhammer [*Emberiza citronella*]) in the Christmas-tree plantations. For the woodlark, Christmas-tree plantations are even among the most important strongholds in the German Federal State of North Rhine-Westphalia.

## 1. Introduction

A large part of Europe's biodiversity is associated with agricultural land (Donald et al., 2006; Henle et al., 2008; Kleijn et al., 2009). Additionally, farmland constitutes the single largest habitat in Europe; more than 40% of the European (EU-27) (Eurostat, 2016) and 54% of the German (BMU, 2007) terrestrial land surfaces are used for agriculture. Consequently, agricultural landscapes play an important role for 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 (Donald et al., 2006; Flohre et al., 2011; Vickery et al., 2001). The two main drivers of the current loss in farmland biodiversity are (i) land-use intensification on 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; Graham et al., 2017; Maes et al., 2005; Newton, 2017). Land-use change affects birds mainly due to the alteration of the food supply and its influence on the breeding habitat (Benton et al., 2002; Newton, 2004; Vickery et al., 2001).

However, anthropogenic transformation of landscapes may also result in the emergence of novel ecosystems. Novel ecosystems are characterised by recent establishment, due to deliberate or inadvertent human action, and new species combinations, with the potential for changes in ecosystem functioning (Hobbs et al., 2006). A characteristic example in Central European farmlands are Christmas-tree plantations. As a result of agricultural overproduction during the early 1980s and, therefore, the introduction of a milk quota within the EU, many

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grasslands in the study area, the low-mountain landscape of the 'Hochsauerland' in Central Europe (cf. Section 2.1), have been converted to Christmas-tree plantations (Fartmann et al., 2017; Rüther, 1990). Since then, their extent has increased continuously. The last significant expansion of Christmas-tree cultivation in the study area began in 2007 following the European storm 'Kyrill' (Fink et al., 2009). More than 2900 ha of Kyrill windthrows on former non-native spruce forests (*Picea abies*) have been planted with Christmas trees after salvage logging (Centre for Forest Ecosystems, 2013). Today, the Hochsauerland and adjacent low-mountain areas are important strongholds of Christmas-tree production in Europe, covering a total area of 18,000 ha (State Parliament NRW, 2013).

As Christmas-tree plantations have emerged as a novel ecosystem only very recently, scientific knowledge concerning their role for biodiversity conservation is very scarce (Fartmann et al., 2017; Gailly et al., 2017). However, Bagge et al. (2012) recently showed that conventionally managed Christmas-tree plantations in Denmark have higher carabid beetle species richness and abundance than organically managed ones. Additionally, Gailly et al. (2017) demonstrated that the introduction of Christmas-tree plantations into landscapes dominated by grassland with low hedge density in the Belgian Ardenne region increases bird species richness and abundance. However, they question the genuine quality of Christmas-tree plantations for birds due to the lack of data on breeding success.

Within the Hochsauerland, recent studies provided evidence that Christmas-tree plantations are characterised by high arthropod densities (ground beetles, spiders) comparable to those of montane heathlands and windthrows (Freienstein et al., 2018; Höppner, 2014) and high seed availability (Streitberger and Fartmann, 2018). Additionally, they are meanwhile regularly used as breeding habitats by the threatened woodlark (*Lullula arborea*) (Fartmann et al., 2017; Höppner, 2014; Legge, 2009; Schulte, 2017). Since the first observation of about 20 breeding pairs in Christmas-tree plantations in 2008 (Legge, 2009), the size of the woodlark population has continuously increased (Fartmann et al., 2017; Schulte, 2017).

The aim of this study is to evaluate the landscape-scale effects of the novel ecosystem Christmas-tree plantation on breeding bird assemblages in an important European stronghold of Christmas-tree production, the intensively used low-mountain landscape of the Hochsauerland (Central Europe) (Fig. 1), in comparison with competing land-use types. For this purpose, we compared environmental conditions as well as species richness and density of breeding birds in landscapes dominated by (i) grassland, (ii) Christmas-tree plantations in open landscapes that had been established on former grasslands, (iii) Christmas-tree plantations that had been established on former windthrows, (iv) windthrows as a result of the European storm 'Kyrill' in January 2007, and (v) non-native spruce forests. Finally, we provide recommendations for the future management of Christmas-tree plantations.

## 2. Materials and methods

### 2.1. Study area

The 541 km$^2$ study area is located in the northern part of the 'Hochsauerland' (51°6′ N/8°5′ and 51°22′ N/8°33′ E, 250–550 m a.s.l.), a low-mountain range in the southeast of the German Federal State of North Rhine-Westphalia (Fig. 1). It is characterised by a rather cool and wet climate (mean annual temperature: 8.0 °C; mean annual precipitation: 1184 mm; meteorological station Eslohe [351 m a.s.l]; period: 1981–2010; Wetterdienst and (DWD), 2017). The dominating soils in the hilly landscape are originally nutrient-poor cambisols (= poorly developed brown soils) on acidic bedrock (Geologisches Landesamt Nordrhein-Westfalen (NRW) 1998). The landscape is characterised by intensive forestry and agriculture. Forests (47% of the total area, mainly non-native spruce forests), and improved grassland (23%, mostly silage grasslands or cattle pastures with high stocking rates) are the dominant habitat types, followed by arable fields and built-up area (11% each). Nutrient-poor habitats and hedges have become rare within the agricultural areas of the study area as a result of intensive land use and associated structural homogenisation of the landscape.

Christmas-tree plantations (mainly caucasian fir [*Abies nordmanniana*]) are now characteristic elements of the low-mountain landscape, covering 3813 ha (7%) of the study area. Christmas-tree plantations are characterised by the application of fertiliser and herbicides. However, intensive fertilisation is avoided as it leads to a rapid height growth of the trees with negative effects on sales opportunities (Matschke, 2005; Maurmann, 2013). Christmas-tree plantations have a rotation cycle of 8 to 12 years. Herbicides are usually applied prior to planting of the young trees and during the first three to four years each spring at the beginning of the growing season and each autumn after lignification of the tree shoots (Körner, 1988; Matschke, 2005). As a result, the rows between the Christmas trees are usually covered by mosaics of bare ground (~5–10% cover), gravel (~5–10%) and weeds (~40%) in summer (Höppner, 2014). In contrast, insecticides are normally not applied. Additionally, the herb layer between the tree rows is often mulched in late summer (Matschke, 2005). During the rest of the growing season there are usually no further management activities. To avoid browsing of the shoot tips by roe deer and partly red deer, the plantations are fenced (Legge, 2009). Hence, there is no public access, and the breeding birds are not disturbed by mountain bikers, hikers or walkers and their domestic dogs.

### 2.2. Sampling design

#### 2.2.1. Plots

We compared five different landscape types characteristic for the study area and dominated by (i) grassland (GRASS), (ii) Christmas-tree plantations in open landscapes that had been established on former grasslands (CTOPEN), (iii) Christmas-tree plantations that had been established on former windthrows (CTWIND), (iv) windthrows as a result of the European storm 'Kyrill' in January 2007 (WIND), and (v) spruce forests (FOREST). Per landscape type, we randomly selected seven quadratic plots with a size of 40 ha and a cover of the focal land-use type of at least 40% within the plot ($N_{plots}$ = 35, Fig. 1).

#### 2.2.2. Habitat composition

For each plot, we mapped the habitat composition according to Riecken et al. (2006) and calculated the area of each habitat type using ArcGIS 10.2 (ESRI Inc.). For further analysis, the habitat types were summarised to the following nine main classifications: arable land, semi-natural grassland, improved grassland, fringe/clearing vegetation, Christmas-tree plantation, shrubland, deciduous forest, coniferous forest, and built-up area (Table 1). Additionally, we calculated the landscape diversity ($H'$) of each plot using the Shannon Index (O'Neill et al., 1988):

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

where $N$ is the total area of a plot and $n_i$ is the area of each habitat type in the plot.

#### 2.2.3. Breeding bird surveys

Mapping of the breeding bird territories was performed in all plots from the end of February to June 2016 (Fischer et al., 2005). Altogether, five surveys at early morning and two at night with an interval of at least 10 days between each visit were conducted. 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 all the study area. Breeding was assumed if a bird showed territorial behaviour twice within a distance of 10 days between each survey (Fischer et al., 2005). Additionally, for detecting

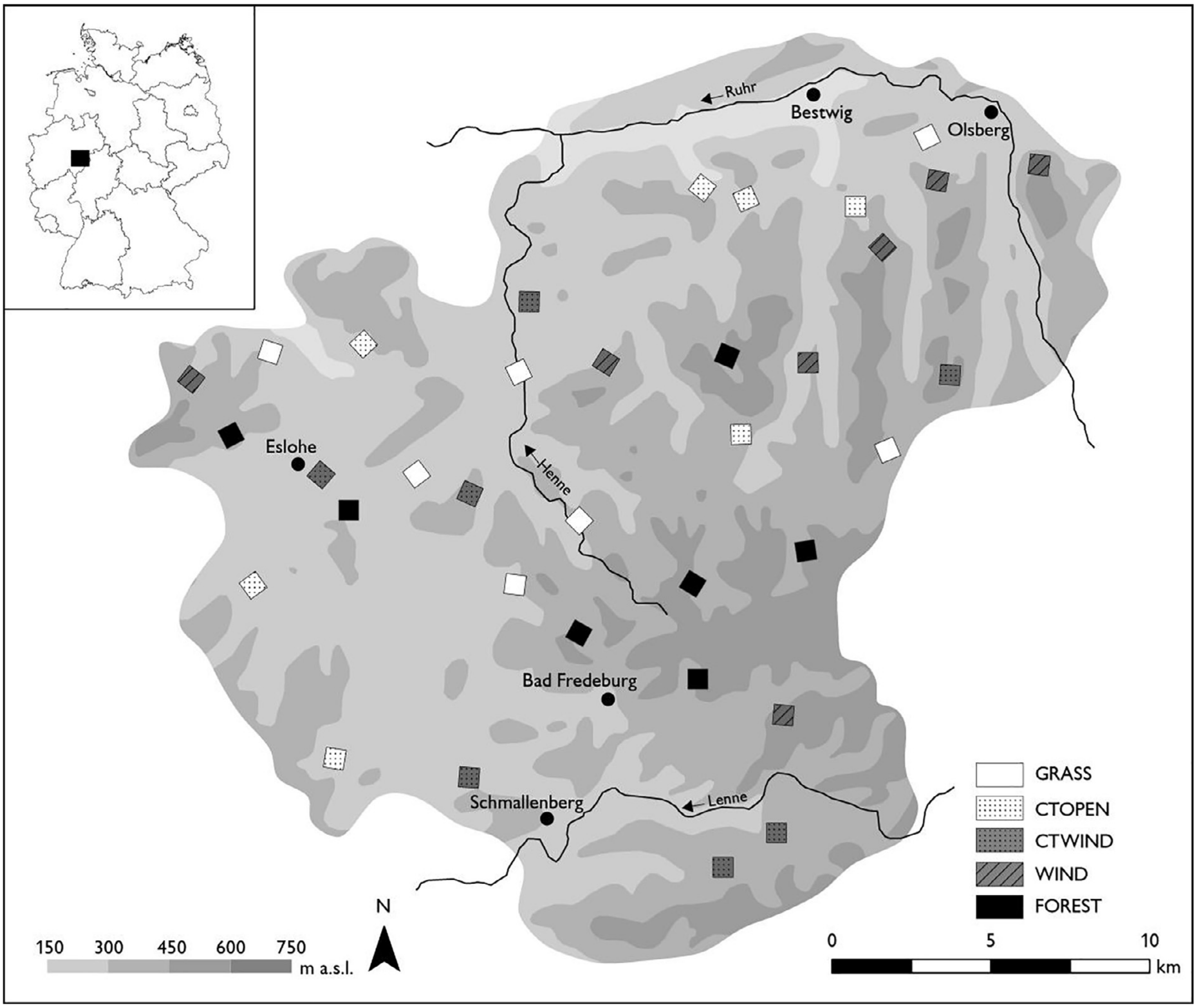


**Fig. 1.** Location of the study area and study sites in Germany.

owls, woodpeckers, and woodlark, we used tape playbacks of their calls and songs (Fischer et al., 2005). Prior to further analyses, breeding bird species were classified as threatened (including near-threatened species) or non-threatened species according to the red data book of North Rhine-Westphalia (Sudmann et al., 2011).

### 2.3. Statistical analysis

As test assumptions of ANOVA (normal distribution and homogeneous variances) usually failed on visually checked histograms (Quinn and Keough, 2002), all sampled numerical parameters (Table 1, Fig. 3) were tested for significant differences among the five landscape types by Kruskal–Wallis $H$ test. As post-hoc test, we applied the Dunn's

**Table 1**
Mean size ( ± SE) of habitat types and landscape diversity ($H'$) within the five landscape types ($N_{plots}$ = 35). Differences among the landscape types were tested by Kruskal–Wallis $H$ test. As post-hoc test, we applied the Dunn's test. In order to account for multiple testing, the $P$ values were adjusted using the Benjamini–Hochberg procedure (Pike, 2011). Different letters indicate significant differences of pairwise comparisons. n.s. = not significant; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

| Parameter | Landscape type | | | | | |
|---|---|---|---|---|---|---|
| | GRASS | CTOPEN | CTWIND | WIND | FOREST | Test statistics |
| *Habitat type (ha)* | | | | | | |
| Arable land | 3.4 ± 1.4 | 2.0 ± 1.4 | 2.8 ± 2.3 | 0.0 ± 0.0 | 0.4 ± 0.2 | $H = 8.11^{n.s.}$ |
| Semi-natural grassland | 0.2 ± 0.2 | 0.1 ± 0.1 | 0.9 ± 0.9 | 0.1 ± 0.0 | 0.2 ± 0.1 | $H = 0.64^{n.s.}$ |
| Improved grassland | $28.9 \pm 1.2^{a}$ | $4.6 \pm 1.5^{ab}$ | $2.7 \pm 1.0^{b}$ | $0.1 \pm 0.1^{b}$ | $2.0 \pm 1.0^{b}$ | $H = 22.00^{***}$ |
| Fringe/clearing vegetation | $0.7 \pm 0.3^{a}$ | $1.0 \pm 0.4^{a}$ | $3.2 \pm 1.3^{ab}$ | $16.7 \pm 2.7^{b}$ | $0.9 \pm 0.3^{a}$ | $H = 18.84^{***}$ |
| Christmas-tree plantation | $0.3 \pm 0.3^{a}$ | $24.0 \pm 2.1^{b}$ | $20.5 \pm 1.0^{b}$ | $3.1 \pm 1.3^{a}$ | $0.9 \pm 0.5^{a}$ | $H = 27.41^{***}$ |
| Shrubland | $1.2 \pm 0.4^{ab}$ | $1.4 \pm 0.3^{ab}$ | $1.7 \pm 0.5^{ab}$ | $5.0 \pm 1.5^{a}$ | $0.5 \pm 0.3^{b}$ | $H = 12.38^{*}$ |
| Deciduous forest | 1.8 ± 0.6 | 3.4 ± 0.7 | 1.9 ± 0.7 | 5.0 ± 0.9 | 3.9 ± 1.1 | $H = 9.65^{*}$ |
| Coniferous forest | $2.4 \pm 1.7^{a}$ | $2.5 \pm 0.9^{ab}$ | $5.2 \pm 1.4^{ab}$ | $8.7 \pm 1.4^{bc}$ | $29.8 \pm 0.8^{c}$ | $H = 23.11^{***}$ |
| Built-up area | 1.2 ± 0.3 | 0.8 ± 0.3 | 1.1 ± 0.2 | 1.1 ± 0.2 | 1.5 ± 0.4 | $H = 2.44^{n.s.}$ |
| *Landscape diversity (H')* | $0.9 \pm 0.1^{a}$ | $1.7 \pm 0.1^{b}$ | $1.8 \pm 0.1^{b}$ | $1.5 \pm 0.1^{b}$ | $0.9 \pm 0.1^{a}$ | $H = 23.21^{***}$ |

test. In order to account for multiple testing, the $P$ values were adjusted using the Benjamini–Hochberg procedure (Dinno, 2017; Pike, 2011). The relationship between the landscape diversity and the area of Christmas-tree plantations was analysed using the regression with the best fit (largest adjusted $R^2$; McDonald, 2014) (see Fig. 4).

Generalised linear model (GLM) were calculated to detect environmental parameters that explain the species richness and territory density of breeding bird assemblages, separately for all and threatened species, in the five landscape types. In order 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 included only top-ranked models within $\Delta AIC_C < 2$ (cf. Grueber et al., 2011).

Prior to GLM analyses, Spearman rank correlations ($r_s$) were conducted to exclude variables with strong inter-correlations ($|r_s| \geq 0.5$) (cf. Dormann et al., 2013). Arable land was correlated with deciduous forest ($r_s = -0.51$, $P < 0.01$) and Christmas-tree plantations with landscape diversity ($r_s = 0.75$, $P < 0.001$). Therefore, we excluded deciduous forest and landscape diversity from the analyses described below; all remaining parameters in Table 1 were included.

To identify indicator species for each landscape type, an indicator species analysis (ISA) (De Cáceres and Jansen, 2016; Dufrêne and Legendre, 1997) was carried out. All statistical analyses were performed using R 3.4.1 (R Development Core Team, 2017).

## 3. Results

### 3.1. Habitat composition

The five studied landscape types differed in habitat composition and landscape diversity (Table 1). GRASS, CTOPEN, CTWIND, and FOREST were significantly dominated by the respective eponymous land-use type. WIND significantly had the highest extent of fringe/clearing vegetation and shrubland, which had established since 2007 on former windthrows. Arable land, semi-natural grassland, deciduous forest, and built-up area had an area of maximally 5 ha (12.5% of the plot) per landscape type and did not differ among the five landscape types.

Landscape diversity was significantly highest at the two types of Christmas-tree plantation landscapes and WIND, differing from the very homogeneous GRASS and FOREST. Across all landscape types, landscape diversity was significantly related to the cover of Christmas-tree plantations per plot (Fig. 2). Landscape diversity was highest in plots with an intermediate area of Christmas-tree plantations (~19 ha, 45% of the plot).

### 3.2. Breeding bird assemblages

Altogether, we detected 61 breeding bird species on the 35 plots, 24 of which are considered threatened for North Rhine-Westphalia (Appendix, Table A1). The seven most common species (> 200 territories) were, with decreasing frequency, chaffinch (*Fringilla coelebs*), dunnock (*Prunella modularis*), blackbird (*Turdus merula*), wren (*Troglodytes troglodytes*), robin (*Erithacus rubecula*), firecrest (*Regulus ignicapilla*), and chiffchaff (*Phylloscopus collybita*). Among the threatened species, yellowhammer (*Emberiza citrinella*), willow warbler (*Phylloscopus trochilus*), linnet (*Carduelis cannabina*), woodlark, and tree pipit (*Anthus trivialis*) had, in decreasing order, the highest numbers of territories (147–35). In two threatened species, the woodlark and the great grey shrike (*Lanius excubitor*), the detected territory numbers are of supra-regional relevance: The 46 territories of the woodlark and the five territories of the great grey shrike account for 4.2 and 10%, respectively, of the maximally estimated population size in North Rhine-Westphalia. The woodlark was almost completely restricted to CTOPEN and CTWIND (Table 2). The great grey shrike territories occurred at three CTOPEN plots and, in each case, one GRASS and WIND plot.

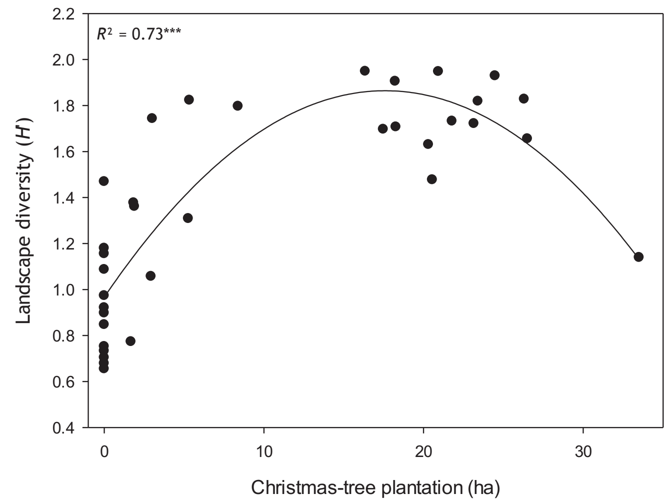


**Fig. 2.** Relationship between the proportion of Christmas-tree plantations and landscape diversity ($H'$) ($N_{\text{plots}} = 35$). $y = 0.967 + (0.0408 \times \text{proportion of Christmas-tree plantations}) - (0.000464 \times \text{proportion of Christmas-tree plantations}^2)$, $^{***}P < 0.001$.

### 3.3. Relationship of bird assemblages to habitat composition

In contrast to the number of all species, the number of threatened species as well as the territory density of all and threatened species differed significantly among the five landscape types (Fig. 3). The density of all species was significantly lowest at GRASS and highest at CTWIND, WIND and FOREST; CTOPEN had an intermediate position. For threatened bird species, CTOPEN, CTWIND, and WIND played a prominent role. The number of species and the density were highest in these three landscape types significantly differing from FOREST and partly from GRASS (territory density: CTOPEN and CTWIND).

For every landscape type, we determined indicator species (Table 2). The highest numbers of indicator species were identified for FOREST, WIND, and GRASS, with five to eight species each. Except FOREST, every landscape type had indicator species that are considered threatened. At the two Christmas-tree plantation landscape types, even all indicator species were threatened species. The indicator species of CTOPEN were tree pipit, yellowhammer, and woodlark. Linnet was the characteristic species in CTWIND.

The area of improved grassland had negative effects on species richness and density of all and threatened species (Table 3, Fig. 3). Except for the density of all species, the area of coniferous forest also negatively affected species richness and density in all models. Additionally, species richness of all and threatened species increased with the area of Christmas-tree plantations. The area of fringe/clearing vegetation also had a positive effect on the species richness of all species. In general, model accuracy was very good ($R^2$: 0.20–0.60).

## 4. Discussion

Our study revealed that the five studied landscape types in the intensively used low-mountain landscape strongly differed in habitat composition and landscape diversity. Landscape diversity was significantly highest at the two types of Christmas-tree plantation landscapes and WIND, differing from GRASS and FOREST. Bird species assemblages clearly responded to the differences in habitat composition. This was especially true for threatened species having a peak of species richness and territory density at the two types of Christmas-tree plantation landscapes and slightly weakened at WIND. GRASS had an intermediate position, and FOREST was almost irrelevant for threatened

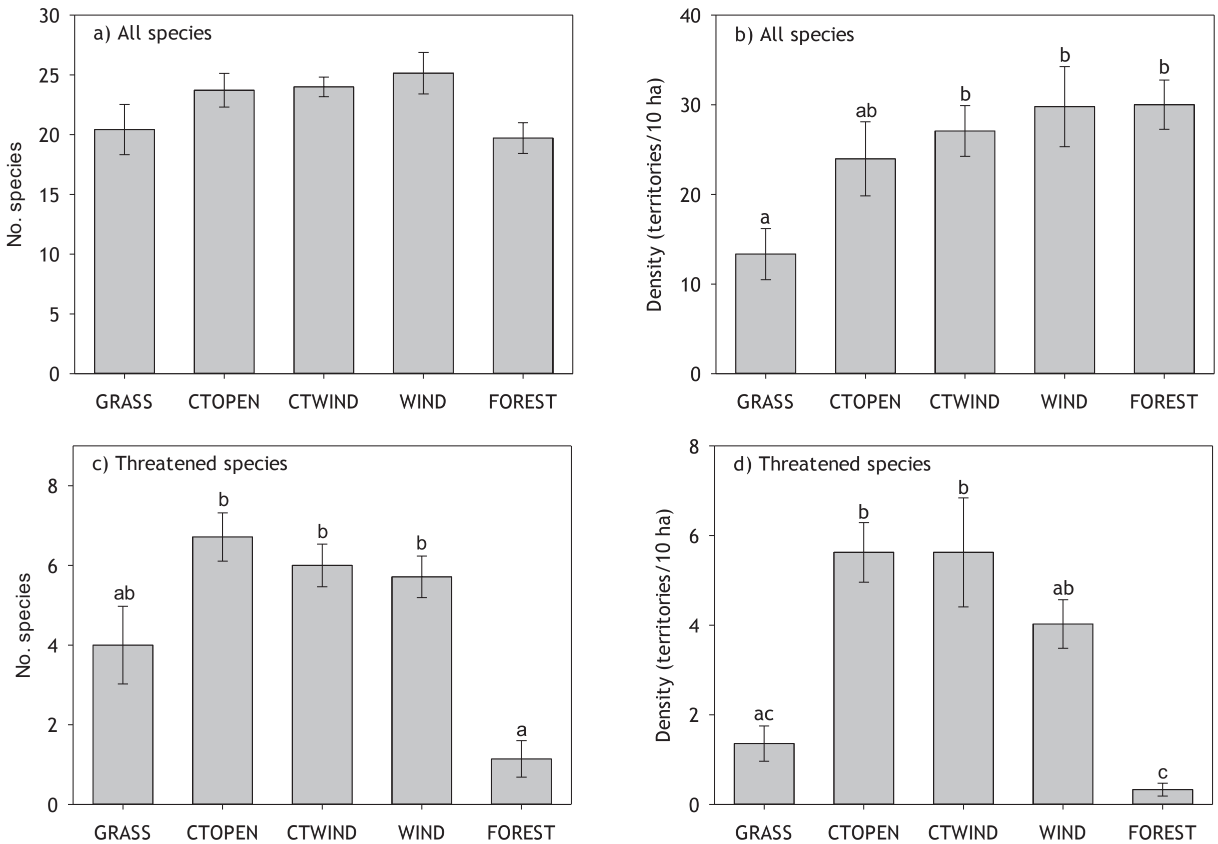


**Fig. 3.** Mean values ( ± SE) of species richness and density of all (a, b) and threatened (c, d) breeding bird species in the five landscape types ($N_{plots}$ = 35). Differences among the landscape types were tested by Kruskal–Wallis *H* test. As post-hoc test, we applied the Dunn's test. In order to account for multiple testing, the *P* values were adjusted using the Benjamini–Hochberg procedure (Pike, 2011). Different letters indicate significant differences of pairwise comparisons. Statistics: a) $H = 7.683$, $df = 4$, $P = 0.10$; b) $H = 12.501$, $df = 4$, $P < 0.05$; c) $H = 24.305$, $df = 4$, $P < 0.001$; d) $H = 24.354$, $df = 4$, $P < 0.001$.

species. All indicator species (linnet, tree pipit, woodlark, and yellowhammer) of the two Christmas-tree plantation types and WIND were threatened species and occurred with high density in the respective landscape types.

Both GRASS and FOREST had very low landscape diversity, with almost three quarters of the plot covered by improved grassland and coniferous forest, respectively. Additionally, due to intensive agriculture and forestry in the study area, the grassland and forest stands are characterised by a very homogenous habitat structure (own observation). Heterogeneity at the landscape and habitat scale is a key factor for the species richness of bird assemblages (Benton et al., 2003; Vickery and Arlettaz, 2012). In line with this, GRASS and FOREST had the lowest species richness of threatened bird species. Additionally, the area of improved grassland and coniferous forest negatively affected the species richness of all and threatened species in the GLM analyses.

In contrast to FOREST, GRASS also had very low territory densities, and the area of improved grassland negatively influenced the density of all and threatened species in the GLM analyses. The vast majority of the improved grasslands in the study area were used as silage grasslands or cattle pastures with high stocking rates (cf. Section 2.1.). Even if birds would start nesting in these uniform grasslands (cf. Wilson et al., 2009), both management regimes would result in an almost complete loss of nests due to frequent mowing and trampling (Gatter, 2000; Newton, 2017; Wilson et al., 2009).

However, improved grasslands are of relevance for some bird species, especially raptors feeding on small mammals, as foraging habitats due to high accessibility to the remaining food resources (Newton, 2017). Indeed, with buzzard (*Buteo buteo*) as well as the threatened kestrel (*Falco tinnunculus*) and red kite (*Milvus milvus*), three of the five indicator species of GRASS were birds of prey. Maximally, up to 12 raptors (one buzzard, nine red kites, two black kites [*Milvus migrans*]) were simultaneously observed hunting in silage grasslands in the study area during harvest (own observation). The white wagtail (*Motacilla alba*), another threatened indicator species of GRASS, feeds on small flies on the ground, such as dung flies regularly occurring in pastures (Davies, 1977).

Despite the low landscape diversity of FOREST and the high homogeneity of the coniferous forest stands in the study area, such forests are known to harbour high densities of tiny insects with beneficial effects on several widespread, insectivorous songbird species (Gatter, 2000, 2004; Mattes, 1988). Consequently, most of the indicator species of FOREST identified in our study (coal tit [*Parus ater*], crested tit [*Parus cristatus*], firecrest, goldcrest [*Regulus regulus*], treecreeper [*Certhia familiaris*], and wren [*Troglodytes troglodytes*]) belonged to this group of species (cf. Flade, 1994).

The two types of Christmas-tree plantation landscapes and WIND had the highest landscape diversity, with beneficial effects on threatened species. The area of Christmas-tree plantations per plot was even a surrogate for landscape diversity, as landscape diversity was highest in plots with an intermediate area of Christmas-tree plantations (~19 ha, 45% of the plot). Besides the strong effects of Christmas-tree plantations on landscape diversity, Christmas-tree plantations are characterised by strong differences in habitat structure between the different plantation parcels, enhancing diversity at the habitat level (Fartmann et al., 2017). A regular rotation cycle of Christmas trees from planting to harvesting lasts between 8 and 12 years (Körner, 1988; Matschke, 2005). Depending on the age of the stands, the habitat structure strongly differs (Matschke, 2005). In the first years, Christmas-tree plantations are characterised by small Christmas trees growing in rows with large areas of bare soil and gravel between the

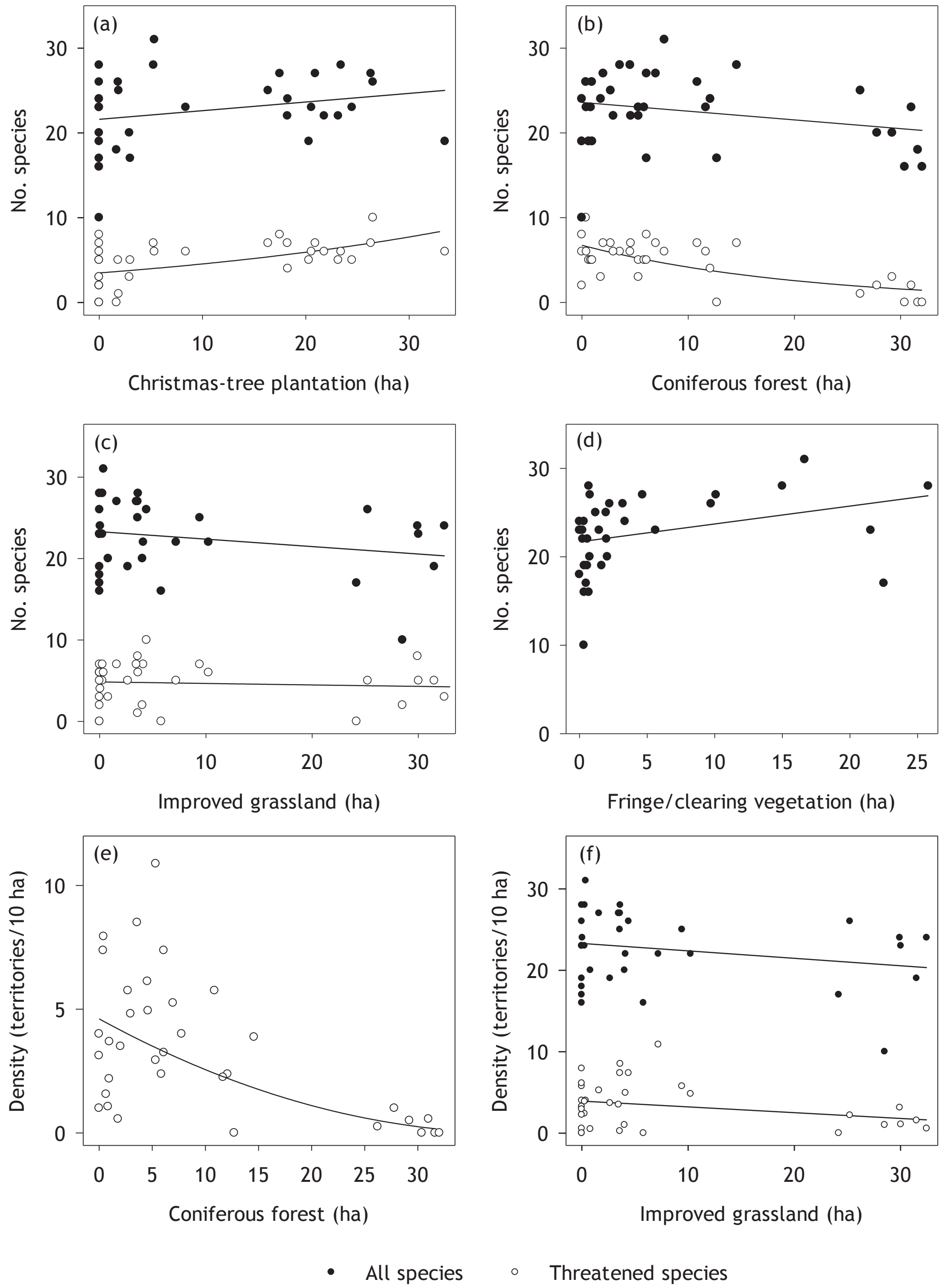


**Fig. 4.** Relationship between species number and density of all and threatened breeding bird species, respectively, and the significant environmental parameters of averaged models ($N_{plots}$ = 35) (see Table 3). The regression slopes were fitted using a single predictor GLM (GLM; Gaussian error structure for the response variables number of all species, densities of all and threatened species; Poisson error structure for the response variable number of threatened species).

rows at the beginning of the growing season (Section 2.1). Three to four years after planting, the application of herbicides is usually ceased (Körner, 1988; Matschke, 2005) and the rows between the trees become increasingly vegetated (Fartmann et al., 2017). During the last third of the rotation cycle, most of the ground is covered by Christmas trees up to 2.5 m in height. As the Christmas-tree producers have to supply the market every year with new trees, Christmas-tree plantations are usually characterised by mosaics of parcels with different tree ages and, hence, different habitat structures (Fartmann et al., 2017). Accordingly, a higher cover of Christmas-tree plantations is also an indicator for high habitat heterogeneity. As a result, the species richness of both all and threatened species increased with the area of Christmas-tree plantations.

The habitat composition and landscape diversity of CTOPEN and CTWIND were similar. The same was true for the species richness and territory density of breeding birds. However, both landscape types were characterised by different indicator species. We assume that this is the result of differences in the habitat structure and resource availability due to a different land-use history. Christmas-tree plantations at CTWIND had been established since 2007 on former windthrows. As a result of mulching of the remaining wood material following salvage logging of the trees, they usually had a higher cover of dead wood (Höppner, 2014). Together with the lack of previous soil tillage, the soil conditions are more diverse, resulting in a higher cover of weeds. Hence, CTWIND had a lower cover of bare ground and more heterogeneous vegetation than CTOPEN. Additionally, the area of fringe/

**Table 2**
Results of indicator species analysis (ISA) (De Cáceres and Jansen, 2016; Dufrêne and Legendre, 1997) for the five landscape types based on territory densities ($N_{plots} = 35$). IV = indicator value; ab = relative abundance (%) comparing the five landscape types, % = percentage of plots within each landscape type with occurrence of the species. Grey-hatched type values: species are indicator species for this landscape type; bold-type values: species are threatened in North Rhine-Westphalia (Sudmann et al., 2011). *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

| Species | IV | *P* | GRASS | | CTOPEN | | CTWIND | | WIND | | FOREST | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | ab | % | ab | % | ab | % | ab | % | ab | % |
| Buzzard (*Buteo buteo*) | 42.9 | * | 100 | 43 | . | . | . | . | . | . | . | . |
| **Kestrel (*Falco tinnunculus*)** | 57.1 | ** | **100** | **57** | . | . | . | . | . | . | . | . |
| **Red kite (*Milvus milvus*)** | 33.3 | * | **78** | **43** | 22 | 29 | . | . | . | . | . | . |
| **White wagtail (*Motacilla alba*)** | 46.8 | * | **82** | **57** | 18 | 14 | . | . | . | . | . | . |
| Blue tit (*Parus caeruleus*) | 47.5 | ** | 47 | 100 | 15 | 29 | 5 | 14 | 21 | 71 | 11 | 43 |
| **Tree pipit (*Anthus trivialis*)** | 61.2 | *** | . | . | **61** | **100** | 22 | 86 | 14 | 29 | 4 | 29 |
| **Yellowhammer (*Emberiza citrinella*)** | 46.3 | ** | 5 | 43 | **46** | **100** | 37 | 71 | 11 | 71 | 1 | 14 |
| **Woodlark (*Lullula arborea*)** | 50.5 | ** | . | . | **51** | **100** | 40 | 100 | 9 | 29 | 1 | 14 |
| **Linnet (*Carduelis cannabina*)** | 63.1 | *** | 2 | 29 | 31 | 86 | **63** | **100** | 4 | 29 | . | . |
| Black woodpecker (*Dryocopus martius*) | 36.4 | * | . | . | 9 | 14 | 18 | 14 | 64 | 57 | 9 | 14 |
| Chiffchaff (*Phylloscopus collybita*) | 36.5 | * | 11 | 100 | 23 | 100 | 20 | 100 | 37 | 100 | 10 | 86 |
| **Willow warbler (*Phylloscopus trochilus*)** | 54.9 | *** | . | . | 15 | 100 | 30 | 100 | **55** | **100** | 1 | 14 |
| **Bullfinch (*Pyrrhula pyrrhula*)** | 49.1 | ** | 4 | 14 | 23 | 43 | 13 | 43 | **57** | **86** | 3 | 14 |
| Blackcap (*Sylvia atricapilla*) | 38.3 | *** | 15 | 100 | 11 | 100 | 17 | 100 | 38 | 100 | 18 | 100 |
| Whitethroat (*Sylvia communis*) | 45.0 | ** | 10 | 71 | 17 | 57 | 27 | 100 | 45 | 100 | 1 | 14 |
| Treecreeper (*Certhia familiaris*) | 56.1 | ** | 4 | 14 | 9 | 29 | . | . | 9 | 29 | 78 | 71 |
| Wood pigeon (*Columba palumbus*) | 39.7 | ** | 12 | 71 | 20 | 71 | 16 | 71 | 12 | 71 | 40 | 100 |
| Chaffinch (*Fringilla coelebs*) | 40.9 | *** | 9 | 100 | 17 | 100 | 15 | 100 | 18 | 100 | 41 | 100 |
| Coal tit (*Parus ater*) | 48.8 | ** | 11 | 29 | 11 | 43 | 13 | 57 | 16 | 71 | 49 | 100 |
| Crested tit (*Parus cristatus*) | 46.0 | ** | 5 | 29 | 8 | 29 | 15 | 71 | 26 | 71 | 46 | 100 |
| Firecrest (*Regulus ignicapilla*) | 50.8 | *** | 10 | 86 | 8 | 71 | 15 | 86 | 16 | 86 | 51 | 100 |
| Goldcrest (*Regulus regulus*) | 50.9 | *** | 11 | 71 | 8 | 57 | 13 | 100 | 18 | 86 | 51 | 100 |
| Wren (*Troglodytes troglodytes*) | 35.7 | ** | 9 | 100 | 15 | 86 | 17 | 86 | 24 | 100 | 36 | 100 |

clearing vegetation was thrice as high at CTWIND compared to CTOPEN.

All four indicator species of the Christmas-tree plantation landscapes build their nests at the ground or in shrubs and young trees (linnet) beneath sheltered vegetation, depend on song posts – such as Christmas trees, fence posts, and tall trees adjacent to the plantations (own observation) – and feed mainly on the ground (Bauer et al., 2005). The three indicator species of CTOPEN – tree pipit, woodlark, and yellowhammer – are insectivorous, at least during the breeding period (Bauer et al., 2005), and prefer low-growing vegetation (yellowhammer) (Whittingham and Evans, 2004; Whittingham et al., 2005) or bare ground (tree pipit, woodlark) for foraging (Bosco, 2014; Bowden, 1990; Burton, 2007). Christmas-tree plantations in the study area are characterised by high arthropod densities (Freienstein et al., 2018; Höppner, 2014). In contrast, the indicator species of CTWIND – the linnet – relies largely on a diet of seeds, even when feeding their young (Wilson et al., 2009). Due to the higher weed cover and larger area of fringe/clearing vegetation (see above), seeds are widely available at CTWIND. Therefore, we explain the high relevance of the Christmas-tree plantations for the four threatened bird species especially by the (i) high availability and (ii) accessibility of suitable food. Additionally, due to the low management activity during the growing season, the lack of public access through fencing, and the lack of mechanical soil

**Table 3**
Model-averaging results (GLM; Gaussian error structure [a, b, d]; Poisson error structure [c]): relationship between species number (a, c) and density (b, d) of all and threatened breeding bird species, respectively, and environmental parameters ($N_{plots} = 35$). Model-averaged coefficients (conditional average) were derived from the top-ranked models ($\Delta AIC_C < 2$). n.s. = not significant; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

| Parameter | Estimate | SE | *Z* | *P* |
|---|---|---|---|---|
| (a) No. of all species ($R^2 = 0.20–0.30$) | | | | |
| (Intercept) | 22.89 | 3.19 | 7.14 | *** |
| Coniferous forest | −0.19 | 0.07 | 2.58 | ** |
| Christmas-tree plantation | 0.14 | 0.06 | 2.13 | * |
| Fringe/clearing vegetation | 0.23 | 0.10 | 2.20 | * |
| Improved grassland | −0.13 | 0.06 | 1.99 | * |
| (b) Density of all species ($R^2 = 0.32–0.39$) | | | | |
| (Intercept) | 28.16 | 3.59 | 7.72 | *** |
| Improved grassland | −0.46 | 0.16 | 2.87 | ** |
| (c) No. of threatened species ($R^2_{McFadden} = 0.54–0.60$) | | | | |
| (Intercept) | 1.87 | 0.33 | 5.45 | *** |
| Coniferous forest | −0.06 | 0.01 | 3.77 | *** |
| Christmas-tree plantation | 0.02 | 0.01 | 2.26 | * |
| Improved grassland | −0.02 | 0.01 | 2.41 | * |
| (d) Density of threatened species ($R^2 = 0.54–0.59$) | | | | |
| (Intercept) | 4.65 | 2.32 | 1.99 | * |
| Coniferous forest | −0.16 | 0.06 | 2.47 | * |
| Improved grassland | −0.13 | 0.04 | 3.22 | ** |

disturbance in the Christmas-tree plantations, the risk of nest loss is low.

Gailly et al. (2017) also showed that Christmas-tree plantations promote bird species richness and abundance in an intensively used landscape. However, they question the genuine quality of Christmas-tree plantations for birds due to possibly negative effects of insecticide and herbicide application on breeding success. In the Christmas-tree plantations of our study area, insecticides are normally not applied (cf. Section 2.1) and arthropod densities (carabid beetles, spiders) are high, comparable to those on montane heathlands and windthrows (Freienstein et al., 2018; Höppner, 2014). In contrast, herbicides are regularly sprayed. However, the applied quantities still allow the establishment of a herb layer with intensive seed production in summer (Section 2.1Streitberger and Fartmann, 2018; Höppner, 2014). Additionally, successful reproduction has regularly been confirmed for the woodlark (Höppner, 2014), and populations of the species have continuously increased in the Christmas-tree plantations of the study area during the last ten years (Fartmann et al., 2017; Schulte, 2017). Hence, we have no evidence that the Christmas tree-plantations in the study area with their current management act as ecological traps for breeding birds.

In terms of conservation, the Christmas-tree plantations are even prime habitats of the woodlark in North Rhine-Westphalia (Fartmann et al., 2017; Schulte, 2017). The threatened species is legally protected at the EU scale by the Birds Directive (Ssymank et al., 1998), and the current population size is estimated to be 750 to 1100 breeding pairs in North Rhine-Westphalia (Grüneberg et al., 2013). With 46 territories, we detected 4% of the maximally estimated population size of the federal state in the Christmas-tree plantations of our study area. In 2016, the population size in the Hochsauerland was even estimated to be around 530–600 breeding pairs also nearly exclusively occurring in Christmas-tree plantations (Fartmann et al., 2017; Schulte, 2017). Consequently, the Christmas-tree plantations of the Hochsauerland are, besides active and former military training areas (Grüneberg et al., 2013), nowadays the most important strongholds of the species in North Rhine-Westphalia (Fartmann et al., 2017).

Due to the young history of the ecosystem, breeding of woodlarks in Christmas-tree plantations has only recently been detected (Behle, 2001; Legge, 2009; Fartmann et al., 2017). Until the middle of the last century, the woodlark was a widespread breeding bird of montane heathlands in the Hochsauerland (Borchard et al., 2013; Legge, 2009). However, most likely due to abandonment and afforestation of heathlands with the associated loss of open habitat structures, the populations vanished (Borchard et al., 2013). Between 1980 and 2007, only single breeding pairs were observed at the 1960 $km^2$ large Hochsauerland (Legge, 2009). Since the first detection of about 20 breeding pairs within the study area in 2008 (Legge, 2009), the observation area was enlarged, and the population size in the Christmas trees continuously increased until the preliminary peak of 530–600 pairs in 2016 (see above). Comparable shifts in habitat use of birds are well known and can occur within a few generations (Fuller, 2012a; Wesolowski and Fuller, 2012).

Since Christmas-tree plantations are a novel ecosystem, our knowledge concerning the plant and animal assemblages is scarce. However, as our study showed, there seem to be many similarities in bird assemblages of Christmas-tree plantations and the more intensively studied young conifer plantations in forestry. It is well documented that all four indicator species of the Christmas-tree plantation landscapes can occur in high densities in such young conifer plantations (Flade, 1994; Graham et al., 2017; Khoury et al., 2009; Burgess et al., 2015; Burton, 2007; Gatter, 2000; Langston et al., 2007; Wotton and Gillings, 2000; Fuller et al., 2004).

Recently, some studies have highlighted the importance of windthrows for threatened bird species (Thorn et al., 2016; Zmihorski, 2010; Zmihorski and Durska, 2011). Besides the high landscape diversity of WIND, the plots had the highest extent of fringe/clearing vegetation and shrubland. In general, both habitat types were across and within the plots characterised by high heterogeneity (own observation). In accordance with this, the area of fringe/clearing vegetation promoted species richness of all species. Both threatened indicator species of WIND, bullfinch and willow warbler, are known to prefer such heterogeneous young-growth stages of woodland succession (Fuller, 2012b,c; Graham et al., 2017; Grüneberg et al., 2013; Wilson et al., 2009).

In conclusion, the novel ecosystem of Christmas-tree plantations fosters the species richness and density of threatened breeding bird species in the intensively used low-mountain landscape of the study area. The species richness of threatened breeding bird species was driven mainly by landscape heterogeneity. The area of the Christmas-tree plantations was even a surrogate for landscape diversity. Densities of the threatened indicator species of the Christmas-tree plantation landscapes were probably promoted by (i) high availability of suitable food (arthropods, seeds) and (ii) high accessibility to the food resources due to bare ground (tree pipit, woodlark) or low-growing vegetation (linnet, yellowhammer) in the Christmas-tree plantations. For the woodlark, the Christmas-tree plantations in the Hochsauerland are even among the most important strongholds in North Rhine-Westphalia.

## 5. Implications for conservation

To increase the availability of seeds and probably of arthropods, on the one hand, and to reduce the amount of herbicides used, on the other hand, we recommend the cessation of herbicide application along the plantation fences and tramlines. In contrast, weed control by grazing Shropshire sheep, which do not browse Christmas trees (Matschke, 2005), would hardly be an alternative to herbicide application, especially since the woodlark and tree pipit vitally depend on bare ground (Bosco, 2014; Bowden, 1990; Burton, 2007; Langston et al., 2007). The same is true for mechanical weed control through milling during the growing season (Arlettaz et al., 2012), as nest loss should increase, although for example the nesting sites of the woodlark are located mainly below the Christmas trees (Höppner, 2014). Additionally, soil erosion rates probably rise after heavy rainfall on the inclined slopes after milling.

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## Appendix A

See Table A1

**Table A1**
Breeding bird species, threat status, and number of territories in the studied plots ($N_{plots}$ = 35). Common name: Newton, 2017; scientific name: Barthel and Helbig, 2005; threat status: Sudmann et al. (2011); NRW population: percentage of the estimated maximum population size in North Rhine-Westphalia according to Grüneberg et al., 2013, only specified for species having a share of more than 2.5%. Threat status: CR = critically endangered, EN = endangered, VU = vulnerable, NT = near threatened.

| Common name | Scientific name | Threat status | Territories | NRW population (%) |
|---|---|---|---|---|
| Common chaffinch | *Fringilla coelebs* | . | 445 | . |
| Dunnock | *Prunella modularis* | . | 325 | . |
| Blackbird | *Turdus merula* | . | 244 | . |
| Wren | *Troglodytes troglodytes* | . | 233 | . |
| Robin | *Erithacus rubecula* | . | 228 | . |
| Common firecrest | *Regulus ignicapilla* | . | 213 | . |
| Common chiffchaff | *Phylloscopus collybita* | . | 206 | . |
| Goldcrest | *Regulus regulus* | . | 180 | . |
| Blackcap | *Sylvia atricapilla* | . | 167 | . |

(continued on next page)

**Table A1** (*continued*)

| Common name | Scientific name | Threat status | Territories | NRW population (%) |
|---|---|---|---|---|
| Song thrush | *Turdus philomelos* | . | 154 | . |
| Yellowhammer | *Emberiza citrinella* | NT | 147 | . |
| Great tit | *Parus major* | . | 131 | . |
| Willow warbler | *Phylloscopus trochilus* | NT | 111 | . |
| Whitethroat | *Sylvia communis* | . | 77 | . |
| Coal tit | *Parus ater* | . | 63 | . |
| Crested tit | *Parus cristatus* | . | 63 | . |
| Linnet | *Carduelis cannabina* | NT | 54 | . |
| Wood pigeon | *Columba palumbus* | . | 54 | . |
| Woodlark | *Lullula arborea* | VU | 46 | 4.2 |
| Blue tit | *Parus caeruleus* | . | 40 | . |
| Tree pipit | *Anthus trivialis* | VU | 35 | . |
| Jay | *Garrulus glandarius* | . | 27 | . |
| Common treecreeper | *Certhia familiaris* | . | 23 | . |
| Mistle thrush | *Turdus viscivorus* | . | 21 | . |
| Bullfinch | *Pyrrhula pyrrhula* | NT | 19 | . |
| Nuthatch | *Sitta europaea* | . | 18 | . |
| Garden warbler | *Sylvia borin* | . | 15 | . |
| Willow tit | *Parus montanus* | . | 13 | . |
| Skylark | *Alauda arvensis* | VU | 11 | . |
| Great spotted woodpecker | *Dendrocopos major* | . | 11 | . |
| Fieldfare | *Turdus pilaris* | . | 10 | . |
| House sparrow | *Passer domesticus* | NT | 9 | . |
| Marsh tit | *Parus palustris* | . | 7 | . |
| Greenfinch | *Carduelis chloris* | . | 7 | . |
| Wood warbler | *Phylloscopus sibilatrix* | VU | 7 | . |
| Common redstart | *Phoenicurus ochruros* | . | 7 | . |
| Red-backed shrike | *Lanius collurio* | NT | 6 | . |
| Short-toed treecreeper | *Certhia brachydactyla* | . | 6 | . |
| White wagtail | *Motacilla alba* | NT | 6 | . |
| Great grey shrike | *Lanius excubitor* | CR | 5 | 10 |
| Common kestrel | *Falco tinnunculus* | NT | 4 | . |
| Carrion crow | *Corvus corone* | . | 3 | . |
| Black woodpecker | *Dryocopus martius* | . | 3 | . |
| Magpie | *Pica pica* | . | 3 | . |
| Red kite | *Milvus milvus* | VU | 2 | . |
| Long-tailed tit | *Aegithalos caudatus* | . | 2 | . |
| Common buzzard | *Buteo buteo* | . | 2 | . |
| Goldfinch | *Carduelis carduelis* | . | 2 | . |
| Common raven | *Corvus corax* | NT | 2 | . |
| Icterine warbler | *Hippolais icterina* | NT | 2 | . |
| Barn swallow | *Hirundo rustica* | VU | 2 | . |
| Grasshopper warbler | *Locustella naevia* | VU | 2 | . |
| Serin | *Serinus serinus* | . | 2 | . |
| Common starling | *Sturnus vulgaris* | NT | 2 | . |
| Lesser whitethroat | *Sylvia curruca* | NT | 2 | . |
| Marsh warbler | *Acrocephalus palustris* | . | 1 | . |
| Middle-spotted woodpecker | *Dendrocopos medius* | NT | 1 | . |
| Whinchat | *Saxicola rubetra* | CR | 1 | . |
| Grey-headed woodpecker | *Picus canus* | EN | 1 | . |
| Long-eared owl | *Asio otus* | VU | 1 | . |
| Tawny owl | *Strix aluco* | . | 1 | . |

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