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Effects of Christmas-tree plantations on phytodiversity: implications for conservation

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Abstract

Perennial crops such as Christmas trees have increasingly been cultivated throughout Europe. However, knowledge on the influence of Christmas-tree plantations (CTP) on biodiversity is still scarce. We examined phytodiversity and soil and habitat-structure characteristics within young (CTP-YOUNG, tree age ≤ 6 years) and old (CTP-OLD, tree age > 6 years) conventionally managed CTP in comparison with the three most dominant habitat types within the study area: (1) intensively managed grasslands (GRASS), (2) windthrows (WIND) and (3) non-native spruce forests (FOREST) ($n_{\text{per sample type}} = 18$). Our study revealed clear differences in soil characteristics, habitat structure and plant-species richness between the five sample types. These differences were most pronounced between three groups of habitats: (1) CTP, (2) GRASS and (3) WIND/FOREST. CTP were characterized by a typical habitat structure composed of a distinct shrub layer, an intermediate herb layer and a low litter cover. In contrast to the other sample types CTP had a comparably high cover of bare ground and stones/gravel. Due to the practiced management CTP were characterized by a unique plant species community composed of a high number of ruderal species and some neophytes. The differences between CTP-YOUNG and CTP-OLD were generally small. Next to management, phytodiversity in CTP was influenced by the size of CTP. Small-scale CTP generally had a higher phytodiversity. For the cultivation of Christmas trees, we recommend the reduction of herbicide use as far as possible. New plantations should be implemented preferentially within homogeneous landscapes composed of habitats with low importance for biodiversity.

Keywords Biodiversity conservation · Land-use change · Landscape heterogeneity · Perennial crop · Ruderal species · Species richness

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Introduction

The current biodiversity loss is a great challenge for nature conservation worldwide. Due to the rapid decrease of species diversity it is hypothesised that we are approaching the sixth global mass extinction event (Barnosky et al. 2011). Amongst the most detrimental threats to biodiversity is land-use intensification (Sala et al. 2000; Maxwell et al. 2016). This is especially true for Europe where more than 40% of the European (EU-27) terrestrial land surface is used for agriculture (Eurostat 2016). However, due to the ancient tradition of land use, agricultural landscapes play an important role for biodiversity conservation in Europe. Many habitats of conservation concern evolved by traditional land use and are dependent on low-intensive management (Halada et al. 2011). As a consequence of land-use intensification since the 1950s, dramatic species declines were triggered for a great variety of different taxa by changes in agricultural management (e.g. Hendrickx et al. 2007; Hooftman and Bullock 2012; Storkey et al. 2012; Meyer et al. 2013; Nilsson et al. 2013; Sanderson et al. 2013).

Due to the severe loss of farmland biodiversity, conservation measures for promoting species diversity within agricultural landscapes are of special importance. Research on the impact of agriculture on farmland biodiversity is therefore an important basis for developing and improving existing conservation strategies (e.g. Loos et al. 2014; Assandri et al. 2017; Löffler and Fartmann 2017). Next to agricultural intensification, the increased establishment of novel cropping systems cultivated for purposes other than food production, impacts farmland biodiversity. One typical example are perennial crops composed of woody species planted as short-rotation coppices for use as energy resources (Pleguezuelo et al. 2015). In contrast to annual crops, short-rotation coppices are characterised by a low disturbance intensity, longer rotation cycles and lower nutrient and herbicide inputs (cf. Dauber et al. 2010). Within homogeneous agricultural landscapes, short-rotation coppices have the potential to increase biodiversity at the landscape level by promoting habitat heterogeneity and species richness (Haughton et al. 2016). However, the effects are dependent on several factors such as the crop type or the field size (cf. Dauber et al. 2010).

Another typical example for perennial crops are Christmas trees which have increasingly been cultivated throughout Europe, especially in Germany since the 1950s (Maurmann 2013). Here, the area used for Christmas-tree production increased by over 300% between 1970 and 2010 (Maurmann 2013). So far, ecological studies regarding Christmas-tree plantations (CTP) mainly focus on silvicultural and management aspects (e.g. Sæbø et al. 2009; Nikiema et al. 2012). In contrast, studies on the environmental influence of CTP are still scarce. This is especially true for their effects on biodiversity. However, the knowledge of these effects is of vital importance for deriving sustainable management recommendations. To date, available studies on species diversity in CTP address primarily birds and arthropods (Hughes and Hudson 1997; Williams et al. 2011; Bagge et al. 2012; Gailly et al. 2017; Fartmann et al. 2018) while other parts of biodiversity have hardly been analysed.

CTP are characterised by a specific management regime, including the application of fertilizer and herbicides, resulting in a unique habitat structure. However, compared to several other crops, fertilizer and herbicide inputs in CTP are low. While intensive fertilization is avoided as it leads to a rapid height growth of the trees with negative effects on sales opportunities (BMLFUW 2008; Matschke 2005; Maurmann 2013), weed control is regularly carried out in CTP. As a consequence, the plantations typically have much bare ground exposed (Bagge et al. 2012; Fartmann et al. 2018). Due to the open habitat structure

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and high availability of food resources (arthropods and seeds) the plantations function as important breeding habitats for threatened bird species dependent on open ground (Fartmann et al. 2018). On the landscape level, CTP promote bird species richness by increasing habitat availability within homogeneous landscapes (Gailly et al. 2017; Fartmann et al. 2018).

In contrast, knowledge regarding the effects of CTP on plant richness is still lacking. Therefore, the objectives of our study were to analyse plant-species diversity within CTP and to evaluate the floristic value of CTP from a conservation viewpoint for deriving implications for the cultivation of Christmas trees. Therefor we focused on the following questions:

- What soil and habitat-structure characteristics are typical for CTP and how do CTP differ from other dominant habitat types in terms of soil and habitat-structure characteristics?
- In which way are CTP characterised by traits of phytodiversity (e.g. total species richness, number of ruderal species) and how do CTP differ from other dominant habitat types in terms of phytodiversity?
- Do differently aged CTP differ with respect to soil and habitat-structure characteristics and phytodiversity?

The study was carried out within one of the most important strongholds of Christmas-tree production in Europe, the "Hochsauerland", a low-mountain landscape located in Central Germany where CTP cover a total area of 18,000 ha (Landtag NRW 2013). In this region, many grasslands were converted to CTP as a result of agricultural overproduction during the early 1980s and, therefore, the introduction of a milk quota within the EU (Rüther 1990). Since then, the area of CTP has continuously been increased. 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*) were planted with Christmas trees after salvage logging (Wald-Zentrum 2013).

We examined different traits of phytodiversity (total species richness, numbers of threatened species, neophytes and ruderal species) and environmental parameters (soil, habitat structure) within young (CTP-YOUNG, tree age $\leq$ 6 years) and old (CTP-OLD, tree age > 6 years) conventionally managed CTP in comparison to the three most dominant habitat types within the study area: (1) intensively managed grasslands, (2) windthrows and (3) non-native spruce forests.

Materials and methods

Study area

The study area, with a size of 541 km^2, 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.sl.), a low-mountain range in the southeast of the German Federal State of North Rhine-Westphalia. It is characterised by a rather cool and wet climate (mean annual temperature: 7.5 °C; mean annual precipitation: 1184 mm; meteorological station Eslohe [351 m a.s.l]; period: 1961–1990; DWD 2017). The dominating soils are nutrient-poor cambisols (= poorly

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developed brown soils) on acidic bedrock (Geologisches Landesamt NRW 1998). The landscape is characterised by intensive forestry and agriculture. The dominant habitat types are forests which occupy 47% of the total area and mainly represent non-native spruce forests, and improved grassland occupying 23% of the total area, followed by arable fields and built-up area (in each case covering 11% of the total area) (Fartmann et al. 2018). Furthermore, CTP (mainly Caucasian fir [*Abies nordmanniana*]) are characteristic elements of the low-mountain landscape covering 3813 ha (7%) of the study area. Within the study area, the vast majority of CTP are managed conventionally with herbicide treatment for weed control and rotation cycles of eight to twelve years (Fartmann et al. 2018).

Vegetation and soil sampling

For vegetation and soil sampling in CTP we distinguished between young (hereafter referred to as CTP-YOUNG) and old (CTP-OLD) plantations (see Introduction). *Abies nordmanniana* was planted within the majority (80%) of the plantations. Further tree species were *A. procera* and *Picea pungens*. In addition to CTP, analyses were carried out within the three most dominant habitat types found within the study area – grassland (GRASS), non-native coniferous forests (FOREST) and windthrows (WIND) which were caused by the storm 'Kyrill' in January 2007. Therefore, our study focuses on four habitat types and distinguishes between five different sample types: CTP (CTP-YOUNG, CTP-OLD), GRASS, FOREST and WIND. For every habitat type five to eight 40 ha sized plots dominated by the equivalent habitat type were randomly selected (in total 25 plots). For every sample type 18 vegetation relevés (samples) were randomly distributed amongst the plots with the equivalent habitat type (=three to six samples per plot). The vegetation relevés had a size of 5 m×5 m. The minimum distance between the relevés was defined to be 30 m. In most cases the distance of the relevés within one plot was much greater. All vascular plants of all vegetation layers (herb, shrub and tree layer) were identified on each of the relevés during May until July 2017 according to Oberdorfer (2001) and Jäger and Werner (2001) and followed the scientific nomenclature of Wisskirchen and Haeupler (1998). Cover of all plant species was estimated by using the Wilmanns scale (Wilmanns 1998) and were converted into the following percentage cover values: r=0.1%, +=0.5%, *1*=1%, *2m*=2.5%, *2a*=10%, *2b*=20.5%, *3*=38%, *4*=63%, *5* =88%. In addition, we analysed habitat structure which included vegetation characteristics and further parameters. Vegetation characteristics comprised the estimation of the cover of the following layers: Christmas trees within CTP, tree layer (woody species with heights > 6 m), shrub layer (shrubs and woody species with heights between 0.5 and 6 m), herb layer, herbs, grasses and cryptogams. Further habitat-structure parameters were the estimated cover of litter, bare ground and stones/gravel. The parameters were estimated by using 5% steps. The mean height of the herb layer and Christmas trees were determined by measuring the maximum height at five randomly selected spots within the relevé.

Soil samples were taken to a depth of 10 cm at three randomly selected locations within every relevé. The three samples were mixed and after air-drying and sieving, the samples were analysed for soil reaction ($CaCl_2$, WTW Multi 3430, pH electrode SenTrix 940-3), calcium acetate lactate soluble phosphate (spectrophotomer, Biochrom Libra S11), potassium (flame photometer, BWB Technologies BWB XP) and mineralised nitrogen (water soluble ammonium and nitrate, ion chromatography, Metrohm 761 Compact IC).

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Phytodiversity

As biodiversity parameters we analysed for each sample the total number of species and Simpson´s diversity index (Simpson 1949), as well as the number of threatened plant species, neophytes and ruderal species (r, cr and sr strategy). Classification of threatened species was based on the red data book of North-Rhine Westphalia (LANUV NRW 2010). All species listed as 'critically endangered', 'endangered', 'vulnerable' and 'near threatened' (red list categories: 1, 2, 3 and V) were included within the analysis. Neophytes were determined according to Haeupler et al. (2003) and NetPhyD and BfN (2013). The BIOLFLOR trait base (Klotz et al. 2002) was used as the basis for the categorisation of ruderal species. For the analysis, species of all layers (herb, shrub and tree layer) were included. However, cultivated, non-native tree species (Christmas trees [*Abies nordmanniana*, *A. procera* and *Picea pungens*], *Picea abies* and *Pseudotsuga menziesii*) were excluded from all analyses.

Statistical analysis

For detecting differences between the sample types, (generalised) linear-mixed models (LMM; GLMM) were applied (R packages lme4, nlme; Bates et al. 2017; Pinheiro et al. 2017) by creating plot as the random factor. Sample type served as a nominal fixed factor and the analysed parameters were used as dependent variables. Depending on the distribution of the variables, either binomial (percentage data), Poisson (count data) or linear (for square-root transformed variables with normal distribution) models were applied. For reducing overdispersion within the models (binomial/Poisson), observation level random effects were added as a random factor (Harrison 2014, 2015). The overall effect of the dependent variables on sample type was analysed by comparing the full models with reduced models without sample type as the fixed factor (ANOVA, likelihood ratio tests). Pairwise differences between the sample types were detected by applying Tukey test as a post hoc test (*glht* function, R package multcomp, Hothorn et al. 2017).

An indicator species analysis (ISA, Dufrêne and Legendre 1997) was carried out with square-rooted species cover values to detect significant indicator species for the different sample types. Vegetation composition was analysed by non-metric multidimensional scaling (NMDS; R package vegan, *metaMDS* function; Oksanen et al. 2019) with the Bray–Curtis distance as a distance measure and a maximum number of 100 random starts in search for a stable solution. Species with an occurrence of less than three were excluded from the analysis. Only environmental variables (soil parameters and habitat structure characteristics) which were non-intercorrelated amongst each other (Spearman correlation coefficient $|r_s| < 0.6$) were included for the overlay of environmental variables (cf. "Appendix") (*envfit* function, R Package vegan; Oksanen et al. 2019).

An LMM was carried out to detect which environmental parameters determine plant species richness within CTP-OLD and CTP-YOUNG. Species numbers were log-transformed for achieving a normal distribution and inserted in the model as the dependent variable. Phosphorus, potassium and mineralised nitrogen content as well as soil acidity (pH) and Christmas-tree height were included in the analysis as the independent variables. As a proxy for habitat structure, we integrated the cover of stones/gravel within the model (cf. "Appendix"). Moreover, the total area size of CTP within a 500 m radius around each vegetation relevé was added as an explanatory variable. Therefor the area of CTP (ha) was calculated based on land-use data from the German Real Estate Cadastre Information System

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(ALKIS) and aerial photographs using ArcGIS 10.2 (ESRI Inc.). For the LMM plot served as the random factor. 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 carried out by using the *dredge* function (R package MuMIn, Bartón 2018), and only included top-ranked models within $\Delta AIC_C < 3$ (cf. Grueber et al. 2011).

The analyses were carried out with R 3.4.2 (LMM; GLMM; NMDS) (R Core Team 2017) and PCORD 5 (ISA).

Results

Soil conditions

Soil conditions differed considerably among the sample types (Table 1): pH values were significantly highest in GRASS and CTP-YOUNG, intermediate in CTP-OLD and lowest in WIND and FOREST. Compared to the four other sample types, soils in GRASS were characterised by a significantly higher concentration of mineralised nitrogen. In contrast, phosphorus and potassium contents were highest in CTP and significantly differing from WIND and FOREST; GRASS had an intermediate position. Phosphorus concentration in GRASS

Table 1 Mean values ± SE of soil and habitat-structure characteristics of the five different sample types

Parameter	GRASS	CTP-YOUNG	CTP-OLD	WIND	FOREST	*P*
Soil characteristics						
pH	5.6 ± 0.1[a]	5.3 ± 0.1[a]	4.7 ± 0.1[b]	3.9 ± 0.1[c]	3.5 ± 0.1[c]	***
N_{min} (mg/100 g)	7.0 ± 0.7[a]	3.4 ± 0.4[b]	3.0 ± 0.2[b]	4.4 ± 0.7[b]	2.7 ± 0.5[b]	***
P (PO_4^{3-}) (mg/100 g)	0.4 ± 0.1[bc]	0.5 ± 0.1[c]	0.7 ± 0.0[c]	0.2 ± 0.0[ab]	0.1 ± 0.0[a]	***
K (mg/100 g)	13.9 ± 2.2[bc]	23.5 ± 1.7[a]	17.5 ± 1.5[ab]	8.2 ± 1.1 [cd]	5.5 ± 1.5[d]	***
Habitat structure						
Cover (%)						
Tree layer	0.0 ± 0.0[a]	0.0 ± 0.0[a]	0.0 ± 0.0[a]	1.1 ± 4.7[a]	39.2 ± 4.0[b]	***
Shrub layer	0.0 ± 0.0[a]	40.9 ± 2.9[b]	51.4 ± 3.6[b]	55.2 ± 5.3[b]	1.3 ± 0.7[a]	***
Christmas trees	.	41.7 ± 2.3[a]	51.1 ± 3.7[b]	.	.	*
Herb layer	89.2 ± 2.8[a]	46.7 ± 4.0[b]	40.3 ± 4.4[b]	51.8 ± 4.5[b]	16.4 ± 4.2[c]	***
Herbs	40.1 ± 4.7[a]	43.1 ± 3.5[a]	40.0 ± 4.4[a]	18.2 ± 2.7[ab]	12.1 ± 3.3[b]	**
Grasses	75.8 ± 3.0[a]	5.3 ± 2.5[b]	1.4 ± 0.8[b]	41.4 ± 5.1[a]	6.7 ± 2.3[b]	***
Cryptogams	4.0 ± 1.4[a]	16.0 ± 4.1[ab]	23.1 ± 4.1[b]	16.8 ± 3.4[ab]	22.3 ± 4.7[b]	**
Litter	45.8 ± 5.5[b]	23.6 ± 3.3[a]	27.2 ± 2.0[ab]	69.4 ± 2.8[c]	72.5 ± 3.7[c]	***
Bare ground	6.1 ± 2.5[bc]	9.1 ± 2.4[c]	6.9 ± 2.3[bc]	0.2 ± 0.1[a]	1.8 ± 1.1[ab]	***
Stones/gravel	0.0 ± 0.0[a]	9.1 ± 2.3[b]	4.8 ± 1.6[b]	0.1 ± 0.0[a]	1.8 ± 0.6[a]	***
Christmas-tree height (cm)	.	97.6 ± 5.9[a]	205.8 ± 14.3[b]	.	.	***
Herb-layer height (cm)	13.6 ± 1.9[a]	46.1 ± 4.8[b]	39.4 ± 4.8[b]	30.1 ± 2.4[b]	11.8 ± 1.6[a]	***

N = 18 per group. Comparison between groups was done by Tukey test, see materials and methods for details. Sample types with no consistent letter indicate significant differences ($P < 0.05$)

n.s. not significant

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

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differed significantly from FOREST, whereas potassium content significantly differed from CTP-YOUNG with the highest and from FOREST with the lowest concentrations.

Habitat structure

Habitat structure significantly differed between CTP and the three other sample types (Table 1). In contrast, the two types of CTP only differed significantly in the cover and height of Christmas trees with higher values in CTP-OLD (Table 1).

A distinct tree layer only occurred within FOREST (Table 1). In contrast, a shrub layer was only pronounced within CTP and WIND. In CTP, the shrub layer was mainly composed of Christmas trees. The herb-layer cover was significantly highest in GRASS, intermediate in CTP and WIND and lowest in FOREST. The composition of the herb layer differed according to the sample type (Table 1). In GRASS and CTP, the cover of herbs was highest and differed significantly from FOREST. In WIND, the herb cover was intermediate. In contrast, the grass cover was significantly higher in GRASS and WIND compared to CTP and FOREST. The herb layer was highest in CTP and WIND significantly differing from GRASS and FOREST (Table 1). In CTP-OLD and FOREST cryptogam cover was highest significantly differing from GRASS; the two other sample types had an intermediate position (Table 1). Litter cover was significantly highest in WIND and FOREST, intermediate in GRASS and CTP-OLD and lowest in CTP-YOUNG. CTP were the habitats significantly richest in bare ground and stones/gravel (Table 1). WIND had the significantly lowest values of bare ground and GRASS those of stones/gravel.

Phytodiversity and species composition

The overall number of detected species was highest in CTP-YOUNG (100 species), followed by WIND (85), CTP-OLD (74), GRASS (65) and FOREST (45). In contrast, mean species number was significantly highest in WIND and GRASS differing from FOREST; CTP had an intermediate position (Fig. 1). When taking abundance into account, differences in species richness were less pronounced. Values of mean Simpson's Diversity Index ranged between 0.6 (FOREST, CTP-YOUNG) and 0.8 (GRASS; WIND); significant differences were only detected among GRASS and FOREST (Fig. 1). CTP-OLD had an intermediate position. The number of threatened species was generally low and did not differ among the five sample types (Fig. 1). Species richness of neophytes and ruderal species was significantly highest in CTP differing from the three other sample types (Fig. 1).

For each of the five sample types, ISA revealed significant indicator species (Table 2). GRASS and WIND were characterised by many different indicator species. Amongst them were *Lolium perenne*, *Taraxacum* sect., *Ruderalia* agg. and *Trifolium repens* for GRASS and *Rubus idaeus*, *Deschampsia flexuosa* and *Luzula luzuloides* for WIND. In contrast, *Mycelis muralis* and *Dryopteris carthusiana* were the only indicator species in FOREST. For CTP, neophytes and ruderal species in particular were identified as indicator species, such as *Epilobium ciliatum*, *Myosotis arvensis* and *Vicia hirsuta* for CTP-YOUNG and *Crepis capillaris*, *Sonchus arvensis* and *Sonchus asper* for CTP-OLD.

The NMDS ordination underlines the previous results on differences in environmental conditions among the studied sample types and distinguished three distinct groups of community composition: the two types of CTP, FOREST/WIND and GRASS (Fig. 2). Along the first axis CTP were clearly separated from FOREST and WIND by a lower

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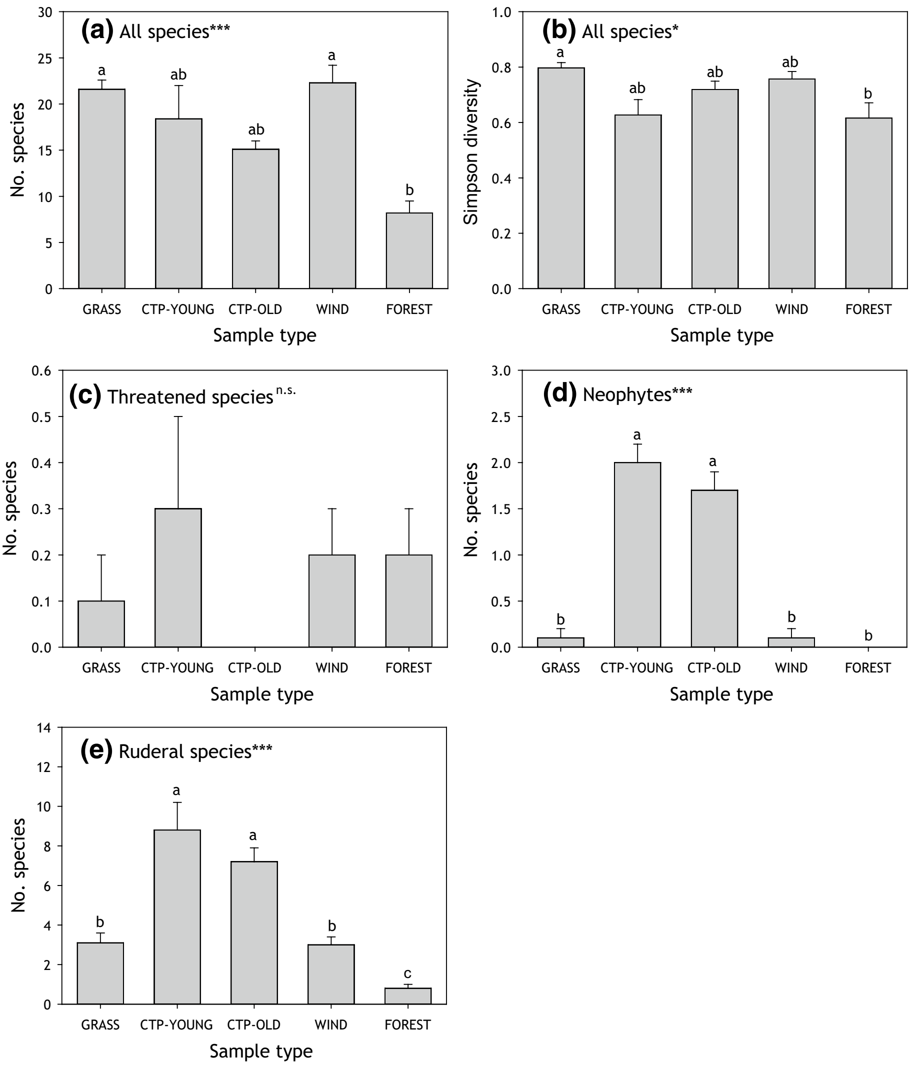

Fig. 1 Mean values ± SE of plant species richness of the five different sample types. $N = 18$ per group. Comparison between groups was done by Tukey test, see materials and methods for details. Sample types with no consistent letter indicate significant differences ($P < 0.05$). * $P < 0.05$, ***$P < 0.001$, *n.s.* not significant

cover of the litter layer and higher potassium contents whereas GRASS had an intermediate position. Furthermore, CTP and GRASS were distinguished from WIND/FOREST by higher pH values, a higher cover of herbs and the absence of the tree layer. Along the second axis FOREST/WIND and CTP were separated from GRASS by a higher cover

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Table 2 Results of ISA (Dufrêne and Legendre 1997) of the five different sample types

Species	GRASS	CTP-YOUNG	CTP-OLD	WIND	FOREST	*P*
Lolium perenne	94.1	.	.	.	.	***
Taraxacum sect. *Ruderalia*	90.9	.	.	.	.	***
Trifolium repens	87.5	.	.	.	.	***
Poa pratensis	87.1	.	.	.	.	***
Cerastium holosteoides	83.3	.	.	.	.	***
Poa trivialis	78.6	.	.	.	.	***
Phleum pratense	73.8	.	.	.	.	***
Rumex acetosa	66.7	.	.	.	.	***
Veronica serpyllifolia	66.7	.	.	.	.	***
Bellis perennis	61.1	.	.	.	.	***
Cardamine pratensis	61.1	.	.	.	.	***
Ranunculus acris	61.1	.	.	.	.	***
Dactylis glomerata	59.9	.	.	.	.	***
Ranunculus repens	54.2	.	.	.	.	***
Alopecurus pratensis	50.0	.	.	.	.	***
Trifolium pratense	47.4	.	.	.	.	***
Holcus lanatus	42.6	.	.	.	.	***
Plantago major	39.7	.	.	.	.	***
Poa annua	36.7	.	.	.	.	***
Bromus hordeaceus	33.3	.	.	.	.	***
Veronica chamaedrys	33.3	.	.	.	.	***
Plantago lanceolata	30.3	.	.	.	.	**
Rumex obtusifolius	26.2	.	.	.	.	**
Festuca rubra agg.	25.3	.	.	.	.	**
Epilobium ciliatum	.	50.4	.	.	.	***
Myosotis arvensis	.	42.3	.	.	.	***
Vicia hirsuta	.	40.7	.	.	.	***
Veronica persica	.	35.8	.	.	.	***
Lapsana communis	.	30.4	.	.	.	***
Cirsium arvense	.	28.6	.	.	.	**
Fallopia convolvulus	.	28.5	.	.	.	***
Viola arvensis	.	25.7	.	.	.	**
Crepis capillaris	.	.	49.9	.	.	***
Sonchus arvensis	.	.	47.1	.	.	***
Sonchus asper	.	.	39.8	.	.	***
Vicia sepium	.	.	37.3	.	.	***
Senecio vulgaris	.	.	35.9	.	.	***
Vicia cracca	.	.	30.2	.	.	**
Geranium dissectum	.	.	29.4	.	.	***
Rubus idaeus	.	.	.	85.5	.	***
Deschampsia flexuosa	.	.	.	73.0	.	***
Luzula luzuloides	.	.	.	59.2	.	***
Galium harcynicum	.	.	.	56.3	.	***
Digitalis purpurea	.	.	.	55.1	.	***

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Table 2 (continued)

Species	GRASS	CTP-YOUNG	CTP-OLD	WIND	FOREST	*P*
Agrostis tenuis	.	.	.	50.3	.	***
Senecio ovatus	.	.	.	50.2	.	***
Juncus effusus	.	.	.	50.0	.	***
Galium aparine	.	.	.	48.8	.	***
Rubus fruticosus agg.	.	.	.	45.3	.	***
Epilobium angustifolia	.	.	.	42.3	.	***
Carex ovalis	.	.	.	38.9	.	***
Dryopteris dilatata	.	.	.	38.8	.	***
Athyrium filix-femina	.	.	.	35.3	.	***
Galeopsis tetrahit	.	.	.	34.0	.	***
Betula pendula	.	.	.	33.3	.	***
Moehringia trinervia	.	.	.	33.1	.	***
Cytisus scoparius	.	.	.	32.0	.	***
Rumex acetosella	.	.	.	26.8	.	**
Veronica officinalis	.	.	.	25.4	.	**
Mycelis muralis	.	.	.	.	*28.8*	***
Dryopteris carthusiana	.	.	.	.	*26.7*	**

Only significant species with an indicator value (IV) ≥ 25 are shown. Species are sorted by "IV" for the considered sample type. Displayed indicator values: Species are indicator species for the accordant sample type. $N = 18$ per sample type

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

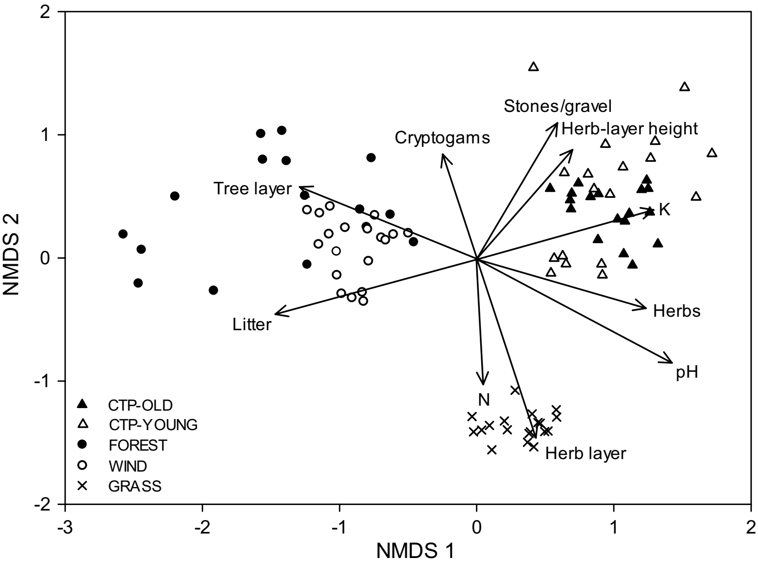

Fig. 2 NMDS ordination with vegetation samples of the five sample types ($N = 90$) and environmental variables as overlay ($P < 0.001$). Four dimensions, stress: 7.7. N = nitrogen content; K = potassium content

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of cryptogams, a lower herb-layer cover and lower concentrations of nitrogen. CTP were associated with the highest cover of stones/gravel and the tallest herb-layer.

According to the model-averaging LMM, species numbers in CTP were significantly negatively affected by a high cover of stones/gravel and a high CTP area within a radius of 500 m around each vegetation sample (Table 3).

Table 3 Model-averaging results (LMM): relationship between the number of species (log-transformed) and environmental variables in young and old Christmas-tree plantations ($N=36$)

Model	Estimate	SE	t	*P*
1				
(Intercept)	4.636184	0.5469777	8.476003	***
Stones/gravel	−0.028445	0.0085782	−3.315968	**
Christmas-tree area (500 m buffer)	−0.025522	0.0090979	−2.805282	**
pH	−0.168107	0.0958816	−1.753276	n.s.
McFadden's Pseudo R^2				0.63
2				
(Intercept)	3.853615	0.3317577	11.615753	***
Stones/gravel	−0.036266	0.0075615	−4.796198	***
Christmas-tree area (500 m buffer)	−0.025669	0.0094395	−2.719311	*
McFadden's Pseudo R^2				0.56
3				
(Intercept)	4.187414	0.3463584	12.089828	***
Stones/gravel	−0.032676	0.0076939	−4.246968	***
Christmas-tree area (500 m buffer)	−0.028775	0.0086927	−3.310243	**
Potassium content	−0.013011	0.007505	−1.733567	n.s.
McFadden's Pseudo R^2				0.62
Model averaging	**Estimate**	**SE**	**Z**	***P***
(Intercept)	4.2179398	0.5864971	6.98	***
Stones/gravel	−0.031338	0.0087163	−3.442	***
Christmas-tree area (500 m buffer)	−0.026403	0.0092093	−2.732	**
pH	−0.061265	0.0991478	−0.605	n.s.
Potassium content	−0.004168	0.0078472	−0.523	n.s.
Christmas-tree height	0.0002452	0.0006505	0.369	n.s.
Phosphorus content	−0.042206	0.151829	−0.271	n.s.
McFadden's Pseudo R^2 (range of all models)			0.56–0.65	

Presented are the top three models (Model 1–3) as well as the complete model-averaging results (full average). Model-averaged coefficients were derived from the top-ranked models (ΔAICc < 3)

Mineralised nitrogen content was not included within the top-ranked models

n.s. not significant

**P* < 0.05; ***P* < 0.01; ****P* < 0.001

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Discussion

Our study revealed clear differences in soil conditions, habitat structure and plant-species richness between the five studied sample types. These differences were most pronounced between three groups of habitats: (1) CTP, (2) GRASS and (3) WIND/FOREST. Soils at CTP had the highest potassium and phosphorus contents. Additionally, CTP were characterized by a typical habitat structure composed of a distinct shrub layer built up of Christmas trees, an intermediate herb layer and a low litter cover. In contrast to the other sample types, CTP had a comparably high cover of bare ground and stones/gravel. In addition to habitat structure, CTP had a unique plant-species community composed of a high number of ruderal species and some neophytes. In contrast, the differences between CTP-YOUNG and CTP-OLD were generally small.

GRASS and CTP were the only habitat types that are regularly fertilized (see introduction). As a result, they had the most nutrient-rich soils. While GRASS was characterised by the highest soil nitrogen contents, those of CTP were comparable to WIND and FOREST. In contrast, CTP had the highest potassium contents whereas phosphorus contents were high in both GRASS and CTP. In general, Christmas trees have relatively low nutritional requirements compared to arable crops (Maurer 2014). The amount of fertilization is strongly dependent on the nutritional demand of the planted tree species and local soil conditions (Matschke 2005; Maurer 2014). Fertilization in CTP must be carried out carefully as overly nutrient-rich conditions can cause an undesired rapid growth of the trees and may cause tree damage (Matschke 2005; Maurer 2014). Specifically, excessive and unbalanced loads of nitrogen are detrimental for Christmas trees as they increase the trees' sensitivity towards diseases, pests and drought (Matschke 2005; BMLFUW 2008; Maurer 2014). Additionally, it leads to rapid height growth with negative effects on sales opportunities. However, deficits in the supply of certain nutrients may also decrease the economic quality of the trees (Maurer 2014). Generally, all the Christmas-tree species planted have a relatively high demand for potassium as deficits in the supply cause the discoloration and falling off of the needles in addition to decreasing the trees' resistance towards pollution and other pressures such as diseases and pests (Matschke 2005).

In contrast to nutrient availability, soil acidity in CTP differed according to the age of the Christmas trees. Soils at CTP-YOUNG were less acidic than those at CTP-OLD. Most likely, the increased soil acidity of the older CTP results from cation removal by nutrient uptake, harvesting and leaching (cf. Körner 1988; Hatten et al. 2014). This assumption is supported by the slightly lower potassium content within the older stands.

Concerning the mean overall plant-species richness CTP had an intermediate position between GRASS/WIND (most species-rich) and FOREST (most species-poor). When taking abundance into account, diversity of CTP-YOUNG was comparable to FOREST and CTP-OLD had an intermediate position as reflected by Simpson's Diversity Index. However, the total number of detected plant species was highest at CTP-YOUNG, and CTP-OLD also harboured many different species. FOREST are intensively managed within the study area and, hence, were characterised by a homogeneous and dense tree cover (cf. Fartmann et al. 2018), an extensive litter layer and low structural diversity resulting in a low herb cover and low species diversity (cf. Ellenberg and Leuschner 2010). In contrast, WIND covered a wide variety of different successional stages with a more vigorous herb and shrub layer as well as a high structural and plant-species diversity. According to the

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ISA, they were characterised by a high number of plant species typical for acidic clear-cuts such as *Rubus idaeus*, *Deschampsia flexuosa* or *Luzula luzuloides* (Ellenberg and Leuschner 2010). In GRASS, plant-species diversity was comparable to WIND. However, communities were mainly composed of widespread and nutrient-demanding grassland species such as *Lolium perenne*, *Taraxacum* sect. *Ruderalia* agg. or T*rifolium repens* (Dierschke and Briemle 2002; Grime 2007).

Vegetation in CTP was strongly determined by weed control. In the conventionally managed plantations of the study area weed growth is controlled by herbicides (see introduction), because a high herb cover in spring reduces tree survival and affects tree quality, e.g. by reduced growth or decreased budding (Sæbø et al. 2009; Maurer 2014). Herbicides are usually applied prior to planting of the young trees and twice a year within young stands during the first three to four years (Körner 1988; Matschke 2005). Typically, soil-acting herbicides are brought out at the beginning of the growing period whereas foliar-acting herbicides are applied towards the end of the vegetation period (Willoughby and Palmer 1997). Within older stands of CTP, herbicide treatment occurs the most irregularly (Maurer 2014). In general, however, the timing of herbicide spraying, and the applied quantities still allow the establishment of a high-growing herb layer (this study) with intensive seed production in summer (Fartmann et al. 2018). Ruderal and some neophytic species were especially able to cope with the environmental conditions at CTP. Most ruderal species have a short-lived, annual life cycle (cf. Klotz et al. 2002) adapted to a high degree of disturbance. However, some perennial species were also dominant within CTP, such as *Sonchus arvensis*. In comparison to annual crops, perennial species are most likely favoured within CTP by the lack of soil tillage (cf. Streit et al. 2002). *Epilobium ciliatum*, a neophytic and perennial species, was one of the most frequent herbs in CTP and an indicator species for CTP-YOUNG. This species seems to be highly resistant to herbicides. In Europe, several herbicide-tolerant populations were identified within agricultural habitats (Matulevičiūtė 2016).

A similar pattern in species richness was also observed in comparing short-rotation coppices (SRC) with other intensively managed habitats (Baum et al. 2012). In contrast to forests and arable fields, SRC provided a higher plant-species diversity. However, species composition in SRC differed according to plantation age. Within older plantations the proportion of woodland species increased in line with increasing tree cover (Baum et al. 2012). In contrast, we found only weak differences in species composition among young and old CTP. The most obvious explanation for this pattern is that the variation in management and habitat structure was too low due to the relatively short rotation cycle of eight to twelve years (cf. study area section). The LMM analysis revealed that species richness in CTP was negatively affected by: (1) the proportion of stones/gravel and (2) by the area of CTP within a radius of 500 m around the sample. Most likely, these parameters can be regarded as a proxy for management intensity. Within large-scale CTP weed control is intensively carried out resulting in a high proportion of open ground and low species diversity. In contrast, management intensity seemed to be lower within smaller CTP embedded within a more heterogeneous landscape. In such CTP, up to 40 to 50 species per sample were found (this study). However, the higher species richness within these samples may also be caused by the greater edge effects from adjacent habitats. The high variation in species richness at CTP, especially at CTP-YOUNG, is also reflected by the high overall species number detected in the two sample types, although mean species richness was at an intermediate level.

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As demonstrated by our study, threatened plant species only occur in low numbers in CTP. However, also within the other habitat types red-list species were very rare. In contrast, prior studies showed that conventionally managed CTP have a high conservation value for some animal groups. The more open ground vegetation in conventionally managed CTP compared to the denser vegetation of biologically managed ones promotes a high abundance of arthropods such as carabid beetles (Bagge et al. 2012). Moreover, CTP are important breeding habitats for threatened bird species due to the high amount of bare ground offering accessibility to food resources (arthropods and seeds) (Fartmann et al. 2018). For the woodlark (*Lullula arborea*), CTP in the Hochsauerland are one of the most important strongholds in North Rhine-Westphalia (Fartmann et al. 2018). Similar observations were also made within another perennial crop type. Vineyards composed of a heterogeneous habitat structure with patches of bare ground and vegetation were also identified as important foraging habitats for the woodlark in Switzerland (Schaub et al. 2010; Arlettaz et al. 2012).

In summary, our study showed that CTP were characterised by a unique plant-species community differing from the most widespread habitats within the low-mountain range of the Hochsauerland. In contrast to grasslands, non-native coniferous forests and windthrows, CTP were characterised by a higher number of ruderal species due to regular disturbance by chemical weed control. Furthermore, species resistant to herbicides were favoured within CTP. From a conservation viewpoint, CTP have a low significance for red-list plant species. However, due to the special habitat structure, they play an important role as habitats for threatened animal species. Especially within homogeneous landscapes, such as the study area, CTP increase species richness at the landscape level due to their unique plant-species composition.

Implications for management

With respect to this study on phytodiversity and previous findings on animal communities (Bagge et al. 2012; Fartmann et al. 2018) it is a challenge to define a suitable management strategy that fosters both flora and fauna in CTP. Our study on plant-species richness showed that herbicide application represses less competitive species, reduces overall species richness and promotes ruderal and herbicide-tolerant species such as *E. ciliatum*. Alternative methods for weed control are (1) grazing by Shropshire sheep which is often carried out within organically managed CTP (SSBA 2008; Maurer 2014) and (2) mechanical removal of weeds by mowing, mulching, milling or the application of plastic foliar (Matschke 2005; Sæbø et al. 2009). Grazed plantations are typically sown and characterised by grassland vegetation (own observation). However, detailed studies on the effects of grazed organically managed CTP on phytodiversity are lacking so far.

In other perennial crop systems like vineyards, positive effects on plant-species richness were found within organically managed sites with mechanical weed control compared to conventional sites where herbicides were applied (Nascimbene et al. 2012; Puig-Montserrat et al. 2017). However, all mechanical techniques for weed removal are labour-intensive and costly. Mowing, mulching and milling would, additionally, increase the nest loss in ground-nesting birds (Fartmann et al. 2018). Moreover, on milled sites, soil erosion rates are likely to rise after heavy rainfall on the inclined slopes.

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Within large-scale plantations where herbicide treatment is still the most practical option for weed control, we recommend the reduction of herbicide use as far as possible, e.g. by the cessation of herbicide application along the plantation fences and tramlines for reducing chemical inputs into the environment. However, within plantations that serve as important habitats for threatened bird species dependent on a high proportion of bare ground such as the woodlark, it is essential to conserve the preferable habitat structure.

New plantations should be implemented preferentially within homogeneous landscapes composed of habitats with low importance for biodiversity. In contrast to non-native spruce forests or improved grasslands, CTP are characterised by a greater landscape diversity as they are composed of parcels with different tree ages and, hence, different habitat structures (Fartmann et al. 2018). Large-scale plantations are essential for promoting threatened bird species such as the woodlark. However, for promoting plant-species diversity in CTP, we recommend the establishment of CTP on smaller spatial scales combined with low land-use intensity (especially low herbicide usage). In general, the establishment of CTP should be avoided on windthrows as these habitats are characterised by a high structural heterogeneity and play an important role for nature conservation. They do not only promote a relatively high plant-species richness, but also function as important habitats for threatened bird species (Fartmann et al. 2018).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Appendix

See Table 4.

Table 4 Overview of intercorrelations (Spearman correlation coefficient $|r_s|>0.6$) of environmental variables (soil and habitat-structure characteristics) excluded from NMDS ordination

Excluded variable	Intercorrelated variable	r_s	P
Shrub-layer cover	Herb-layer height	0.70	***
Grass cover	Herb-layer cover	0.72	***
	Stones/gravel	−0.69	***
Bare ground	Stones/gravel	0.62	***
Phosphorus content	Litter	−0.61	***
	Potassium content	0.70	***

***$P<0.001$

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