

# Short Rotation Coppice (SRC) Plantations Provide Additional Habitats for Vascular Plant Species in Agricultural Mosaic Landscapes

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Published online: 13 April 2012

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**Abstract** Increasing loss of biodiversity in agricultural landscapes is often debated in the bioenergy context, especially with respect to non-traditional crops that can be grown for energy production in the future. As promising renewable energy source and additional landscape element, the potential role of short rotation coppice (SRC) plantations to biodiversity is of great interest. We studied plant species richness in eight landscapes (225 km<sup>2</sup>) containing willow and poplar SRC plantations (1,600 m<sup>2</sup>) in Sweden and Germany, and the related SRC  $\alpha$ -diversity to species richness in the landscapes ( $\gamma$ -diversity). Using matrix variables, spatial analyses of SRC plantations and landscapes were performed to explain the contribution of SRC  $\alpha$ -diversity to  $\gamma$ -diversity. In accordance with the mosaic concept, multiple regression analyses revealed number of habitat types as a significant predictor for species richness: the higher the

habitat type number, the higher the  $\gamma$ -diversity and the lower the proportion of SRC plantation  $\alpha$ -diversity to  $\gamma$ -diversity. SRC plantation  $\alpha$ -diversity was 6.9 % ( $\pm 1.7$  % SD) of species richness on the landscape scale. The contribution of SRC plantations increased with decreasing  $\gamma$ -diversity. SRC plantations were dominated more by species adapted to frequent disturbances and anthropo-zoogenic impacts than surrounding landscapes. We conclude that by providing habitats for plants with different requirements, SRC  $\alpha$ -diversity has a significant share on  $\gamma$ -diversity in rural areas and can promote diversity in landscapes with low habitat heterogeneity and low species pools. However, plant diversity enrichment is mainly due to additional species typically present in disturbed and anthropogenic environments.

**Keywords** Agriculture · Biodiversity · Bioenergy · Poplar (*Populus*) · Structural heterogeneity · Willow (*Salix*)

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## Introduction

Against the background of global biodiversity loss largely caused by intensive agriculture [1–5], the diversity of entire agricultural landscapes, the  $\gamma$ -diversity, is of great research interest. The  $\gamma$ -diversity addresses the species diversity of a landscape with more than one kind of natural community, and it includes the diversity within ( $\alpha$ -diversity) and among communities ( $\beta$ -diversity, terminology of Whittaker [6]). Unlike species richness, species diversity takes the proportional abundances of species into account [7]. Many scientific papers address the question of the importance of structural heterogeneity in agricultural landscapes and agree that landscape heterogeneity is beneficial for biodiversity [i.e. 8–12]. According to Forman [13], a matrix of large patches of plant communities supplemented with small patches scattered throughout the

landscape characterizes an optimum landscape as small patches provide different benefits for biodiversity compared to large patches.

The cultivation of bioenergy crops as renewable energy source is debated widely [cf. 14–17]. To reach the EU target of producing 20 % of the primary energy consumption from renewable energies in the year 2020, vast areas of land will be necessary for energy crop cultivation [18–20] for biomass production to be a promising option [i.e. 14, 21]. The large areas needed and economic cost of transporting raw biomass material to end-use locations raise concerns about large-scale biomass crop monocultures [18]. Short rotation coppice (SRC) plantations are perennial lignocellulosic energy crops with high biomass yields; they are expected to play a major role (together with perennial grasses like miscanthus, reed canary grass and giant reed) in increasing the amount of renewable energy from biomass in Europe [22, 23]. The potential contribution of SRC plantations to biodiversity as an additional landscape element in agricultural areas is described in various studies [e.g. 24–33], which reported predominantly positive effects.

The aim of our study is to analyse the suitability of SRC characteristics and landscape matrix characteristics for predicting the contribution of  $\alpha$ -diversity of SRC plantations to vascular plant  $\gamma$ -diversity in fragmented agricultural landscapes. As an alternative to the equilibrium theory of island biogeography by MacArthur and Wilson [34] and Duelli [35, 36] developed the mosaic concept for agricultural landscapes claiming habitat variability (number of biotope types per unit area), habitat heterogeneity (number of habitat patches and ecotone length per unit area) and the proportional area of natural (untouched), semi-natural (perennial vegetation or cultures with low input) and intensely cultivated areas (mainly annual crops and monoculture plantations) as the most suitable factors for predicting biodiversity of an agricultural mosaic landscape. Evidence for this theory was found by Simmering et al. [11]: while at the patch scale, habitat type, area and elongated shape were the main determinants of plant species richness, non-linear habitat richness, the gradient from anthropogenic to semi-natural vegetation and the proportions of natural vegetation and rare habitats were predictors for species richness at the multi-patch (1 ha each) scale, in a highly fragmented agricultural landscape in central Germany. A positive relationship between vascular plant species richness, number of habitat types and habitat patches per area was also found by Waldhardt et al. [12].

The plant species richness of willow and poplar SRC plantations smaller than 10 ha and grown for biomass energy was related to  $\gamma$ -diversity of the corresponding five Swedish and three German landscapes. In reference to the mosaic concept [35, 36], we explore the hypotheses that the share of SRC plantation  $\alpha$ -diversity on  $\gamma$ -diversity depends on (1) landscape structure and (2)  $\gamma$ -diversity itself. In

contrast to landscapes with homogenous structures, we expect a higher  $\gamma$ -diversity but lower SRC plantation  $\alpha$ -diversity in areas with heterogeneous structures characterized by high numbers of habitats and habitat patches with long edges. Further, we expect a higher  $\gamma$ -diversity in areas with higher proportions of semi-natural vegetation and rare habitats, and a higher SRC plantation  $\alpha$ -diversity share in species-poorer landscapes than in species-richer ones.

## Material and Methods

### Study Areas and Sites

Our survey on plant species diversity was conducted on eight landscapes of 15×15 km, corresponding to 225 km<sup>2</sup> surface area. Five areas were located in Central Sweden in the Uppland province and three in Northern Germany in the states of Brandenburg (one study area) and Lower Saxony (two study areas). We selected study areas (landscapes) in which SRC plantations were a representative element. Within each landscape, we chose one or several SRC plantations of 1 to 10 ha, and we delimited the landscapes so that the SRC plantations were situated centrally. We chose SRC plantations for which we had sufficient information regarding plant material and management history. The SRC plantations contained mainly willow clones but also poplars of various ages and rotation regimes. Former land uses also varied (for further descriptions of SRC study sites see Table 1). Due to overlaps with another research project we used four landscapes in which two SRC plantations each were considered (SRC study sites Franska/Kurth, Hjulsta, Lundby), and one landscape in which three SRC plantations were regarded (study sites Bohndorf I, II and III). The SRC plantations located in the same landscape cannot be considered independently in statistical analyses. Thus, we used mean species numbers, shoot ages and plantation ages for SRC plantations located in the same landscape.

The Swedish sites were exposed to lower temperatures and received less precipitation than the German sites: mean annual temperature was about 5.5 °C for the Swedish study sites and 8.5 °C for the German sites. During the growing season (May–September) mean monthly temperature was 13.5 °C for the Swedish and 15 °C for the German sites. Annual precipitation was about 530 mm (monthly mean during the growing season: 55 mm) for the Swedish sites and about 640 mm (monthly mean during the growing season, 60 mm) for the German sites (data bases: long-term recordings from 1961 to 1990 [37, 38]).

The Swedish study sites were characterized by cohesive soils with high clay content. The bedrock is predominantly granite and gneiss. Sand deposits, which were covered with sandy soils, were the prevailing parent material at the German

**Table 1** Overview of the SRC study sites

Landscape	SCR site	Country	Geographical location N E	Size (ha)	Estab. No.	Rot. No.	Last harvest	Sampled crops	Previous land use
Åsby (AS)	Åsby	S	59°59'07" 17°34'57"	8.2	1996	4	2008	Willow: 'Tora'	Arable land
Bohndorf (BD)	Bohndorf I	D	53°10'33" 10°38'52"	1.2	2006	2	2009	Willow: 'Tordis', 'Inger'	Grassland
Bohndorf (BD)	Bohndorf II	D	53°10'31" 10°37'53"	1.5	2008	1	–	Willow: 'Tordis'	Grassland
Bohndorf (BD)	Bohndorf III	D	53°10'18" 10°37'37"	1.7	2007	1	–	Willow: 'Tordis'	Grassland
Cahnsdorf (CD)	Cahnsdorf	D	51°51'30" 13°46'05"	1.6	2006	2	2008	Poplar: 'Japan 105'	Arable land
Djurby (DJ)	Djurby	S	59°41'20" 17°16'34"	2.3	1990	5	2006	Willow: 'L78101', 'L78021'	Arable land
Franska/Kurth (FK)	Franska	S	59°49'10" 17°38'28"	0.7	1994	5	2007	Willow: 'Anki', 'Astrid', 'Bowles Hybrid', 'Christina', 'Gustaf', 'Jorr', 'Jorun', 'Orm', 'Rapp', 'Tora', 'L78021'	Arable land
Franska/Kurth (FK)	Kurth	S	59°48'29" 17°39'25"	1.2	1993	4	2007	Willow: 'L81090', 'L78021'	Arable land
Hamerstorf (HT)	Hamerstorf	D	52°54'36" 10°28'06"	3.2 <sup>a</sup>	2006	1	–	Poplar: 'Hybrid 275', 'Max 4', 'Weser 6'; Willow: 'Tora', 'Tordis', 'Sven', '1 unknown'	Grassland ( <i>Populus</i> ), arable land ( <i>Salix</i> )
Hjulsta (HS)	Hjulsta I	S	59°31'55" 17°03'00"	3.0	1995	4	2008	Willow: 'Jorr'	Arable land
Hjulsta (HS)	Hjulsta II	S	59°32'01" 17°02'54"	6.2	1995	4	2008	Willow: 'Jorr'	Arable land
Lundby (LB)	Lundby I	S	59°40'42" 16°57'18"	1.2	1995	3	2005	Willow: 'L78021'	Arable land
Lundby (LB)	Lundby II	S	59°40'44" 16°57'43"	9.5	2000	2	2005	Willow: 'Tora'	<i>Salix</i> (died), before 1995: arable land

D Germany, S Sweden

<sup>a</sup> *Populus*, 2.1; *Salix*, 1.8 ha

sites. The landscape structure is described in the result section under the subheading “Landscape structure and the landscape SRC diversity effect on  $\gamma$ -diversity”.

### Spatial Analyses

Spatial analyses were conducted to test how SRC plantations contribute to species diversity of the surrounding landscape and to look for structural elements that are indicative for the SRC contribution to landscape  $\gamma$ -diversity. The spatial scale  $\gamma$ -diversity referred to is not explicitly defined [7, 39], but Whittaker [40] distinguished  $\gamma$ -diversity (species diversity of a landscape comprising more than one community type) from  $\epsilon$ -diversity that describes the diversity of geographical areas across climatic or geographic gradients. The reference area for  $\gamma$ -diversity is about 100 km<sup>2</sup>, but for  $\epsilon$  diversity it is about 10<sup>6</sup> km<sup>2</sup> [41]. We defined the landscape scale in terms of areas of 225 km<sup>2</sup> for the evaluation of  $\gamma$ -diversity, and those areas were overlaid with CORINE (Coordinated Information on the European Environment) Land Cover data [42]. The availability of those data for both Sweden and Germany enabled us to evaluate structural landscape attributes on the same database. Base year for the land cover data was 2006. CORINE provides land cover data on three different levels [42]. Higher levels cumulate land cover classes of the lower level. The broadest classification is ‘level 1’ distinguishing the five land cover classes ‘Artificial surfaces’, ‘Agricultural areas’, ‘Forest and semi-natural areas’, ‘Wetlands’ and ‘Water bodies’. All five classes of level 1 were present in our study areas. Twelve classes were present on level 2 and 21 on level 3 (Table 1).

### Floristic and SRC Vegetation Assessment

For comparing SRC vegetation data with the diversity of the higher landscape scale, species lists from the nation-wide German floristic mapping [43] and region-wide Swedish mapping (for the province of Uppland) [44] were used. The data were provided by the German Federal Agency for Nature Conservation (BfN) and by the Swedish Species Information Centre (ArtDatabanken, SLU) for 5 × 5-km map excerpts. Nine map excerpts—one with the SRC in the centre, and eight bordering map excerpts—were used to determine the reference areas for the higher landscape scales

in order to avoid any SRC being located close to the margin of the map area. The entire set of maps encompassed approximately 225 km<sup>2</sup> area (15 × 15 km). Flora species lists were simplified to species level to avoid overestimations.

SRC vascular plant species abundance was recorded in 2009 from May until July in Germany and from July until August in Sweden. At each SRC site, the species in 1,600 m<sup>2</sup>, corresponding to 144 plots of about 11 m<sup>2</sup> size, were assessed in four 400 m<sup>2</sup> areas (20 × 20 m). For each plot a species list was compiled. The nomenclature follows Rothmaler [45].

### Data Analysis

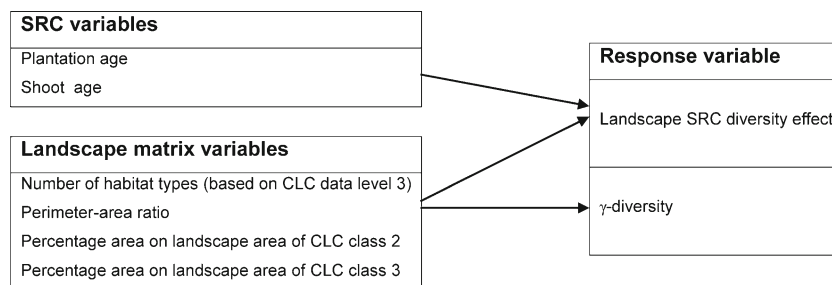
In a first step, species–area curves from SRC vegetation mappings were calculated to determine the minimum area for representative species numbers [46] and to test the representativeness of our 1,600 m<sup>2</sup> plots for deriving SRC plantation  $\alpha$ -diversity values. For all area units (one plot to 144 plots), species numbers of all possible plot permutations [cf. 47] were calculated and averaged per unit area by EstimateS 8.2.0 [56].

In a second step, the relationship between the SRC diversity and the  $\gamma$ -diversity was investigated. A linear positive relationship would indicate that the share of SRC diversity on  $\gamma$ -diversity does not change with increasing  $\gamma$ -diversity. The contribution of SRC plantation  $\alpha$ -diversity to plant  $\gamma$ -diversity of the surrounding landscapes, defined here as ‘landscape SRC diversity effect’, was calculated by Eq. 1 where  $\alpha$ -diversity is the species number recorded in 1,600 m<sup>2</sup> SRC plantation, and  $\gamma$ -diversity is the species number found on landscape scale (225 km<sup>2</sup>).

$$\text{landscape SRC – diversity effect} = \frac{\alpha - \text{diversity}}{\gamma - \text{diversity}} \quad (1)$$

Linear regression analysis and test of homoscedasticity of residuals was applied using  $\gamma$ -diversity as predictor variable and landscape SRC diversity effect as response variable. To determine whether SRC variables and landscape matrix variables were significant predictors of the ‘landscape SRC diversity effect’ and of ‘ $\gamma$ -diversity’ (landscape matrix variables only, Fig. 1), multiple regression analysis was conducted. For the response variable ‘ $\gamma$ -diversity’, Poisson regression for count data was used (procedure PROC GENMOD, SAS 9.2)

**Fig. 1** SRC variables and landscape matrix variables included in multiple regression analyses for the response variables ‘landscape SRC diversity effect’ and ‘ $\gamma$ -diversity’. *CLC class 2* agricultural areas, *CLC class 3* forest and semi-natural areas



and overdispersion was corrected by Pearson’s  $\chi^2$ . The landscape matrix variable ‘perimeter–area ratio’ ( $P$ : perimeter,  $A$ : patch area, cf. [48]) was calculated by Eq. 2:

$$P/A = \sum_{i=1}^m P_i / \sum_{i=1}^m A_i \tag{2}$$

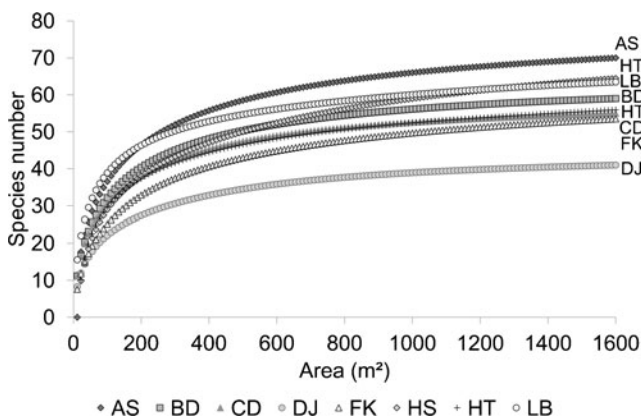
The decision on the best-fitted model was based on the Akaike information criterion (AIC), in which a smaller value indicates a better fit of a model. However, the AIC does not provide information on the absolute model fit, i.e. its significance has to be tested. Inter-correlations among explanatory variables were investigated with Pearson’s product moment correlation. Since no significant correlations were found (significance level:  $p < 0.05$ ), multiplicative interactions were not included in multiple regression analysis.

To compare landscape SRC diversity effect and  $\gamma$ -diversity, the plants were assigned to plant communities according to Ellenberg et al. [49]. The Shapiro–Wilk test was applied to test the proportions of plant communities for normal distribution. For normally distributed data the  $t$  test was applied to compare plant community proportions of SRC plantations with those of the landscape. For data not normally distributed the non-parametric Mann–Whitney  $U$  test (two-sided) was chosen.

**Results**

**Representativeness of SRC Vegetation Samplings and Its Relationship to Landscape  $\gamma$ -Diversity**

The species–area curves validated our sample size of 1,600 m<sup>2</sup> per SRC plantation as suitable for comparisons with the  $\gamma$ -diversity (Fig. 2). The increase in species number with area size slowed down rapidly from area sizes above



**Fig. 2** Species–area curves of the SRC plantations. All possible permutations of the 144 plots per SRC plantation were calculated and averaged per area unit (1 plot=11.11 m<sup>2</sup>). Abbreviations of SRC plantation names see Table 1

approximately 200–300 m<sup>2</sup> sampled area. At areas between circa 600 and 1,000 m<sup>2</sup>, 90 % of the species recorded in 1,600 m<sup>2</sup> were detected. As the sample size is representative, SRC plantation size was excluded from multiple regression analysis.

No linear relationship was found for SRC  $\alpha$ -diversity vs. landscape  $\gamma$ -diversity ( $R^2=0.16, p=0.3290$ , Fig. 3a) indicating a variable contribution of SRC diversity to landscape diversity with increasing  $\gamma$ -diversity.

**Landscape Structure and the Landscape SRC Diversity Effect on  $\gamma$ -Diversity**

All study areas were dominated by non-irrigated arable land (34–58 % land cover) and coniferous forests (19–31 % land cover, Table 2). With the exception of 30 % water body cover at study area Hjulsta and 10 % cover of discontinuous urban fabric at study area Franska/Kurth, the proportion of all other land cover was below 8 %. The number of habitat types in the study areas ranged from 10 to 16 (CORINE land cover (CLC) data level 3) for 110 to 139 habitat patches. No relationship between number of habitats and number of habitat patches was found.

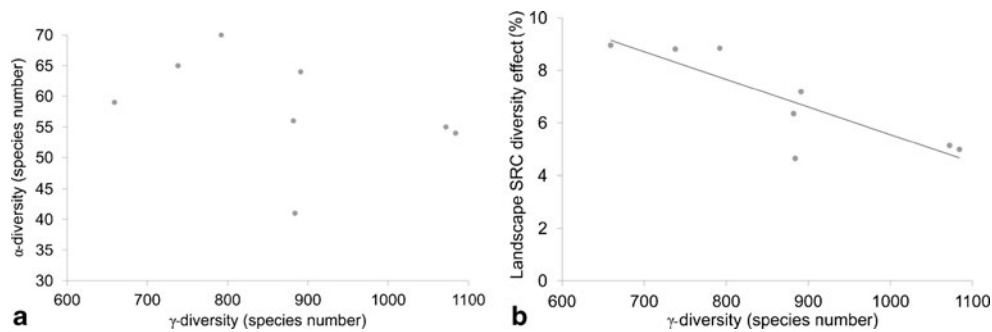
The species number for landscape ( $\gamma$ -diversity) ranged from 659 to 1,084 (Table 3). The SRC plantations encompassed 41 to 70 species. The species proportion of 1,600 m<sup>2</sup> SRC plantations on 225 km<sup>2</sup> of the surrounding landscape varied between 4.6 and 9.0 % (mean,  $6.9 \pm 1.7$  % standard deviation). The lower the species number of the landscape, the higher was the landscape SRC diversity effect (Fig. 3b,  $R^2=0.72, p=0.0077$ ).

**Explanatory Variables on  $\gamma$ -Diversity and Landscape SRC Diversity Effect**

The significant model with the best AIC value was the one including all four landscape matrix parameters (Table 4), whereas only the number of habitat types influenced  $\gamma$ -diversity significantly (Table 5). The  $\gamma$ -diversity increased with increasing number of habitat types.

Multiple regression models with the response variable ‘landscape SRC diversity effect’ were calculated for all possible combinations of the variables: SRC plantation age, SRC shoot age, number of habitat types, perimeter–area ratio, percentage area CLC class 2, and percentage area CLC class 3. Two models were significant ( $p < 0.05$ ) and the ‘landscape SRC diversity effect’ was best explained by the model including the number of habitat types and the SRC shoot age (Table 6). Both the number of habitat types and the SRC shoot age were negatively related to the ‘landscape SRC diversity effect’ but this was only significant for the number of habitat types (Table 7, overall model:  $R^2=0.71, p=0.0459$ ). Linear regression analysis resulted in an increasing ‘landscape SRC





**Fig. 3** Relationship of  $\alpha$ - and  $\gamma$ -diversity: **a** scatterplot of SRC species number ( $\alpha$ -diversity) and landscape species number ( $\gamma$ -diversity) and **b** linear regression analysis of the landscape SRC diversity effect on  $\gamma$ -

diversity (%) vs.  $\gamma$ -diversity.  $R^2=0.72$ ,  $p=0.0077$ . Regression equation:  $y=-0.0105x+16.08$ . Area SRC plantations, 1,600 m<sup>2</sup>; area landscapes, 225 km<sup>2</sup>;  $N=8$

**Table 2** CORINE land cover levels and land cover proportions of the study landscapes

CLC code	CLC level 1	CLC level 2	CLC level 3	AS	BD	CD	DJ	FK	HS	HT	LB
111	Artificial surfaces	Urban fabric	Continuous urban fabric					1		<0.5	
112	Artificial surfaces	Urban fabric	Discontinuous urban fabric	2	2	4	1	10	<0.5	6	3
121	Artificial surfaces	Industrial, commercial and transport units	Industrial or commercial units			1		4		1	1
122	Artificial surfaces	Industrial, commercial and transport units	Road and rail networks and associated land	1			1	1		<0.5	<0.5
124	Artificial surfaces	Industrial, commercial and transport units	Airports			<0.5				<0.5	
131	Artificial surfaces	Mine, dump and construction sites	Mineral extraction sites	<0.5	<0.5	<0.5					
133	Artificial surfaces	Mine, dump and construction sites	Construction sites	<0.5		<0.5					
141	Artificial surfaces	Artificial, non-agricultural vegetated areas	Green urban areas			<0.5		1		<0.5	<0.5
142	Artificial surfaces	Artificial, non-agricultural vegetated areas	Sport and leisure facilities	<0.5	<0.5	<0.5	<0.5	1			<0.5
211	Agricultural areas	Arable land	Non-irrigated arable land	57	56	55	58	35	34	46	57
231	Agricultural areas	Pastures	Pastures	1	3	10	2	1	1	3	2
242	Agricultural areas	Heterogeneous agricultural areas	Complex cultivation patterns	<0.5	<0.5		<0.5	1	1	2	<0.5
243	Agricultural areas	Heterogeneous agricultural areas	Land principally occupied by agriculture, with significant areas of natural vegetation	1	3	4	1	2	1	4	2
311	Forest and semi-natural areas	Forests	Broad-leaved forest		3	1	<0.5	1	2	2	
312	Forest and semi-natural areas	Forests	Coniferous forest	26	31	19	25	31	20	31	29
313	Forest and semi-natural areas	Forests	Mixed forest	3	1	1	1	3	7	5	1
324	Forest and semi-natural areas	Scrub and/or herbaceous vegetation associations	Transitional woodland-shrub	6		1	5	3	3		3
333	Forest and semi-natural areas	Open spaces with little or no vegetation	Sparsely vegetated areas			1					
411	Wetlands	Inland wetlands	Inland marshes			1	1		<0.5		<0.5
511	Water bodies	Inland waters	Water courses					<0.5			
512	Water bodies	Inland waters	Water bodies	1			2	8	30		

**Table 3** Diversity of landscapes ( $\gamma$ -diversity, 225 km<sup>2</sup>) and SRC plantations (1,600 m<sup>2</sup>)

Country	Area and SRC site	Species numbers		Landscape SRC Diversity effect (%)
		SRC	Landscape	
S	Åsby	70	792	8.8
D	Bohndorf	59	659	9.0
D	Cahnsdorf	55	1,072	5.1
S	Djurby	41	884	4.6
S	Franska/Kurth	54	1,084	4.9
D	Hamerstorf	56	882	6.3
S	Hjulsta	65	738	8.7
S	Lundby	64	891	7.1

D Germany, S Sweden

diversity effect' with decreasing number of habitat types ( $R^2=0.60, p=0.0242$ ).

**Plant Communities**

The SRC plantations had a higher proportion of species assigned to plant communities of frequently disturbed and anthropo-zoogenic habitats than landscape species pools. The proportion of species in the plant communities 'herbaceous vegetation of frequently disturbed areas' and 'anthropo-zoogenic heathlands and lawns' was greatest in both the landscape species pools and the SRC plantations (Fig. 4). The greatest difference between plant communities in the landscape species pools and the SRC plantations occurred for the proportion of 'freshwater and bog vegetation' species, which was 14 % in the landscape species pools and almost

**Table 4** Relative goodness-of-fit-test of the multiple Poisson regression models explaining the  $\gamma$ -diversity: only models with significant variables are shown

Number in model	AIC	SBC	Variables in model	Significance
1	58.4212	58.5801	c	sig
2	51.4753	51.7136	cd	c sig
2	51.8684	52.1067	ce	c sig
2	51.4586	51.6969	cf	c sig
3	45.9765	46.2942	cde	c sig
3	45.2899	45.6077	cdf	c sig
3	44.6970	45.0147	cef	c sig
4	39.2852	39.6824	c d e f	c sig

Response variable:  $\gamma$ -diversity (species number)

AIC Akaike information criterion, SBC Schwarz criterion, c number of habitat types, d perimeter–area ratio, e percentage area CLC class 2, f percentage area CLC class 3, Sig. significant

absent in the SRC plantations. 'Deciduous forests and related heathland' species reached 13 % in SRC plantations and 14 % in the landscape species pool. Nineteen percent of the species found in SRC plantations and 8 % of the landscape species pool comprised indifferent species with no real affinity for a particular community. The standard deviations showed that variations between SRC plantations were greater than between landscape species pools.

**Discussion**

**High Landscape SRC Diversity Effect on  $\gamma$ -Diversity**

The results show that  $\alpha$ -diversity of small-scale (<10 ha) SRC plantations (1,600 m<sup>2</sup> in area) can contribute considerably to plant species richness in larger landscapes ( $\gamma$ -diversity, 225 km<sup>2</sup>) accounting for a share of 6.9 % ( $\pm 1.7$  % SD, Table 3) on average. This is in line with Kroihner et al. [31] who found an 8 to 12 % contribution to landscape species richness when comparing similar-sized SRC stands with landscape units nine times smaller (25 km<sup>2</sup>). For other land uses (arable land, forests, fallow and grassland), Simmering et al. [11] also found a similar mean share of 10 % of  $\alpha$ -diversity of different sized patches to  $\gamma$ -diversity, although these findings related to a considerably smaller agricultural area (0.2 km<sup>2</sup> area). The species–area relationship (cf. Fig. 2) indicated a study size of 1,600 m<sup>2</sup> per SRC plantation is representative for this type of analysis. In accordance with our results, Kroihner et al. [31] showed the increase in species slowed down rapidly above 200–400 m<sup>2</sup> sample area for a poplar SRC plantation in central Germany. We conclude that larger SRC plantations of several hectares on homogenous sites will not result in any further increase in plant species richness and their 'diversity effect' over smaller SRC plantations, and probably rather decrease diversity. Therefore, we recommend planting several smaller SRC plantations instead of one large one, i.e. larger than 10 ha, the maximum plantation size studied here. SRC plantations of different ages, rotation regimes and tree species enhance structural diversity providing habitats for species with different requirements and are thus beneficial for species diversity [50, 51].

**Less Species and Habitats in a Landscape Increase the Importance of SRC Plantations for  $\gamma$ -Diversity**

Our study is the first report to show a clear relationship between landscape structure (number of habitat types),  $\gamma$ -diversity and the contribution of SRC plantations to  $\gamma$ -diversity across two European landscapes (Fig. 3, Table 7): In accordance with the mosaic concept [35, 36], the species number for the landscapes increased with increasing number

**Table 5** Multiple Poisson regression analysis: results of the effect of landscape matrix variables on  $\gamma$ -diversity

Analysis of maximum likelihood parameter estimates							
Parameter	DF	Estimate	Standard error	Wald 95 % confidence limits		Wald $\chi^2$	Pr> $\chi^2$
Intercept	1	5.9413	0.4992	4.9629	6.9197	141.65	<.0001
Number habitat types	1	0.0820	0.0130	0.0565	0.1074	39.82	<.0001
P/A ratio	1	-0.0069	0.0143	-0.0350	0.0212	0.23	0.6295
(%) CLC 2	1	-0.0011	0.0025	-0.0059	0.0038	0.18	0.6695
(%) CLC 3	1	0.0022	0.0072	-0.0118	0.0162	0.09	0.7596
Scale	0	1.6182	0.0000	1.6182	1.6182		

The scale parameter was estimated by the square root of Pearson's  $\chi^2$ /DOF

*P/A ratio* perimeter–area ratio, (%) *CLC* percentage surface on landscape area covered by CLC class, *CLC class 2* agricultural areas, *CLC class 3* forest and semi-natural areas

of habitat types. The more diverse the landscapes and the higher the number of habitat types, the lower was the share of SRC plantations on vascular plant  $\gamma$ -diversity. This indicates that SRC plantations are most beneficial for flora diversity in rural areas with low habitat type heterogeneity, by providing habitats suitable for many species.

Unlike Poggio et al. [52], who analysed the relationship between the quotient perimeter/area and  $\gamma$ -diversity in cropped fields and edges, we found no increasing diversity with increasing landscape complexity expressed by the perimeter-to-area ratio. Edges between biotope types often contain a rich flora and fauna [13, 36], so that smaller mosaic patches with their comparatively longer ecotones enhance biodiversity of a landscape [36]. Wagner and Edwards [53] showed edges of arable fields and narrow habitats contributing more to species richness than the interior of arable fields and meadows. However, the species present at the edges are intermixed subsets of the adjacent plant communities, and only few species are expected to be present only at edges [13]. We speculate that land cover data on a greater scale than CORINE land cover could provide further information on the relationships between diversity and patch sizes as well as edge lengths. Our results do not confer with one hypothesis of the mosaic concept which claimed the surface proportions of natural, semi-natural and intensely cultivated areas influenced biodiversity, which was also confirmed by Simmering et al. [11]. The landscapes studied here were all dominated by non-irrigated

arable land and coniferous forests; all other habitat types comprised only very small percentages of land cover. Thus, the landscapes we analysed may be unsuitable for sound exploration of this hypothesis because only few habitat types dominated the landscapes and their land cover percentages were similar for all landscapes.

#### SRC Plantations Increase Habitat Variability on Landscape Scale

Due to our study design we were not able to identify plant species that are exclusively found in SRC plantations, since they were also included in the assessments on landscape scale. However, it could be demonstrated that the SRC stands provide a large habitat variability suitable for species of many different plant communities. This becomes apparent particularly when considering the large difference in area between SRC plantations and the landscapes regarded (cf. Fig. 4): three plant communities each contained more than 10 % of the species present (19 % species had no real affinity for a particular community), whereas, in the landscape species pools, the percentage species of four communities accounted for more than 10 %. The SRC plantations species composition differs greatly from other land uses common in agricultural landscapes. This was shown by Baum et al. [54] who compared species diversity of arable lands, forests and grasslands and found that species composition of SRC plantations differed especially from arable lands and coniferous forests. SRC

**Table 6** Relative goodness-of-fit of the multiple regression models explaining the 'landscape SRC diversity effect': only models with significant variables are shown

Number in model	$R^2$	AIC	SBC	Variables in model	p model
1	0.60	5.403	5.56185	SRC shoot age	0.0242
2	0.71	4.8601	5.09839	SRC shoot age, number of habitat types	0.0459

*AIC* Akaike information criterion, *SBC* Schwarz criterion



**Table 7** Parameter estimates of multiple regression analysis modelling the influence of the number of habitat types and the SRC shoot age on the ‘landscape SRC diversity effect’

Variable	Estimate	Standard error	Pr> t
Intercept	16.347	2.846	0.0022
Number habitat types	−0.646	0.213	0.0291
SRC shoot age	−0.513	0.375	0.2296

Overall model:  $R^2 = 0.71$ ,  $p = 0.0459$

plantations can contribute to landscape diversity by creating new habitats with species composition different from other land uses. Even though SRC plantations are an extensive land use, they contributed mainly to plant diversity by contributing species of disturbed and anthropogenic environments. The proportion of species assigned to plant communities of frequently disturbed and anthro-po-zoogenic habitats was higher in SRC plantations than in the landscape species pools. SRC plantations contain predominantly common species and only few studies report the presence of rare species [cf. 25]. Analyses of Baum et al. [54] have shown that SRC plantation age does not affect species number, but species composition. They found a positive relationship between SRC plantation age and SRC tree cover along with a decrease in grassland species proportion and an increase in woodland species proportion. Considering this temporal habitat heterogeneity promoting light-demanding and ruderal species after SRC establishment and rotation cuttings and woodland species later on, SRC plantations can host many different species groups in comparably small areas. The SRC plantations contain a subset of the landscape species pool that comprises on average a share of 6.9 %, and by creating new habitats with species composition different from other land uses, these plantations have a high value for landscape diversity.

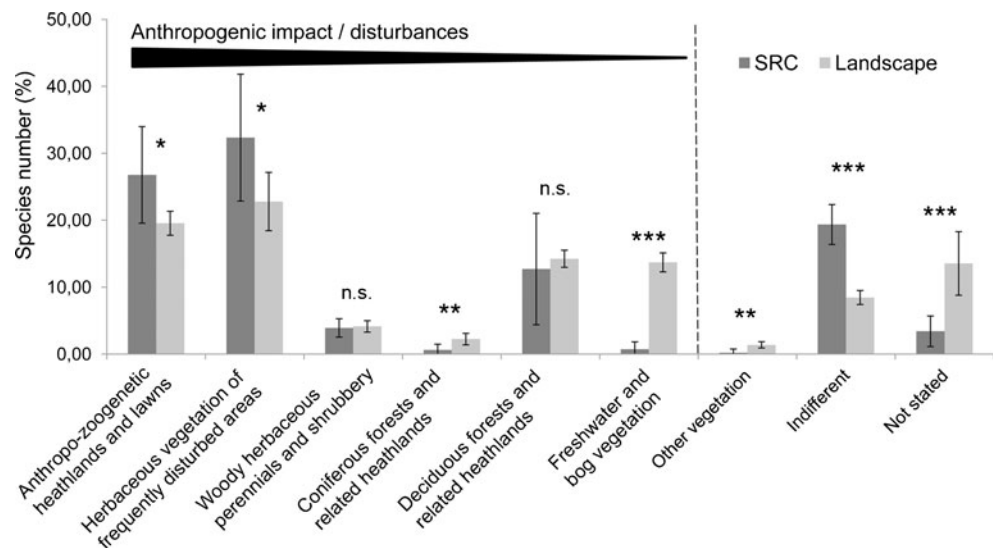
Our results and those of many other authors (cf. introduction) have shown landscape heterogeneity as beneficial for biodiversity. The expected increase in bioenergy crop production in coming years may have negative effects on biodiversity if it results in the establishment of large monocultures [18, 55]. But, by avoiding large monocultures, planting bioenergy crops can also be an opportunity for increasing structural landscape heterogeneity and creating new habitats which enhance biodiversity in current agricultural landscapes, whereby woodland and SRC plantations are especially beneficial [15].

**Conclusion**

Our results show that SRC plantations provide habitats for plants with different requirements and thereby have a significant share on  $\gamma$ -diversity. Therefore, these plantations positively affect species diversity on the landscape scale, in particular in landscapes with lower habitat diversity. The number of habitat types and the species number in a landscape can be used to predict the contribution of SRC plantations to vascular plant diversity in fragmented agricultural landscapes. Especially in rural areas with low habitat type heterogeneity, SRC plantations are beneficial for plant diversity, where plant diversity enrichment is mainly due to the occurrence of additional species present in disturbed and anthropogenic environments.

CORINE land cover data can be used for landscape structure analyses on higher landscape scales. However, on lower scales, restrictions due to low scale of land-use data must be considered in landscape structure analysis in relation to the mosaic concept: edge effects may be neglected of habitats not distinguished by CLC. Further analyses using consistent land cover information in both Sweden and Germany will be useful

**Fig. 4** Mean percentage species proportion assigned to plant communities and standard deviation of the landscapes (225 km<sup>2</sup>,  $N=8$ ) and SRC plantations (1,600 m<sup>2</sup>,  $N=8$ ). Species proportions were not significantly different between landscape and SRC plantation for ‘Woody herbaceous perennials and shrubbery’ ( $p=0.7213$ ) and ‘Deciduous forests and related heathlands’ ( $p=0.6017$ ). Significances: \* $p<0.05$ ; \*\* $p<0.01$ ; \*\*\* $p<0.001$



for further detailed landscape structure analyses of SRC plantation effects on landscapes.

**Acknowledgements** This study was conducted under the framework of the FP7 ERA-Net Bioenergy Project “RATING-SRC” funded by the German Federal Ministry of Food, Agriculture and Consumer Protection (BMELV), the Agency for Renewable Resources (FNR) and the Swedish Energy Agency. We would particularly like to thank Rudolf May from the Federal Agency for Nature Conservation (BfN) and Mora Aronsson from the Swedish Species Information Centre/ArtDatabanken, Swedish University of Agricultural Science (SLU) for providing plant species lists on a higher landscape scale, and also Marianna Holzhausen and Till Kirchner (vTI Eberswalde) for preparing the geographical data. We thank two anonymous reviewers for constructive comments on an earlier version of this paper.

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