

Biodiversity in short-rotation coppice

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ABSTRACT

Although short-rotation coppice (SRC) is a sustainable cultivation technique, biodiversity issues keep policy makers from encouraging farmers to establish SRC. From the 47 reviewed publications of this review 91% reported on poplar or willow SRC, and 63% focused on animal diversity. The α - and β -diversity were most often studied by quantifying species richness and abundance. SRC had a positive effect on fungal diversity, which was negatively correlated to coppice rotation length, due to a higher nutrient demand after coppicing. In comparison with agricultural monocultures SRC provides a higher biodiversity, but it remains lower than that of mixed deciduous forests. Besides the planted genera and species, an understorey of generalist species similar to the previous land use develops and evolves to a forest-like understorey. At every coppice rotation the light availability changes and the planted area evolves from a bare field to a shrub-like vegetation, which later approaches a forest with a closed canopy. These changes in the plant community influence animal diversity. Bird populations similarly evolve from open-space to forest communities, continuously co-existing in shifting ratios. Arthropods and small mammals use the SRC to fulfil all of their habitat needs, while birds and large mammals only use the SRC for a limited number of resources. Recommendations for policy makers and SRC growers are provided, and areas for future research have been identified. It is concluded that introducing well-managed SRCs can enrich biodiversity in an agriculture-dominated landscape, but that SRCs most probably have a negative effect on biodiversity when introduced into a highly forested landscape.

1. Introduction

Governments worldwide are striving to reduce our dependency on fossil fuels by promoting the use of sustainable and renewable energy sources. Most agree that a mix of solar, wind and hydro energy is required, but energy from biomass should be added to this list [1]. Bioenergy has the important advantage that energy can be stored and used when required. Forestry and (agricultural) waste streams will not be able to fulfill the expected increase in biomass demand – this creates an opportunity for biomass harvested from short-rotation coppice (SRC) [2,3]. SRC is a biomass cultivation technique covering the middle ground between forestry and agriculture: fast-growing tree genera such as poplar (*Populus*) and willow (*Salix*) are densely planted in rows and regularly coppiced (2–8 yr coppice rotations) at ground level. As a result biomass and revenue for the grower are generated at the end of each coppice rotation [4]. Biomass from SRC is envisaged as being part of the solution for guaranteeing energy security, while at the same time mitigating climate change [5,6]. Although with current power-generation technology, SRC's contribution is “limited” to fossil fuel

substitution – thereby reducing the net rate of increase of atmospheric CO₂ concentration – with the future development of carbon capture and sequestration technology, SRC has the potential to contribute to the long-term objective of reversing the build-up of atmospheric CO₂ [7].

Despite SRC's expansion potential, the large-scale deployment of SRC is hampered by uncertain productivity figures and persistent misconceptions among growers and the public. Next to the negative perception of burning wood, one of the most headstrong misconceptions about SRC is its allegedly detrimental effect on biodiversity [7–9]. While European forests' standing biomass has increased over the past decades, forest biodiversity has diminished [10] and plantations – amongst others, SRC – are usually seen as a risk to biodiversity [11,12]. However, previous studies and reviews on biodiversity in SRC focused on a (very) narrow range of species or genera and have – thus far – failed to present the complexity inherent to biodiversity and, thus, a complete overview. It is, therefore, timely to assemble the scientific evidence on the dynamics of plant and animal communities in SRC in a comprehensive and up-to-date review of the available data. The insights and evidence from this review can contribute to underpin policies

Abbreviations: α , α -diversity (species level); β , β -diversity (habitat level); γ , γ -diversity (landscape level); ha, hectare; m, metre; SRC, short-rotation coppice; yr, year
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designed to ensure SRC establishment has a positive effect on biodiversity.

2. Database construction

A number of diversity indices at different organisational levels have been quantified for different taxa in SRC. The most common diversity indices are the species richness (= the number of species per unit area) and the abundance (= the number of individuals per species). From these indices, the Shannon-Wiener index [13], the Simpson index [14] and the species evenness [15] can be calculated. The levels at which these indices are calculated are classified as α -, β - and γ -diversity [16]. When the number and/or abundance of species occurring in a specific habitat (i.e., the SRC in this case) are quantified, this refers to the α -diversity. The β -diversity, in turn, reflects the differentiation among habitats, i.e., the difference between SRC and surrounding habitats in the same landscape. Combining the α - and β -diversity generates the γ -diversity, a measure for the total species diversity in a landscape.

An extensive literature survey was conducted to establish a database of research related to biodiversity issues in SRC. Scientific peer-reviewed publications were collected by searching the Web of Knowledge for the terms “SRC” and “diversity”, and by then back-tracking the literature cited in those publications. There was no restriction on the year of publication; the oldest publications dated back to 1978. Only publications in English were considered. Publications on observational data (47) were included in the analysis; although six modelling studies and nine review papers were retrieved, these were omitted from the analysis. Coppicing intervals exceeding eight years were considered too long for SRC and were, therefore, also omitted from further analysis. Internal reports that were neither peer reviewed nor published in open accessible scientific databases were not considered.

3. Results and discussion

An overview of the publications analysed for this review, as well as a summary of the most relevant parameters and findings for each analysed publication have been presented in Table 1. More than half of the studies (33) assessed biodiversity of a willow SRC, while poplar was the second most studied SRC genus (20); other SRC genera were only occasionally reported on (Fig. 1). Together, studies on poplar and on willow SRC made up 91% of all publications in the database (Table 2). The largest number of studies was performed on SRCs in, and equally spread between, the UK (22), the US (22) and Sweden (20; Table 2). The remaining SRCs were mainly situated in Germany, Belgium and Italy (Fig. 1).

The majority of studies (63%) reported on animal diversity (mainly arthropods and birds), followed by plants (i.e., excluding the planted SRC species, except for one; 22%) and fungi (12%) (Fig. 1, Table 2). Few publications specifically studied the integration of SRC into the landscape (γ -diversity), while mostly the α - (biodiversity within an SRC) and β -diversity (in comparison to other land uses) were quantified (Table 2). Overall, species richness and species abundance were both studied in almost half of the publications (44%), while alternative indices were examined in less than 7% of the publications (Table 2).

3.1. Fungal diversity

Studies on the fungal diversity of SRCs are limited to (ecto)mycorrhizae, with a symbiotic relationship between a fungus and the plant roots. Mycorrhizae facilitate nutrient uptake by the plant, thereby increasing the plant's aboveground biomass growth. This implies that mycorrhizae also enhance the phytoremediation potential of SRC by improving the uptake of pollutants from contaminated soils [62,63]. Beside several physical site conditions, the fungal species colonising a specific root system depends on the host plant genotype and the management of the SRC.

Mycorrhizal fungi are host species-specific: in general, *Glomus*, *Laccaria* and *Scutello* spp. are more symbiotic with poplar SRC [62], while *Cortinarius*, *Hymenogaster* and *Hebeloma* spp. as well as several Russulales genera are more specific to willow SRC [21]. Furthermore, mycorrhizal communities differ between willows grown as SRC and (adjacent) natural stands: fungal genera *Tomentella*, *Tuber* and *Geospora* spp. prefer the latter one [21]. The low (aerial) spore dispersal potential is a possible limitation to the colonisation of new areas within or outside the SRC [21,22].

While every management intervention most likely influences the mycorrhizal community, only the effect of coppicing on mycorrhizal colonisation has been investigated for SRC. Shorter rotations positively affect mycorrhizal formation and root colonisation of the SRC species [20] and co-occurring plant species in the understorey [19]. Short rotations (1–2 yr) promote fungal genera *Laccaria*, *Peziza* and *Tuber* spp., while *Inocybe* and *Sclerotinia* spp. are promoted by longer coppicing intervals (3–4 yr) [20]. One possible explanation is that an increased demand for mineral nutrients is signalled to the roots upon coppicing, thereby stimulating mycorrhizal growth [20]. Another explanation is that plant-fixed carbon is reduced by coppicing, thereby reducing the potential mycelium expansion and enhancing mycelium growth from spores [19].

The combination of a host species preference with the major influence of the SRC management regime results in large differences between mycorrhizal communities associated with SRC and agricultural land. Probably due to the improved soil quality, the mycorrhizal community was richer after several rotations in a 10-yr old poplar SRC in Italy as compared to intensively managed or uncultivated systems [17,19]. The higher fungal species richness and abundance under SRC might reflect a lower risk of nutrient losses and imply a more sustainable soil management as compared to common agricultural practices [19].

3.2. Plant diversity

Before the establishment of an SRC the soil is ploughed, and frequently fertiliser and/or herbicide treatments are applied [64]. After a bare, ploughed soil is prepared for the SRC, different plant types are introduced by man and nature. The SRC grower introduces the SRC plants at a high density in a regular planting design, while seeds and rhizomes already present in the seed bank spontaneously germinate. Other seeds find their way to the SRC by natural dispersion. Some added value to biodiversity can also be arranged by managing the stand edges.

3.2.1. Introduced vegetation

3.2.1.1. Planted material. The most obvious biodiversity of an SRC consists of the planted material itself. In general, operational SRCs are established with commercially available genotypes, usually pure species and hybrids of the genera *Populus* and *Salix*, or in a few publications/studies from the genera *Eucalyptus* and *Robinia*. Commonly, species from only one genus or different genotypes from one species are used in any SRC. SRC growers face a trade-off when deciding upon the number of genotypes to plant when establishing an SRC. A homogeneous feedstock – achieved with homogeneous planting material – is preferred for efficient handling by SRC coppice machinery; the ideal would be reducing the genotypic diversity to one genotype only [65]. This also guarantees a very homogeneous end-product, as is preferred for industrial use. On the other hand, selecting only one genotype for an entire SRC increases the risk of massive field losses due to unfavourable genotype-environment interactions [64,66], pests (see Section 3.3.3 for a discussion on beetles) and diseases [67] on the susceptible genotype.

In practice, a mixture of genotypes is usually planted [68]. Diversity in planting material generates diversity in the morphology of shoots, branches and leaves, leading to more structural niches and increased

Table 1

Database of the 47 peer-reviewed publications containing observational data on biodiversity in short-rotation coppice (SRC). The taxonomic group studied, the SRC genus studied and the country in which the study was carried out, the level of diversity (α -, β -, γ -diversity), variables and diversity indices studied, as well as the main conclusions from each publication are presented.

Taxonomic group	SRC genus	Country	Level	Variable	Diversity index	Main conclusions	Ref
Bacteria Mycorrhizae Plants Arthropods Earthworms Round worms Microbes	Willow	Belgium	β	Agricultural land Energy grass	Species richness Abundance Ellenberg	Arable land < SRC	[17]
Mycorrhizae	Willow	Belgium	β	Grassland	Abundance	Grassland < SRC	[18]
Mycorrhizae	Poplar	Italy	α	Coppicing	Abundance	Coppicing positively affected mycorrhizae	[19]
			β	Agricultural land Fallow land	Species richness		
Mycorrhizae	Poplar	Germany	α	Coppice rotation length	Species richness	Coppicing favoured mycorrhizae formation	[20]
Mycorrhizae	Willow	Sweden	β	Natural stands	Species richness Abundance	Different taxa in SRC and natural stands	[21]
Mycorrhizae	Willow	UK	α	Temporal variation Spatial variation	Abundance	Temporal and geographical variation Influenced by pH	[22]
Mycorrhizae Earthworms	Willow	France	β	Agricultural land Grassland Natural stands	Species richness Abundance Shannon-Wiener	Arable land < SRC SRC < grassland SRC < natural stands	[23]
Plants	Alder	Sweden	α	Fertilisation	Species richness	Disruption in species composition at establishment, no stabilisation in 5 yr	[24]
Plants	Willow Eucalyptus	China	β α	Bog SRC age Burning	Abundance Species richness Abundance Shannon-Wiener Evenness	Species richness related to soil nutritional status Second rotation < first rotation Regeneration with seedlings < SRC	[25]
Plants	Poplar	France	α	SRC age SRC species Stem density	Species richness	Mean species richness decreased with SRC age Understorey not influenced by herbicides, SRC species or stem density Previous land use influenced young SRCs	[26]
Plants	Poplar	Germany	α	SRC age SRC species Irrigation Fertilisation	Species richness Abundance Shannon-Wiener	Species richness increased initially, decreased after coppicing SRC species-dependent understorey composition SRC age-dependent understorey composition No fertiliser or irrigation effect	[27]
Plants	Poplar	Sweden	β	Agricultural land Deciduous forest	Species richness	Arable land < SRC SRC < deciduous forest	[28]
Plants	Poplar Willow	Germany Sweden	β	Agricultural land Grassland Coniferous forest Mixed forest	Species richness Abundance Shannon-Wiener Sørensen	Highest species richness in SRC Species composition lowest similarity with arable lands and forests Species composition highest similarity with grassland and mixed forests Species composition correlated to SRC tree cover, SRC age and coppicing	[11]
Plants	Poplar Willow	Germany Sweden	γ	Landscape	Species richness	Higher contribution of SRC when γ -diversity is low	[29]
Plants	Willow	Denmark	α	SRC age Coppicing	Abundance	No willow flowering the year following coppicing Increased flowering with coppice rotation length	[30]
Plants	Willow	Poland	β	Grassland Fallow land	Species richness Shannon-Wiener Evenness Simpson	Unfertilised SRC < grassland < fertilised SRC Unfertilised SRC < fallow land < fertilised SRC	[31]
Plants	Willow	Sweden	β	Agricultural land Bog	Species richness Abundance	Negative effects of fertilisation and herbicides Disruption in species composition at establishment, slow stabilisation Decreasing species richness with increasing coppice rotation length	[32]
Plants Arthropods Plants Arthropods	Poplar Willow Willow	Belgium France UK	β β	Agricultural land Agricultural land Fallow land Landscape	Species richness Abundance	Arable land < SRC Incorporation of SRC increases γ -diversity	[33]
Arthropods	Alder Hazel Willow	Denmark	α β	SRC size Leys	Species richness Abundance	SRC hedges beneficial for parasitoid diversity	[34]
Arthropods	Poplar	Italy	α β	SRC age Deciduous forest Agricultural land	Species richness Shannon-Wiener Evenness Forest Affinity Index	Species richness neither correlated with SRC age nor land use Shannon-Wiener neither correlated with SRC age nor land use Dominance in SRC simpler than forests SRC more comparable to forest with increasing age	[35]
Arthropods	Poplar Willow	UK	α	SRC size	Abundance	SRC edge colonised before interior zone	[36]
Arthropods	Sweetgum	US	α β	Grass cover Agricultural land Energy grass	Species richness	SRC < energy grass SRC = arable land No grass cover effect	[37]

(continued on next page)

Table 1 (continued)

Taxonomic group	SRC genus	Country	Level	Variable	Diversity index	Main conclusions	Ref
Arthropods	Willow	Germany	α	SRC species	Species richness Abundance	Increase species richness with increasing diversity in SRC species	[38]
Arthropods	Willow	Sweden	α	Coppicing	Species richness Abundance	Coppicing favoured leaf beetles 5 yr-coppice rotation length disrupts biological control	[39]
Arthropods	Willow	UK	α	SRC species	Abundance	Increase in monocultures, decrease in mixtures of SRC species	[40]
Arthropods	Willow	UK	α	SRC species	Abundance	SRC species preference	[41]
Arthropods	Willow	UK	α	SRC age	Abundance	Positively affected by SRC age and free-living natural stands	[42]
Arthropods	Willow	UK	β	SRC species	Abundance	SRC species specific resistance	[43]
Arthropods	Willow	UK	β	Agricultural land Fallow land	Species richness Abundance	Arable land = fallow land < SRC	[43]
Arthropods	Willow	US	α	Fertilisation	Species richness Abundance	Fertiliser type correlated differently to species studied	[44]
Arthropods		US	α	Tillage	Species richness	Soil preparation negatively correlated to species richness and abundance	[45]
Birds	Poplar	US	β	Forest Shrub land Agricultural land	Abundance Species richness Abundance	Higher species richness and abundance after soil preparation Arable land < SRC < forest & shrub land Heterogeneity increases species richness and abundance	[46]
Birds	Poplar Willow	UK	α	SRC age SRC species	Species richness Abundance	Poplar < willow Positive SRC age effect on resident birds	[47]
Birds	Poplar Willow	UK	α	SRC species	Abundance	Species-dependent preference for SRC species	[48]
Birds	Poplar Willow	US	α	SRC species	Species richness	SRC species preference for nesting	[49]
Birds	Poplar Willow	US	α	SRC size SRC age	Species richness Abundance	SRC maintains arable land- and forest-related species Species richness increased with differences in SRC age	[50]
Birds	Willow	UK	α	SRC size	Species richness	SRC attracted shrub and forest species to arable land	[51]
Birds	Willow	UK	β	Agricultural land Grassland	Abundance	SRC interior < SRC edge Arable land & grassland < SRC Arable border & grass-bordered hedgerow < SRC-bordered hedgerow	[52]
Birds	Willow	UK	β	Natural stands	Species richness Abundance	Natural stand < SRC	[52]
Birds	Willow	Sweden	β	Agricultural land Coniferous forest	Species richness	Species richness intermediate between arable land and coniferous forest Species richness highest when SRC height exceeded 2 m Habitat features outside SRC influence species richness	[53]
Birds	Willow	Sweden	α	SRC age	Species richness	SRC favoured brush species Species composition shifted after planting and coppicing	[54]
Birds Mammals	Poplar	US	β	Agricultural land Forest Shrub land	Species richness Abundance	Arable land = SRC < forest for mammals Arable land < SRC < forest for birds	[55]
Birds Mammals	Poplar	US	β	Agricultural land Forest Shrub land	Species richness Abundance	Replacing arable land with SRC had no negative effect on diversity	[56]
Birds Mammals	Poplar	US	β	Agricultural land Forest	Species richness Abundance	Arable land = SRC SRC < forest Species composition is a mixture of grassland and forests	[57]
Birds Mammals	Willow	US	α	SRC age Coppicing Shrub land Landscape	Species richness Abundance	SRC increased γ -diversity More small mammals in the year after coppicing More birds with increasing SRC age	[58]
Mammals	Poplar	Italy	β	Forest Agricultural land	Abundance	Single rows < double rows Negative correlation with distance to forests	[59]
Mammals	Poplar	US	α	SRC age	Species richness Abundance	SRC age negatively influenced species richness and abundance	[60]
Mammals	Willow	Sweden	α	Food abundance Height	Abundance	4 yr < 1 yr < 2–3 yr Higher foliage, lower food abundance	[61]

vegetation heterogeneity [32,68]. Furthermore, the nutrient content of the leaves differs among genotypes and species, and causes different decomposition rates [32]. The combination of these factors leads to variation in understorey (plant and animal) species composition [11,27]. From the standpoint of the SRC grower, a multi-genotypic SRC provides more resistance to insects, pests and diseases, and thus limits the economic risks linked to biomass losses [68].

3.2.1.2. Stand edges. Uncultivated stand edges are necessary landscape elements around SRCs to allow agricultural machinery (needed for planting, fertilisation, herbicide application, and coppicing) access to the SRC [68]. Stand edges can also be used as physical subdivisions of large SRCs [30]. In commercial SRCs, these stand edges often reach widths of 8–10 m [69] and are important structures: increasing

biodiversity when grass and/or other herbaceous species are allowed to develop, or even be sown. As long as active management of the stand edges is maintained, plant species richness will increase (in the beginning) or stabilise (when a maximum is reached), as will the floral richness and vegetation structure [58,68,70] (Fig. 2). This diversity attracts invertebrate species, in turn providing ecosystem services such as pollination and predation [30].

3.2.2. Naturally occurring vegetation

After planting an SRC, the understorey develops from the seed bank. The understorey develops over time within the first and following rotations, with some kind of reset at every coppice event, leading to a mixture of successional stages.

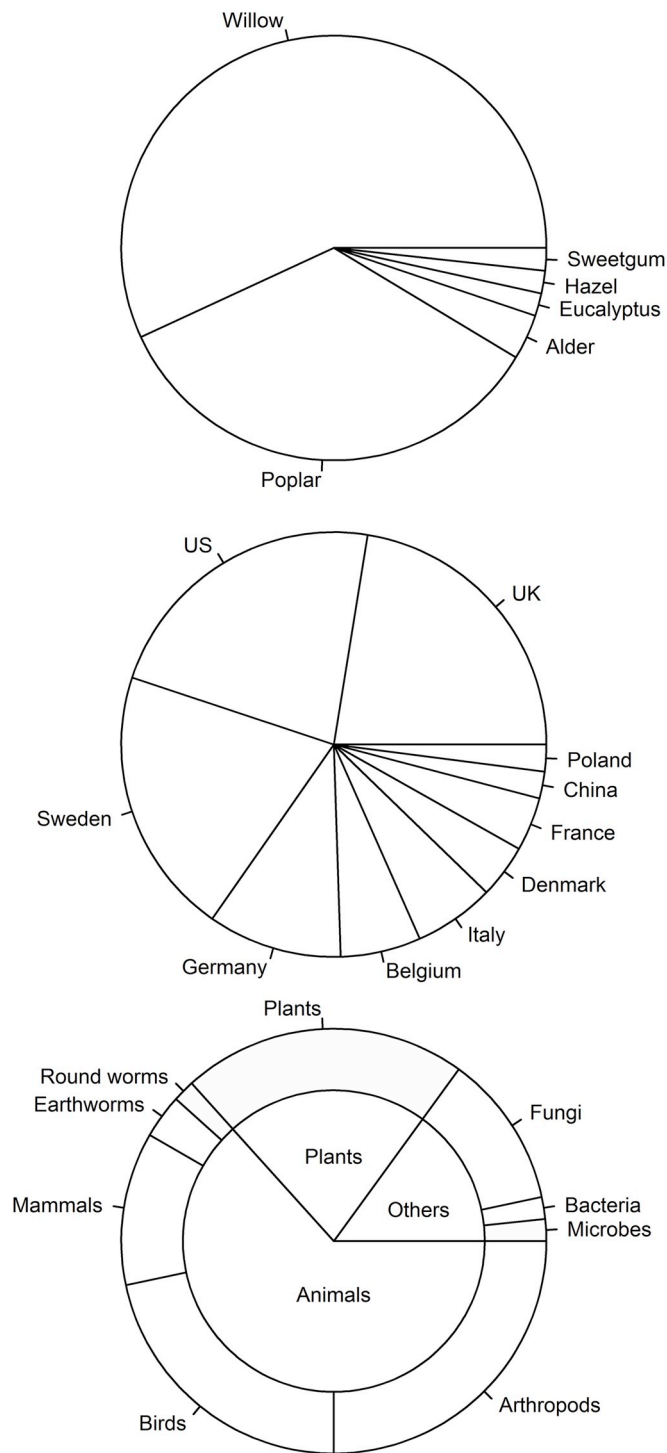


Fig. 1. Relative distribution of the 47 observational studies according to the short-rotation coppice genus (upper panel), the country where the study was performed (middle panel) and the studied taxonomic group (bottom panel).

3.2.2.1. From seed bank to maturity. Plants sprouting from seeds, rhizomes, tillers or living roots present in the soil are considered harmful. These plants prevent good establishment of the SRC species, because of competition for the same resources. Mechanical and/or chemical “weed” control is, therefore, applied before and/or after planting of the SRC species. Herbicide use decreases the species richness and abundance of germinating seeds [71]. Seeds and vegetative tissue surviving herbicide treatments can colonise the areas free from vegetation, where the planted SRC species has not yet

Table 2

The absolute (#) and relative (%) number of publications integrated for this analysis in terms of the studied taxonomic group, the SRC species studied, the country in which the study was performed, the diversity level studied and the diversity index analysed.

		#	%
Taxonomic group	Animals	32	60
	Bacteria, microbes	2	4
	Fungi	6	11
	Plants	13	25
SRC species	Willow	33	57
	Poplar	20	34
	Alder	2	3
	Eucalyptus	1	2
	Hazel	1	2
	Sweetgum	1	2
	UK	11	22
Country	US	11	22
	Sweden	10	20
	Germany	5	10
Diversity level	Belgium	3	6
	France	3	6
	Italy	3	6
	Denmark	2	4
	China	1	2
	Poland	1	2
	α	28	50
	β	25	45
	γ	3	5
	Diversity index	Species richness	37
Abundance		36	42
Shannon-Wiener		6	7
Evenness		3	4
Forest Affinity		1	1
Simpson		1	1
Sørensen		1	1



Fig. 2. The 8-m wide stand edge of an operational short-rotation coppice (on the left) in Lochristi (Belgium), established as a grass cover enriched with herbaceous species. The short-rotation coppice is integrated into an agriculture-dominated landscape (mainly maize; on the right) with a row of natural willow stands (behind). Picture taken by SPP Vanbeveren on 21 August 2018.

established a root system. Since herbicide treatments are common practice for SRCs, seed bank densities, species richness and abundance in SRC are comparable to those found on agricultural land [71,72].

Because SRCs are usually established in spring, no fresh seeds arrive at the time of planting, and the emerging vegetation, therefore, resembles the vegetation of former land uses [32,71]. Cultivation of the soil and planting of the SRC create different soil structures, each favouring different species: furrows and cracks from ploughing, and smooth surfaces where the planting machine has compressed the soil [73].

In general, planting- and coppice-related disturbances cause the soil to receive more light and become warmer, thereby favouring generalist plant species, which are then outcompeted within the following rotation by (fewer) forest species [26,32]. The generalist species are mostly ruderals, known as weed species in cropland and along roadsides [9,32,33]. A higher number of forest and tall herb species were found in the first rotation of an SRC when the previous land use was a forest or a tree-plantation, in contrast to SRC established on a meadow or cropland (which favoured meadow species) [26]. Also, in an SRC established on a former bog, the bog species dominated the understorey in the first rotation [24]. Seldomly, do rare species appear on newly established SRCs [32].

With time (and independent from previous land use) the canopy of the SRC closes and the available light on the understorey diminishes [9]. With the reduced incoming light on the understorey, forest understorey species are favoured over grassland species [11,27], while the total plant species richness decreases [26,71]. The number of invasive species increased with a closing canopy when the SRC was established on a former bog [24]. Planted SRC genotype and planting density influence the dynamics of canopy closure, and thus, also the composition and evolution of the understorey [11,58].

Understorey composition was not correlated with previous land use for rotations after the first rotation [26]. Nevertheless, in Sweden, understorey composition reached equilibrium faster in SRCs established on former meadows as compared to SRCs established on former bogs [32]. When several SRCs were consecutively established after each other, the diversity in meadow plants decreased in France [26].

3.2.2.2. Factors affecting the understorey vegetation. Beside the naturally occurring spatio-temporal variation, the ways in which SRCs are established and managed, are more than likely to influence their biodiversity. The coppice rotation length and planting density are selected before planting as these are interdependent: the longer the rotation, the lower the planting density. In the US, planting density was positively correlated with bird populations [58]. Within each rotation, the canopy structure evolves from a bare field to a shrub-like stand, and further to a closed canopy with stems exceeding 10 m [74]. The coppice rotation length, therefore, determines what stage of canopy development can be reached. Stem height and canopy cover of SRC plants were positively correlated with coppice rotation length, whereas ground cover was negatively correlated [56,58]. In the first year of a rotation, a dense herbaceous cover is combined with a shrub-like growth of the SRC plants [58]. The most important structural changes occur between the first and the second year: during the first year most biomass is allocated to the leaves, but from the second year most is allocated to the SRC plant stems. During later years the canopy structure simplifies, as a dense canopy of SRC plants develops and the understorey diminishes [58]. This rapidly changing canopy structure is an important determinant of structural landscape-scale diversity (see Section 4) and animal distribution (see Section 3.3).

Size and shape affect the α -diversity on an SRC and the interaction with other land uses nearby [68]. Small or irregularly shaped SRCs – or SRCs with a large edge to area ratio – host a larger α -diversity of understorey plants as compared to large rectangular SRCs [28,29,32]. Furthermore, several smaller SRCs likely increase the γ -diversity, while the reverse is expected from large (> 10 ha) plantations (in Germany and Sweden) [29]. Even within one SRC the species richness decreased from the edge towards the interior [28], probably because plant seeds colonised the edge more easily through wind or animal dispersal (in Sweden) [32]. Once across the edge of the SRC, the vegetation becomes rather uniform and less attractive for many animal species, and more difficult to colonise for most plant species.

The effects of irrigation, fertilisation and herbicide application on biodiversity in SRC are rarely reported in the literature [68] and the few studies available are based on short-term effects. No [27,75] or negative [32,71] correlations were reported between fertilisation and plant

species richness or abundance in SRC. In a peat bog (with a very small seed bank) converted to SRC, fertilisation favoured surviving bog species in the first year after establishment [24]. Herbicide application is considered pivotal for a successful SRC establishment because it favours the SRC plants over all others. Applying herbicides in the establishment phase will cause a decline in the phytodiversity, and when applied in between rotations, this decline is only enhanced [32].

The only major disruption in the lifetime of an SRC is the recurrent coppicing, whereby all aboveground biomass is removed. Coppicing is a very sudden and extreme change in the vegetation structure and can have positive and negative effects on the α - and γ -diversity [68]. However, positive effects entirely depend on the non-simultaneous coppicing of different parts of large-scale SRCs [68] – or different SRCs in the same landscape [30] – to generate a spatio-temporal mosaic of differently aged SRCs, canopy structures, refuges for animals, flowering species, etc. Furthermore, manual coppicing is preferred over machine coppicing for biodiversity consequences as the former generates more gaps and a more irregular structure [32]. However, manual coppicing has been shown to be financially inefficient on easily accessible (flat) terrain [76].

3.2.3. SRC versus other land uses

Biodiversity remains an important characteristic for determining potential areas for SRC expansion. Several studies have investigated the difference in plant biodiversity between SRC on the one hand and forests, grasslands, agricultural land or abandoned land on the other. Overall, SRC can positively contribute to plant diversity when thoughtfully integrated into the landscape [11,28,32]. Most importantly, it should be kept in mind that although SRCs are less intensively managed, as compared to agricultural land, SRCs mainly contribute to plant diversity by adding generalist species typical for disturbed and anthropogenic environments in temperate climates [68]. Hence, large and uniform SRC monocultures [29] replacing sensitive, unexploited ecosystems should be avoided [32].

The mosaic concept states that the landscape species richness increases as the number of (heterogeneous) habitats making up the landscape expands. Or in other words: the lower the γ -diversity, the higher the added value for biodiversity of establishing SRC [28,29]. Also, more species and individuals are able to reach the SRC as the surrounding landscape becomes more diverse [32,58]. Furthermore, the added value that SRC can bring to biodiversity is dynamic over time – the age of the SRC can account for many structural characteristics [58].

Abandoned land is most likely to be converted to SRC, as competition with other land uses is limited. Furthermore, such abandoned, often contaminated land is already characterised by common species with lower biodiversity values as compared to SRC [32]. In terms of plant diversity, SRC did not significantly differ from (marginal) grasslands [11]. Only a few studies have compared SRC, abandoned land and grassland; so generalisation of these results might be unwise.

The literature clearly shows that SRC has a plant biodiversity potential situated between agricultural land and deciduous forest [68]. Replacing arable land with SRC [11,29] or integrating SRC into an agricultural landscape [32,58] will definitely benefit plant biodiversity. The reason for this is the lower management (and disturbance) intensity of SRC as compared to agriculture [68]. The higher floristic heterogeneity in an SRC, as compared to adjacent agricultural land, contributes to a larger variation of habitats (suitable for, e.g., drought-sensitive species) [28,70]. Coniferous and mixed forests host fewer plant species as compared to old-growth deciduous forests which maintain a higher plant species richness [11,28,32].

3.3. Animal diversity

Animal diversity in one specific landscape entity is more difficult to describe as compared to plant diversity at the same level. The place

where a plant establishes – either from seed or as a vegetative cutting – has to provide all the resources the plant needs, while animals are spatially highly dynamic [35,53,58,77]. Consequently, the landscape surrounding the SRC is more important to animal diversity than the characteristics of the SRC itself [53,57,59]. For example, the abundance of forest-related birds in SRC is positively correlated to the area of forest nearby [57], and only dominant small mammals from adjacent forests survive in SRC [57,78].

The species richness and abundance of birds [46,47,51,53,57,70,78], mammals [58,79], butterflies [9,70], soil mites [45], other arthropods [17,33,35,70,80] and earthworms [17] in SRC are higher than in agricultural land (i.e., annual cultivation of row crops), pasture and residual habitat (urban areas, roads, etc.), but lower than in forest, shrub land and natural grassland. To nuance this general trend, relatively small SRCs host a bird species richness comparable to large forested areas, but lower than the edge zones of forests [51,53]. The age of the SRC also influences the species richness and abundance (see Section 3.3.4).

Individual species might show opposite trends to the one described in the previous paragraph, as a result of the shifting community dynamics in SRC [78]. For example, SRC hosts an overall higher arthropod species richness than agricultural land [43], but carabid beetles are more abundant in cereal crops [37]. The same goes for mammals: while deer use forests and SRC alike in winter, squirrels appear to treat SRC as agricultural land and avoid it [79].

For many animals, SRC is most likely not fulfilling all of their habitat demands and, therefore, need other landscape elements nearby [57]. Yet, SRC provides important resources that are otherwise not sufficiently present in the landscape. Smaller animals (e.g., arthropods and small mammals) do not necessarily have a spatial niche larger than the size of an SRC.

3.3.1. SRC establishment

Soil cultivation prior to planting had a negative effect on soil mites in the establishment year but the effect decreased during the following years [45]. There was no effect of planting technique (manual or mechanised) on mite communities. The effects on species richness and abundance were larger on predatory Gamasida than on saprophagous and mycophagous Oribatida. This reflected the drastically changing prey availability and tempered changes in understorey vegetation, which still resembles the vegetation of the previous land use in the first few years since establishment (see Section 3.2.2).

The planting scheme, planting density and coppice rotation length indirectly affect animal diversity by determining the rate of canopy closure in every rotation. Small mammals prefer double rows over single rows because of its higher degree of canopy cover [59]. Similarly, a higher planting density enhances canopy closure and thereby sustains higher bird abundances [51,71]. Longer coppice rotations allow more recovery time for soil invertebrates [45] and allow the SRC trees to grow bigger, thus generating more nesting opportunities for birds [53].

3.3.2. SRC plant species

Different genotypes grow in different ways, thereby creating different habitats within and between rotations, creating mixtures of leaves and decomposing litter, and thus, attracting a larger diversity of animals [23]. A higher number of such (micro-) habitats within an SRC hosts a higher diversity of arthropods [38]. Positive effects of habitat heterogeneity within an SRC plantation on bird species richness were reported [46], but this result was not confirmed [49]. However, birds temporally prefer certain SRC species for hiding and nesting; this is related to the branching pattern of the SRC plant species [49]. SRC established with willow attracts a higher bird species richness and abundance when compared to poplar SRC; this was explained by the more complex branching pattern of willow and its more abundant associated arthropod communities [47,51,71]. Poplar SRC is preferred over willow SRC by bird species favouring open space, as for example,

partridge [48].

Beside the species or genera planted, the sex of the planted material also influences animal diversity. Dioecious genera (e.g., poplar and willow) produce either nectar on female plants, or nectar and pollen on male plants. Thus, planting a mixture of male and female plants creates an important food source for many pollinators [30]. By careful selection, a mixture of willows can be planted with varying flowering times, so as to provide pollen and nectar over extended time periods [30].

3.3.3. Management

Fertilisation, irrigation and weed control have a major influence on animal diversity. These management interventions promote SRC growth, thereby accommodating the SRC species while hindering all other (plant and animal) species [56,57]. Weed control suppresses understorey development, and in turn this limits animal diversity by simplifying decomposing litter and habitat heterogeneity [45,80]. The type of fertiliser applied determines its effects on decomposers: plastic mulch and sewage sludge had negative effects on soil mite populations, while the number of soil mites was positively correlated with the amount of chicken manure applied [44]. The effects of weed control and fertilisation were most pronounced in the first growing season after application; these effects were nullified by changing plant communities in later growing seasons [45].

Pesticides are applied on SRC against defoliating leaf beetles, mainly from the Chrysomelidae-family (e.g., *Phratora vulgatissima*, *Galerucella lineola* and *Lochmea caprea*) [36,39,40,80]. However, these pesticides are not species-specific and reduce the invertebrate food web complexity [70], thereby reducing food abundance for insectivores [59]. Pesticides are usually not very effective, as adult beetles overwinter on mature trees outside the SRC [39,42]. Their spring emergence varies among species over several weeks [36], making the selection of a good pesticide application time problematic. Several weeks after having infested the SRC edge, beetles favoured specific SRC genotypes to disperse throughout the SRC interior [36,41]. One way towards biological pest management is to impede beetle dispersal by planting genetically diverse mixtures and avoiding mono-genotypic rows and blocks [40,41].

Pesticide application raises environmental concerns and is economically expensive [39], making it preferable to control leaf beetles and other pests biologically [43,68]. Unfortunately, biological control of leaf beetles is disrupted by coppicing, as the leaf beetles' predators (e.g., *Orthotylus marginalis* and *Anthocoris nemorum*) overwinter in the SRC [39]. To overcome or to reduce the effects of such a disruption, extended coppice rotation lengths and phased coppicing of different parts of the SRC are suggested options [39,68]. Also, the undisturbed SRC soil and understorey favour parasitoids of pests present in nearby crops [33,34].

3.3.4. Temporal variation

The dynamic habitat characteristics provided by an SRC provide different functions to different species over time [60,81]. Therefore, describing the function that an SRC provides to a certain (animal) species or group of species over time should always take the SRC age into account [57]. By definition, an ageing SRC is characterised by an increasing canopy height. Between soil preparation and the end of the first growing season, the SRC attracts (generalist) bird and mammal species associated with open fields and meadows [50,57–59,80]. The abundant understorey vegetation of a young SRC provides food and cover able to sustain a high species richness and abundance throughout the year [51,60,78]. From the second growing season onwards, open-field bird species are gradually replaced by forest-associated bird species, although a mixture remains till the end of the rotation [46,50–52,57]. Some bird and mammal species, however, only colonise an SRC close to the next coppice, thereby quickly losing their newfound home upon coppicing [46,60].

The species richness and abundance of birds, other than birds of

prey, increased with increasing SRC age [47]. This can be explained by increased nesting opportunities [47,50,51,53,58] and increased food abundance, such as leaf-feeding larvae, stem-feeding aphids and pollinating winged invertebrates [9]. The richness and abundance of mammal species decreased with SRC age because of declining food variability for small mammals and food availability for large mammals [57,58,60]. However, the lack of understorey vegetation in well-maintained SRCs is beneficial for some specialist small mammals [57]. Population sinks are a threat when habitats are as dynamic as SRCs [46], but nest predation or breeding success did not differ from those experienced by the same species in other habitats [50]. To maintain a maximal animal diversity, an SRC should contain several age classes at any given time [47,54,56,60]. Nevertheless, the bare land left after coppicing is rapidly covered by the trees' regrowth, limiting the efficacy of this strategy [70].

3.4. Landscape diversity

Implementing SRC into the landscape remains a crucial factor as this results in beneficial or harmful consequences for the γ -diversity. The homogeneity arising from row crops (such as SRC) poses the largest risk to biodiversity, as this kind of habitat requires specialised species and this results in – by definition – lower abundances [35]. Therefore, diversity in vertical and horizontal structure should be maximised to accommodate as many plant and animal species as possible [46,47]. In large SRCs heterogeneity arises automatically when individual trees fail to resprout after planting or coppicing [46,56], but also the size of the SRC area itself can play an important role in biodiversity.

Although large SRCs support a higher bird species richness than small SRCs [46,50], the higher edge to area ratio of small SRCs can boost both plant and animal diversity [47,51,57,58]. The edge zone of an SRC is able to sustain a higher species richness, and abundance of invertebrates [9] and birds [48,52,53,71] as compared to the interior zone. This also implies that results obtained from small SRCs cannot be extrapolated to large SRCs, as these have a lower edge to area ratio [52,56–58]. Also, the relative surface area of edges surrounding the SRC increases with decreasing area. These edges support more butterflies [80] and birds [48,53] than the SRC itself and are more diverse than field edges surrounding agricultural land [70].

SRC should be implemented carefully in any landscape. When introduced into an agriculture-dominated landscape, SRC is likely to increase the structural diversity [48], but when introduced into an open or forest-dominated landscape, no overwhelming positive or negative effects should be expected [56,58]. Yet, SRC can play a crucial role in forest-dominated landscapes by connecting different forest patches [56,81], buffering sharp habitat edges [e.g. between agricultural land and coniferous forests; 55, 81], or providing shrub vegetation for non-forest species [54,78]. Planting different genotypes at random instead of in mono-genotypic blocks and maintaining different age classes positively contribute to biodiversity and even decrease the risk of economic losses due to pests and diseases [48,80,82].

4. Practical implications and recommendations

The following practical implications and recommendations are based on the above review of the existing literature and within the limit of coverage of this review. The elaborations are, therefore, limited and based on the above specific findings. Planning and management of SRC could and should be directed towards creating a strong positive impact on biodiversity, while conserving (or marginally affecting) biomass productivity. It should be understood that: (i) phytodiversity is composed of common, ruderal species and initially resembles that of the former land use, but it evolves to a vegetation composition more typical of forests, and (ii) animals use SRC for one or more aspects (shelter, nesting, foraging), but seldom seem to completely depend on SRC for fulfilling all of their needs. Creating a structurally diverse habitat with

spatial and temporal dynamics with SRC should be aimed for by:

- allowing patches with high mortality
- planting different (native) genotypes (and sexes)
- phased planting and coppicing of large SRCs
- allowing a certain amount of understorey growth
- maximising the edge to area ratio
- introducing biodiverse stand edges
- stimulating biological control over herbicides, fungicides, pesticides and fertilisers
- creating a credit system (cfr. carbon credits) as to stimulate SRC farmers

It became clear from this review that several studies have already been performed on biodiversity in SRC. The interpretation of the results should be done with caution as the studies analysed in this review were neither representative for all biodiversity indices nor for all types of SRC in all climates. The majority of studies were conducted on SRC established with poplar and willow in temperate climates; they, therefore, poorly represent SRC established with e.g. eucalypt and *Robinia* in tropical climates. The current review manuscript differs from all previous reviews as each of the last mentioned ones only handled a very narrow aspect of biodiversity (e.g. wildlife and game [71], willow [82], boreal climates [77]), while our current literature review combines all aspects of biodiversity together. Furthermore, seven from the nine reviews were conducted more than ten years ago and the most recent review dates back to 2011 [78] and focused on birds and mammals only. So, the current review has a value of synthesizing and updating all studies on the issue of biodiversity in SRC. Nevertheless, many uncertainties that require further studying, remain:

- Although biodiversity can be quantified by different indices, species richness and abundance were primarily used to assess the biodiversity in SRC. More complex indices (e.g. the Shannon-Wiener or Simpson index) were hardly quantified and allow more comprehensive interpretations of reality.
- In most of the reviewed publications one specific SRC characteristic (e.g., age or planted genotype) was related to biodiversity, or an SRC was compared to other (surrounding) land uses. The results from these studies remain very case-specific; to generate stronger far-reaching results the ambitions of individual studies should increase accordingly.
- Little is known about the effect of SRC on biodiversity when established on marginal or abandoned land. As these areas are envisioned for developing SRC in the future, the specific effects relating to this kind of land (poor soils, slopes) will be more representative than the effects of SRC established on arable land.

5. Conclusions

As many species become threatened by global changes, biodiversity conservation should be prioritised to conserve those species that contribute to climate change mitigation (and the production of renewable energy). If biodiversity is not taken into account when deciding on the agronomic methodology to be applied for generating biomass for bioenergy, its ecological profitability would be greatly diminished. SRC covers the middle ground between agriculture and forestry, both in terms of management and biodiversity. This review summarised the specific findings of scientific peer-reviewed publications; this should be kept in mind when interpreting or extrapolating the results. While SRC is most likely to negatively influence biodiversity in a forest-dominated landscape, it has a high potential to enhance biodiversity in structurally homogeneous, agriculture-dominated landscapes. Because it is envisaged that SRC is mainly established on abandoned (agricultural) land, the significant enhancement of biodiversity in these landscapes provides additional value.

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