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Review

Willow Short-Rotation Coppice as Model System for Exploring Ecological Theory on Biodiversity–Ecosystem Function

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Abstract: Plantations of willow (*Salix* spp.) are today grown as short-rotation coppice (SRC) for the sustainable production of biomass. While developing these production systems in the past, much ecological knowledge on plant–plant, plant–environment and trophic interactions has been generated. This knowledge can contribute to the further development of biodiversity–ecosystem function (BEF) theory, which frequently lacks a sound understanding of the complex mechanisms behind the observed patterns of diversity-productivity relationships. Thus, willow SRC systems are suitable models to explore BEF theory; they are simple enough to allow the study of the complex ecological mechanisms involved and they have many similarities to grassland systems in which much of recent BEF theory development has been achieved. This paper briefly reviews the current observational and mechanistic knowledge on diversity–productivity relationships in willow SRC, as well as the most important above- and below-ground trophic interactions that are likely to affect them. If the available knowledge is integrated and combined with further experimental work targeting mechanisms behind patterns, research on willow SRC as a model offers a great opportunity for filling the gaps in the understanding what presently hampers the development of predictive BEF theory.

Keywords: biodiversity–ecosystem function (BEF); diversity–productivity relationships; herbivory; mycorrhiza; trophic interactions; Salix; short-rotation forestry

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1. Introduction

Willows (genus *Salix*, family Salicaceae) are fast-growing deciduous trees and shrubs occurring mostly in temperate and arctic zones of the northern hemisphere [1]. Intensively managed willow plantations are commercially grown for biomass production in many regions of the world, and the short-rotation coppice (SRC) systems most often used are gaining interest worldwide mainly due to their efficient and sustainable land use along with an increasing demand for biomass resources [2]. Willow SRC plantations consist of densely grown (10,000 to 20,000 plants ha^{-1}), high-yielding genotypes of willow cultivated on agricultural land; and the shoots are typically harvested during winter for biomass on the basis of two- to five-year cutting cycles [3]. The rootstock remains in the ground after each shoot harvest, with new shoots re-sprouting the following spring. Thus, in an ecosystem function perspective, the regular shoot harvests every second to fifth year allow for the study of temporal patterns in shorter (two to five years) and longer time scales (>five years). Additionally, the controlled removal of above-ground plant parts while rootstock is sustained implies that competitive exclusion and extinction of individual genotypes is reduced. In the cases where several genotypes are grown in the same plantation, willow SRC systems, with the above characteristics, are attractive for the study of diversity–productivity relationships and the development of (predictive) biodiversity–ecosystem function (BEF) theory. This is supported by the high level of functional diversity present across the various species and genotypes used in willow SRC systems as evidenced by the results from controlled pot experiments, (e.g., [4–7]), and experimental field trials (Table 1).

Table 1. Ranges of functional trait values observed in similar-aged willow genotypes field-grown in SRC systems in Sweden and UK; the smallest (Minimum) and highest (Maximum) values observed in any of the genotypes grown in the respective trial are shown.

Trait	Minimum	Maximum	Genotypes and Growth Conditions	Source
Shoot biomass per plant (kg)	0.3	1.5	6 genotypes, 4 treatments	[8]
Total leaf area (m^2)	0.6	2.5		
Root biomass fraction (-)	0.1	0.2		
Specific leaf area (mm^2 g^{-1})	9524	13,089		
Leaf N concentration (%)	1.7	3.3		
Bud burst date (day of year)	76	115	6 genotypes, 4 treatments	[9]
Biomass yield (Mg ha^{-1} $year^{-1}$)	6	16	5 genotypes, 1 treatment	[10]
Specific leaf area (mm^2 g^{-1})	12,129	14,923		
Final individual leaf area (mm^2)	2060	4573		

Originally initiated by a number of influential ecosystem studies carried out in grasslands, it has more recently been reported in a broad range of ecosystems worldwide that greater species diversity increases productivity [11,12]. However, generalizations have not been forthcoming due to conflicting interpretations of the same results [13], high complexity of the processes involved, and to an associated lack of predictive BEF theory especially when several trophic levels are taken into consideration [14]. Importantly, investigators have focused more often on the consequences of interspecific diversity for plant growth and productivity, involving the use of taxonomic predictors of diversity, rather than on the functional mechanisms behind observed patterns. For example, it is unclear which genetically-based differences in plant phenotype, and under which environmental conditions, result in differential niche occupation and thereby significantly contribute to diversity–productivity relationships; and which trait differences (or combinations) are unaccompanied by strong differences in resource use and therefore result in similar niche occupation (with no diversity–productivity effects realized). In addition, theoretical approaches based on the functional traits of the involved species or genotypes are beginning to replace studies based upon taxonomic predictors [15]; they are however challenging. This is because functional traits may influence processes at different levels of organization (e.g., trophic levels), at different time scales, and as such their influence may change over time [15]. For example, mixtures of species (or genotypes) with contrasting traits could use resources more effectively and reduce losses, but the positive effects may depend on the characteristics of the mixture components and the environmental conditions (e.g., resource availability), and change over time.

By linking emerging knowledge on plant functional traits, plant diversity and ecosystem processes at several trophic levels, BEF theory could be further developed with regard to a better understanding of the underlying mechanisms and their interactions (Figure 1). Examples of this are previous works in willow SRC that have focused on plant functional traits in relation to environment [8,16–18], plant interactions with insect herbivores and root-associated fungi [6,7,19,20], and plant–plant interactions [21]. This review briefly summarizes some of the current knowledge on willow SRC research that is relevant for BEF theory development in terms of diversity effects on growth and productivity, and the associated trophic interactions above- as well as below-ground. Consideration of other trophic levels in addition to producers is important, not least because individual ecosystem processes can be more strongly affected by the overall diversity of functional traits and the diversity of microorganisms influencing decomposition and nutrient cycling, than by tree species richness [22].

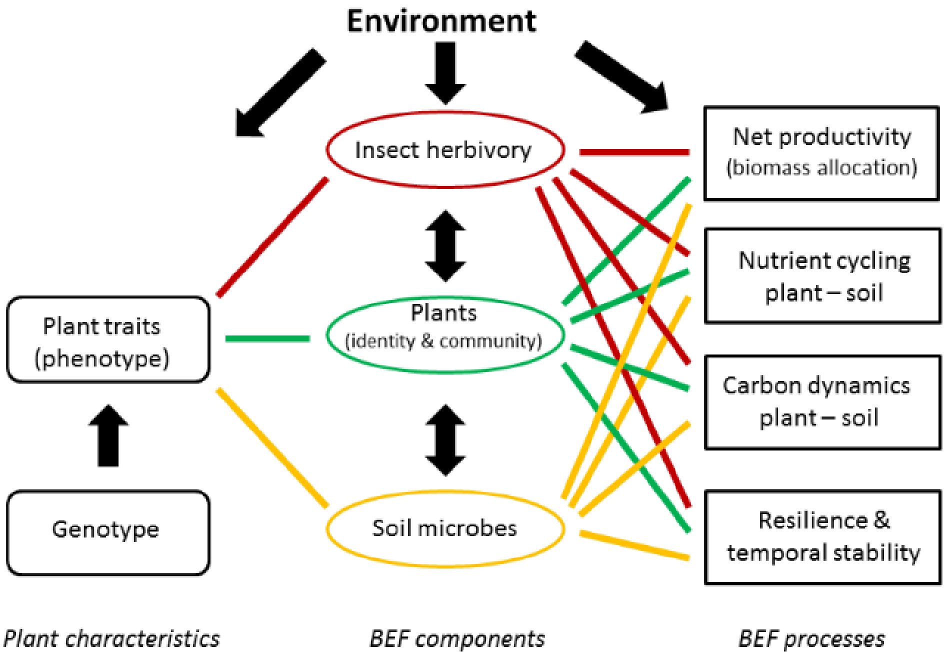

Figure 1. Conceptual overview of important relationships between plant (willow) traits and the biodiversity–ecosystem function (BEF) components and processes to be targeted when developing predictive BEF theory using willow short-rotation coppice (SRC) as a model. The BEF components relate to plant growth and productivity (green), insect herbivory as an important above ground trophic interaction (red), and soil microbes representing an important part of below ground trophic interactions (yellow). The BEF processes listed are considered important for the functioning of plant communities. Modified from [23].

2. Tree Diversity and Productivity

The commercial SRC cultivation practice is based on intensive management actions including weed control [2]. On the one hand, the weed control strategy strongly affects the establishment, development and biomass productivity of the main crop in willow SRC systems [24,25]; suggesting SRC systems to be grown with a minimum of ground vegetation in order to maximize biomass productivity. On the other hand, plantations of willow SRC grown on agricultural land often have greater plant diversity compared to stands of cereals, spruce and fallow ground, for example [26,27], suggesting a hitherto unexplored opportunity that a diverse ground vegetation could benefit biogeochemical cycling and productivity. With regard to the main crop, most commercial willow SRC grown for biomass production currently consist of single species or genotypes. Apart from the environmental (climate, soil) and management conditions, the growth and productivity in willow SRC are strongly affected by the specific characteristics of the plant material used in the plantation (Figure 1). Instead of growing pure stands, the cultivation of mixed stands including fast-growing components (species or genotypes) could be one way to enhance stand growth by making use of selection effects according to BEF theory [11]. Already early theoretical ecological frameworks [28,29] suggested that the more complex ecosystems become in terms of their food webs, the more efficient they are in utilizing resources, and a corollary of this is that enhanced biodiversity would improve biogeochemical cycling and productivity [11,30]. Observational studies in differently-composed tree stands suggest indeed that the composition of a plantation in terms of pure stands, consisting of single species or genotypes, or mixed stands can positively affect productivity [31,32]. Several mechanisms have been invoked to explain why biodiversity can have such a positive effect on productivity [11,33], but a clear understanding of the mechanisms underpinning

BEF is still missing [14,34,35]. In willows, the effect of species or genotype mixture on growth was explored in a controlled growth container study in which plants were cultivated in two environments differing in resource (nutrient) supply [36]. This study demonstrated that the specific functional trait combinations of two individual species/genotypes affect their response to mixture as compared to pure culture; and the results support the hypothesis that mixtures perform equally well or better than pure cultures especially in low-resources environments. In field-grown stands, no clear evidence has been found so far for a strong positive effect of stand diversity on productivity in young willow SRC [21,37], but it is possible that a (positive) diversity effect on productivity will evolve as these plantations grow older. Despite of the absence of a clear diversity effect on stand productivity after three years of growth, it was demonstrated that the addition of two of the genotypes ('Jorr' and 'Loden') resulted in enhanced community biomass production, while others ('Tora' and 'Björn') were found to reduce community biomass production in the mixed stands [21]. In terms of BEF, evidence was found for a negative selection effect due to the genotype 'Tora' performing better in mixed than in pure communities in two of the experimental sites (Freiburg, Uppsala) [21]. The results imply that increasing genetic richness has no significant effect on community productivity during the first three years of growth; and provide evidence that specific functional trait combinations of individual genotypes affect community productivity in either a positive or a negative direction. The trait profiles of the individual genotypes used in these trials, along with their temporal trajectories, may be further explored and linked to the genotype-specific effects on community productivity (e.g., Figure 2). The generated knowledge could then be used to test general predictions of BEF theory, especially when additional data on processes including more than one trophic level are considered [14]. For example, the corresponding work could be done in the willow SRC trials previously discussed [21], as these are part of the TreeDivNet network, which is the largest network of biodiversity experiments worldwide and provides a unique platform for BEF related research in a global perspective [32].

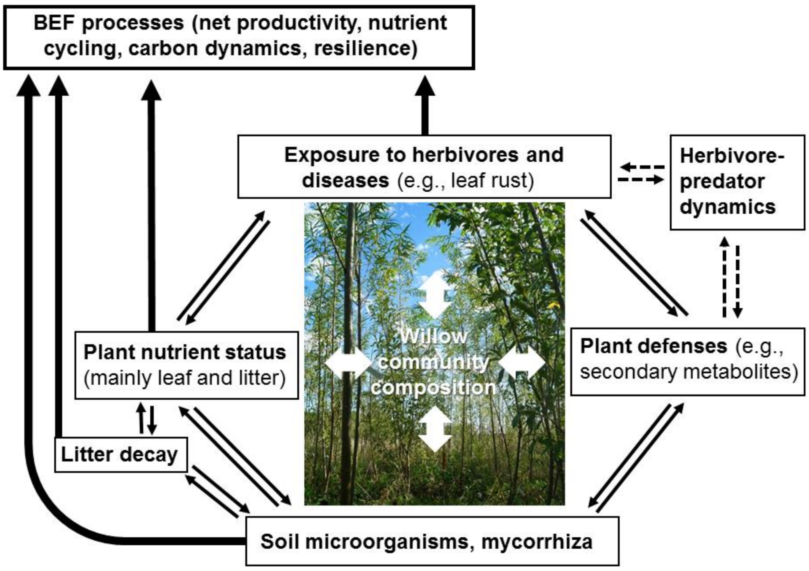

Figure 2. Overview of the links between ecosystem characteristics and processes currently researched in willow SRC systems (thin arrows), separated into bottom-up (solid lines) and top-down (dashed lines) interactions; and their connections to the overall ecosystem processes important for biodiversity–ecosystem function (BEF) (thick arrows). Bottom-up processes are those in which plant growth is affected by the utilization of limited resources (e.g., nutrient elements), while top-down processes are those in which plant growth is affected by the action of predators feeding on herbivores. Photo: Mixed willow SRC plantation near Uppsala, Sweden; the willow shoots are three years old (courtesy S. Hoeber, SLU).

3. Tree Diversity and Above-Ground Trophic Interactions

With regard to further theory development of BEF and the questions of if and how genotype and species diversity affect ecosystem functions, diversity experiments have investigated how plant performance (growth and survival) and their vulnerability to herbivory or rust infestation are affected by community diversity [35,38–40] (Figure 2). In this context, community diversity is increasingly acknowledged to provide associational resistance to herbivores and rust infestation; lower levels of herbivory and rust disease have been found in mixed than in mono-specific plots [41,42]. However, the opposite—associational susceptibility—can also occur [43,44].

The example of associational effects, which classically results from both bottom-up and top-down processes (e.g., Figure 2), illustrates the point that improved understanding of BEF requires the development of predictive models that accommodate both of these essential processes. In this context, willow SRC systems are excellent model systems, because they provide these.

Work done on BEF to date reveals no conclusive patterns with regard to how above ground trophic interactions respond to the genetic diversity of plant communities. Much of the data generated on this issue is conservation oriented and reported from wild populations, yet production-oriented cropping systems also play an increasingly important source of data [45]. This is driven by the demand for reduced utilization of chemical pesticides and fungicides, and an increasing awareness of the importance of biodiversity and ecosystem functions in production systems [46]. A recently published meta-analysis of 60 experimental studies on arthropods illustrates some of the complexities of relating stand genetic diversity with herbivore damage [47]. The results from that analysis lead to a few general conclusions: Both insect herbivores and their predators were higher in diverse wild plant communities, and herbivore abundance was lower in cropping systems that had higher crop genetic diversity, yet predator abundance was not affected there. One crucial factor to take into account is if the herbivores are generalists or specialists on their host plants. The meta-analysis [47] revealed that damage caused by generalists was lower in diverse systems and that specialist herbivores were unaffected. In short, it was concluded that plant genetic diversity does indeed affect arthropod communities (both herbivores and predators) yet there is limited potential for the use of crop mixtures as a means of pest control in agricultural systems [47].

These reported patterns are important advances; however, the mechanisms underlying the variability in results are yet to be discovered. This makes for a limited predictive power as BEF stands today. Willow systems, and especially those related to SRC, allow for rigorous tests of BEF theory development with regard to aboveground trophic interactions in production systems. In particular, they can play an instrumental role in identifying key components that link plant diversity levels and damage caused by herbivores that are useful for generalizations regarding both production and conservation systems. Further, mixed stands of SRC willow could provide suitable test systems for the adaptation and durability of rust resistance in the light of BEF theory, which also is an important research subject in plant pathology [38]. Willow SRC models allow for investigations that standardize many elements (genetic stand composition, soil nutrient status, levels of biotic influence, harvest regime) so that the effects of one or a few factors can be addressed in a specific experiment.

Over time, research efforts based upon willow model systems have led to emerging patterns on an array of abiotic and biotic factors affecting willow–pest interactions including at least two trophic levels. The reported interactions often address insect herbivores [6,41,48–55], but also fungal and bacterial diseases [39,40] or mammalian herbivores [56]. Other studies accommodate a third trophic level and give insights into how plant (willow) community structure affects the natural enemy pressures on herbivores [20,53,57–59]. The abiotic factors considered include mostly soil nutrient status [54] and water regime [6,60]. While no conclusive general principles can be made on how biotic and abiotic factors affect willow–pest interactions, a few patterns can be noted from the studies mentioned above. There is genetically-based variability in many willow interactions including several trophic levels: resistance to fungal and bacterial diseases, susceptibility to insect and mammalian herbivores, resistance to certain insect herbivores, production of a variety of secondary metabolites that serve as defense against herbivores and pathogens, soil nutrient status and water regimes. The variability in these traits, coupled with the ease of establishing structured experiments based on willows, allows for a uniquely mechanistic approach to theory building within the BEF framework and the questions of if and how genotype and species diversity affect ecosystem functions that are realized through the integration of processes at several trophic levels.

4. Tree Diversity and Below-Ground Trophic Interactions

Soil microbial communities, of which mycorrhizal fungi are an integral component, are important controls of soil health and plant productivity in ecosystems [61]. *Salix* spp. belong to the low number of dual-mycorrhizal plants forming both arbuscular and ectomycorrhizal symbiosis. For this reason they were used as model organisms, for the evaluation of the specific benefits of fungal diversity in plant nutrition and biomass production [62] (Figure 2). In general, mycorrhizal fungi regulate nutrient transfer between plants and soil via mycelial networks [63], and the utilization of mycorrhizal networks for influencing sustainability and productivity in biomass production systems such as willow SRC has been proposed [64,65]. Mycorrhizal networks are supported by plant-derived carbon, and increases in plant diversity have been associated with increased carbon storage in grassland [66] and forest soils [67]; however, the mechanisms behind are unclear. In most systems, mycorrhizal fungi receive 10 to 50% of plant-fixed carbon [68], and mycorrhizal fungal necromass constitutes an important pathway of carbon into long-term soil pools [69]. The quantity and composition of the microbial-mediated carbon flow from plant to soil depend on the functional traits of the microbial species involved [70], and the mycorrhizal fungal community composition is one of the main drivers of carbon and nutrient cycling in many soils (e.g., [71]). It has indeed been suggested to consider the quantity and quality of plant species-specific root colonization with mycorrhiza as plant traits for exploring patterns of soil carbon cycling [72]. Apart from mycorrhiza, it has been shown that the total soil microbial community composition—including both symbiotic and saprotrophic fungal and bacterial communities—reflects the quality of soil organic matter (SOM) so accurately that the soil microbial community may be used to predict SOM quality [73]. The SOM quality strongly affects its decomposition, and is therefore critical for the longevity and sustainability of the carbon pool accumulating in soil [73]. Hence, plant trait diversity potentially affects both quantity and quality of the carbon flow from above to below ground as well as the longer-term sustainability of the soil carbon pool.

In willows, the identity of the mycorrhizal partner has been shown to significantly influence the uptake of various nutrient elements, among them nitrogen and phosphorus, into the host plants [19,74], pointing at a strong influence of these fungi on the below-ground trophic interactions related to the productivity and function of these ecosystems (Figure 2). Arbuscular mycorrhizal fungi increased the stem phosphorus content of willows in vegetation filter systems up to 33% [75]. In addition, the diversity and abundance of root-associated fungi also affect the chemical composition of the foliage and consequently the above-ground trophic interactions related to the plants' predisposition to herbivore attacks and infection by pathogens, like rust fungi [7,19] (Figure 2). Conversely, both the willow genotype identity and the length of the rotation period (cutting cycle) have been shown to affect the diversity of mycorrhizal fungi or saprophytic microorganisms under willow SRC, along with the activity of hydrolytic enzymes affecting nutrient cycling [76,77]. Although the diversity of ectomycorrhizal fungi in planted willow SRC has been found to be lower compared to adjacent natural willow stands [78], willow SRC was concluded to enrich the biodiversity of soils when compared to conventional agriculture-dominated landscapes, and the ectomycorrhizal fungi contribute considerably to that enrichment [79].

In spite of the many observational studies demonstrating patterns of functional relationships with regard to below-ground trophic interactions affecting BEF, quantitative investigations of the functional interactions between willow diversity, soil microbiology and nutrient cycling are rare. In a study with focus on the plant–soil interactions in willow SRC, mixing of genotypes with strong eco-physiological differences was hypothesized to change the diversity and abundance of root-associated fungi and phosphorus mobilization in the mycorrhizosphere, based on different expressions of root traits [80]. A most interesting result was that interspecific root competition increased the richness and root colonization by endophytic fungi more than by ectomycorrhizal fungi; and also increased the activities of hydrolytic soil enzymes involved in the phosphorus mineralization. This suggests a selective promotion of endophytic root colonization and changed competition for nutrients by mixtures of *Salix* genotypes compared to the pure cultures. These results indicate that the specific suite of traits in mixtures have significant effects on the soil processes related to phosphorus cycling, which are not committed by the pure cultures of the individual genotypes.

Based on their no-till management, willows grown in SRC also promote the soil faunal abundance and diversity, and thereby, the soil food web relating to below ground trophic interactions [65]. Thus, the soil fauna plays a pivotal but little understood role in both carbon and nutrient cycling. For example, in a comparison of different ecosystem types, the divergence of feeding channels within the soil food web was investigated using willows [81], and the willow system was identified as an appropriate model system for the exploration of BEF theory, linking the abundance of herbivores, microbivores, micropredators, omnivores and macro-predators with soil carbon and nitrogen cycling. In a recent review on the relationship between below-ground biodiversity and ecosystem services across European forests, soil biodiversity was concluded to be generally positively related to ecosystem services, but the authors identified huge knowledge gaps regarding especially the functional relationships between the diversity of soil biota and ecosystem services [82]. Willow SRC systems are promising models for performing research to close some of those knowledge gaps, not least because much knowledge is already available in these systems on the functional relationships relevant for BEF and the integration of various trophic levels.

5. Discussion and Conclusions

Much work has been already done on diversity–productivity relationships and BEF theory development, based mostly on observational investigations in grassland and forest systems. Even if we are rapidly gaining insights into the ecological and plant physiological interactions that affect production systems, we are far from able to predict them only by means of manipulating community structures. In addition, much of the research on diversity–productivity relationships was indeed focused towards the study of the consequences of interspecific diversity for plant productivity. The approaches using taxonomic predictors are less promising when using willow SRC, because the plant material used in this production system is usually taxonomically diverse and most often includes hybrid varieties with elements from various taxonomic entities or species [83]. Instead of using taxonomic predictors, approaches based on the functional traits of the involved species or genotypes seem more promising for exploring the mechanistic links between plant functional traits (or trait differences) and resource use or niche occupation, for example. There are, however, challenges as the functional traits of interest may influence processes at various trophic levels and their influence may even vary over time [14,15]. The willow SRC production system is based upon individual genotypes of known genetic pedigree that can be vegetatively propagated. In addition, much information is already available on the impact of abiotic factors such as water and nutrient (mostly nitrogen) supply on the growth of different willow genotypes [4,16,17,84]. This allows for a multidisciplinary approach where the role of fundamental attributes of individual willow genotypes (such as physiological growth traits, phytochemical production related to pest resistance, ability to compete with other plants) can be assessed in a community and ecosystem approach. As the previous sections have shown, for willow SRC much evidence is already available on the relationships between plant functional traits and the processes important (e.g., resource use), and this information includes processes at various trophic levels (Figure 2). Significant advances in the development of BEF theory that take into consideration both above and below ground trophic interactions can therefore be made by using willow SRC as model systems. For example, genotype by environment interactions can be stringently tested since willow genotypes and species are easily propagated and subjected to various abiotic and biotic treatments in field and laboratory situations. Apart from BEF theory development, results from such studies can also provide the basis for long-term plant production strategies that can increase plant resistance to pests and diseases and promote sustainable plant production methods (e.g., for producing biomass for biofuel use [2]).

There are many arguments underpinning the notion that willow SRC plantations are suitable model systems to explore BEF theory:

- Willows are perennial and fast-growing.
- Willow genotypes are easily cloned, reducing a source of variation in the system.
- Willows are dual mycorrhizal (i.e., associated with arbuscular and ectomycorrhizal fungi), providing the consideration of both partly contrary impacts of the two main types of mycorrhiza formation on carbon cycling.
- Willows promote the soil faunal abundance and diversity and are appropriate model systems for the investigation of the soil food web based on their no-till management.
- Well-established field and greenhouse experimental willow model systems with varying levels of genotypic diversity are already part of professional biodiversity networks [32].
- Regular shoot harvests allow for the study of temporal patterns in shorter (i.e., within one cutting cycle of three-year) and longer time scales (i.e., across subsequent cutting cycles).
- Short-rotation willow systems have characteristics that are similar in functionality to other perennial systems such as grasslands, for which much of the relevant BEF theory development has been achieved.
- The short-rotation practice of controlled removal of above ground plant parts while below ground parts are sustained implies low risk for competitive exclusion and extinction of genotypes, and thereby enhanced opportunities for the study of the mechanisms underlying plant–plant and plant–environment (abiotic and biotic) interactions in a BEF context.

In addition, major advances in BEF theory development hitherto came from experimental and modelling work done on diversity–productivity interactions in microbial and on grassland communities [85,86], which are species-rich systems. With so many species interactions, variability can be difficult to explore, although statistical models have been developed to address their complexity [87–89]. We suggest that the simplicity of the willow SRC system in itself contributes to and complements advancements in BEF theory; it allows for species interactions to be stringently manipulated experimentally and assessed. By working with willow SRC systems of fewer species, interactions of biological importance that occur across trophic levels could be revealed.

Due to the various advantages mentioned, and the notion that willow SRC systems seem to be simple enough to allow the study of the complex mechanisms involved in plant–plant and plant–environment (abiotic and biotic) interactions in a BEF context, we consider this model system attractive for future research that could fill the gaps in our understanding of what presently hampers the development of predictive BEF theory.

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