Perennial grass bioenergy cropping systems: Impacts on soil fauna and implications for soil carbon accrual

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ABSTRACT
Perennial grass energy crop production is necessary for the successful and sustainable expansion of bioenergy in North America. Numerous environmental advantages are associated with perennial grass cropping systems, including their potential to promote soil carbon accrual. Despite growing research interest in the abiotic and biotic factors driving soil carbon cycling within perennial grass cropping systems, soil fauna remain a critical yet largely unexplored component of these ecosystems. By regulating microbial activity and organic matter decomposition dynamics, soil fauna influence soil carbon stability with potentially significant implications for soil carbon accrual. We begin by reviewing the diverse, predominantly indirect effects of soil fauna on soil carbon dynamics in the context of perennial grass cropping systems. Since the impacts of perennial grass energy crop production on soil fauna will mediate their potential contributions to soil carbon accrual, we then discuss how perennial grass energy crop traits, diversity, and management influence soil fauna community structure and activity. We assert that continued research into the interactions of soil fauna, microbes, and organic matter will be important for advancing our understanding of soil carbon dynamics in perennial grass cropping systems. Furthermore, explicit consideration of soil faunal effects on soil carbon can improve our ability to predict changes in soil carbon following perennial grass cropping system establishment. We conclude by addressing the major knowledge gaps that should be prioritized to better understand and model the complex connections between perennial grass bioenergy systems, soil fauna, and carbon accrual.

KEYWORDS
biodiversity, bioenergy, carbon accrual, perennial, soil ecology, soil fauna, sustainability, switchgrass, trophic interactions
1 | INTRODUCTION

Bioenergy production will likely be a key element for reaching renewable energy and carbon (C) emission mitigation targets to limit further climate change. Stimulated by global food insecurity and environmental concerns, focus has shifted away from first-generation biofuels produced from food crops to second-generation biofuels produced from non-food sources (Nanda et al., 2015; Valentine et al., 2012). Following extensive research by the U.S. Department of Energy into diverse biomass sources, perennial grasses such as switchgrass (Panicum virgatum) are now widely believed to be the future of bioenergy in North America (McLaughlin & Kszos, 2005; U.S. Department of Energy, 2011; Wright & Turhollow, 2010) (Table 1). Multiple key advantages of perennial grass production over first-generation and annual crops have been identified, suggesting that dedicated perennial grass energy crops have the greatest potential for sustainable biomass production. Perennial grasses can successfully grow on degraded, marginal soils that are unsuitable for annual crop production, minimizing competition between bioenergy and food crops for land even as biomass feedstock demands increase (Tilman et al., 2009). Additionally, perennial grasses require less intensive management and fewer chemical inputs than their first-generation counterparts to achieve economically viable yields, providing numerous environmental benefits such as reduced nitrogen (N) leaching and greenhouse gas emissions (Robertson et al., 2017). There is also growing evidence that perennial grass bioenergy cropping systems (PGCS) promote greater biodiversity and ecosystem services, such as increased pollinator abundance and biological pest suppression, than annual, more intensively managed systems (Bellamy et al., 2009; Landis et al., 2018; Meehan et al., 2012; Núñez-Regueiro et al., 2021; Robertson et al., 2012; Werling et al., 2014). A final prominent advantage is the expectation that PGCS have greater potential to accrue and store soil organic C (SOC) (Anderson-Teixeira et al., 2009; Fargione et al., 2008; McGowan et al., 2019). However, uncertainties remain over the potential for land-use changes associated with PGCS establishment to influence SOC stability and storage (Agostini et al., 2015). As the viability of bioenergy as a C mitigation strategy hinges on the ability of bioenergy cropping systems to accrue SOC, further knowledge of SOC dynamics under PGCS is crucial for understanding the long-term sustainability of these systems.

Given the critical importance of SOC accrual for the successful expansion of bioenergy crop production (Lemus & Lal, 2005), research into SOC dynamics under PGCS has greatly expanded in recent decades. Such efforts have reaffirmed the fundamental roles of plants and soil microbes in SOC cycling. Primary production largely determines the amount of fresh SOC entering soils both belowground via the root system and aboveground as litter. High SOC inputs to PGCS result from the substantial belowground productivity characteristic of perennial grasses as well as surface litter retention in the absence of tillage (Anderson-Teixeira et al., 2013; Carvalho et al., 2017). Once in soils, the fate of these inputs largely depends on soil microbes, with their community dynamics and activity driving both SOC decomposition and stabilization (Kallenbach et al., 2016). Compared to annual cropping systems, the increased activity and densities of microbes, especially for fungi, in PGCS suggest greater potential SOC stabilization and storage within these systems (Jesus et al., 2016; Liang et al., 2015; Zhang et al., 2015; Searle and Malins, 2014; Sanderson and Adler, 2008).

| Species               | Description          | Yield range (Mg ha⁻¹ yr⁻¹) | Advantages                                                                 | Limitations                     |
|-----------------------|----------------------|----------------------------|---------------------------------------------------------------------------|--------------------------------|
| Big bluestem (Andropogon gerardii) | warm-season (C₄) grass | 6.8–11.9¹ 3.2–11.4² | Dominant native grassland species, productive across a wide geographic range | Limited research into energy crop potential |
| Miscanthus (Miscanthus × giganteus) | warm-season (C₄) grass | 4–44¹ 5–38⁴ 1.4–40.9⁹¹ | Vigorous growth with high yield potential under suitable conditions | Narrow genetic base, sterile, non-native to N. America, poor overwintering at northern latitudes |
| Reed canary grass (Phalaris arundinacea) | cool-season (C₃) grass | 1.6–12.2¹ 5.5–10.2⁶ | Broad genetic variability, productive at low temperatures | Lower N and water efficiencies than C₄ grasses, potential to become invasive |
| Switchgrass (Panicum virgatum) | warm-season C₄ grass | 0.9–34.6¹ 1–35⁴ 5.2–11.1⁴ | Dominant native grassland species, broad genetic variability, productive across a wide geographic range | Weed competition can hinder crop establishment |

¹Lewandowski et al. (2003); Zhang et al. (2015); ²Searle and Malins (2014); ³Sanderson and Adler (2008).
et al., 2012). Furthermore, insights into the interactions between soil microbes and soil characteristics emphasize the importance of microbe-soil dynamics for understanding SOC stabilization within PGCS (Kravchenko et al., 2019; Tiemann & Grandy, 2015). Taken together, SOC accrual in PGCS is thought to occur as a consequence of complex interactions between microbes, plant-derived SOC, and soil, with climate and soil characteristics serving as bottom-up regulators of microbial activity and SOC access. However, this view of SOC accrual ignores the contributions of soil fauna, a vital component of soil ecosystems with the potential to exert both bottom-up and top-down control over microbes.

Soil fauna (henceforth “fauna”) comprise much of the biodiversity belowground and perform wide ranging functions essential for crop production and overall ecosystem stability (Table 2). All of the basic processes governing SOC—addition, loss, transformation, and translocation—are influenced directly or indirectly by fauna to some degree (Fox et al., 2006; Osler & Sommerkorn, 2007; Seastedt, 1984). Despite recognition that faunal activity can substantially affect SOC fluxes, the extent to which fauna influence SOC stocks, and hence the ability of soils to accrue SOC, remains uncertain (Schmitz et al., 2014). Further insight into the potential for fauna to regulate SOC stocks in addition to fluxes is needed to improve our understanding of SOC dynamics overall. Indeed, wide discrepancies between major ecosystem models and limited predictive power remain major obstacles for simulating SOC cycling, even with the explicit inclusion of microbial dynamics. This suggests that current models fail to completely incorporate the key controls and mechanisms governing SOC dynamics, further emphasizing the need to consider faunal effects on SOC (de Vries et al., 2013; Filser et al., 2016; Grandy et al., 2016). However, major uncertainties regarding fauna community structure, function, and ecological interactions must be addressed before their explicit incorporation into SOC models is possible. While investigations into these knowledge gaps are necessary across diverse ecosystems, we argue that they are especially needed in managed systems such as PGCS due to the opportunity for new knowledge to inform management practices to promote SOC accrual.

From the limited research specific to bioenergy cropping systems, evidence suggests that PGCS better support native fauna abundance and diversity than annual, more intensively managed systems. However, questions remain regarding faunal responses to different attributes of PGCS, such as crop type, diversity, and management requirements. Less clear is the potential for such cropping system effects to alter the strength or direction of faunal effects on SOC accrual in PGCS. To address these uncertainties, our objectives are to (1) review the effects of fauna on SOC dynamics, reporting findings from North American PGCS when available and drawing inferences from studies in other managed and natural ecosystems when not, (2) discuss how crop traits and management practices typical of PGCS influence or are likely to influence fauna community structure and function in ways likely to strongly impact their effects on SOC, and (3) identify the critical knowledge gaps hindering our ability to parameterize faunal effects on SOC dynamics, using data from switchgrass bioenergy cropping systems to illustrate where future research in this topic is most needed. We synthesize findings from studies conducted specifically in the context of bioenergy as

| Functional roles          | Ecological importance                                                                 | Examples                              |
|---------------------------|--------------------------------------------------------------------------------------|---------------------------------------|
| **Microfauna**            |                                                                                      |                                       |
| Microbivores              | Regulate microbial prey populations; mineralize nutrients                             | Rhabditis spp.                        |
| Herbivores/plant parasites| Cause plant damage, disease, or death                                                | Meloidogyne incognita                 |
| Predators/omnivores       | Regulate prey populations; mineralize nutrients                                       | Dorylaimus spp.                      |
| Entomopathogens           | Infect and kill insects, including some important pest species                        | Heterorhabditis bacteriophora         |
| **Mesofauna**             |                                                                                      |                                       |
| Decomposers/microbivores  | Enhance decomposition rates by fragmenting plant litter; mineralize nutrients; regulate microbial prey | Oribatid mites, collembola            |
| Predators/omnivores       | Regulate prey populations; mineralize nutrients                                       | Mesostigmatid mites                   |
| **Macrofauna**            |                                                                                      |                                       |
| Ecosystem engineers       | Alter the physical and chemical conditions of the soil                               | Earthworms, ants, moles               |
| Decomposers               | Degrade organic material; mineralize nutrients                                        | Isopods, millipedes, earthworms       |
| Predators                 | Regulate prey populations; mineralize nutrients                                       | Carabid beetles, centipedes           |
they exist, though limited research into fauna and their effects on SOC within PGCS necessitates drawing inferences from studies conducted in other, comparable arable and natural lands. While we narrow our focus in this review to North American PGCS, further investigations into the interconnections between belowground biodiversity and SOC dynamics will doubtlessly be an important aspect in better understanding the sustainability and efficacy of bioenergy cropping systems dominant in other parts of the world.

2 | SOIL FAUNA EFFECTS ON SOC DYNAMICS

2.1 | Direct effects: SOC inputs and losses from fauna

Fauna-derived SOC inputs include living biomass, necromass, exuviae, fecal pellets, and other biosynthesized materials. Temperate grasslands support high faunal densities compared to other biomes (Petersen & Luxton, 1982). Similarly, greater densities under PGCS relative to annual systems have been reported for diverse faunal groups: detritivorous invertebrates (Hedde et al., 2013) including collembola (Bellamy et al., 2009), mites (Zahorec et al., 2021), and earthworms (Emmerling, 2014; Felten & Emmerling, 2011; but see Briones et al., 2019) as well as carabid beetles (Ward & Ward, 2001). Additionally, fecal pellets can be found in abundance in the surface layers of grassland soils (Davidson et al., 2002). While this could indicate a greater quantity of fauna-derived SOC under PGCS, these inputs likely comprise only a small fraction of total SOC stocks. At the Kjettslinge field experiment, fauna only contributed between 1.63% and 5.48% to total soil biomass, even less when root biomass was considered (Andrén et al., 1990). Similarly, faunal biomass C was estimated as less than 4% that of soil microbes in temperate grasslands (Fierer et al., 2009). The low relative biomass of fauna suggests that the vast majority of SOC in PGCS will be of plant or microbial origin, with only minor faunal inputs to total SOC stocks.

Direct losses of SOC from fauna result from SOC consumption, most prevalently through detritivory and microbivory, and subsequent respiration of unassimilated C. How much SOC is lost from PGCS by faunal respiration is unknown, though it can be assumed that fauna make lesser contributions to total soil respiration than microbes. Studies from other systems indicate that faunal respiration accounts for as much as ~10% of total soil respiration (Andrén et al., 1990; Reichle, 1977; Schaefer, 1990), though lower faunal contributions are also possible (Jiang et al., 2016; Persson et al., 1980). While microbes should have the greatest direct influence on SOC losses from PGCS, it remains unclear if fauna will have significant, albeit secondary, direct effects on SOC loss.

The balance between direct faunal SOC inputs, including biomass and biosynthesized products, and respiratory losses determines the net contribution of fauna on SOC stocks. Historically, this was estimated by combining faunal community structure, life history, and energetics data to calculate mean annual SOC flow through fauna. This requires a great deal of taxa-specific information which is largely unexplored except for a relatively small number of soil food web studies. Even less understood is the relative stability of faunal SOC inputs, which is necessary to determine if faunal SOC gains are ultimately accrued. It is now known that molecular recalcitrance is a poor predictor of SOC stability (Schmidt et al., 2011), challenging traditional assumptions that faunal input C:N ratios should reliably correlate with their turnover times. Faunal fecal production is predicted to stimulate aggregate formation (Maaß et al., 2015) and can enhance dissolved OC (DOC) leaching (Joly et al., 2020), both of which could promote long-term fecal-SOC storage. Further research into partitioning of faunal-SOC inputs in PGCS into active, slow, and passive SOC pools will be necessary to understand the true direct contributions of fauna to SOC accrual.

2.2 | Indirect effects: interactions with microbes and organic matter

While fauna have only weak direct effects on SOC gains and losses, their numerous indirect effects on SOC may be significant regulators of SOC dynamics (Seastedt, 1984; Wolters, 2000; Yang & Gratton, 2014). These indirect effects can be categorized as direct or indirect microbial interactions or organic matter decomposition effects. While this attempts to make broad distinctions between the predominant mechanisms driving these interactions for ease of discussion, these categories are often overlapping. We focus our attention primarily on fauna interactions with microbes and plant-derived organic matter as they have received the greatest research attention to date and point readers to Bonkowski et al. (2009) for greater detail on fauna–plant interactions.

2.2.1 | Effects on microbes

Microbivory can strongly affect SOC decomposition and stability by exerting top-down control over microbial activity and community dynamics. Detritivorous and microbivorous fauna have been found to alter microbial activity (Crowther et al., 2012; Wickings & Grandy, 2011), biomass...
(Bradford et al., 2002; Trap et al., 2016), and community composition (Janoušková et al., 2018), with the strength and direction of faunal effects depending on microbivore identity and grazing intensity. A major way in which faunal grazing can stimulate microbial activity is by enhancing microbial turnover and subsequent N mineralization (Bardgett & Chan, 1999). Fauna have significant influence over N availability in soils, with ~30% of total N mineralization attributed to their activity (Verhoef & Brussaard, 1990). This can have important implications on microbial and plant growth, especially when N is limiting as is the case for many marginal soils. Faunal grazing can stimulate microbes via other mechanisms as well, such as grazing triggering compensatory growth (Bengtsson et al., 1993; Hanlon & Anderson, 1979; Hedlund & Augustsson, 1995), though further research is needed to determine the extent to which such mechanisms observed in simplified microcosm studies occur in natural settings. Taken together, microbivory can significantly influence microbial activity, growth, and composition. Thus, microbivory can thus indirectly affect SOC by altering the quantity of microbial SOC inputs or losses as well as how microbes access and utilize organic matter. The strength and direction of the effect on SOC will ultimately depend on the balance between stimulatory and inhibitory effects of microbivory as well as the identities of the microbes preyed upon.

Fauna also have important bottom-up effects on microbes by influencing the physical and chemical properties of soils. These bottom-up effects can arise due to changing microclimatic conditions in response to faunal activity. Tunneling and burrowing by macrofauna “ecosystem engineers” can profoundly alter soil porosity, water and gas movement, temperature, and chemistry, all of which are important abiotic controls over microbial activity. Ant activity has been shown to have a range of impacts on microbial diversity and activity in north temperate grasslands (Wills & Landis, 2018), with potentially important implications for how these microbes process SOC. Additionally, fauna alter the molecular, chemical, and physical structure of organic matter via mechanisms including bioturbation, ingestion/excretion, and litter fragmentation, subsequently impacting its accessibility to microbes (Filser et al., 2016; Wickings & Grandy, 2011). Macrofauna can also enhance the incorporation of C in microaggregates within larger macroaggregates, indicating their potential for macrofaunal activity to enhance SOC stabilization by increasing the amount of C physically protected from microbial decomposition (Fonte et al., 2007; Franco et al., 2020). Thus, faunal activity can influence microbial activity by regulating microbial access to SOC which in turn affects SOC stabilization. Lastly, belowground herbivory by fauna can have important consequences for rhizosphere microbes, though more research is necessary to understand the implications of these multitrophic interactions on SOC dynamics (Gan & Wickings, 2020).

### 2.2.2 Organic matter decomposition

Detritivorous fauna, particularly meso- and some macrofauna, play a significant role in organic matter decomposition with important consequences for plant residue stabilization and turnover. There is general consensus from litter bag studies that fauna accelerate decomposition, with the strongest positive faunal effects found in grasslands (García-Palacios et al., 2013). Furthermore, Seastedt (1984) reported an ~22% average increase in grass litter decomposition rate with faunal access to litter bags. On the contrary, faunal suppression had no noticeable effect on litter mass loss in miscanthus (Miscanthus × giganteus), switchgrass, or prairie bioenergy cropping systems, though fauna had largely recolonized insecticide treated units by the end of the study (Zangerl et al., 2013). As faunal effects on litter mass loss vary with climate and litter quality (González & Seastedt, 2001; Sauvadet et al., 2017), more research within PGCS is needed to predict the impact of fauna on litter turnover in these systems.

Detritivorous fauna strongly influence the physical and chemical properties of litter which can significantly affect how decomposer microbes and soil surfaces interact with litter C. These effects, which are not always captured in litter bag studies, are expected to have important implications for SOC fate and stability. Litter C becomes more accessible to microbes following faunal fragmentation, gut processing, and excretion (Edwards, 2000; Petersen & Luxton, 1982), such that fauna help to facilitate the flow of C from litter to microbial pools. Faunal litter processing is also expected to influence the production and leaching of DOC (Cragg & Bardgett, 2001; Joly et al., 2020; Osler & Sommerkorn, 2007), a critical component of stabilized SOC for its ability to associate with mineral surfaces (Cotrufo et al., 2019). Both mechanisms can have substantial impacts on overall SOC stability, as was found in a 3-year decomposition study conducted in a tallgrass prairie. Positive effects of fauna on big bluestem (Andropogon gerardii) decomposition during the first 18 months increased microbial uptake of litter-C during the early stages of decomposition (Soong et al., 2016). Another early-stage effect of fauna was increased incorporation of litter-C and N into silt- and clay-sized SOC pools, suggesting enhanced DOC leaching. When simulated in DayCent, these faunal effects on litter C transfer into microbial and slow SOC pools increased total SOC by 11% over two centuries. This study puts forth compelling evidence that by altering the properties of organic matter, fauna can indirectly promote...
SOC accrual by affecting when and how microbes as well as mineral surfaces associate SOC inputs.

3 | CROPPING SYSTEM EFFECTS ON SOIL FAUNA

In the previous section, we reviewed the diverse ways fauna influence SOC dynamics. We find evidence from the current literature that fauna make relatively minor direct contributions to SOC gains and losses. In contrast, indirect faunal effects on SOC, as mediated by their impacts on microbes and organic matter decomposition, can strongly influence the fate and stabilization of SOC. It can be surmised that such indirect effects of fauna should therefore have the greatest potential to impact SOC accrual potential, with direction of their effects on SOC accrual depending on how fauna alter the interactions between SOC, microbes, and the mineral soil. Theoretically, faunal effects that enhance food web C efficiency and SOC stabilization can promote SOC accrual, whereas the opposite can result in SOC depletion as respiratory losses outpace SOC gains (Figure 1). The strength of faunal effects on SOC accrual should depend in part on the activity and structure of faunal communities, which is largely dependent on aboveground land use. For this reason, understanding how land use impacts fauna and their ability to indirectly affect SOC is essential to understanding their potential contributions to SOC accrual. This is especially important in PGCS, wherein management practices can be readily implemented to promote positive faunal effects on SOC accrual.

While studies exploring the impacts of bioenergy cropping system establishment on native biodiversity continue to emerge, few have evaluated the responses of soil fauna (Dauber et al., 2010; Immerzeel et al., 2014; Lask et al., 2020). As stated earlier, current research indicates that PGCS can better support native fauna compared to annual cropping systems. However, the potential variability in faunal community structure, diversity, and activity across diverse PGCS remains largely uninvestigated. Physiological and morphological trait variation across different candidate perennial grass energy crops is expected to have differing effects on fauna. Indeed, Emery et al. (2017) reported significant differences in nematode community composition between switchgrass and miscanthus, with miscanthus communities dominated by plant-parasitic nematodes. Plant diversity and management differences across PGCS may also impact faunal communities with potential implications for their effects on SOC. Therefore, to understand how SOC dynamics in PGCS are influenced by fauna, it will be important to consider how faunal communities and activities are affected by different PGCS characteristics. We begin by discussing the potential bottom-up effects of perennial grass energy crops on fauna by serving as sources of food and habitat, followed by cropping system characteristics, specifically crop diversity and N additions, as they pertain to faunal communities.

**FIGURE 1** Conceptual diagram showing C transfers between living (circles) and non-living (square) SOC pools with levers representing the interactions where fauna theoretically have the greatest potential to positively or negatively influence SOC accrual. These interactions include (1) effects on SOC (largely particulate OM) quality and/or accessibility to decomposer microbes, (2) trophic interactions with microbes which alter community-level microbial turnover and functioning, and (3) indirect effects on microbes (e.g., microhabitat modifications via bioturbation) that subsequently affect how microbes and SOC interact. Each of these interactions are primarily indirect, with direct faunal effects from SOC inputs (e.g., necromass) and outputs (CO₂) expected to have only minor influence on SOC accrual. Living plants omitted for simplicity and substantial uncertainties regarding the mechanisms and relative significance of fauna–plant and fauna–microbe–plant interactions on SOC accrual.
3.1 | Perennial grasses as the base of soil food webs

Perennial grass energy crops represent a diversity of physiological, morphological, and phenological traits. These traits largely determine the quality and quantity of SOC inputs in soils and thus serve as important bottom-up regulators of consumers in soil food webs. Unlike aboveground food webs, the influence of plant-specific traits in shaping soil fauna communities is expected to be greatest at large spatial and temporal scales, whereas interspecific interactions between soil biota are assumed to be the primary drivers of soil community dynamics at local levels (Wardle, 2006).

The quality of perennial grass residues has important implications for soil food web structure. Bacteria and their consumers dominate the rhizosphere where labile, high-quality substrates (e.g., root exudates) are most heavily concentrated, whereas more C-rich litter selects for increased fungi and fungivore activity (Figure 2). Grass litter is relatively low quality, with warm-season C4 grasses generally producing higher C:N, more recalcitrant residues than cool-season C3 grasses (Baer et al., 2002; Vivanco & Austin, 2006). Across five PGCS at the Kellogg Biological Research Station, average surface litter C:N over 7 years ranged from 36.2 in native C3 and C4 polycultures to 64.4 for miscanthus monocultures (Robertson, 2021). Residue quality may impact fauna by altering soil food web structure, as C:N is known to influence microbial community composition (Liang et al., 2017; Waldrop & Firestone, 2004). Furthermore, the production of high C:N energy crops on bacterial-dominated soils typical of agroecosystems may lead to N competition between fauna and microbes (Ernst et al., 2009), which may be especially important in marginal soils. However, the limited responses of diverse faunal groups to residues of differing quality may indicate that residue quality impacts on fauna may only become appreciable when C:N differences are very large (Porazinska et al., 2003; Sauvadet et al., 2016). For instance, earthworm densities were similar under miscanthus and SRC willow systems despite miscanthus, a C4 grass, producing higher C:N litter, but densities in

![Diagram of SOC flows through soil food web channels](image-url)

**FIGURE 2** Potential pathways of SOC flows through soil food web channels. Arrows represent C transfers color-coded by C origin: root-derived (green), living heterotroph biomass (blue), and litter-derived (yellow). (1) Much of the photosynthetically fixed C (photosynthate) produced by grasses is allocated belowground through the roots, (2) fueling root symbionts and other rhizospheric microbes, predominantly bacteria. (3) Microbial, especially bacterial, predation is high in the rhizosphere and promotes N mineralization, while (4) parasites, pathogens, and other pests attack crop roots. In contrast, saprotrophic microbes, predominantly fungi, and detritivores subsist on more recalcitrant litter, in which (5) shredding by decomposer fauna promotes further decomposition by microbes, which are also (6) often ingested along with the litter they colonize. (7) Belowground and surface-dwelling predators prey upon consumers from both food webs. In addition to cycling between trophic groups, (8) C can exit soils via respiration or (9) become stabilized and, at least for some time, protected from further decomposition.
these PGCS were strongly reduced compared to those in an annual arable system (Briones et al., 2019). Soil food webs also exhibit a relatively high degree of omnivory and generalism, and hence, minor or moderate differences in residue quality between perennial grass energy crops may be largely negligible.

Primary productivity influences soil food web structure by controlling the quantity and relative partitioning of above- and belowground plant C entering soils. How much plant productivity ultimately enters soil food webs as belowground production or litter depends on interactions between species- or variety-specific traits and external factors. Across three PGCS established in Illinois, United States, belowground biomass and surface litter inputs were highest in miscanthus, intermediate in switchgrass, and lowest in native prairie cropping systems (Anderson-Teixeira et al., 2013). The quantity of litter and belowground inputs is also regulated by climatic variables such as mean annual temperature and precipitation as well as soil characteristics. Indeed, belowground biomass and litter production differed greatly for both switchgrass and native prairie systems depending on PGCS site geography (von Hadern et al., 2019). As soil food webs are thought to be largely donor controlled, productivity helps determine the faunal densities PGCS can sustain. Thus, perennial grass energy crops that provision greater residue quantities to soil can theoretically support more abundant belowground communities. However, few empirical studies have specifically investigated the effects of residue quantity on fauna. While positive effects of fauna on above- and belowground productivity have been observed, it remains uncertain what, if any, feedbacks these changes in residue quantity have on faunal communities (Bais et al., 2006). Fauna consumers are widely believed to be less constrained by resource competition compared to those aboveground, and many possess physiological adaptations to persist during periods of resource scarcity or environmental unfavorability. Indeed, litter quantity was found to have only transient effects on fauna in a cultivated soil, with faunal densities similarly high across soils with differing amounts of litter after 11 months, even in treatments with no litter (Sauvadet et al., 2016). Thus, the influence of primary productivity in PGCS, and thus residue quantity, may have only minor effects on fauna.

3.2 Perennial grasses as habitat provisioners and modifiers

Plants exert significant influence over the physical and climatic conditions of surface soils which has important implications for soil microclimate and habitat conditions. Many traits characteristic of perennial grasses linked to their enhanced environmental sustainability can also benefit fauna. The greater root biomass associated with perennial grasses enhances soil porosity, facilitating water drainage and gas exchange as well as creating channels for faunal movement (Marshall et al., 2016). This improved soil structure increases the volume of soil accessible to fauna, connectivity between resource patches, and spatial heterogeneity within the soil matrix. This may become increasingly important in subsurface soils as organic matter becomes scarcer and bulk density increases with depth. Meso- and microfauna should be especially sensitive to root effects on soil structure, as they rely on pre-existing pore spaces to move throughout the soil. Tallgrass species such as big bluestem tend to have greater fine and coarse root production at depth compared to shortgrass species (e.g., blue grama, Bouteloua gracilis, also a C4 grass) with shallower root systems (Craine et al., 2002). Switchgrass and miscanthus root systems can extend several meters below the soil surface, though environmental conditions, soil characteristics, and management can significantly influence the depth and distribution of their roots (Ma et al., 2000; Mann et al., 2013). Other traits affecting root architecture may also influence fauna in PGCS, especially microfauna and root-associated groups. For instance, under blue grama-dominated fields, increased specific root length and branching intensity corresponded to elevated and depressed densities of root feeding nematodes, respectively (Otfinowski & Coffey, 2020). While variation in perennial grass root architecture has been shown to have important implications for SOC decomposition (de Graaff et al., 2013), the extent to which fauna effects on SOC may be impacted by root architecture differences between species remains unknown.

Furthermore, the lack of tillage in PGCS allows the accumulation of a stable litter at the soil surface. The litter layer provides habitat for surface-dwelling species and regulates soil microclimate conditions as it buffers the underlying soil from diurnal temperature fluctuations and moisture loss (Andrade et al., 2010), both of which can have important impacts on fauna. Although the effects of litter on fauna in the context of PGCS specifically remains to be investigated, litter has been linked to greater densities for earthworms (Melman et al., 2019), isopods (Souty-Grosset & Faberi, 2018), microarthropods (Santos et al., 1978), and other surface-dwelling species (Facelli, 1994) in a range of habitat types. As fauna are highly sensitive to soil temperature and moisture, PGCS management practices that influence litter layer thickness and stability are predicted to have substantial effects on fauna communities. For instance, baling after harvest can strongly depress the amount of aboveground residues that become incorporated into the litter layer (Anderson-Teixeira et al., 2013; Kantola et al., 2017), which may negatively impact fauna.
3.3 | Cropping system diversity effects

While plant diversity is a driver of aboveground faunal diversity and abundance in PGCS (Webster et al., 2010), the effects on belowground communities are expected to be much more complex. Faunal responses to increasing plant richness are largely idiosyncratic across systems (de Deyn et al., 2004; Hooper et al., 2000; Wardle, 2006). As faunal communities exhibit high functional redundancy and resiliency, plant composition, particularly plant functional trait composition, is predicted to influence fauna more strongly than plant diversity per se (Beugnon et al., 2019). To date, the potential relationships between plant richness, plant functional diversity, and faunal diversity remain poorly understood within PGCS. Restored prairie cropping systems containing a mix of native grasses, legumes, and forbs supported more diverse ant communities than switchgrass (Helms et al., 2020). In contrast, nematode diversity under switchgrass stands was similar regardless of whether switchgrass was grown in monoculture or within a diverse prairie polyculture (Bliss et al., 2010). While nematodes have smaller spatial distributions than meso- and macrofauna and thus the potential effects of diversity may not have been fully captured, it is also likely that different size classes, and thus different functional groups, may exhibit variable responses to plant diversity.

While plant and faunal diversity appear to be relatively uncoupled, plant diversity has been found to influence other aspects of belowground communities that may become important when considering faunal effects on SOC. Greater plant richness can increase the quality range for residues entering soil food webs, potentially allowing more trophic levels to coexist than when plant richness, and thus residue quality diversity, is low. Indeed, there is evidence that plant diversity aboveground is associated with increased soil food web complexity. Eisenhauer et al. (2011) reported functional shifts in nematode communities as a function of grassland plant richness, with high-diversity grasslands supporting increased fungivorous and predatory nematodes and relatively lower herbivorous nematodes compared to species-poor grasslands. Furthermore, Helms et al. (2020) analyzed arthropod food webs across diverse bioenergy cropping systems and found restored prairie polycultures supported longer food chains than switchgrass monocultures. Plant diversity may also influence fauna community structure indirectly. For instance, perennial grass energy crop monocultures produce significantly fewer fine roots than perennial polycultures (Sprunger et al., 2017), which can influence the quality and quantity of root-derived SOC entering soil food webs as well as soil microhabitat or microclimate conditions.

A final aspect of plant diversity to consider is the potential effect of unplanned non-crop diversity (e.g., weeds). No-till, low-input PGCS can contain relatively high weed diversity and biomass, especially after initial planting (Holguin et al., 2010; Werling et al., 2014). Weeds, which inflate plant diversity and habitat heterogeneity within PGCS, can serve as additional habitat and food sources for fauna. Weed biomass and diversity can promote soil arthropod abundance and diversity with potentially significant impacts on soil food web structure. Following herbicide application and subsequent herbicide-resistant weed invasion, Wardle et al. (1999) observed increased faunal abundances in agricultural fields, indicating that fauna were more strongly impacted by plant community changes than the herbicide itself. Additionally, Semere and Slater (2007) reported greater carabid beetle diversity and abundance associated with miscanthus bioenergy cropping systems compared to reed canary grass (Phalaris arundinacea), and that these differences resulted from the greater abundance of weeds in miscanthus rather than crop type. As PGCS generally receive no or low weed control, weeds may provide beneficial diversity effects for belowground communities, the extent to which warrants further investigation.

3.4 | Impacts of nitrogen addition

Land-use intensification has consistently strong adverse effects on soil fauna (de Vries et al., 2013). Reduced management intensity and land conversion (e.g., conventional annual cropping systems to grassland) have a range of potential benefits on soil communities (Felten & Emmerling, 2011; Postma-Blauw et al., 2010; Tsiafouli et al., 2015) which are expected to favor fauna in minimally managed PGCS. While management practices known to be detrimental to fauna (e.g., annual tillage) are largely absent, many PGCS still receive some degree of N fertilization. Within the United States, a range of 67–110 kg N ha$^{-1}$ yr$^{-1}$ is recommended for native warm-season grasses, while cool-season grasses have greater N demands (Brezda, 2000). Although this is a reduction compared to the amount of N required for annual systems, the strong effects of N additions on soil chemistry have the potential to impact fauna even at relatively low fertilization rates. For this reason, the potential for N additions in PGCS to affect fauna and their effects SOC dynamics warrant investigation.

N additions can indirectly affect fauna via their substantial impacts on soil microbial communities (Fierer et al., 2012; Geisseler & Scow, 2014). Increased bacterial dominance (de Vries & Bardgett, 2012; de Vries et al., 2006) as well as reductions in sensitive functional groups
such as arbuscular mycorrhizal fungi and Gram-negative bacteria (Leff et al., 2015; Oates et al., 2016; Zhang et al., 2018) have been associated with increased N fertilization. These changes in microbial community structure may have cascading effects on higher trophic levels. The lower fungi-to-bacteria ratios of N-fertilized soils should favor bacterivores and disfavor fungivores, as has been reported with nematodes (Emery et al., 2017; Gruzdeva et al., 2007; Murray et al., 2006; but see Ikoyi et al., 2020). However, faunal responses to N addition are difficult to generalize, perhaps in part due to the types of N additions applied varying across studies (Table 3). A recent meta-analysis reported generally negative effects of fertilization on faunal diversity, with high variability in faunal response depending on the type, amount, and duration of N additions (de Graaff et al., 2019).

**Table 3** Responses of soil biota to N fertilizer application. Effects are distinguished as: +, positive; –, negative; NA, no effect. Fertilizer type (O, organic; I, inorganic) included when specified. Responses are color-coded as follows: results from perennial grass systems in green, other perennial systems in blue, and annual systems in orange.

| Abundance | Diversity |
|-----------|-----------|
|           | – | + | NA | – | + | NA |
| Macrofauna | 1 | 2 (I) | 3 (I) | 5 (O) | 6 (O, I) | 5 (O) | 6 (O, I) |
| Earthworms | 4 (I) | 5 (O) | 1 | 1 |
| Carabid beetles | 5 (O) | 6 (O, I) | 5 (O) | 5 (I) | 6 (O, I) |
| Mesofauna | 7 |
| Collembola | 1 (O, I) | 8 (O, I) | 1 |
| Prostigmatid mites | 8 (O, I) |
| Microfauna | 11 (O) |
| Nematodes | 2 (I) | 9 (O) | 10 (O, I) | 11 (O) | 1 | 13 (I) | 9 (O) |
| Bacterivore | 12 (I) | 2 (I) | 9 (O) | 10 (O, I) | 11 (O) | 14 (I) | 2 (I) |
| Fungivore | 2 (I) | 3 (I) | 10 (I) | 9 (O, I) | 11 (O) | 12 (I) |
| Plant parasite | 9 (O) | 10 (O, I) | 13 (I) |
| Omnivore | 11 (O, I) | 12 (I) |
| Predators | 2 (I) | 3 (I) | 9 (O) |
| Protists | 11 (O) | 15 (O, I) | 16 (I) |

References: 1Cluzeau et al., 2012; 2Murray et al., 2006; 3Blanchart et al., 2006; 4Ma et al., 1990; 5Raworth et al., 2004; 6Sadej et al., 2012; 7Crossley et al., 1992; 8Wang et al., 2016; 9Hu and Qi, 2010; 10Zhang et al., 2016; 11Forge et al., 2005; 12Ikoyi et al., 2020; 13Emery et al., 2017; 14Gruzdeva et al., 2007; 15Lentendu et al., 2014; 16Zhao et al., 2019.
conducted in more conventional annual, largely maize (Zea mays), cropping systems. As N tends to cycle more efficiently and be less limiting under PGCS, it is possible that the soil communities they support will respond less strongly than fauna in annual, more intensely managed systems.

Furthermore, the effect of N additions alone cannot be decoupled from other potential effects from the use of legumes or organic fertilizers, such as increased plant diversity. Additionally, both inorganic and organic N additions can significantly impact the quality and quantity of plant residues, resulting in additional indirect effects on fauna. For instance, the concentration of C compounds exuded by switchgrass roots doubled at high compared to low N availability (Smercina et al., 2021), which may further promote bacteria-based food webs over fungal-base webs. To date, no standardized investigations into N addition effects on diverse faunal groups across large geographic scales, as have been done for microbes (Zhang et al., 2018), have been attempted to our knowledge. Thus, potential patterns in faunal responses to N additions in grassland ecosystems remain obscure, as are any implications they may subsequently have on SOC accrual. The potential for N additions to impact soil food web structure, which can alter the balance between C and N mineralization and immobilization as microbes and fauna compete for N and subsequently affect SOC accrual, warrants further investigation in PGCS.

4 | IDENTIFYING THE UNKNOWNS

Substantial work had gone into identifying the factors driving SOC accrual in PGCS, with the ultimate goal of predicting SOC changes following cropping system establishment. As switchgrass has been identified as a promising herbaceous energy crop for biomass production within the continental United States (Wright & Turhollow, 2010), it has been the subject of considerable research to understand its potential impacts on SOC stocks. Current evidence suggests that switchgrass cropping systems (SWCS) establishment is generally associated with SOC gains exceeding the 0.25 Mg C ha$^{-1}$ yr$^{-1}$ minimum necessary for cropping system C neutrality (Agostini et al., 2015; Frank et al., 2004; Liebig et al., 2008; Martinez-Feria & Basso, 2020). However, variability in SOC accrual potential across sites is high, with SWCS establishment resulting in SOC losses in some circumstances. Understanding the sources of this variability will be necessary to better model SOC dynamics in switchgrass and other PGCS. To date, research into potential sources of variation in SOC changes has focused on climate, soil characteristics, management practices, and, increasingly, microbial dynamics (Garten & Wullschleger, 2000; Tiemann & Grandy, 2015). As was detailed in previous sections, fauna have diverse influences over SOC, largely through their effects on microbes and decomposition dynamics, with potentially significant implications for the SOC accrual ability of PGCS soils. Thus, we argue that the explicit incorporation of fauna community structure and activity can improve our ability to accurately model SOC dynamics, predict SOC changes with PGCS establishment, and account for site-specific variability. However, there remain critical knowledge gaps relating to which, how, and to what degree do soil fauna influence SOC that must first be addressed before this can be achieved. Here, we describe these major knowledge gaps, with particular focus on how they can be addressed within SWCS.

While much data exist and continue to be generated on abiotic, plant, and microbial dynamics from diverse switchgrass ecosystems, soil fauna communities remain one of the last major unexplored ecosystem components of SWCS. Little data exist on the faunal biodiversity associated with switchgrass, and even less is known of the spatial or temporal variability of these communities (Table 4). Understanding faunal biodiversity within SWCS will be important for identifying dominant or potential “keystone” groups which may have outsized influence on SOC. In an example from a Sitka spruce forest, the dominant litter-dwelling arthropod Onychiurus latus, a fungivorous collombola, altered that natural distribution of saprotrophic fungi by preferentially grazing upon the competitively superior Marasmius androsaceus (Newell, 1984a, 1984b). Since M. androsaceus was also found to enhance the decomposition rate of litter, O. latus may also be indirectly slowing litter decomposition in this forest by allowing the competitive inferior fungus to strive where it is abundant. Beyond species richness and identification, knowledge on faunal functional richness and food web dynamics can be useful to predict which faunal effects are likely to have the greatest impact on SOC. For instance, the expansive, deep rooting systems of switchgrass may favor bacterial-based food webs and promote high abundances of microfauna, thus enhancing N mineralization by stimulating microbial turnover. This in turn could alleviate switchgrass-microbe competition for N, which can promote SOC gains by preventing SOC mining by N-limited microbes or improving switchgrass biomass production.

Uncovering the taxonomic and functional composition of faunal communities will also be useful for identifying key invertebrate–fauna interactions in relation to SOC dynamics within SWCS. While the prospect of identifying such interactions remains a daunting task, insights into the identities of key microbes associated with switchgrass can serve as a starting point. Numerous microbial...
taxa and functional groups (e.g., arbuscular mycorrhizal fungi) comprising the switchgrass microbiome have been found to increase switchgrass biomass production and stress tolerance (Hestrin et al., 2021). By regulating the abundance or activity of these microbes, fauna have the potential to alter the quantity of switchgrass productivity that ultimately enters SOC pools. Documented effects of soil fauna on arbuscular mycorrhizal fungi, as well as the responses of plants to such interactions, range from positive to negative (Dauber et al., 2008; Gange, 2000; Hol & Cook, 2005; Paudel et al., 2016). In SWCS, the combined reduction of AMF and nematodes altered the lignin composition of aboveground switchgrass tissues (Basyal et al., 2021), which may influence its subsequent decomposition.

Another major knowledge gap is that, of the diverse ways soil fauna can influence SOC (see Figure 1), it remains essentially unknown how these effects operate within SWCS. Furthermore, the mechanisms driving many of these effects are not clearly understood, especially regarding how they influence SOC stability. Litter bag studies, widely used to study the role of fauna in residue decomposition by tracking residue mass loss overtime, provide no information on how residues were lost. Hence, despite the overall positive trend of fauna on litter mass loss from these studies, how much mass loss can be directly attributed to faunal ingestion as opposed to indirect faunal effects (e.g., enhanced microbial decomposition or DOC leaching in the presence of fauna) remains unclear.

A similar issue arises from studies measuring soil respiration in the presence or absence of fauna; increased respiration in the presence of fauna may arise from compensatory growth of grazed microbes, microbial utilization of labile C compounds in fecal pellets, or more suitable microclimate conditions for microbes. As each of these potential mechanisms has differing implications on SOC stability and fate, such investigations provide incomplete information into the true nature of faunal effects on SOC. Investigations conducted within SWCS into the role of fauna on SOC should therefore be designed such that the fate of SOC as it is transferred between pools with different turnover times is measured, rather than simply short-term SOC gains or losses. This was effectively done by Soong et al. (2016), who in addition to measuring the effect of fauna on litter mass loss examined the incorporation of litter C into organic matter fractions as well as microbes.

As mechanisms behind faunal effects on SOC are better understood, the direction, strengths, and variability of these effects must be quantified and validated in order to be parameterized and incorporated into SOC models as is currently being done for soil microbes (Wieder et al., 2014). It has already been stated that faunal activity, particularly that of detritivorous groups, generally increases decomposition rates. Thus, reported decomposition rates for switchgrass residues measured in the absence of fauna may be underestimated. However, the degree to which faunal influence residue decomposition will depend on the quality
of the residue, which strongly varies between switchgrass tissue types (Johnson et al., 2007). While knowledge on the quantity and quality of switchgrass net primary productivity that becomes incorporated as SOC continues to expand across climate gradients and soil types (Agostini et al., 2015; von Haden et al., 2019), to our knowledge, only one study (Zangerl et al., 2013) has attempted to quantify the contribution of fauna to switchgrass residue decomposition. The degree to which switchgrass residues of different quality are fed upon and by which fauna in SWCS can have significant implications for the fate of these inputs as they are made more or less available for subsequent microbial degradation. Furthermore, it will be important to investigate the variability of fauna effects across different climate conditions and soil types as well as under different levels of N fertilization as each of these factors can strongly influence soil fauna community structure, activity, and interactions with microbes. Temporal variability must also be considered, as seasonal variation in soil fauna communities will influence how and how strongly soil fauna communities affect SOC.

5 | CONCLUSIONS

Substantial research has been devoted in recent decades to evaluating the environmental impacts of perennial grass energy crop production in North America. There is general consensus that PGCS are a more sustainable alternative to annual, first-generation energy crops, owing to their higher potential to offset C emissions with less risk for indirect land use effects and lower management requirements (Robertson et al., 2017). Still, there remain critical gaps that challenge assumptions of the long-term success and sustainability of perennial grass energy crop production. Critically, high variability in SOC stock responses to PGCS establishment, coupled with SOC modeling limitations, remains significant barriers to bioenergy expansion. SOC accrual, a prerequisite for bioenergy, can be conceptualized as the consequence of interconnected physical, chemical, and biological processes and interactions. Research developments continue to elucidate the critical roles of plants, their residues, and microbes in SOC formation, decomposition, and stabilization. However, comparatively little research has focused on the potential contributions of fauna. As such, their contributions to SOC accrual in PGCS can currently only be speculated at. Despite this, we have shown that soil fauna have diverse effects on soil microbial community structure and activity and organic matter decomposition dynamics, the results of which can influence the interactions between microbes, plant residues, and mineral soils. Thus, faunal activity has the potential to indirectly regulate SOC stability. Much research is needed to elucidate the direction, strength, and primary mechanisms driving these faunal effects in PGCS, yet it will be important to gain a more comprehensive understanding of the biotic factors regulating SOC accrual.

While the influence of fauna on SOC accrual ability remains obscure, the strong influence of aboveground land use on fauna is well documented. In order to understand the role of fauna on SOC dynamics in PGCS, it will be necessary to consider how PGCS characteristics moderate faunal community structure and function. While current evidence suggests that PGCS favor fauna relative to annual cropping systems, little is known about how faunal communities differ across the diverse range of potential PGCS. Perennial grass traits expected to have the greatest potential impact on fauna are those that influence the quality (e.g., C:N) and/or quantity (e.g., belowground biomass) of residue inputs to soil food webs or influence the faunal habitat conditions. PGCS design, such as monoculture or polyculture, and N additions are also expected to have potentially important impacts on fauna. Greater understanding into how faunal communities, as well as their interactions with microbes and organic matter, are affected by these characteristics can help to predict faunal effects on SOC across diverse PGCS.

Greater investigation of the primary faunal effects on SOC and the extent to which they can influence SOC accrual potential within varying PGCS could eventually lead to the incorporation of fauna in SOC models. At present, however, the basic knowledge of the structure and functioning of native faunal communities within PGCS is incredibly scarce. Even for switchgrass, the “model” perennial grass energy crop in North America, the taxonomic and functional richness of faunal communities it is associated with is practically unknown. Furthermore, which of the numerous diverse faunal effects could be having the greatest impact on SOC in PGCS, and to what extent, can only be speculated at in the absence of empirical study. It will also be necessary to consider how both faunal community structure and their effects on SOC vary both spatially and temporally. While this list of knowledge gaps is far from exhaustive, prioritizing research in these areas is a crucial next step to improve our understanding of fauna, an obscure yet ubiquitous component of PGCS, and their role in SOC dynamics.

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DATA AVAILABILITY STATEMENT
There is no data available as no new data were generated in the production of this review.

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