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Biomass and biofuel crop effects on biodiversity and ecosystem services in the North Central US

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1. Introduction

The adoption of biomass cropping systems to supply feedstocks to bioenergy and bioproducts industries has the potential to alter the mix of ecosystem services realized from agricultural landscapes [1]. In the North Central US, current biomass cropping systems are primarily monocultures of the annual crops corn and soybean. However, the diversity of systems used for biomass crops in the region is likely to be augmented in the future by dedicated crops based on perennial plants [2]. Assessing what biomass crops to grow, where to grow them, and how they should be managed represents a complex combination of socio-political, economic, and ecological decisions that will determine the mix of ecosystem services we derive from agricultural lands.

An ecosystem services framework has been useful in evaluating the relative merits of different bioenergy production systems. Gasparatos et al. [1] reviewed the impact of first-generation biofuel production systems on biodiversity, and resulting provisioning, regulating and cultural services. They found that while some provisioning (fuel) and regulating services (climate regulation) may be enhanced, this often comes at the expense of biodiversity, and other provisioning (food, water) and regulating (air quality, erosion control) services. Joly et al. [3] also used an ecosystem services framework to examine the impacts of biofuel production systems on biodiversity and ecosystem services. They conclude that the land transformations that have taken place globally to produce biofuels have resulted in serious biodiversity declines. However, they also conclude that the effects of biofuel production on ecosystem services is highly context and location-specific, with some systems having the potential to enhance ecosystem services. Indeed, a recent synthesis examining the impacts of second-generation bioenergy cropping systems in Europe suggest that transitioning from first-generation feedstocks to dedicated lignocellulosic feedstocks may frequently improve ecosystem services [4].

The development of biomass crops has been underway in the US since the 1970s, with significant crop improvement efforts conducted under the auspices of the US Department of Energy (US DOE) [5]. In the mid-2000s, the desire to reduce dependence on foreign sources of oil and the environmental load of fossil fuel combustion, coupled with advances in the potential to derive transportation fuels from cellulosic biomass, fostered a resurgence of research into biomass cropping systems. During this time, there was also a growing consensus that a focused national effort was needed to enable the emergence of a cellulosic biofuel industry. In 2006, the US DOE Office of Science and the Office of Energy Efficiency and Renewable Energy released a report that outlined a 15-year strategy of research, technology development, and systems integration aimed at supporting a cellulosic biofuels sector [6]. This report was seen as the original research roadmap supporting the formation of three national Bioenergy Research Centers charged with providing the fundamental science to underpin an environmentally sustainable and economically competitive advanced cellulosic biofuels industry. In 2007, the Great Lakes Bioenergy Research Center (GLBRC) was one of three national research centers funded by the US DOE to pursue this mission [7, 8].

Corn and soybean have long dominated the agricultural landscape of the North Central US. In recent years, 35 to 40% of the US corn crop has been used to produce ethanol that is blended into Nitrogen and phosphorous typically are added to these cropping systems to maintain productivity and manage livestock manure. These inputs, particularly when combined with tillage can result in excessive leaching of nitrogen to ground- and surface-waters and to overland movement of phosphorous attached to soil particles to surface waters [9] resulting in local to continental eutrophication of water bodies [10]. Also, significant amounts of the nitrogen added as inorganic fertilizer can be lost via volatilization or microbe-mediated nitrification and dentirification [11, 12], contributing to ecosystem disservices that include excessive deposition locally and accumulation of greenhouse gases globally. Largely because of high inputs, the net energy gain of developing biofuels from annual crops appears to converge near zero [13]. Increasing production of annual crops through intensification on existing crop land or conversion of marginal lands [14] threatens other ecosystem services important to the sustainability of agricultural landscapes e.g. natural pest suppression [15].

Concerns about the sustainability of current biofuel cropping systems prompted research to derive fuels and other bioproducts from cellulosic biomass sourced from dedicated energy crops and/or food crop residues [16, 17]. However, harvesting residues of annual crops does not address the environmental concerns stated above, and could exacerbate these problems by driving the planting of even more land to annual crops. Alternatively, the addition of dedicated cellulosic crops significantly broadens the options for potential feedstock producing cropping systems, providing opportunities for coupling ecosystem service improvements and ecologically sustainable production [18]. Perennial plants such as native prairies grasses, tropical grasses, and short rotation trees show promise as sustainable biomass crops because they minimize erosion by covering the soil year-round and minimize energy costs of agronomic management stemming from fossil fuel use for planting equipment and production and application of pesticides and fertilizers [19, 20]. However, the benefits of incorporating perennials into current agricultural landscapes as part of a sustainable biomass cropping system has received less research attention (but see [21, 22]). Understanding how perennial biomass cropping systems – specifically those planted with native species – could be integrated into North Central US cropping systems to enhance multiple ecosystem services has been a focus of the GLBRC Biodiversity Team.

Here, we review more than 35 studies conducted by the GLBRC Biodiversity Team, where we compared the potential effects of alternative biomass cropping systems on the organisms and processes that provide important supporting, provisioning, regulating and cultural services in agricultural landscapes. The following central questions directed our research: 1) How does the choice of biomass crop(s) influence biodiversity and the potential to provide ecosystem services that can be delivered at the level of a crop field and to the overall landscape? 2) How do different management practices affect the ecosystem services provided by alternative systems?, and 3) How does the configuration of biomass and other crops in an agricultural landscape influence ecosystem services provided to other crops? Our hypothesis was that perennial biomass cropping systems, particularly those with higher plant species diversity, would provide more ecosystem services and reduce associated disservices compared to annual cropping systems. We addressed this hypothesis by estimating how crop yields and other ecosystem services provided by a variety of cellulosic biomass crops differed and how these relationships varied when measured at plot-, field-, and landscape-levels of spatial organization

2. Materials and methods

Below we provide an overview of methods used in the studies we review. Details about the specific sites and methods used can be found in the individual publications cited (**Table 1**).

2.1 Sites

Research sites were located in southern Wisconsin and Michigan and consisted of a combination of intensively-managed plot-level experiments, replicated scale-up fields, and a network of commercial-sized fields embedded within representative agricultural landscapes (**Fig 1**). In 2008, the Biofuel Cropping Systems Experiments (BCSEs) were established in each state to compare and contrast 10 different cropping systems with each system planted in 30 x 40-m plots in 5 replicate blocks. In Michigan, the BSCE was established at the W.K. Kellogg Biological Station (KBS, 42°23′47″ N, 85°22′26″ W, 288 m a.s.l.) and in Wisconsin at the Arlington Agricultural Research Station (ARL, 43°17′45″ N, 89°22′48″ W, 315 m a.s.l.).

Treatments were designed to provide a gradient of increasing plant species diversity and included both annual and perennial cropping systems: continuous corn, corn-soybean-canola rotation, switchgrass, miscanthus, hybrid poplar, mixed-species native grasses, successional vegetation, and restored prairie (**Table 2**). Split-plot treatments included; stover removal in continuous corn, nitrogen addition in restored prairie, and no nitrogen addition in perennial crops (see [20] for details of cropping systems management). In 2009, "Scale-up" fields (9 to 17 ha) were established at two sites in Michigan to measure biomass production and other ecosystem services at scales typical of production fields with differing land use histories (see table 1 in [23]) and landscape positions. At each site, one field was planted to restored prairie, switchgrass, or continuous corn and managed as in the BSCE.

We also worked with local landowners and extension specialists to identify a set of commercial-sized corn/soybean, switchgrass, and reconstructed prairie fields (3 to 30 ha) across varying landscapes in southern Michigan and Wisconsin. These "Extensive sites" were selected so that all three cropping systems were in close proximity to each other, and embedded within a range of agricultural landscape compositions typical of southern Michigan and Wisconsin. The landscapes surrounding these sites ranged from highly simplified landscapes (i.e., fields surrounded by high proportions of annual cropland within 1.5 km) to moderately complex (i.e., fields surrounded by a combination of croplands, grasslands, forest, or wetlands). The wide spatial distribution of the Extensive sites allowed us to capture gradients in soil type, climate, and overall cropping practices. Because of the current lack of a market for biomass in our states, these sites did not have a history of annual harvests as would be the case in a biomass cropping system, although haying and burning to promote plant diversity often occurred.

2.2 Plants

We evaluated the relationship between plant species diversity (number of species) and above ground biomass production by sampling fields planted to bioenergy crops at two spatial scales – the BCSE experimental plots and larger Extensive and Scale-up fields. These larger fields differed in fertility, time of establishment, land use history, surrounding landscape, and a variety of other factors; however our capacity to evaluate how these differences moderate the effect of biodiversity on yield was limited by small sample size [23, 24].

An initial analysis of how ecosystem services, including above-ground production, varied with cropping system was done by comparing species composition and a variety of services from prairie (n=10) and switchgrass (n=10) Extensive sites in Michigan. Aboveground production and species composition was determined from hand harvests done at peak biomass (August-September) in 2008 and 2009 [23, 24]. We also estimated productivity in the KBS and ARL BCSE from hand harvests (July, corresponding to peak biomass) and by machine at the end of the growing season (September-October) corresponding to the more typical time and methods for biofuel harvest. Because stability in production may be an important ecosystem service, we calculated how variation in aboveground biomass production (i.e. stability, calculated as mean divided by the standard deviation) of the four herbaceous perennial cropping systems of the BCSE representing a gradient of species richness varied (see **Table 1**). Finally, we explored if harvest frequency (1 versus 2) affected biomass production in restored prairie treatments at the Michigan Scale-up sites for three years [23, 24].

2.3 Insects

The adoption of biomass cropping systems is anticipated to affect insect communities and resulting ecosystem functions in complex and cascading ways [25]. To evaluate the effects of different biomass cropping systems, as well as the influence of management and landscape context on insect biodiversity responses, we sampled potential insect pollinators using water-pan traps, netting at flowers, and sentinel flower observations in a subset of the Extensive sites [26-28]. Water pan traps were also used to collect aphids colonizing different fields [28, 29]. To measure the relative abundance of other insect taxa over the course of a growing season we also used sweepnet sampling [30, 31], or placement of yellow sticky card traps [28, 30, 32]. We then used data from these sampling efforts to measure the relative abundance of different taxonomic groups, as well as family (or species-level, for pollinators and some predators), richness and diversity.

The choice and management of biomass crops can affect arthropods that contribute to both pollination and insect pest suppression, two processes that support provisioning and regulating ecosystem services. Pollination potential within the biomass crops was assayed by examining seed mass of potted sentinel sunflowers (*Helianthus annuus*) placed within different biomass crops [26]. Pest suppression potential was measured by the placement of sentinel prey corn earworm eggs (*Helicoverpa ze*a), or soybean aphids (*Aphis glycines*) in the field [30, 32]. Some prey were exposed to ambient populations of naturally occurring arthropod predators while others where shielded from the activity of predators using cages. The difference in the number of prey remaining alive after a given period of time (24 to 72 h, depending on the experiment) was used as an index of biological control potential.

2.4 Birds

Production of biomass crops is anticipated to alter bird communities at field and landscape scales [33, 34]. To assess the likely impacts of different biomass crop types on bird diversity and abundance, we first conducted a meta-analysis of the existing literature [35]. This meta-analysis focused on four major biomass crops that were currently cultivated or being considered for production in the US including corn, switchgrass, pine, and poplar. The analysis contrasted vertebrate animal abundance or density, and diversity in potential biomass crops versus reference habitats that these crops may replace. A second analysis contrasted the abundance of vertebrates in annual crops versus perennial grasslands that were part of the Conservation Reserve Program (CRP) [35]. Subsequent field studies in southern Michigan utilized the Extensive site network and additional sites to examine the diversity and abundance of migratory and breeding birds in relation to biomass crop habitat and landscape variables [31, 36-38]. Finally, the opportunity to sight rare birds was considered as a cultural service as part of an assessment of multifunctionality (section 2.6) [29].

2.5 Microbes

The central role microbes play in mediating soil biogeochemical processes [39] motivated our soil biodiversity research. We primarily relied on linked measurements of the microbial community and biogeochemical process rates to explore these relationships [40], although we also conducted laboratory measurements of soil microbial growth efficiencies from diverse habitats to gain insight into how land management influences microbial communities and their processes [41]. At the onset of our studies, it was unclear whether the effects of establishing biomass crops on soil microbial community composition would be detectable, given the variability caused by heterogeneity of soil properties and legacy effects from prior land uses [42]. In most of our studies, we characterized microbial communities via extraction of biomarkers such as cell membrane lipids, wall amino sugars, and DNA from soil samples. We analyzed community DNA via both targeted and shotgun metagenomic sequencing. The former approach was used to characterize composition of functional groups such as methane consumers or nitrogen fixers in addition to the entire community. Our analyses of these data focused more on community composition and dissimilarity than on diversity per se, because methods like lipid profiling cannot be properly analyzed or interpreted for diversity metrics [43].

We used the network of Extensive sites to compare how cropping systems and soil properties shaped microbial community composition and microbial residues [44, 45]. We also tracked soil microbial community changes during cropping system establishment at the Wisconsin BCSE [46] and then again after establishment to evaluate the effects of nitrogen fertilization [47]. Finally, using Michigan and Wisconsin Extensive and BCSE sites, we compared soil microbial communities from soil bulk samples across multiple cropping systems [48] and in switchgrass between rhizosphere and bulk soil samples [49].

2.6 Multifunctionality

The development of a biomass-based agricultural bioeconomy has been viewed as an opportunity to increase the functionality of US agriculture [50]. We assessed the multifunctionality of potential biomass cropping systems for our region in a variety of ways. Initially, we used GIS-enabled spatially explicit modeling to predict the effects of potential bioenergy driven land use and land cover changes on bird communities [33], biological control potential [51], and pollinator abundance and diversity [27]. We tested our hypotheses that more diverse, perennial systems would provide a greater range of ecosystem services with an analysis exploring relationships of biomass crop choice (corn, switchgrass and restored prairie) to the biodiversity of multiple taxa (plants, insects, bird, and microbes) and to a subset of services those taxa supply (biomass yield, pollination and pest suppression, opportunity to observe rare birds, and methane consumption) [29]. Data from the establishment-phase (i.e., years 1 through 6) of the BCSE provided yield comparisons to improve our understanding of the productivity potentials from a wider range of biomass cropping systems [20]. Finally, using GIS layers of existing land cover, coupled to models of potential biomass crop services and disservices, we developed a spatially-explicit decision-support system to allow stakeholders to evaluate the multifunctionality of user-defined placement of biomass crops on their farms [52, 53].

3. Results and discussion

3.1 Diverse and monoculture plantings of perennials were similarly productive.

In field surveys of existing plant communities in the Extensive sites, we did not find significant differences in biomass production between switchgrass and prairie plantings. Although there was considerable variation among sites in biomass production, this was not related to planted or observed plant species richness and may reflect differences in initial management (including seed mixture), site fertility, or past land use [24]. We found similar results for the BCSE fields where yields were either similar across diversity gradients or higher in switchgrass monocultures depending on the year and nitrogen fertilization treatment [54].

Evidence from surveys of switchgrass plantings in SW Michigan [29] and from experimental plots and extensive sites of the GLBRC [24] show that other species establish in switchgrass monocultures (reflecting seed bank or colonization from surrounding landscape). Because these plantings are not managed to maintain a monoculture (plots not weeded or sprayed), other species invade and so low diversity plots have more species than originally planted. Dickson and Gross [24] show that this can occur rapidly (within 2 years). Also, experimental studies that were designed to explore the relationship between species richness and productivity have shown that these relationships rapidly deteriorate when intensive weeding is stopped [55]. Without a 'monoculture' treatment that is maintained as such, the relationship between actual (or planted) species richness and productivity is not likely to be detected or maintained. This complicates efforts to related planted species richness with productivity; but there may still be positive effects on other ecosystem services [29].

Past land use can also have a significant and persistent effect on the establishment of diverse perennial communities. Grman et al. [56] found that management, especially the seed mix composition, was a major determinant of plant species composition across 27 restored prairies in southwestern Michigan, while past land use also had some effect on composition. In particular, sites restored from pasture had a higher proportion of non-native, C_3 grasses, which may have inhibited establishment of sown native species [56]. Munson and Lauenroth [57] found that species composition and prior land use were important determinants of productivity in CRP lands, and that previously established non-native species reduced the establishment of native species. Although their study did not explicitly analyze connections between species diversity and productivity, they did find that a diverse community had higher productivity in a wet year, but not dry years. Our results from the restored prairies in the Michigan Scale-up sites provide further evidence that past land use may be an important determinant of the potential for restored prairies to deliver provisioning ecosystem services. While restored prairies at both sites were established at the same time, with identical seed mixes and management, the eventual species composition and aboveground productivity of the two sites differed. At the site previously enrolled in the Conservation Reserve Program we observed a higher species diversity, more abundant forbs and lower productivity than the site more recently in row-crop agriculture, where C4 grasses dominated [23]. Because the relationships between species diversity or richness and productivity can depend on species composition [58-60], some of the variation between study sites and experimental settings in our results likely are the result of different plant communities, despite the use of the same or similar seed mixtures.

We also explored the effects of dual versus single harvesting on biomass production and species diversity in a plot-level experiment within the restored prairies of the two Michigan Scale-up sites. Our results showed that at the site where a low-diversity prairie dominated by C_4 grasses was established, single harvests produce more biomass than the sum of dual harvests; however, at the more diverse site, single and double harvests had similar biomass yields [23]. Double harvests increase light and potentially provide an opportunity for low-stature forbs, including annuals, to flower and so provide opportunities for supporting pollinator-based services (K. Gross, unpublished data).

3.2 Plant diversity did not have a consistent effect on yield stability.

Although diverse prairie plantings and switchgrass were found to produce similar amounts of biomass, diverse plantings may differ in their resilience to environmental fluctuations and so provide more consistent production from year to year. This may arise because of differences in traits among species in a more diverse planting that buffer against drought or other perturbations that can limit productivity [61, 62]. Over the first five years in the BCSE plots, species richness had only a small positive effect on the stability (μ/σ) of biomass production. This relationship was weaker at ARL (Wisconsin) compared to KBS (Michigan) (K. Stahlheber, unpublished data). At KBS, the two cropping systems with the highest species richness (restored prairie and unplanted successional field) had the highest stability in biomass production, indicating significantly less variation from year to year. At ARL, by contrast, the five-species native grass cropping system had the most consistent biomass production. This suggests that other attributes of the community beside species richness such as the identity and productivity of the dominant species may be more predictive of the stability in biomass production (K. Stahlheber, unpublished data).

3.3 Biomass crop and landscape structure influenced pollinators and pollination.

Patterns of arthropod abundance and diversity were generally consistent across our different studies, with relatively greater abundance and diversity of arthropods in grasslands (switchgrass and restored prairies) than in annual cropping systems such as corn or soybean. At the local level, pollinators such as wild bees were two to three times more abundant in grasslands compared to corn [28]. At the landscape level, increasing the amount of grasslands around focal fields (generally evaluated at the 1.5-km scale), increased bee species richness and abundance [26]. Moreover, wild bee assemblages tended to be comprised of bees that were more specialized when the landscape had more grassland, while in landscapes with more annual and wind-pollinated crops, assemblages had more generalists, and honey bees (*Apis mellifera)* were relatively more abundant. Variation in bee communities, which was influenced by the prevalence of grassland in the landscape, was also associated with differences in pollination potential, i.e. when wild bees were more abundant, sentinel flowers placed at our experimental sites had a greater seed set [26]. We hypothesize that bee communities and their pollination potential will vary if the prevalence of grasslands in the landscape were to change [27], as may occur if growing perennial-plant biomass were to become more economically viable and thus more widespread, or if corn-based bioenergy production were to continue to increase at the expense of grasslands [14],

3.4 *Biomass crop and landscape structure influenced natural enemies and pest suppression.* A similar pattern to that of pollinators was observed with other insects in biomass production landscapes. Working in the Scale-up and Extensive sites in Michigan, Robertson et al. [31] found that switchgrass and restored prairies had 230% and 320% higher arthropod family-level diversity, respectively, than in corn, with a corresponding 750% and 2700% increase in arthropod biomass, respectively. Gardiner et al. [28] found that predatory flies and lady beetles (Coccinellidae) generally were more abundant in prairie sites compared to corn. Using a broader array of sites and different sampling techniques, Werling et al. [30] similarly found that predator biomass and family-level richness was highest in perennial grassland-based biomass crops. Moreover, within a crop type, increasing the diversity of flowering plants increased predator biomass.

At the landscape level of spatial resolution, increasing the proportion of grasslands, forest cover, or landscape diversity all had positive effects on predatory insect abundance, biomass, or diversity [28, 30, 32]. Although the overall pattern is one of higher natural enemies in either grasslands sites, or in landscapes with a significant proportion of perennial cover, there were some exceptions. For example, Gardiner et al. [28] found the relative abundance of *Coleomegilla* *maculata*, a pollen-feeding lady beetle was more abundant in corn and corn-dominated landscapes. Similarly, Liere et al. [32] found that increasing the proportion of soybeans in the landscape in their study was also associated with a greater abundance of natural enemies.

The mechanisms by which biomass cropping systems positively affect arthropod biodiversity at local and landscape levels of spatial resolution have not been thoroughly examined. The perenniality of biomass crops entails a greater persistence of these habitats through time, compared to annual cropping systems that are replanted each year. This feature alone could increase diversity and abundance of arthropods [63]. Moreover, increased diversity in these grasslands could be due to more flowering dicots [30] supporting a greater diversity and temporal continuity of prey that are used by generalist predators. In fact, a greater arthropod resource base in these grasslands was proposed as a key mechanism by which a greater diversity of birds was supported in biomass grasslands [37]. The studies of Gardiner et al. [28] and Liere et al. [32] which show the potential of positive effects of annual crops on beneficial insects, suggest that these habitats may provide limiting resources such as prey items for these consumers. Future studies examining the mechanisms by which perennial grasslands support beneficial arthropods will be essential to understand how biomass crop management and placement in the landscape will enhance or reduce their numbers at local and landscape scales.

Differences in predatory arthropods among biomass crops was also associated with variation in biological control potential. Werling et al. [30] found that predation of sentinel eggs was greatest in perennial grasslands compared to corn, and predation rates further increased as plant diversity within a habitat increased. However, this effect saturated as plant diversity reached 5 to 10 species. In parallel with the effects on natural enemy abundance and diversity, an increasing amount of grassland or forested habitat in the landscape was also associated with increased predation rates [30]. The effects of the landscape on natural enemies, and the negative effects of natural enemies on prey species, raises the possibility of indirect effects of landscape on prey suppression. Liere et al. [32] experimentally demonstrated this causal pathway showing that as landscape diversity increased, the abundance of predatory and parasitic arthropods in soybean increased, which was then associated with more intense prey suppression, and increased soybean yield. To our knowledge, this is one of the first studies to demonstrate this full causal pathway.

Furthermore, this finding suggests that increasing landscape diversity by the addition of dedicated biomass crops could enhance pest suppression services in associated annual crops. Indeed, we found that farms in more diverse agricultural landscapes in North Central US use less insecticides than those in more simplified landscapes [64, 65]. Explicitly incorporating biocontrol services into bioeconomic models suggests that farmers may be willing to supply some forms of biomass (crop residues) at lower prices [66].

3.5 ***Perennial grasslands supported greater bird abundance and diversity.***

Fletcher et al. [35] showed that the diversity of vertebrates in general, and birds specifically, would be negatively affected by the conversion of reference habitats to either pine, poplar, or row crop production systems and that bird species of conservation concern should be most negatively impacted [67]. In contrast, conversion of row crops to grasslands was predicted to increase the diversity and abundance of birds at landscape scales [33] In field experiments, a total of 35 bird species utilized switchgrass and restored prairies during spring migration, including species of national conservation concern like Henslow's sparrow (*Ammodramus henslowii*) [38]. During the breeding season, 29 species of birds were found in corn, 35 in switchgrass, and 45 in prairie habitats [37] Field size was positively correlated with bird species richness in switchgrass and restored prairies but not corn, and overall richness was lower in landscapes with more forest cover. Perennial grasslands contained higher arthropod diversity and biomass, potentially providing more food for grassland birds [31]. During fall migration, a total of 30 species were found in switchgrass and 38 in perennial grasslands including nine species of obligate grassland specialists of which four are of conservation concern [37]. Overall, these studies suggested that perennial grass biomass cropping systems have considerable potential to enhance bird abundance and diversity in the North Central US, particularly for grassland specialist species of conservation concern [33, 67].

3.6 ***Perennial grass cropping systems were enriched in plant-associated microbes.***

Cropping systems that promote soil fungi should rely less on nutrient inputs and result in greater soil organic carbon accumulation than systems dominated by soil bacteria [68]. Biomass of arbuscular mycorrhizal fungi (AMF) was greater in switchgrass and restored prairie systems than in the corn system across the network of Extensive sites in Wisconsin [44]. A similar difference was observed between the corn and restored prairie systems of the Wisconsin BCSE only two years after cropping system establishment, although not in the year following establishment [46]. These changes were likely driven by increased rhizosphere size and activity because microbial lipids from these groups increased in switchgrass rhizospheres relative to bulk soil at these sites [49]. These microbes, AMF and Gram-negative bacteria, have previously been reported to receive more carbon from plant exudates [69], making it likely these organisms associate directly with grasses. We observed that nitrogen fertilization substantially reduced the amount by which biomass from these groups increased in perennial systems [47], matching previous findings from other groups [70]. These results are consistent with the classical perspective of symbiotic plant-microbe associations as revolving around exchanges of nutrients and energy [71], although inorganic nitrogen fertilization may be directly deleterious to AMF and other soil microbes [72].

In the Extensive sites, microbial community composition and abundance varied with plant composition, with switchgrass microbial communities intermediate between corn and prairie fields [44]. At the Wisconsin BCSE, switchgrass and restored prairie treatments had similar microbial lipid composition under fertilization, but plant-associated microbial lipids were more abundant in fertilized prairie [47]. We observed lower levels of labile nitrogen in the prairie than in the switchgrass treatment [54], suggesting plant diversity may have influenced the soil microbial community indirectly through regulation of soil chemistry rather than directly through associations.

Soil microbial biomass, as estimated by membrane lipids, responded to perennial biomass cropping system establishment with unexpected speed and intensity [48, 73]. We observed minimal differences among cropping systems the year after BCSE establishment [48], which was consistent with previous reports of minimal changes to microbial community composition several years after land use change [74]. By the following year, however, microbial biomass clearly differed among cropping systems [46]. DNA-based estimates of community diversity responded less strongly to cropping system establishment [55, 80], possibly because DNA from nonviable organisms can linger in the soil [75]. That said, we observed seasonal variability in the composition of rhizosphere nitrogen-fixing bacteria (B. Zhang and J. Tiedje, unpublished data), and it has been proposed that soil microbial communities can turn over on much shorter time scales than previously thought [76]. It remains to be seen whether microbial community function, and thus microbially-mediated ecosystem processes, respond to biomass cropping system establishment with similar alacrity.

3.7 *Carbon cycle dynamics reflect interactions among biomass crops, microbes, and soils.*

We found a variety of factors that influenced carbon cycling processes, including cropping systems, microbial communities, and soil properties. The richness of methane-oxidizing microorganisms increased with the removal of conventional agricultural management and was correlated to higher rates of methane consumption [77]. Richness of all bacterial taxa did not respond systematically to this same gradient, however, and was uncorrelated to total soil respiration [77]. Overall, microbial community composition appears to be less clearly correlated to carbon cycle processes conducted by taxonomically and metabolically diverse groups [77]; such processes include the formation and turnover of microbial residues, which are critical regulators of soil carbon accumulation [78]. Across the Extensive sites, microbial residue turnover, as inferred from soil neutral sugar concentrations [79], reflected abiotic soil properties rather than cropping systems or microbial community composition [49]. Despite the importance of abiotic factors, cropping system rhizosphere properties could also influence this process, as we found lower amino sugar concentrations in switchgrass fields than in adjacent soils [49]. Similarly, we observed substantial differences in microbial growth efficiency across a range of land use types, although it is unclear whether these reflected changes in microbial community composition [45]. Our work forms part of a broader conversation on integrating microbial properties into soil carbon models [80] and has led us to develop a model that provides a framework for incorporating microbial physiology. Despite this progress, linking cropping system properties to microbial community composition and physiology remains a major challenge to understanding and modeling soil carbon cycle processes [81, 82].

3.8 Exploring trade-offs and synergies in biomass cropping system multifunctionality.

Farmer decisions about whether to plant diverse or simple biomass cropping systems will depend on their understanding of the relative synergies and trade-offs associated with each system. Many of the potential synergies stemming from diverse or perennial biomass cropping systems can only be realized by careful choice of the crop and its placement in the landscape. In a synthesis of our data, we found that crop choice plays a critical role in determining biodiversity and ecosystem service trade-offs [29]. Corn is very productive in our region, out-yielding current cultivars of switchgrass and restored prairie by approximately 2-3-fold when both the grain and stover components are considered. Comparisons of perennial grass yields to corn stover showed that they are quite similar [20].

However, perennial grasslands enhanced several ecosystem services including methane consumption in the soil, plant pollination, crop pest suppression, and grassland bird sightings, and also decreased pest arrival into crop fields [29]. The spatial arrangement of biomass crops in the landscape is critical to levels of biocontrol and abundance of grassland birds, which has important ramifications for those choosing where in the landscape biomass crops should be planted. For example, in the North Central US, it is estimated that production of biomass crops on marginal lands – i.e., lands where the costs of crop production are not covered by the sale of commodities – could provide approximately 25% of the federal renewable fuel targets while mitigating greenhouse gas emissions [83]. However, using spatially explicit modeling we showed that if corn were to be planted on marginal lands at the expense of existing grasslands it would lead to a 7 to 65% decline in bird species richness across 20% of the region. Conversely, if restored prairie plantings were to replace existing corn on marginal soils, bird species richness would increase 12 to 207% [33], and similar results were found for bee abundance and diversity [27]. In a related study, the expansion of corn on to marginal soil grasslands was projected to result in a 10 to 64% decline in biocontrol, while expansion of grasslands on to marginal corn sites could increase biocontrol 13 to 205% on over half of the annual cropland in the region [51]. These findings demonstrate that biomass cropping systems based on perennial grasslands have the potential to enhance habitats for both grassland birds and beneficial insects.

We have used models to compare ecosystem service outputs from different biomass cropping systems and to communicate the ecosystem service trade-offs and synergies to farmers and policymakers. Meehan, Gratton [52] explored trade-offs associated with switching from annual crops to perennial biomass crops in 67 small watersheds in southern Wisconsin. They found that strategic replacement of annual crops by perennial grasslands in riparian zones could increase energy production, carbon sequestration, pollinator abundance, and biological control, while simultaneously decreasing phosphorus loadings, nitrous oxide emissions, and unfortunately, farmer income. While the social benefits of making these changes are large relative to the lost income, environmental markets and policies are not yet in place to offset these costs to farmers.

To help stakeholders and policymakers visualize the impact of bioenergy-driven land use and land cover change, we developed the web-based Smartscape™ decision-support system [84] that incorporates multiple models relating land use and land cover changes to subsequent supply of many key ecosystem services [53]. The system allows users to create spatially explicit biomass cropping system scenarios at local (e.g., farm fields) to regional (e.g., south central Wisconsin) levels of spatial resolution and compare their performance against a variety of ecosystem service metrics (**Fig 2**). Axes in the radar plot are oriented such that more desirable performance outputs are more positive and individual scaled to the maximum of each axis.

By visualizing the direction and magnitude of tradeoffs and synergies between multiple ecosystem services, the merits of different cropping systems and their placement in the landscape can be more accurately understood and evaluated. Perhaps more importantly, multiple stakeholders can engage in this modeling process, which can build trust and "buy-in" among constituents with disparate philosophies, attitudes, and goals [85].

4. Synthesis

4.1 *Communicating our overall findings.*

The choice of biomass crop, and the methods by which they are established and maintained, are key drivers of biodiversity across multiple taxa and the ecosystem services they support. As our results show, the outcomes of these management decisions are complex and yet some stakeholders desire simple guidance. For example, the questions we most often hear are: Are biofuels good or bad? or Which cropping system is the "best" for biofuel production? Our research supports only one answer to these simple questions: it depends. In our region, perennial biomass crops, particularly those based on native perennial grasses, show significant promise to enhance multiple ecosystem services. However, corn (grain + stover) is two to three times more productive than the relatively unimproved and unfertilized cultivars of switchgrass and restored prairie plantings we examined [29]. We also found benefits of mixed stands of grasses and forbs in contrast to monocultures of grasses, in particular for reducing variability in yield, the abundance of natural enemies, pollinators, and overall arthropod populations supporting bird communities [29]. However, mixtures of grasses and forbs may also present limitations in processing depending upon pretreatment, deconstruction, and conversion technologies.

Moreover, the importance of where biomass crops will be grown on the landscape has also emerged as a major theme from our research. For example, the overall amount of grasslands in the landscape was shown to be an important factor influencing both pollinator and natural enemy communities [27, 51], as well as bird communities [33]. Land use history will also have strong effects on the establishment and species composition of mixed-species cropping systems [23, 24]. In addition strategic placement of perennial grasslands could be utilized to reduce soil erosion and nutrient loss, although many of these scenarios also showed trade-offs with farmer income based on current prices and support programs [52]. The ability to visually portrait these tradeoffs via the Smartscape™ output has been helpful in our outreach work.

To communicate our findings in a way that captures the nuances of these key dimensions, members of the GLBRC Sustainability leadership team developed a simple mnemonic device called the "4-P's", which we characterize as *strategically Placed, Productive, Perennial, Polycultures* [86]. Although this shorthand has some limitations, it has proved useful in translating our complex results for diverse stakeholder audiences, including researchers from disparate scientific disciplines within the GLBRC. With the 4-P's we can highlight the need to understand where and under what conditions we might expect particular plant production (*Productive*), the value of perennial systems such as native grasslands in reducing disturbance and maintaining soil processes and wildlife (*Perennial*), the role that species or genetic diversity plays in our systems (*Polycultures*) and how benefits of biomass crops affect processes at the landscape scale and how they in turn are influenced by their landscape surroundings (strategic *Placement*). We expect that in the future we may also include additional dimensions including considerations for how cropping systems are managed.

4.2 *Implications for implementation.*

From the outset, our work was informed by a research plan designed to compare alternative biomass cropping systems and determine their biodiversity responses, while others in GLBRC studied the biogeochemistry and economics of these systems. Our long-term goal is to provide science-based information to decision makers to aid in the development of bioenergy policies that facilitate the design of optimal biomass production systems supporting a range of ecosystem services that society values. Whether biomass crops will become an integral part of our agricultural landscapes remains to be seen. Despite attempts at creating a national energy policy that supports renewable sources of energy, demand for cellulosic biomass has been low. There are various reasons for this situation, not the least of which is that current fossil fuel prices are very low because of novel sources of natural gas production. In addition, we continue to be dependent on annual crops for fuel production because these crops have alternative markets, are familiar to farmers, and are usually profitable under current economic policies [19, 87-89]. Moreover, development of infrastructure for using cellulosic feedstocks for ethanol production has only recently begun in our region [90]. Another way to improve adoption perennial biomass feedstocks is to tie biomass production to alternative uses beyond biofuels. For example, cellulosic biomass pre-treatments can be used as sources of high protein feed for ruminant animals [91]. In this way, even in the initial absence of a market for biofuels, demand for high value intermediate products or co-products, such as sugars or protein, can jump start an integrated food-energy system that also supports desirable environmental goals [92].

Recognizing the ecosystem service needs and demands of a diverse stakeholder community may be one way to enhance the use of perennial biomass crops in agricultural landscapes. For example, the advantages of perennial grasslands have long been recognized by land managers working to reduce soil erosion and eutrophication of waterbodies in agricultural landscapes [21, 93]. Planting of perennial grasses, strategically placed in the landscape, has the potential to improve downstream water quality [21], which could offset economic losses from reduced production of corn, soybeans, or other annual crops planted close to riparian areas. While grassland-based biomass cropping systems alone may not be economically competitive with corn, the ability to take advantage of other ecosystem services they provide makes them a superior choice compared to annual crops. Finding other similar synergies between the benefits of perennial grasslands (e.g., carbon sequestration, greenhouse gas reduction, year-to-year stability and wildlife habitat improvement), and stakeholder groups working toward their own goals (e.g., flood reduction, climate stabilization, hunting opportunities), can make these cropping systems more compelling.

In addition to obvious technical, logistical and economic challenges with implementing and integrating biofuel cropping systems into our existing agricultural landscapes, there are remaining gaps in our ecological knowledge that also need to be addressed [4]. For example, it is unclear what the environmental consequences of increasing intensification of biomass crop production as demand higher productivity becomes paramount (e.g., fertilizer use, annual harvests) [94]. Also, until now dedicated biomass crops have largely been restricted to small areas, in localized parts of the US. Widespread adoption could transform areas that had previously had small amounts of perennial land to a larger fraction, with consequences for biodiversity-related responses that are area dependent (e.g. [33, 95]). How these effects actually scale-up will be valuable tests of landscape models at realistic scales [27, 51, 52]. As biofuel crops are adopted and managed for production at widespread scales, the long-term consequences of dedicated biofuel production systems will become clearer. Until then, we must extrapolate from relatively small-scale work, modeling and general principles to build an understanding of the ecosystem service tradeoffs of different biofuel cropping systems.

5. Conclusions

Funding by the US DOE has allowed the GLBRC Biodiversity Team to examine the implications of planting cellulosic biomass crops on biodiversity and ecosystem services in the North Central US. By combining results from research conducted at different spatial scales and studying multiple taxa, we have developed an understanding of how selection of biomass crops and their management can affect ecosystem services in future agricultural landscapes. Our work shows that there is potential for selected biomass crops – especially those that mimic the species diversity and composition of native grasslands – to provide multiple ecosystem services. While there are synergies among some services and biomass production, there are also trade-offs that need to be communicated to stakeholders and policymakers [53]. Our work has also shown that management practices, particularly establishment techniques, fertilization and harvesting regimes can alter biodiversity the biodiversity in a biomass crop and consequently the ecosystem services that can be provided. Management practices that limit soil disturbance and fertilization and promote plant diversity are likely to result in more and sustained ecosystem services. Additionally, the landscape surrounding individual fields is an important determinant of the types of ecosystem services that are provided from biomass crops. Marginal lands, where soil fertility or other factors limit crop production may offer opportunities to support renewable fuel goals, without reducing food production [83]. Our research suggests that for the North Central US, bioenergy cropping systems based on – strategically-Placed, Productive, Perennial, Polycultures – are the most likely to ensure delivery of a balanced set of ecosystem services and should be incentivized.

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Figure captions

Figure 1. Locations of GLBRC Biofuel Cropping System Experiments (BCSE's), Scale-up fields, and a subset of the Extensive site network.

Figure 2. Examples of Smartscape^{TM} (dss.wei.wisc.edu) output.

Table 1

Table 1. GLBRC studies covered in this review categorized by taxonomic focus, ecosystem function/process measured or modeled, and the related ecosystem service.

Ecosystem service	**Taxonomic focus**	**Ecosystem function/process**	**Reference(s)**
Nutrient cycling (supporting)	Microbes	Nitrogen fixation	[48, 49]
Biomass (provisioning)	Plants	Above ground productivity	[20, 23, 24, 54]
	Plants	Herbivory/Disease	[25, 32, 66, 94]
	Plants	Regional productivity	[83]
Pest suppression (regulating)	Arthropods	Predation	[15, 25, 28, 30, 32, 51, 52, 64, 65]
Pollination (regulating)	Arthropods	Pollination	[25-28]
Climate stabilization (regulating)	Microbes	Methane consumption	[40]
	Microbes	CO_2 production and consumption	[40, 41, 96]
	Plants/ Microbes	Nitrous oxide emission	[47, 54, 73]
	Plants/ Microbes	Soil organic matter accumulation	[45, 49]
Biodiversity appreciation (cultural)	Birds	Habitat occupancy, community composition	[31, 33, 35-38, 67]
Multiple services	Multiple	Multiple	[18, 29, 52, 53, 63, 87-89, 97]

Table 2. Cropping systems established at the Great Lakes Bioenergy Research Center's Bioenergy Cropping System Experiment (BCSE) at Arlington, Wisconsin and Hickory Corners, Michigan[1].

System #	Rotation	Crop	Common and Scientific Names
1	Continuous	corn	corn (*Zea mays* L.)
2	Annual	corn[2]	corn
3	rotation	soybean	soybean (*Glycine max* [L.] Merr.)
4	of:	canola	canola (*Brassica napus* L.)
5	Continuous	switchgrass	switchgrass (*Panicum virgatum* L.)
6	Continuous	miscanthus	*Miscanthus x giganteus*
7	Continuous	native grass mix	big bluestem (*Andropogon gerardii* Vitman) Canada wild rye (*Elymus Canadensis* L.) indiangrass (*Sorghastrum nutans* [L.] Nash) little bluestem (*Schizachyrium scoparium* [Michx.] Nash) switchgrass, "Southlow"
8	Continuous	poplar	NM-6 hybrid poplar (*Populus nigra* x *Populus maximowiczii*)
9	Continuous	old field	plant community defined by pre-existing seed bank and novel recruitment
10	Continuous	restored prairie	**grasses** big bluestem Canada wild rye indiangrass junegrass (*Koeleria cristata* [Ledeb.] Schult.) little bluestem switchgrass, "Southlow" **leguminous forbs** roundhead bushclover (*Lespedeza capitata* Michx.) showy tick-trefoil (*Desmodium canadense* (L.) DC.) white wild indigo (*Baptisia leucantha* Torr. & Gray) **non-leguminous forbs** black-eyed susan (*Rudbeckia hirta* L.) butterfly weed (*Asclepias tuberosa* L.) cup plant (*Silphium perfoliatum* L.) meadow anemone (*Aneomone canadensis* L.) New England aster (*Symphyotrichum novae-angliae* [L.] G.L. Nesom) pinnate prairie coneflower (*Ratibida pinnata* [Vent.] Barnhart) showy goldenrod (*Solidago speciosa* Nutt.) stiff goldenrod (*Solidago rigida* L.) wild bergamot (*Monarda fistulosa* L.)

[1]For full details see [20] Table S1, and GLBRC BCSE agronomic protocol http://lter.kbs.msu.edu/protocols/122

[2]System numbers refer to the entry point crop at the start of the rotation. In 2012, the corn-soybean-canola system was replaced by a continuous corn + cover crop system and a corn-soybean + cover crop system with two entry points.

Figure 1
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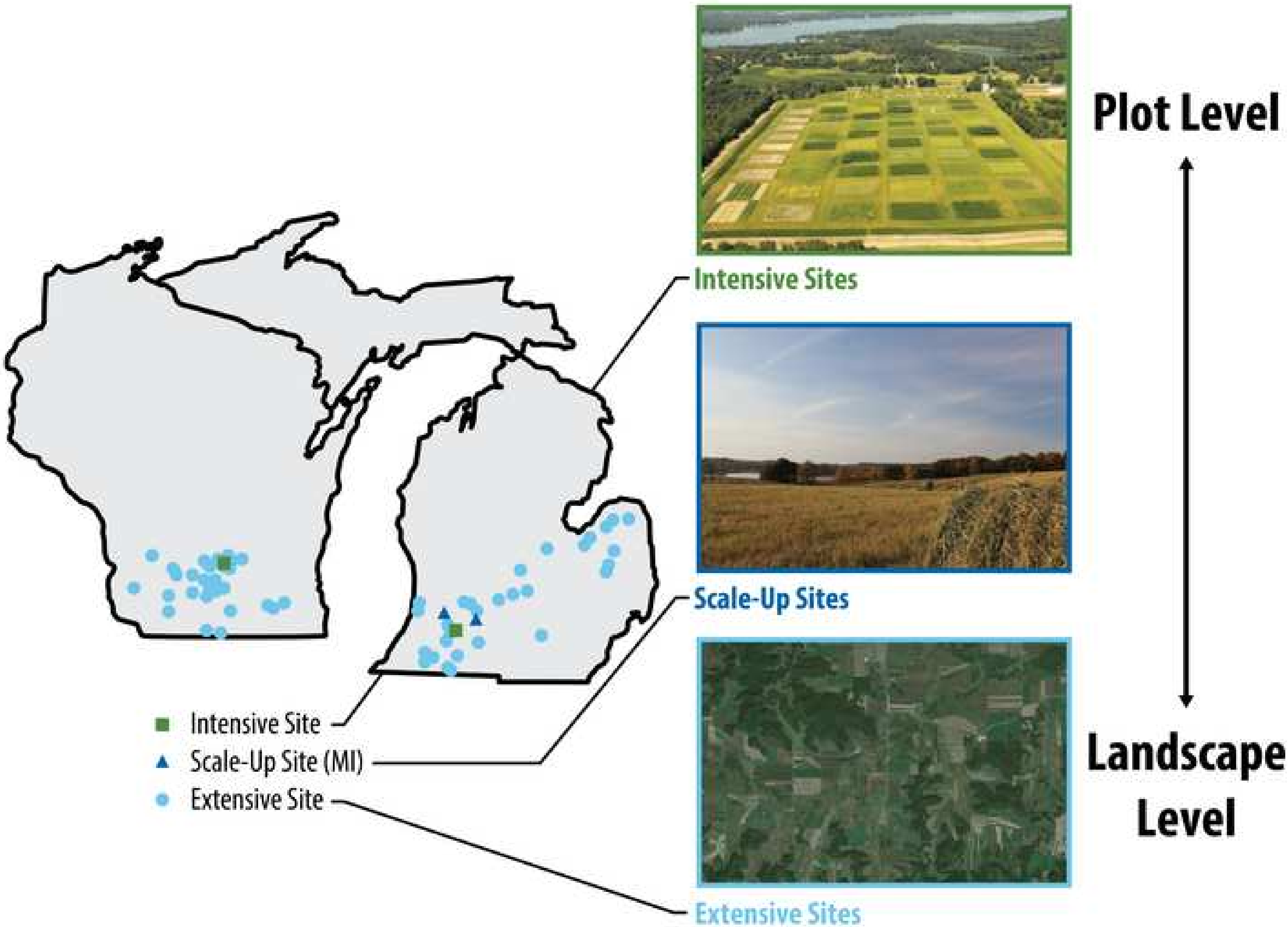

Figure 2
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