

ORIGINAL RESEARCH

Optimizing pollinator conservation and crop yield among perennial bioenergy crops

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Abstract

In order to both combat the decline of biodiversity and produce food, fuel, and fiber for a growing human population, current agricultural landscapes must transition into diversified, multifunctional systems. Perennial cellulosic biofuel crops have potential to meet both of these challenges, acting as multifunctional systems that can enhance biodiversity. What is not well understood, and what we test here, are the tradeoffs among different perennial crops in their performance as biofuels and in biodiversity conservation. Working in an established bioenergy experiment with four native, perennial, cellulosic biofuel crop varieties—ranging from monoculture to diverse restoration planting—we tested the effect of biofuel crop management on flower communities, pollinator communities, and crop yield. The greatest abundance and diversity of pollinators and flowers were in treatments that were successional (unmanaged), followed by restored prairie (seeded mix of native grasses and forbs), switchgrass, and a mix of native grasses. However, biofuel crop yield was approximately the inverse, with native grasses having the highest yield, followed by switchgrass and prairie, then successional treatments. Restored prairie was the optimal biofuel crop when both pollinator conservation and crop yield are valued similarly. We add to mounting evidence that policy is needed to create sustainable markets that value the multifunctionality of perennial biofuel systems in order to achieve greater ecosystem services from agricultural landscapes.

KEYWORDS

agricultural management, biofuel crops, conservation, landscape diversity, Pareto optimality, restored prairie, switchgrass

1 | INTRODUCTION

Human actions have caused a global biodiversity crisis with rapid and widespread rates of biodiversity decline (Dirzo et al., 2014; van Klink et al., 2020; Wagner et al., 2021; Wepprich et al., 2019). Simultaneously, humans are faced with the challenge of sustainably and equitably supporting a growing human population (Bennett et al., 2021; Foley et al., 2011; Kremen & Merenlander, 2018). Agricultural

landscapes are the greatest source of biodiversity loss and have the greatest potential for sustainable conservation (IPBES, 2019). Agriculture currently occupies over 38% of the world's land area, with a projected increase in crop demand of 100%–110% from 2005 to 2050 (Tilman et al., 2011; World Bank, 2016). A majority of agricultural landscapes rely on chemical and energy intensive inputs to produce a single crop (Ramankutty et al., 2018). However, in order to both conserve biodiversity and produce food, fiber, and fuel

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for humans, input-intensive agricultural landscapes need to transition into multifunctional working landscapes (Díaz et al., 2019; Jordan & Warner, 2010).

Diversified agricultural landscapes can mitigate the loss of biodiversity while sustainably supporting a growing human population (Albrecht et al., 2020; Fischer et al., 2006). An increase in natural habitat in working landscapes increases resources available for a range of species and can increase connectivity among habitat patches for some species that are otherwise relegated to protected areas (Fischer et al., 2006; Isbell et al., 2017; Nicholls & Altieri, 2013). In addition to the benefits for biodiversity, diversified landscapes provide important ecosystem services that can promote agricultural yield, including increased soil health, carbon sequestration, and pollination (Kremen & Merenlander, 2018; Morandin & Kremen, 2013; Schulte et al., 2017). The effect of diversifying working landscapes has the potential to create synergies or tradeoffs for biodiversity and the yield of food, fiber, and fuel (Goldstein et al., 2012; Meehan et al., 2013; Nelson et al., 2009; Raudsepp-Earne et al., 2010; Robertson et al., 2017), possible outcomes that we test here. Weighing tradeoffs among environmental and economic factors is crucial for creating sustainable agricultural landscapes that recognize biodiversity and social impacts (Senapathi et al., 2015; Wiens et al., 2011).

One method of landscape diversification is to convert marginal lands—lands that are under cultivation but consistently underperforming (Basso et al., 2019)—to natural or seminatural habitats that can also produce bioenergy (Cai et al., 2011; Núñez-Rogueiro et al., 2019; Robertson et al., 2008). Biofuel agriculture is needed in most climate mitigation scenarios that limit atmospheric warming to 1.5°C by 2100 due to its ability to reduce life cycle carbon emissions (Gelfand et al., 2020; IPCC, 2018). The impact of biofuel agriculture on biodiversity depends on previous land use and biofuel crop choice, including crop diversity (polyculture vs. monoculture; Bennett et al., 2014; Robertson et al., 2017; Tilman et al., 2009; Wiens et al., 2011). Currently, most biofuels are input-intensive monocultures of annual grain crops, such as maize (*Zea mays*; U.S. Environmental Protection Agency, 2018). As an alternative to annual grain crops, perennial cellulosic plants such as native grass species can be planted as a biofuel crop. With current production infrastructure, perennial cellulosic biofuels yield less ethanol per hectare than annual crops (Roozeboom et al., 2019), but potential exists to decrease this gap (Brandes et al., 2018). In addition to biomass production, perennial cellulosic biofuels increase ecosystem functions such as carbon sequestration and biodiversity (Hill et al., 2006; Landis et al., 2018; Werling et al., 2014), and ecosystem services, such as pollination, in the broader landscape (Bennett & Isaacs, 2014; Robertson et al., 2017). While switchgrass (*Panicum virgatum*) is widely considered for its potential as a native perennial monoculture crop (Mitchell et al., 2012), polycultures of native perennial species can be more productive (Tilman et al., 2006)

and can also increase benefits for biodiversity (Robertson et al., 2017; Wiens et al., 2011). Such polycultures include those that we assess: mixes of native grasses (Hill, 2009; Tilman et al., 2006), unmanaged lands allowed to develop early successional plant communities, and restored prairies planted with high-quality grasses and forbs (Fargione et al., 2009).

An important ecosystem service among different biofuel crops is the potential habitat and foraging and/or nesting resources provided to beneficial insects (Landis & Werling, 2010). Pollinators are of high conservation value due to recent declines (Potts et al., 2010), and due to their high ecosystem service value in natural and agricultural systems through the pollination of wild plants and crops (Klein et al., 2007). A major component structuring pollinator communities is the quantity and quality of floral resources available and the associated pollen and nectar resources (Ebeling et al., 2008; Kremen et al., 2018; Potts et al., 2003; Williams et al., 2015). Within agricultural landscapes, more diverse plantings increase the resources and habitat available for pollinators (Ebeling et al., 2008; Isbell et al., 2017; Kremen et al., 2018; Mallinger et al., 2016). In addition, pollinators can spill over from diverse plantings into nearby habitats, which can be especially important for nearby crops by providing pollination services that benefit yields (Bennett & Isaacs, 2014). Pollinator conservation has been of particular interest across the globe in regard to biofuel crops and changing bioenergy landscapes (Bennett et al., 2014; Gardiner et al., 2010; Graham et al., 2017; Romero & Quezada-Euán, 2013; Stanley & Stout, 2013; Werling et al., 2014). However, the tradeoff between pollinator conservation and crop yield, and therefore farmer benefit, is unknown (Garibaldi et al., 2014). Measuring these tradeoffs, as we do here, increases the chance of identifying candidate biofuel crops that can both benefit farmers and biodiversity (Dale et al., 2014; Landis et al., 2018; Power, 2010; Waldron et al., 2012), a task that is essential prior to policy adoption and implementation (Landis & Werling, 2010; Robertson et al., 2017).

Working in an experiment with four native, perennial, cellulosic biofuel crop treatments, ranging from monoculture to diverse restoration planting, we tested for optimal candidate crops with respect to two variables: pollinator conservation and crop yield. We asked three questions: (1) How do candidate biofuel crops affect floral abundance and diversity available to pollinators? (2) How do candidate biofuel crops affect pollinator abundance and diversity? (3) What are the tradeoffs among crop yield and pollinator conservation across candidate crops?

2 | METHODS

2.1 | Study sites

We conducted this study at the Biofuel Cropping System Experiment at the US Department of Energy's Great Lakes

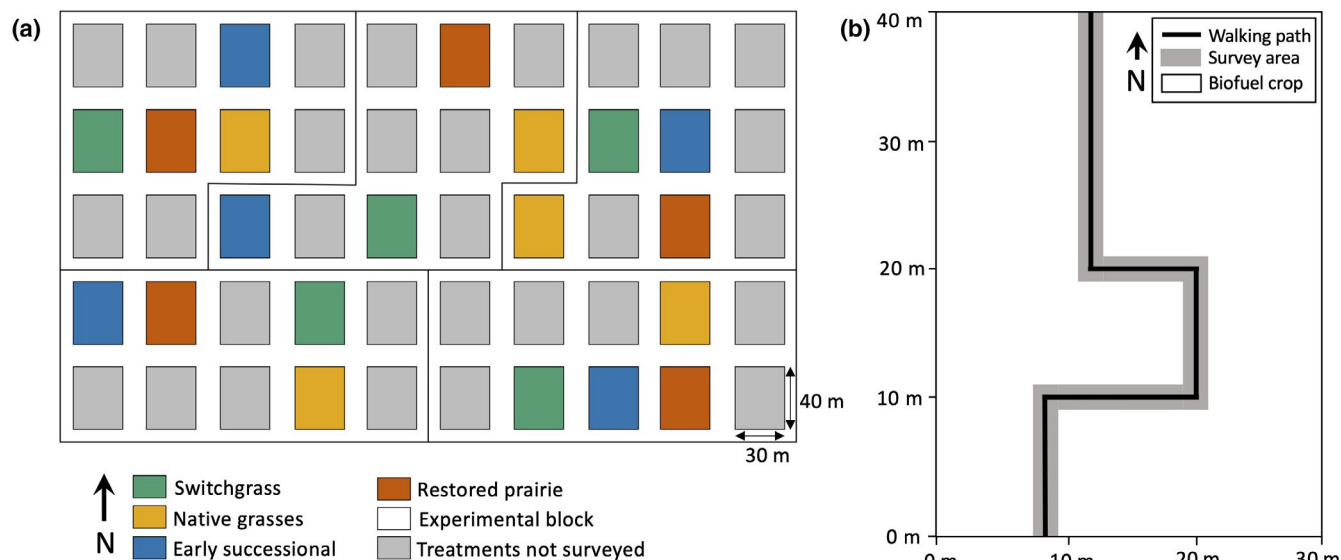


FIGURE 1 (a) The layout of experimental plots in the Great Lakes Bioenergy Research Center sites at Kellogg Biological Station. The intercrop distance between experimental plots is 15 m. (b) The layout of a single plot in the Great Lakes Bioenergy Research site at Kellogg Biological Station. Each plot is 30 × 40 m and contains a single biofuel crop. The survey area is where both pollinators and flower surveys were conducted. Pollinator surveys occurred as timed walks along the walking path, surveying 1 m on either side. Flower surveys were conducted in the same area following pollinator surveys

Bioenergy Research Center experimental landscape (Figure 1). This site is located at the W.K. Kellogg Biological Station's Long-Term Ecological Research site in Hickory Corners, MI (occupied Anishinaabe land). Our study in 2018 occurred within an experiment that was established in 2008 to test the environmental, biogeochemical, and agricultural performance of potential biofuel crops. Prior to the establishment of this experiment in 2008, alfalfa was farmed in the landscape (Sanford et al., 2016). The experiment was a complete block design consisting of five replicate blocks (Figure 1a). Within each block, we studied four treatments that represented four bioenergy cropping systems: switchgrass, native grasses, early succession, and restored prairie. These four bioenergy crops were perennial, consisting of native grasses and/or forbs. Each plot was 30 m by 40 m with a permanent path in the same location in each plot for sampling (Figure 1b). See Gelfand et al., (2020) for detailed soil and climate information at this experimental site.

2.2 | Agricultural management

The switchgrass treatment was seeded in monoculture in 2008, although about 20% of biomass in these switchgrass plots consisted of other species that naturally recruited into the system by 2014 (Werling et al., 2014; see Table S1 for flowering species observed in each treatment in 2018). The native grasses treatment was a mix of one perennial C_3 grass (*Elymus canadensis*) and four C_4 grasses (*P. virgatum*, *Andropogon gerardii*, *Schizachyrium scoparium*, and *Sorghastrum nutans*) seeded in polyculture. The restored prairie treatment was seeded in

native prairie species including the same C_3 and C_4 grasses as in the native grasses treatment plus one C_3 grass (*Koeleria cristata*), three leguminous forbs (*Desmodium canadense*, *Lespedeza capitata*, and *Baptisia leucantha*), and nine non-leguminous forbs (*Rudbeckia hirta*, *Anemone canadensis*, *Asclepias tuberosa*, *Silphium perfoliatum*, *Monarda fistulosa*, *Ratibida pinnata*, *Solidago rigida*, *Solidago speciosa*, and *Symphyotrichum novae-angliae*). The early successional treatment was not seeded, and inhabiting species are those that have colonized the plots via surrounding habitats, from within the seedbank, and potentially from nearby experimental plots. The species sown in each treatment in 2008 and 2009 are described in Table S2.

The land for all four crop treatments was prepared in the same way in 2008. Switchgrass and native grasses treatments were herbicided in 2009 and 2010 to suppress weed competition. Fertilizer was applied annually in the switchgrass, native grasses, and successional treatments at 56 kg of Nitrogen per hectare applied as 28% N fertilizer. Fertilizer was not applied to the restored prairie treatment as per standard agricultural practice for these candidate biofuel crops (Sanford et al., 2016). Plots were harvested annually in the fall, also as per standard practice in these cropping systems (Stahlheber et al., 2016).

2.3 | Flowers

Four sampling rounds of flowers and pollinators occurred monthly between June and October of 2018. We

conducted flower surveys within 5 days of each pollinator survey in every plot to quantify resources available to pollinators. We measured flower richness and abundance along a 2 × 60 m transect in each plot (Figure 1b). We only recorded actively flowering forbs; we did not record grasses. Table S1 lists plant species with open flowers that we detected in each treatment. For each species along the transect, we counted the total number of individuals with open flowers. Then, for 10 individuals of each species (or all individuals if fewer than 10 were observed within the transect), we counted the number of open flowers on each plant. We used those open flower counts to calculate an average number of open flowers per forb species per transect. We multiplied those values by the total number of flowering individuals of that species on the transect, thus providing an estimate of total floral abundance for each species on each transect. In some cases, we counted floral units rather than individual flowers. For instance, we considered a head of a *R. hirta* the equivalent to an individual flower (Table S1).

To determine the effects of bioenergy crop on flower abundance, we used linear mixed effects models with a negative binomial distribution. Main effects of the model were biofuel crop and sampling round, and the random effect was the experimental block. We rarefied flower richness by abundance using the “iNext” package in R to control for the effects of flower abundance on flower species richness (Chao et al., 2014; Hsieh et al., 2016). To determine the effects of bioenergy crops on rarefied flower richness, we used a linear mixed effects model with a normal distribution. The response variable was the rarefied number of plant species with open flowers, the main effect was biofuel crop, and the random effect was the experimental block. Sampling round was not included in this model because we did not have enough observations to calculate rarefied richness for each plot per sampling round; a single measure was calculated across all sampling periods.

2.4 | Pollinators

To test the effects of bioenergy crops on pollinators, we conducted pollinator surveys in each plot. Pollinator diversity and abundance were measured along the same 2 × 60 m transects as the flower surveys (Figure 1b). Each plot was surveyed twice per day per sampling round, with one survey occurring between 10 a.m. and 12 p.m., and the second survey occurring between 1 and 4 p.m. To limit bias, only two scientists conducted all surveys, each of which consisted of walking a single transect over a 10-min period and recording all insects actively visiting a flower and the associated species of flower they were visiting. We defined pollinator groups a priori based on our knowledge of pollinator diversity in the system

(Gardiner et al., 2010). Pollinators were visually identified into 13 groups: *Andrena* spp., *Apis mellifera*, *Bombus* spp. (includes *Xylocopa*, only three total were detected), butterflies, large dark bees (brown or black bees, >16 mm), large green bees (>10 mm including *Agapostemon* spp.), medium dark bees (brown or black bees, 10–16 mm), moths, small dark bees (brown or black bees, <10 mm), small green bees (<10 mm), syrphid flies (non-*Toxomerus* spp. syrphids), *Toxomerus* spp., and wasps. These groups were chosen as they are possible to identify on the wing. We chose to visually identify pollinators rather than destructively sample pollinators because we noticed strong treatment effects across groups that can be visually identified. Visual identification could allow more accurate measurements in the field (without having to stop and execute the collections) and prevents disrupting other pollinators which could skew abundance. We were able to assess key differences without destructive sampling of pollinators. The alternative of collecting pollinators requires long time lags in data processing and high levels of funding for species-level identification. We use the term “pollinator group richness” to equal the number of pollinator groups we recorded.

To determine the effect of bioenergy crop on pollinator abundance and pollinator group richness, we used linear mixed effects models. We constructed the pollinator abundance model using a negative binomial distribution with pollinator abundance as the response variable, biofuel crop and sampling round as the main effects, and experimental block as the random effect. There was one outlier (*z*-score = 8.1, threshold of *z*-score > 3) in the pollinator abundance dataset that was removed from the linear regression analyses. We constructed the pollinator group richness model similarly, but used a normal distribution with pollinator group richness (number of pollinator groups) as the response variable.

The relationship between the pollinator community and the floral community was determined in separate models. Four simple linear regressions were created to investigate the relationships between (1) pollinator abundance and flowering plant abundance; (2) pollinator group richness and flowering plant abundance; (3) pollinator abundance and flowering plant richness; and (4) pollinator group richness and flowering plant richness. All four models were separated because floral abundance and floral richness were correlated despite rarefaction, and treatment caused differences in floral abundance.

2.5 | Crop yield

Plots were harvested after the first frost of the season, on October 25, 2018, using a JD 7350 self-propelled forage harvester equipped with a JD 676 cutting head. Yield was defined as dry harvested biomass (Mg/ha). Yield was measured by chopping plant material into a Gnuse forage wagon fitted with load cells.

To determine the difference in yield among crops, we used a linear mixed effects model with a normal distribution. Crop yield in dry matter yield (Mg/ha) was the response variable, treatment was the main effect, and experimental block was the random effect. We used R package “lme4” (Bates et al., 2015) to construct models with normal distributions and “glmmADMB” (Fournier et al., 2012; Skaug et al., 2013) to construct models with negative binomial distributions. A Tukey test was used for post-hoc analyses for all models using R package “multcomp” (Hothorn et al., 2008).

2.6 | Optimizing crop yield and pollinator conservation

Pareto optimality—a concept from economics and engineering—was used to determine the tradeoffs between biofuel yield and ecosystem service generation (pollinator conservation). Pareto optimality establishes a set of tradeoffs in which one criterion must decrease in order for another to increase. It is a tool for determining the efficient use of resources (Kennedy et al., 2008; Polasky et al., 2005; Tendler et al., 2015). A Pareto frontier is the boundary in graphical space that connects all optimal points. Because the optimum is dependent on how the two variables are valued or preferred against each other, there is a range of optimal points. If the variable on the y-axis is preferred, the corresponding optimal point would be located where the slope of the Pareto frontier is shallow; if the variable on the x-axis is preferred, the corresponding optimal point would be located where the slope

is steep. If the variables on the x- and y-axes are valued similarly, the optimal point will fall where the slope is intermediate. Points will not fall on the Pareto frontier if they are not optimal for any tradeoff between the two variables.

We constructed a Pareto frontier for crop yield (an economic return) and pollinator conservation (an ecosystem service), using the “rPref” package in R. Pollinator group richness was used as a measure of pollinator conservation (Senapathi et al., 2015). Mean pollinator group richness and mean yield across all plots were used to calculate the Pareto frontier. We used the “rPref” package to calculate optimal datapoints with respect to a preference for both high crop yield and high pollinator conservation (Roocks, 2016). Points do not fall on the Pareto frontier if they are not optimal between crop yield and pollinator conservation. All graphical plots were constructed using R package “ggplot2” (Wickham, 2016) and the “Rmisc” package (Hope, 2013) was used to calculate standard error.

3 | RESULTS

3.1 | Flowers

Flower abundance did not differ among successional (mean: $17734.7 \pm \text{SE: } 5355.7$), restored prairie (4730.1 ± 1732.4), and switchgrass (5717.2 ± 2255.6) treatments. These treatments were all significantly higher in floral abundance than the native grasses treatment (1128.7 ± 893.8 ; $\chi^2 = 51.9$, $p < 0.001$; Figure 2a). Results did not change when the number of individual plants replaced flower abundance as the

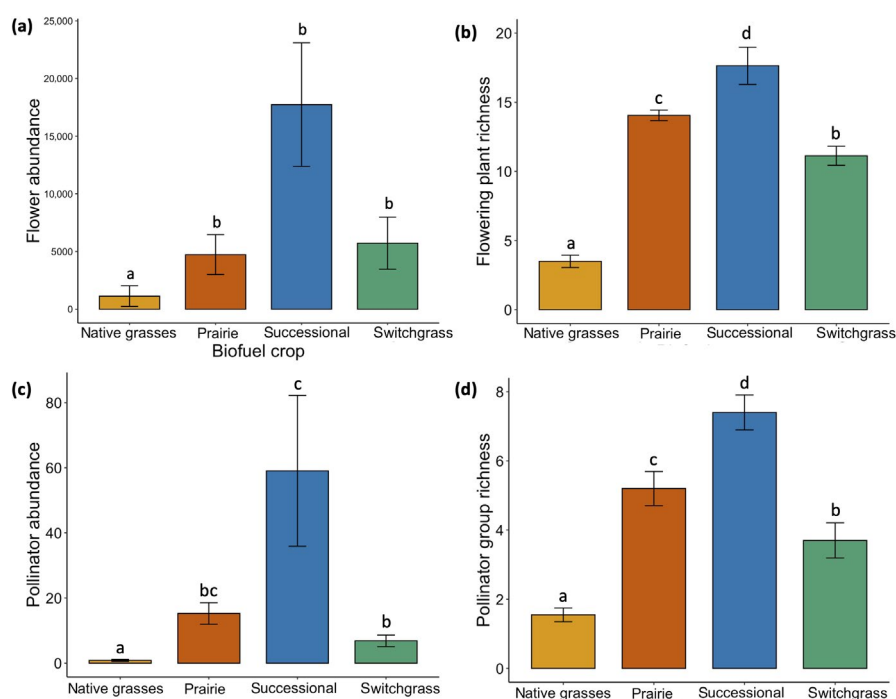


FIGURE 2 (a) Flower abundance, (b) flowering plant richness, (c) pollinator abundance, and (d) pollinator group richness recorded in each of the four biofuel crop treatments. Each bar represents an average across replicated plots and sampling rounds ± 1 SE. Letters indicate significant differences

response variable. Flower richness was highest in the successional treatment (mean: 17.6 ± 1.3) followed by prairie (14.1 ± 0.4), then switchgrass (11.1 ± 0.7), then the native grasses treatment (3.5 ± 0.5 ; $\chi^2 = 235.1$, $p < 0.001$; Figure 2b).

3.2 | Pollinators

Across four sampling rounds, we visually identified 1640 pollinator individuals. Pollinator abundance was highest in successional (mean: $59.1 \pm \text{SE: } 23.2$) and restored prairie (15.3 ± 3.3) treatments, followed by switchgrass (6.9 ± 1.8 ; although restored prairie was not statistically different than successional or switchgrass treatments), and lowest in the native grasses treatment (0.9 ± 0.3 ; $\chi^2 = 153.4$, $p < 0.001$; Figure 2c). A similar pattern resulted for pollinator group richness, with the highest richness in the successional treatment (7.4 ± 0.5), followed by prairie (5.2 ± 0.5), then switchgrass (3.7 ± 0.5), then the native grasses treatments (1.6 ± 0.2), although prairie was not statistically different than switchgrass or successional treatments ($\chi^2 = 76.5$, $p < 0.001$; Figure 2d). Native bees, honeybees, and non-bee pollinators all responded similarly to the biofuel crop treatments when analyzed independently.

Flowering plant abundance and richness were always significantly, positively related to pollinator abundance and richness (pollinator abundance and flower abundance $R^2 = 0.29$, $p < 0.001$; Figure 3a; pollinator group richness and flowering plant abundance $R^2 = 0.47$, $p < 0.001$; Figure 3b;

pollinator abundance and flowering plant richness $R^2 = 0.25$, $p < 0.001$; Figure 3c; pollinator group richness and flower richness $R^2 = 0.49$, $p < 0.001$; Figure 3d).

3.3 | Crop yield

Crop yield (Mg/ha) was highest in native grasses (mean: 7.1 ± 0.5) and prairie (mean: 5.8 ± 0.7) treatments, followed by switchgrass (mean: 5.5 ± 0.3), although prairie was not statistically different from native grasses or switchgrass treatments). The successional treatment (mean: 2.3 ± 0.2) had the lowest crop yield ($\chi^2 = 87.4$, $p < 0.001$; Figure 4).

3.4 | Optimizing crop yield and pollinator conservation

The Pareto frontier analysis created an optimal boundary for valuing high crop yield and high pollinator conservation (Figure 5). The frontier, which connects all optimal points, included the native grasses, restored prairie, and successional treatments. The only treatment not included on the boundary was switchgrass. The frontier shows that restored prairie treatment was the optimal crop when pollinator conservation and biofuel crop yield are valued equally. The native grasses treatment was the optimal crop when crop yield was valued higher than pollinator conservation. The successional treatment was the optimal crop when pollinator conservation was valued higher than crop yield.

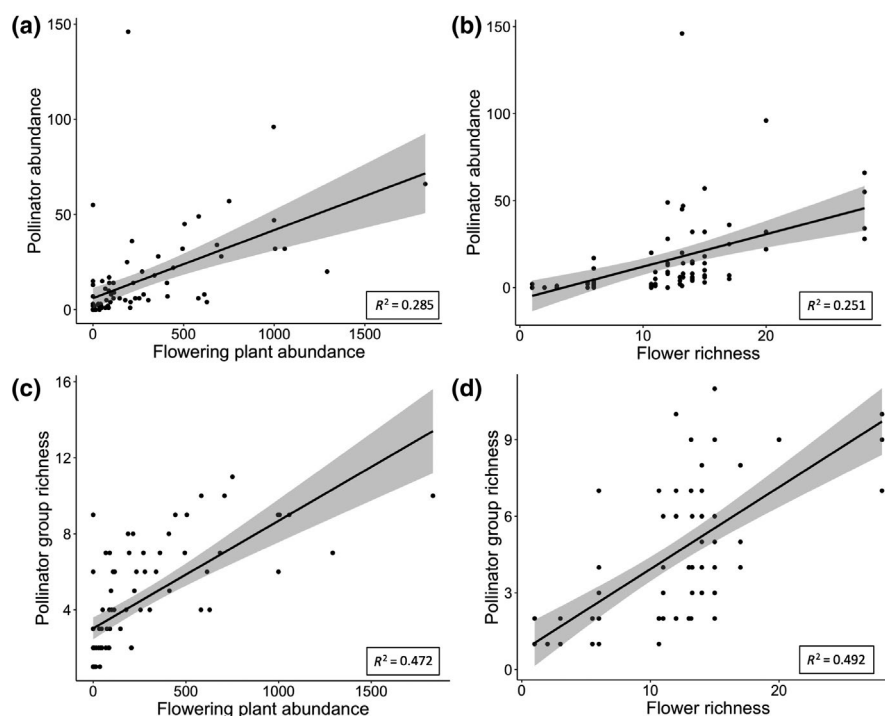


FIGURE 3 (a) Pollinator abundance as a function of flowering plant abundance, (b) pollinator abundance as a function of flower richness, (c) pollinator group richness as a function of flowering plant abundance, and (d) pollinator group richness as a function of flower richness. Each plot depicts a linear model with a 95% confidence interval shaded in gray. Raw data points are shown for each plot for all four sampling rounds. One data point in panels (a) and (c) that describes pollinator abundance (z -score > 3) is not shown

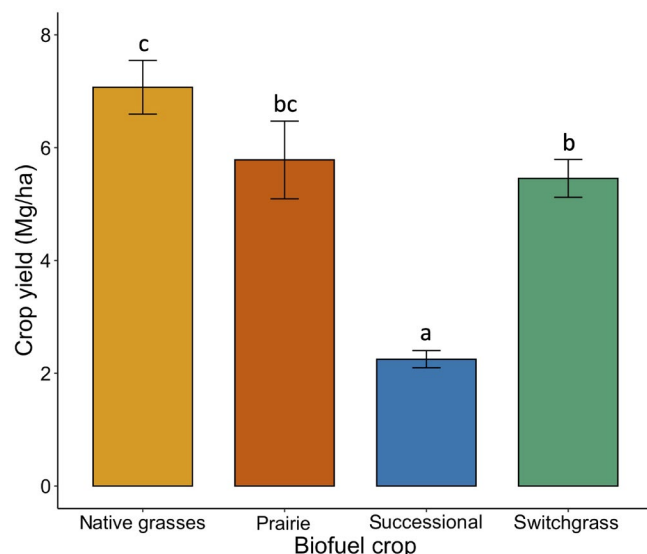


FIGURE 4 The yield of dry harvested biomass (Mg/ha) of each biofuel crop treatment. For comparison, maize yielded on average 9.388 Mg/ha in this same replicated experiment in 2018. Letters indicate significant differences among crop yields

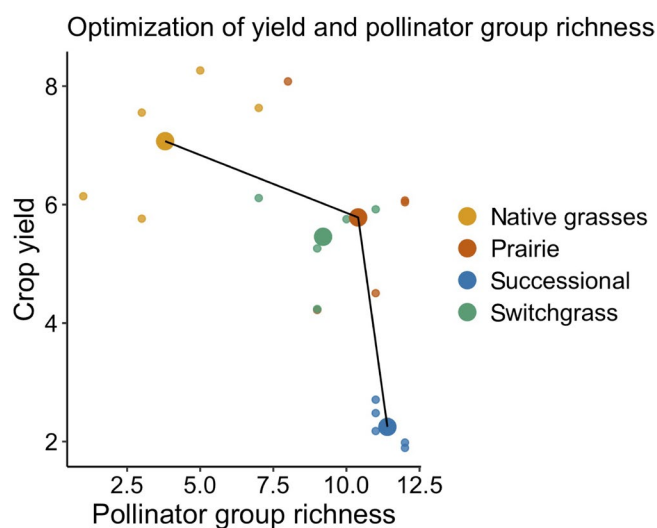


FIGURE 5 A Pareto frontier for mean crop yield (Mg/ha) and mean pollinator group richness across biofuel crop treatments. The Pareto frontier is shown as a solid black line; this describes the optimal values for crop yield and pollinator group richness over a range of preferences. The means for each treatment are the larger, bolded points and the data points for each plot are the smaller points

4 | DISCUSSION

Our results reveal that choice of perennial biofuel crop produced a measurable tradeoff between crop yield and pollinator conservation, mediated by the flower community. Higher floral abundance and diversity drove higher pollinator abundance and diversity in all treatments, but the treatments with the most flowers did not have the highest yield. We found

that restored prairie best balanced objectives to achieve high crop yield and high pollinator richness. These results indicate that working landscapes with biofuels may need to balance conservation with production goals.

The agricultural management of each of the four perennial native biofuel crops established a distinct floral community, as expected. The abundance and diversity of flowers in each treatment explained the abundance and diversity of pollinators. All combinations of flower and pollinator abundance and diversity were positively correlated, with the strongest correlation occurring between pollinator group richness and flower richness. Therefore, agricultural management determined the pollinator community in each biofuel crop. Incorporating a greater abundance and, more importantly, a greater richness of native flower species in agricultural landscapes can attract a more abundant and more diverse community of pollinators.

The richness and abundance of pollinators was highest in the successional treatment, followed by restored prairie, switchgrass, and lowest in the native grasses treatment. Unlike our study that showed a clear ordering of pollinator richness and abundance, past studies have had inconsistent results—some finding higher bee species richness and abundance in restored prairie than switchgrass (Graham et al., 2017; Ridgway, 2016), while another found no difference (Gardiner et al., 2010). When measuring across a broad range of pollinators, we found a greater abundance and richness of pollinators in prairie than in switchgrass treatments. This result adds evidence to other studies that have found an increase in insect species richness from maize to switchgrass to prairie (Harrison & Berenbaum, 2013; Kempster, 2013). Biofuel crop choice impacts biodiversity, and the more species-rich the crop, the higher diversity of pollinators and associated services the crop can conserve within and around biofuel landscapes.

The yield of each crop was inversely related to floral diversity and abundance (Figure 5). The high yields in native grasses were likely due to the number of tall, tightly spaced grasses with highly productive species. The switchgrass treatment was similar, but a thick cover of tall grasses interspersed with more forbs likely caused the lower yield than that of the native grasses. The restored prairie treatment shifted that balance by maintaining tall grasses throughout, but with more forbs than the switchgrass treatment. The low yields in the successional treatment were likely due to the inconsistent, patchy plant cover across the plot. The 2018 yield results presented here are similar to that of the post-establishment yields that were measured in these plots in 2009–2014 (native grasses: mean $5.0 \pm \text{SE } 1.2$ Mg/ha per year; restored prairie: 3.3 ± 0.7 ; successional: 2.5 ± 0.5 ; switchgrass: 7.3 ± 0.9 ; Gelfand et al., 2020). Whereas in 2018 native grasses and restored prairie had the highest yields, switchgrass outperformed prairie and native grasses when averaged

over 2009–2014. In early years, switchgrass is a monoculture, and is slowly filled in with a greater diversity of plants. This change in plant diversity over time corresponds with a change in yield, and results in changes in pollinator diversity. Perennial biofuel crop yield is largely determined by species composition, agricultural management, and year since establishment (Jarchow et al., 2012; Sanford et al., 2016), as seen in our study. These variables should be considered with biodiversity and other environmental and economic variables in selecting a biofuel crop.

Our yield results fall within the expected range for candidate native, perennial biofuel crops (Gelfand et al., 2020; Roozeboom et al., 2019). The yield of these candidate bioenergy crops is lower than that of maize, but this lower productivity does not imply that they are unsuitable for bioenergy. It does imply that it will take more landcover to get the same ethanol produced as these candidate biofuel crops. As we find that these candidate crops benefit biodiversity and ecosystem services, an increase in landcover would then further benefit biodiversity and ecosystem services. For example, the successional treatment had the lowest yield in our study. But, restored prairie and successional treatments had the highest greenhouse gas benefits (the lowest greenhouse gas intensities) compared to these other candidate crops and maize (Gelfand et al., 2020). Increasing the area planted of a crop that benefits biodiversity and ecosystem services, especially on consistently low-yielding land (Basso et al., 2019), creates a more multifunctional and sustainable outcome.

We found that restored prairie treatments provided the optimal response in the tradeoff between production and conservation goals. Farmers who strongly value crop yield over pollinator conservation would farm consistent with a crop that falls along a shallow slope on the Pareto front in Figure 4b. In our study, this corresponds to the native grasses treatment where yield was high, but it performed the lowest for pollinator conservation. Oppositely, farmers who strongly value pollinator conservation over crop yield are depicted by a steep slope on the Pareto front. This end corresponds to the successional treatment that had the highest diversity of pollinators, but the lowest yield. Pollinator conservation and crop yield are attributed similar values where the slope of the Pareto frontier is intermediate between shallow and steep. Restored prairie is the optimum over this range of preferences where pollinator conservation and yield are both valued similarly. Switchgrass treatments performed poorly as they were not the highest in production nor conservation value, and they did not perform optimally when both variables are valued similarly.

Restoring prairie as a biofuel crop in agricultural landscapes could meet both global challenges of combatting biodiversity decline and supporting the growing human population. Tallgrass prairie was a dominant ecosystem in central North America pre-European colonization, but is currently

endangered due to row crop expansion (Samson & Knopf, 1994). Restoring prairie for harvest is not equivalent to replacing natural grassland ecosystems; however, grasslands are historically fire maintained ecosystems and harvest can imitate the biomass removal of fire (Stahlheber et al., 2016). In addition, best practices for wildlife for biomass production and harvest of grasslands have been established to prevent creating habitat sinks (McGuire & Rupp, 2013). Therefore, planting prairie could restore habitat for other native organisms in the region. Planting could occur as the conversion of suitable marginal land, the implementation of buffer strips, the conversion of annual biofuel crops, or introducing prairie strips to agricultural landscapes. Such transformative efforts would meet the level of change needed to create multifunctional landscapes.

In the broader context of bioenergy crops, all of the perennial crops we studied were more diverse than the most common bioenergy crop in the upper Midwestern US: maize. Bee abundance and pollination services are higher in switchgrass and restored prairie than maize (Gardiner et al., 2010; Werling et al., 2014), and as maize has close to zero floral resources within the landscape, it is likely that all four of our tested biofuel crops outcompete maize in terms of pollinator conservation. This agrees with a modeling scenario in which annual bioenergy crops reduced wild bee abundance and diversity and perennial bioenergy crops increased bee abundance and diversity (Bennett et al., 2014). In considering other measures of biodiversity and ecosystem services, restored prairie harbors more diverse ant communities, more diverse predatory arthropod communities, and have higher predation of pest eggs by arthropod predators than switchgrass or maize biofuel crops (Helms et al., 2020; Werling et al., 2014).

Choice of biofuel crop should also consider tradeoffs among other variables, among them climate and water quality. Perennial crops provide climate benefits through carbon storage. They also provide a greater richness of methanotrophs and the consumption of methane occurring in restored prairie and switchgrass compared to maize (Werling et al., 2014). Perennial biofuel crops also provide aesthetic and recreation benefits such as birdwatching during the growing season with a higher richness of breeding birds and a higher abundance of grassland birds in prairie and switchgrass than maize (Werling et al., 2014). Current biofuel markets and policies support annual biofuels such as maize and do not account for the environmental impact of those crops (Landis et al., 2018). These markets and policy should shift to value the multifunctionality of perennial biofuels (Jordan & Warner, 2010; Mishra et al., 2019).

The management and costs of these different crops also play an important role in their value as biofuel crops. Successional, switchgrass, and native grass treatments were fertilized every year while the restored prairie was not

fertilized. The initial cost of the seed mix for restored prairie was higher than the seed mixes for the other three treatments due to the number of species sowed; however, the restored prairie biofuel crop treatment required the least amount of management and costs over time. Restored prairie is the optimal biofuel crop for optimizing pollinator conservation and crop yield with the additional environmental and economic benefits.

Our results have implications for pollinator conservation and biofuel futures. Pollinators respond to increased floral diversity across spatial scales from within fields to across landscapes (Isbell et al., 2017; Kennedy et al., 2013; Kremen & Miles, 2012). In our study, honeybees and non-managed native pollinators both responded similarly to the biofuel crop treatments. Therefore, planting a greater abundance and diversity of perennial, native biofuel crops can positively impact a range of wild and managed pollinator populations and communities within and across landscapes. Compared to low diversity of native grasses, diversifying biofuel landscapes by planting crops such as restored prairie can both support pollinator conservation and maintain yield.

Biofuel agriculture has the potential to diversify agricultural landscapes, increase habitat for beneficial insects and other biodiversity, provide climate benefits, and provide other ecosystem services. Incorporating a greater abundance and, more importantly, a greater richness of native flower species in agricultural landscapes can attract a more abundant and more diverse community of pollinators. Directed policies could encourage the use of multifunctional, resilient crops that benefit both farmers and biodiversity across diverse agroecosystems.

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DATA AVAILABILITY STATEMENT

All data files and code used in this manuscript are archived and open to the public at <https://doi.org/10.5281/zenodo.4603740>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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