DIVERSIFYING AGRICULTURAL LANDSCAPES FOR BIODIVERSITY AND ECOSYSTEM SERVICES

By

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ABSTRACT

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This dissertation focuses on strategies to restore biodiversity and ecosystem services in agricultural landscapes through diversifying the plant community at the landscape level. Biodiversity and ecosystem services are declining globally, and a leading cause of this decline is large-scale row crop agriculture which results in habitat loss and pollution. Simultaneously, the human population is growing, as are human demands for resources produced by agriculture. Diversifying agricultural landscapes is one method to both mitigate the loss biodiversity while providing essential human resources. I conducted three studies that test if diversifying cropping systems can increase biodiversity and ecosystem services and maintain or even increase agricultural yield. In Chapter 1, I tested the ability of multiple native, perennial bioenergy crops (alternatives to annual bioenergy crops) to provide both crop yield and conserve pollinators. I measured pollinator abundance and species richness, flower abundance and species richness, and crop yield across four native perennial biofuel crop varieties: successional land (unmanaged), restored prairie, a mix of native grasses, and seeded switchgrass. Successional land had the most diverse community of pollinators but the lowest crop yield, native grasses had the highest yield but the least diverse pollinator community, and switchgrass and restored prairie were intermediate. If both pollinator conservation and crop yield are valued similarly, restored prairie was the optimal biofuel crop. Chapter 2 tested the effects of crop management practices in row crop agriculture, including the establishment of a conservation practice called "prairie strips" on biodiversity and ecosystem services. Prairie strips are strips of farmland retired from production and actively restored with native prairie plant species. I synthesized the tradeoffs and synergies of a suite of biodiversity and ecosystem service measures across a land use intensity gradient, as well as their spillover from prairie strips into cropland. The lowest land use intensity consistently had the highest levels of biodiversity and ecosystem services other than crop yield. Treatments with prairie strips had higher pollination services and a higher abundance of butterflies and spiders than other row crop treatments. Crop yield in a treatment with low land use intensity and prairie strips remained as highest land use intensity treatment, even when including the area taken out of production for prairie strips. Biodiversity and ecosystem services decreased with increasing distance from prairie strips and this effect was more pronounced in the second year of the prairie strips than the first for several measures. These results show that, even in early establishment, prairie strips can contribute to the conservation of biodiversity and ecosystem services without a disproportionate loss of crop yield. Chapter 3 further investigated one of the measures addressed in Chapter 2: butterfly biodiversity. I measured butterfly and plant species richness and abundance across three years in the same land use intensity gradient. Butterfly abundance and richness increased as land use intensity decreased. Prairie strips harbored unique butterfly communities and had a higher abundance of butterflies than other row crop treatments, including conservation land. Across the 1 ha plot of which 5% was prairie strip, butterfly abundance was higher in row crops with prairie strips than in row crops without prairie strips, likely as a result of prairie strips and other crop management practices in treatments with prairie strips, such as reduced pesticides. Altogether, this work presents evidence that restoring habitat within farms can support biodiversity and ecosystem services without disproportionately impacting crop yields. Furthermore, when strategically placed, these conservation strategies can prevent unnecessary greenhouse gas emissions, and potentially increase crop yield.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Biodiversity is a measure of the variety of life on earth, with inherent value in its existence and vastness. Biodiversity is also valuable for its essential role to perform ecosystem functions that sustain life on earth. Human activity is causing a decline in biodiversity globally with an estimated one million species currently threatened with extinction, and the rate of loss is accelerating. The loss of biodiversity can be mitigated if action is taken, but delayed response will incur greater economic and ecological costs. Immediate transformative change is needed in policy and action to conserve and restore biodiversity (IPBES 2019).

The greatest threats to terrestrial biodiversity are land use change, overexploitation, pollution, and climate change (in descending order; IPBES 2019). Agriculture is the principal cause of land use change, occupying 37% of earth's land (World Bank 2018). Agriculture is also a global source of pollution due to fertilizer and pesticide use, and climate change due to emissions from soil management and other sources (Novotny 1999, Paustian et al. 1995). Simultaneously, the human population is growing, as are human demands for food, fuel, and fiber (IPBES 2019). Furthermore, active and impending climate change hastens the need for developing resilient farming systems (Lipper et al. 2018). The result is an urgent need to transform agricultural landscapes into multifunctional systems that both meet human resource needs and mitigate biodiversity loss (Kremen & Merenlander 2018, Schulte et al. 2021, Basso 2021).

Agricultural diversification is one method of mitigating the loss of biodiversity while still providing resources essential for human life (Kremen et al. 2012, Tscharntke et al. 2021). The composition and configuration of landscapes are important factors determining their ability to support biodiversity and ecosystem services (Tscharntke & Brandl 2004, Kremen et al. 2007, Mitchell et al. 2014, Landis 2017). In agricultural landscapes, diversifying landscape composition and configuration can positively affect biodiversity and ecosystem services by increasing the amount of natural habitat, landscape connectivity, and structural complexity (Tscharntke et al. 2005, M'Gonigle et al. 2015, Lamy et al. 2016). An open question, and one that I address here, is: can landscape diversification increase biodiversity and maintain or even increase agricultural yield and ecosystem services? We take an experimental approach to understand the mechanisms by which landscape diversity affects biodiversity and the functioning of agroecosystems.

Methods of diversification in working landscapes include increased genetic diversity of crops, the addition of crop rotations and cover crops, diversification of the number and complexity of crops within the landscape, and habitat restoration within or surrounding crops (Fischer et al. 2006, Isbell et al. 2017, Schulte et al. 2017, Renard & Tilman 2019). Restoring land within agricultural landscapes benefits biodiversity by increasing available habitat and increasing habitat connectivity within the broader landscape (Fischer et al. 2006, Kremen & Merenlander 2018). Restoring habitat in agricultural landscapes can also support ecosystem services which can have global effects (e.g., carbon sequestration, water purification, prevention of nutrient runoff) and that can increase agricultural yield (e.g., pollination, decomposition, soil microbial activity) (Werling et al. 2014, Schulte et al. 2017, Tamburini et al. 2020). This multitude of goods, services, and functions increases resilience as climates shift and extreme weather events become more common (Liebman & Schulte 2015). While diversification may increase biodiversity, ecosystem services, and crop yield, the resulting tradeoffs and synergies among these for specific agricultural diversification strategies are unknown.

With mounting evidence that diversifying agricultural landscapes is essential for conservation, widespread implementation has yet to occur for at least three reasons: funding and policy, concerns of farmland displacement, and detailed assessments of place-based strategies. Diversifying an agricultural landscape requires implementation costs that are not feasible for farmers without aid, and political action is required to financially support farmers. Another concern is that removing crop land from production will lead to the displacement of agricultural land elsewhere. But advances in precision agriculture can direct efforts to parts of a farm that are consistently underperforming and locations that have the most potential to conserve biodiversity and provide ecosystem services (Chaplin-Kramer et al. 2019, Basso 2021). In addition, studies of specific diversification strategies are needed to direct policy and to discern the interactions among biodiversity, ecosystem services, and crop yield for specific practices. Taking action at the necessary scale will require an understanding of both impacts on conservation and crop yield. Understanding this relationship can inform land management decisions for designing resilient working landscapes that both support biodiversity and yield goods and services (Robertson et al. 2017, Kremen & Merenlander 2018).

I contribute to this body of knowledge with three studies that elucidate the tradeoffs and synergies among biodiversity, ecosystem services, and yield across two diversified cropping systems: perennial bioenergy cropping systems and row crop farms with prairie strips. One specific strategy for diversifying bioenergy cropping systems is planting native, perennial grassland as a bioenergy crop rather than annual grain crops such as maize. Perennial bioenergy landscapes support biodiversity and ecosystem services, but currently produce lower yield than annual grain crops (Robertson et al. 2017, Roozeboom et al. 2019). Most climate change mitigation scenarios include biofuel agriculture, and understanding how different crops impact biodiversity and crop yield is crucial for developing sustainable bioenergy policies (Gelfand et al. 2020). Chapter 1 of this dissertation examines the performance of multiple native perennial bioenergy cropping systems in their ability to optimize pollinator conservation and bioenergy crop yield.

Another method of landscape diversification is the implementation of prairie strips in monoculture row crop farms. Prairie strips are strips of farmland retired from production and actively restored with native prairie plant species. This conservation practice is designed to be practicable for farmers and is a part of the USDA Conservation Reserve Program, which subsidizes farmers for the cost of implementing prairie strips (Luther et al. 2022). Prairie strips have the potential to promote biodiversity and ecosystem services on farms without sacrificing crop yield (Kordbacheh et al. 2020, Schulte et al. 2017). However, this management practice has not been tested against a range of other crop management practices for its impact on biodiversity, ecosystem services, and crop yield, and has not been measured early in prairie strip establishment. Chapter 2 seeks to elucidate the tradeoffs and synergies among biodiversity, ecosystem services, and crop yield across a land use intensity gradient that ranges from cropping systems without prairie strips to cropping systems with prairie strips to conservation land. We also measured how prairie strips spillover into adjacent cropland. To understand the details by which prairie strips affect diversity and ecosystem function as in Chapter 2, for Chapter 3 I expand on one response—butterfly biodiversity—in detail.

Approximately 26% of annual cropland in the Midwest USA is consistently underperforming with the inputs of nutrients and greenhouse gas emissions into that area providing relatively low yields. Continuing to farm this land wastes resources and results in unnecessary nitrogen pollution and greenhouse gas emissions (Basso et al. 2019). These underperforming areas of cropland could be targeted for restoration as prairie strips or for yield as native perennial bioenergy crops without displacing cropland to another location. With my dissertation, I use an experimental approach to assess the potential of these strategies to conserve biodiversity and ecosystem services and produce crop yields.

LITERATURE CITED

LITERATURE CITED

Basso, B. (2021). Precision conservation for a changing climate. *Nature Food*, *2*(5), 322–323. https://doi.org/10.1038/s43016-021-00283-z

Basso, B., Shuai, G., Zhang, J., and Robertson, G. P. (2019). Yield stability analysis reveals sources of large-scale nitrogen loss from the US Midwest. *Scientific Reports*, *9*(1), 5774. https://doi.org/10.1038/s41598-019-42271-1

Chaplin-Kramer, R., Sharp, R. P., Weil, C., Bennett, E. M., Pascual, U., Arkema, K. K., Brauman, K. A., Bryant, B. P., Guerry, A. D., Haddad, N. M., Hamann, M., Hamel, P., Johnson, J. A., Mandle, L., Pereira, H. M., Polasky, S., Ruckelshaus, M., Shaw, M. R., Silver, J. M., Vogl, A. L., and Daily, G. C. (2019). Global modeling of nature's contributions to people. *Science*, *366*(6462), 255–258. https://doi.org/10.1126/science.aaw3372

Fischer, J., Lindenmayer, D. B., and Manning, A. D. (2006). Biodiversity, ecosystem function, and resilience: Ten guiding principles for commodity production landscapes. *Frontiers in Ecology and the Environment*, *4*(2), 80–86. https://doi.org/10.1890/1540-9295(2006)004[0080:BEFART]2.0.CO;2

FAO. (2018). *World Food and Agriculture – Statistical Pocketbook. 2018*. Rome. 254 pp. License: CC BY-NC-SA 3.0 IGO.

Gelfand, I., Hamilton, S. K., Kravchenko, A. N., Jackson, R. D., Thelen, K. D., and Robertson, G. P. (2020). Empirical Evidence for the Potential Climate Benefits of Decarbonizing Light Vehicle Transport in the U.S. with Bioenergy from Purpose-Grown Biomass with and without BECCS. *Environmental Science & Technology*, *54*(5), 2961–2974. https://doi.org/10.1021/acs.est.9b07019

Isbell, F., Adler, P. R., Eisenhauer, N., Fornara, D., Kimmel, K., Kremen, C., Letourneau, D. K., Liebman, M., Polley, H. W., Quijas, S., and Scherer-Lorenzen, M. (2017). Benefits of increasing plant diversity in sustainable agroecosystems. *Journal of Ecology*, *105*(4), 871–879. https://doi.org/10.1111/1365-2745.12789

Intergovernmental Platform on Biodiversity and Ecosystem Services. (2019). Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Díaz, S., Settele, J., Brondízio, E.S., Ngo, H. T., Guèze, M., Agard, J., Arneth, A., Balvanera, P., Brauman, K. A., Butchart, S. H. M., Chan, K. M. A., Garibaldi, L. A., Ichii, K., Liu, J., Subramanian, S. M., Midgley, G. F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., Polasky, S., Purvis, A., Razzaque, J., Reyers, B., Chowdhury, R. R., Shin, Y. J., Visseren-Hamakers, I. J., Willis, K. J., and Zayas, C. N., (editors). IPBES secretariat, Bonn, Germany. 56 pages. https://doi.org/10.5281/zenodo.3553579

Kordbacheh, F., Liebman, M., and Harris, M. (2020). Strips of prairie vegetation placed within row crops can sustain native bee communities. *PLOS ONE*, *15*(10), e0240354. https://doi.org/10.1371/journal.pone.0240354

Kremen, C. and Merenlender, A. M. (2018). Landscapes that work for biodiversity and people. *Science*, *362*(6412), eaau6020. https://doi.org/10.1126/science.aau6020

Kremen, C., Williams, N. M., Aizen, M. A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S. G., Roulston, T., Steffan-Dewenter, I., Vázquez, D. P., Winfree, R., Adams, L., Crone, E. E., Greenleaf, S. S., Keitt, T. H., Klein, A.-M., Regetz, J., and Ricketts, T. H. (2007). Pollination and other ecosystem services produced by mobile organisms: A conceptual framework for the effects of land-use change. *Ecology Letters*, *10*(4), 299–314. https://doi.org/10.1111/j.1461-0248.2007.01018.x

Lamy, T., Liss, K. N., Gonzalez, A., and Bennett, E. M. (2016). Landscape structure affects the provision of multiple ecosystem services. *Environmental Research Letters*, *11*(12), 124017. https://doi.org/10.1088/1748-9326/11/12/124017

Landis, D. A. (2017). Designing agricultural landscapes for biodiversity-based ecosystem services. *Basic and Applied Ecology*, *18*, 1–12. https://doi.org/10.1016/j.baae.2016.07.005

Liebman, M. and Schulte, L. A. (2015). Enhancing agroecosystem performance and resilience through increased diversification of landscapes and cropping systems. *Elementa: Science of the Anthropocene*, *3*, 000041. https://doi.org/10.12952/journal.elementa.000041

Lipper, L., McCarthy, N., Zilberman, D., Asfaw, S., and Branca, G., (editors). (2018). *Climate Smart Agriculture: Building Resilience to Climate Change* (Vol. 52). Springer International Publishing. https://doi.org/10.1007/978-3-319-61194-5

Luther, Z. R., Swinton, S. M., and Van Deynze, B. (2022). Potential Supply of Midwest Cropland for Conversion to In-Field Prairie Strips. *Land Economics.* (Early access Dec. 28, 2021).

M'Gonigle, L. K., Ponisio, L. C., Cutler, K., and Kremen, C. (2015). Habitat restoration promotes pollinator persistence and colonization in intensively managed agriculture. *Ecological Applications*, *25*(6), 1557–1565. https://doi.org/10.1890/14-1863.1

Mitchell, M. G. E., Bennett, E. M., and Gonzalez, A. (2014). Agricultural landscape structure affects arthropod diversity and arthropod-derived ecosystem services. *Agriculture, Ecosystems & Environment*, *192*, 144–151. https://doi.org/10.1016/j.agee.2014.04.015

Novotny, V. (1999). Diffuse pollution from agriculture - a worldwide outlook. *Water Science and Technology, 39*(3), 1-13. https://doi.org/10.2166/wst.1999.0124

Paustian, K., Robertson, G. P., and Elliott, E. T. (1995). Management impacts on carbon storage and gas fluxes (CO2, CH4) in mid-latitude cropland. Pages 69-84 *in* Lal, R., Kimble, J. M., Levine, E., and Stewart, B. A., (editors). *Soil Management and the Greenhouse Effect, Advances in Soil Science.* CRC Press, Boca Raton, Florida, USA.

Renard, D. and Tilman, D. (2019). National food production stabilized by crop diversity. *Nature*, *571*(7764), 257–260. https://doi.org/10.1038/s41586-019-1316-y

Robertson, G. P., Hamilton, S. K., Barham, B. L., Dale, B. E., Izaurralde, R. C., Jackson, R. D., Landis, D. A., Swinton, S. M., Thelen, K. D., and Tiedje, J. M. (2017). Cellulosic biofuel contributions to a sustainable energy future: Choices and outcomes. *Science*, *356*(6345), eaal2324. https://doi.org/10.1126/science.aal2324

Roozeboom, K. L., Wang, D., McGowan, A. R., Propheter, J. L., Staggenborg, S. A., and Rice, C. W. (2019). Long-term Biomass and Potential Ethanol Yields of Annual and Perennial Biofuel Crops. *Agronomy Journal*, *111*(1), 74–83. https://doi.org/10.2134/agronj2018.03.0172

Schulte, L. A., Dale, B. E., Bozzetto, S., Liebman, M., Souza, G. M., Haddad, N., Richard, T. L., Basso, B., Brown, R. C., Hilbert, J. A., and Arbuckle, J. G. (2021). Meeting global challenges with regenerative agriculture producing food and energy. *Nature Sustainability*. https://doi.org/10.1038/s41893-021-00827-y

Schulte, L. A., Niemi, J., Helmers, M. J., Liebman, M., Arbuckle, J. G., James, D. E., Kolka, R. K., O'Neal, M. E., Tomer, M. D., Tyndall, J. C., Asbjornsen, H., Drobney, P., Neal, J., Van Ryswyk, G., and Witte, C. (2017). Prairie strips improve biodiversity and the delivery of multiple ecosystem services from corn–soybean croplands. *Proceedings of the National Academy of Sciences*, *114*(42), 11247–11252. https://doi.org/10.1073/pnas.1620229114

Tamburini, G., Bommarco, R., Wanger, T. C., Kremen, C., van der Heijden, M. G. A., Liebman, M., and Hallin, S. (2020). Agricultural diversification promotes multiple ecosystem services without compromising yield. *Science Advances*, *6*(45). https://doi.org/10.1126/sciadv.aba1715

Tscharntke, T. and Brandl, R. (2004). Plant-Insect Interactions in Fragmented Landscapes. *Annual Review of Entomology*, *49*(1), 405–430. https://doi.org/10.1146/annurev.ento.49.061802.123339

Tscharntke, T., Grass, I., Wanger, T. C., Westphal, C., and Batáry, P. (2021). Beyond organic farming – harnessing biodiversity-friendly landscapes. *Trends in Ecology & Evolution*, *36*(10), 919–930. https://doi.org/10.1016/j.tree.2021.06.010

Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., and Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters*, *8*(8), 857–874. https://doi.org/10.1111/j.1461-0248.2005.00782.x

Werling, B. P., Dickson, T. L., Isaacs, R., Gaines, H., Gratton, C., Gross, K. L., Liere, H., Malmstrom, C. M., Meehan, T. D., Ruan, L., Robertson, B. A., Robertson, G. P., Schmidt, T. M., Schrotenboer, A. C., Teal, T. K., Wilson, J. K., and Landis, D. A. (2014). Perennial grasslands enhance biodiversity and multiple ecosystem services in bioenergy landscapes. *Proceedings of the National Academy of Sciences*, *111*(4), 1652–1657. https://doi.org/10.1073/pnas.1309492111

CHAPTER ONE

Optimizing pollinator conservation and crop yield among perennial bioenergy crops[1]

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 plantings – 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

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markets that value the multifunctionality of perennial biofuel systems in order to achieve greater ecosystem services from agricultural landscapes.

Introduction

Human actions have caused a global biodiversity crisis with rapid and widespread rates of biodiversity decline (Dirzo et al. 2014, Wepprich et al. 2019, van Klink et al. 2020, Wagner et al. 2021). Simultaneously, humans are faced with the challenge of sustainably and equitably supporting a growing human population (Foley et al. 2011, Kremen & Merenlander 2018, Bennett et al. 2021). Agricultural landscapes are the greatest source of biodiversity loss and have the greatest potential for sustainable conservation (Intergovernmental Platform on Biodiversity and Ecosystem Services 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 for humans, input-intensive agricultural landscapes need to transition into multifunctional working landscapes (Jordan & Warner 2010, Díaz et al. 2019).

Diversified agricultural landscapes can mitigate the loss of biodiversity while sustainably supporting a growing human population (Fischer et al. 2006, Albrecht al. 2020). 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, Nicholls & Altieri 2013, Isbell et al. 2017). 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 (Morandin & Kremen 2013, Schulte et al. 2017, Kremen & Merenlander 2018). The effect of diversifying working landscapes has the potential to create synergies or tradeoffs for biodiversity and the yield of food, fiber, and fuel (Nelson et al. 2009, Meehan et al. 2013, Raudsepp-Earne et al. 2010, Goldstein et al. 2012, 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 (Wiens et al. 2011, Senapathi et al. 2015).

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 semi-natural habitats that can also produce bioenergy (Robertson 2008, Cai et al. 2011, Núñez-Regueiro et al. 2019). 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 (Rogelj et al. 2018, Gelfand et al. 2020). The impact of biofuel agriculture on biodiversity depends on previous land use and biofuel crop choice, including crop diversity (polyculture vs. monoculture) (Tilman et al. 2009, Wiens et al. 2011, Bennett et al. 2014, Robertson et al. 2017). 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, Werling et al. 2014, Landis et al. 2018), 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 (Wiens et al. 2011, Robertson et al. 2017). Such polycultures include those that we assess: mixes of native grasses (Tilman et al. 2006, Hill 2009), 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 (Potts et al. 2003, Ebeling et al. 2008, Williams et al. 2015, Kremen et al. 2018). Within agricultural landscapes, more diverse plantings increase the resources and habitat available for pollinators (Ebeling et al. 2008, Isbell et al. 2017, Mallinger et al. 2016, Kremen et al. 2018). 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 (Gardiner et al. 2010, Stanley & Stout 2013, Romero & Quezada-Euán 2013, Werling et al. 2014, Bennett et al. 2014, Graham et al. 2017). 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 (Power 2010, Waldron et al. 2012, Dale et al. 2014, Landis et al. 2018), 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?

Methods

Study sites

We conducted this study at the Biofuel Cropping System Experiment at the U.S. Department of Energy's Great Lakes Bioenergy Research Center (GLBRC) experimental landscape (Figure 1.1). 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 1.1 a). 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 30m by 40m with a permanent path in the same location in each plot for sampling (Figure 1.1 b). See Gelfand et al. (2020) for detailed soil and climate information at this experimental site.

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 1.1 for flowering species observed in each treatment in 2018). The native grasses treatment was a mix of one perennial C3 grass (*Elymus canadensis*) and four C4 grasses (*Panicum virgatum, Andropogon gerardii, Schizachyrium scoparium, Sorghastrum nutans*) seeded in polyculture. The restored prairie treatment was seeded in native prairie species including the same C3 and C4 grasses as in the native grasses treatment plus one C3 grass (*Koeleria cristata*), three leguminous forbs (*Desmodium canadense, Lespedeza capitata, 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 1.2.

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).

Flowers

Four sampling rounds of flowers and pollinators occurred monthly between June and October of 2018. We conducted flower surveys within five days of each pollinator survey in every plot to quantify resources available to pollinators. We measured flower richness and abundance along a 2x60m transect in each plot (Fig. 1b). We only recorded actively flowering forbs; we did not record grasses. Table 1.1 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 ten individuals of each species (or all individuals if fewer than ten 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 *Rudbeckia hirta* the equivalent to an individual flower (Table 1.1).

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.

Pollinators

To test effects of bioenergy crops on pollinators, we conducted pollinator surveys in each plot. Pollinator diversity and abundance were measured along the same 2x60m transects as the flower surveys (Figure 1.1 b). Each plot was surveyed twice per day per sampling round, with one survey occurring between 10am-12pm, and the second survey occurring between 1-4pm. To limit bias, only two scientists conducted all surveys, each of which consisted of walking a single transect over a ten-minute 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, >16mm), large green bees (>10 mm including *Agapostemon* spp.), medium dark bees (brown or black bees, 10-16mm), moths, small dark bees (brown or black bees, <10mm), small green bees (<10mm), 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.

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).

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 efficient use of resources (Polasky et al. 2005, Kennedy et al. 2008, 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.

Results

Flowers

Flower abundance did not differ among successional (mean: 17734.7 ± 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) (χ^2=51.9, p<0.001, Figure 1.2 a). Results did not change when the number of individual plants replaced flower abundance as the 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) (χ^2=235.1, p<0.001, Figure 1.2 b).

Pollinators

Across four sampling rounds, we visually identified 1640 pollinator individuals. Pollinator abundance was highest in successional (mean: 59.1 ± 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) (χ^2=153.4, p<0.001, Figure 1.2 c). 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 (χ^2=76.5, p<0.001, Figure 1.2 d). 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 1.3 a; pollinator group richness and flowering plant abundance R^2=0.47, p<0.001, Figure 1.3 b; pollinator abundance and flowering plant richness R^2=0.25, p<0.001, Figure 1.3 c; pollinator group richness and flower richness R^2=0.49, p<0.001 Figure 1.3 d).

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 (χ^2=87.4, p<0.001, Figure 1.4).

Optimizing crop yield and pollinator conservation

The Pareto frontier analysis created an optimal boundary for valuing high crop yield and high pollinator conservation (Figure 1.5). 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.

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 (Ridgway 2016, Graham et al. 2017), 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, Kempski 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 (Fig. 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 ± 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 (Roozeboom et al. 2019, Gelfand et al. 2020). 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 Fig. 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 which 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 plays 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 (Kremen & Miles 2012, Kennedy et al. 2013, Isbell et al. 2017). 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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APPENDIX

Table 1.1. List of plant species with open flowers present in each treatment, and method used for counting floral abundance and plant abundance.

	Treatments present					
Flower species	Native grasses	Restored prairie	Successional	Switchgrass	Flower equivalent	Plant equivalent
Achillea millefolium	x	x	x		flower	flower cluster
Ambrosia artemisiifolia			x		raceme	plant
Anthemis cotula			x		head	plant
Asclepias syriaca			x		flower	umbel
Aster sp. 1	x	x	x	x	head	plant
Aster sp. 2			x	x	head	plant
Centaurea maculosa			x		head	plant
Daucus carota	x	x	x	x	flower	umbel
Desmodium sp.		x			flower	plant
Dianthus armeria		x	x		flower	plant
Erigeron annuus		x	x	x	flower	plant
Euthamia graminifolia	x	x	x	x	flower	raceme
Geum canadense			x		flower	plant
Hieracium kalmii			x	x	flower	plant
Hieracium sp.			x		head	plant
Hypericum perforatum			x	x	flower	plant

Table 1.1 (cont'd)

Lactuca serriola			x	x	flower	plant
Medicago lupulina		x			head	plant
Monarda fistulosa	x	x	x	x	flower	head
Oenothera biennis			x	x	flower	plant
Oxalis sp.			x		flower	plant
Phytolacca americana			x		flower	plant
Plantago lanceolata			x		head	plant
Potentilla sp.			x		flower	plant
Ratibida pinnata	x	x	x	x	head	plant
Rudbeckia hirta		x	x	x	head	plant
Silene latifolia	x		x	x	flower	plant
Silphium perfoliatum		x	x	x	head	plant
Solanum carolinense			x		flower	plant
Solidago canadensis	x	x	x	x	raceme	plant
Solidago rigida		x	x		raceme	plant
Solidago speciosa		x			raceme	plant
Solidago sp.		x	x	x	raceme	plant
Symphyotrichum novae-angliae	x	x	x	x	head	plant
Torilis japonica			x	x	flower	umbel
Trifolium pratense		x	x		head	plant
Verbascum thapsus			x		flower	plant
Verbena urticifolia			x		flower	plant

Table 1.1 (cont'd)

Veronica persica		x		flower	plant
Vicia americana	x			flower	plant
unknown 1	x			flower	stem
unknown 2	x			flower	raceme
unknown 3	x			flower	head
unknown 4			x	head	flower

Table 1.2. Seeded species and seeding rates for experimental treatments. Due to an intense rain event within two weeks of planting in 2008, most of the seed was lost from treatment plots. After evaluation of the plant composition in the experimental plots in the following summer, a decision was made by scientists and practitioners to replant seed in the switchgrass, native grasses, and restored prairie treatments in 2009. The rates of additional seeding were calculated by restoration practitioners to make the total seeding rate equal to the attempted seeding rate of 2008. Surveying, seeding rates, and planting densities were conducted by a local native seed and restoration company Native Connections in Kalamazoo, MI, USA (occupied Anishinaabe land) following local best-management practices (Sanford et al. 2016).

Treatment	Species	Grass/forb	Oz per acre
Native grasses	*Schizachyrium scoparium* (Michx.) Nash	grass	45.4
	Sorghastrum nutans (L.) Nash	grass	34.1
	Andropogon gerardii	grass	34.1
	Elymus canadensis	grass	22.7
	Panicum virgatum var. Southlow	grass	22.7
Restored prairie	*Elymus canadensis*	grass	17
	Sorghastrum nutans (L.) Nash	grass	17
	Schizachyrium scoparium (Michx.) Nash	grass	17
	Andropogon gerardii	grass	17
	Desmodium canadense	forb	5
	Lespedeza capitata	forb	5

Table 1.2 (cont'd)

	Baptisia lactea var. lactea (Raf.) Thieret	forb	5
	Rudbeckia hirta L.	forb	5
	Anemone canadensis L.	forb	5
	Asclepias tuberosa L.	forb	5
	Monarda fistulosa L.	forb	5
	Silphium perfoliatum L.	forb	5
	Ratibida pinnata (Vent.) Barnh.	forb	5
	Solidago rigida L.	forb	5
	Solidago speciosa L.	forb	5
	Symphyotrichum novae-angliae L.	forb	5
	Koeleria cristata	grass	11.4
	Panicum virgatum var. Southlow	grass	11.4
Switchgrass	*Panicum virgatum* var. Cave-in-Rock	grass	201.6
Successional	-	-	-

Figure 1.1. (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.

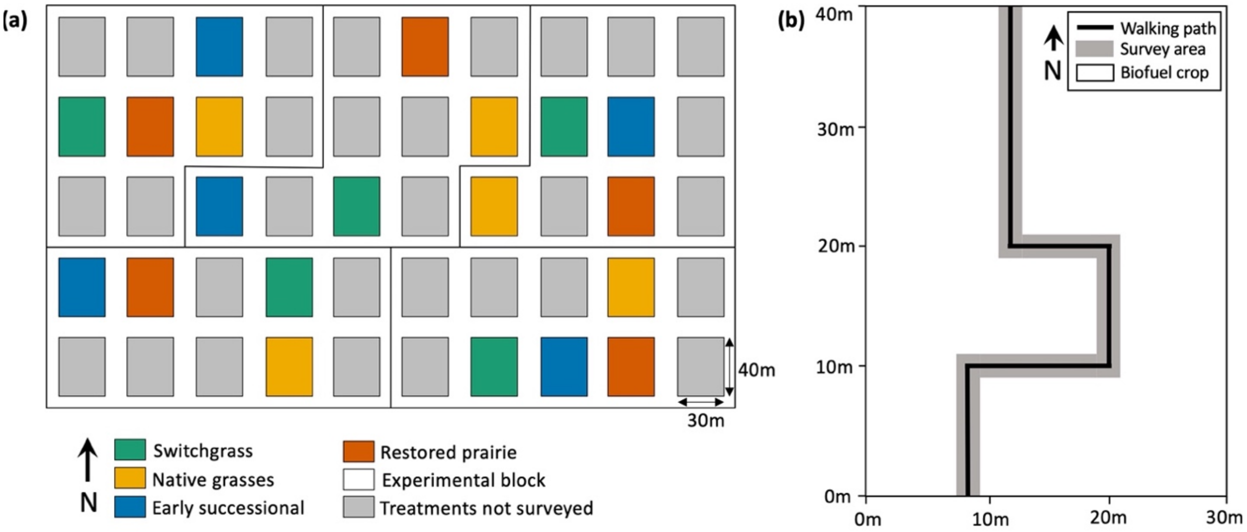


Figure 1.2. (a) Flower abundance, (b) flowering plant richness, (c) pollinator abundance, and (d) pollinator group richness recorded in each of the four biofuel crop treatments. Each bar represents an average across replicated plots and sampling rounds ±1 SE. Letters indicate significant differences.

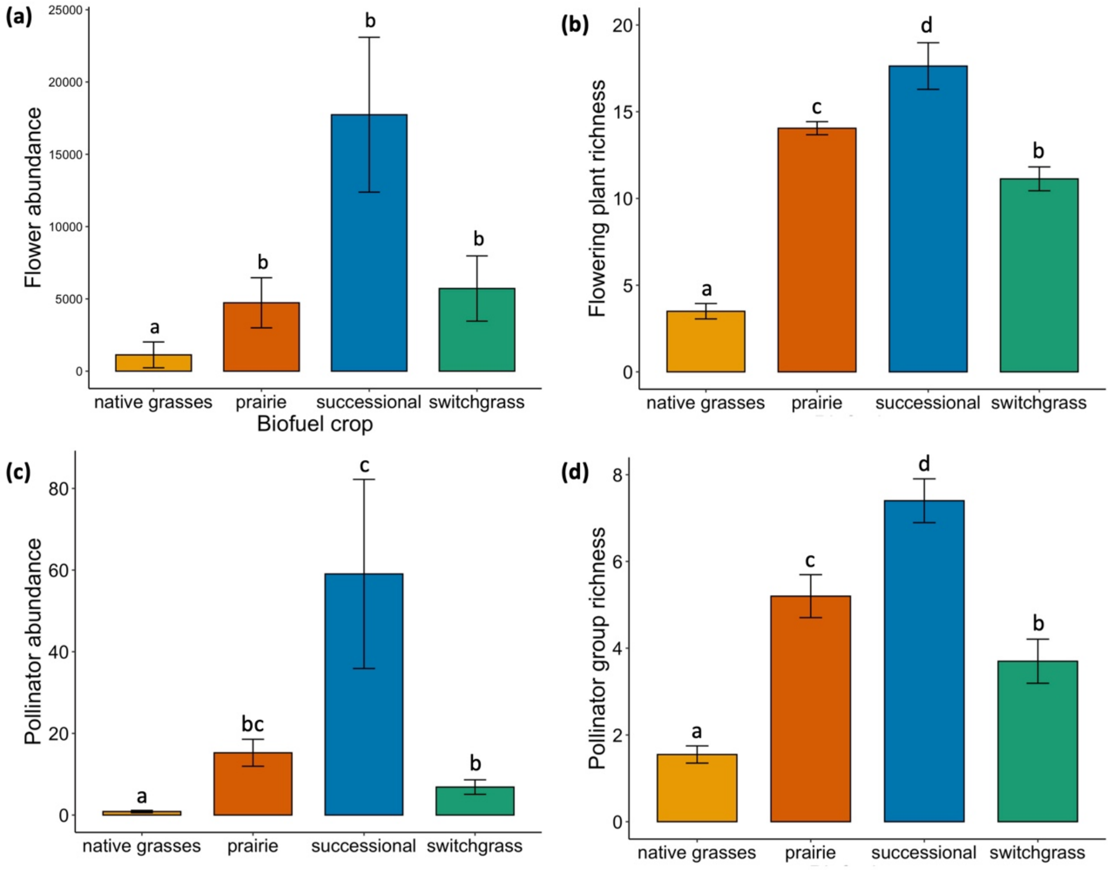


Figure 1.3. (a) Pollinator abundance as a function of flowering plant abundance, (b) pollinator abundance as a function of flower richness, (c) pollinator group richness as a function of flowering plant abundance, and (d) pollinator group richness as a function of flower richness. Each plot depicts a 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.

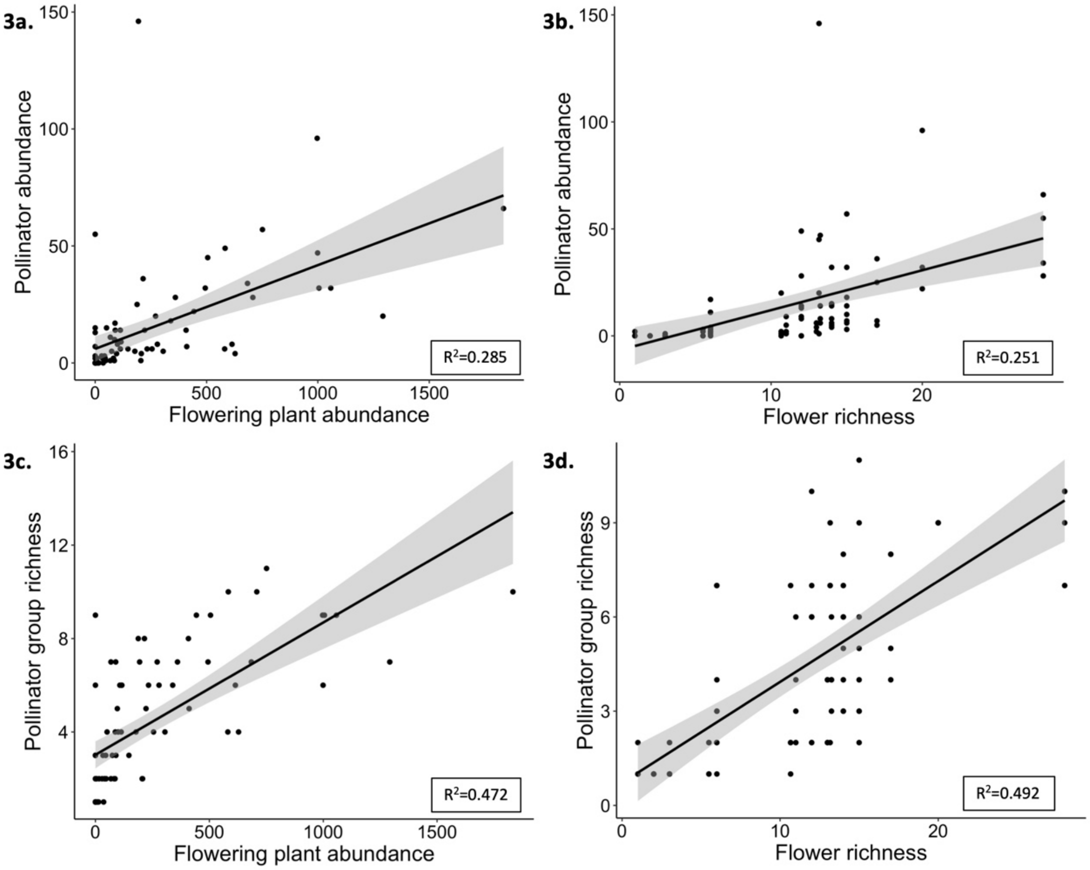


Figure 1.4. The yield of dry harvested biomass (Mg/ha) of each biofuel crop treatment. For comparison, maize yielded on average 9.388 Mg/ha in this same replicated experiment in 2018. Letters indicate significant differences among crop yields.

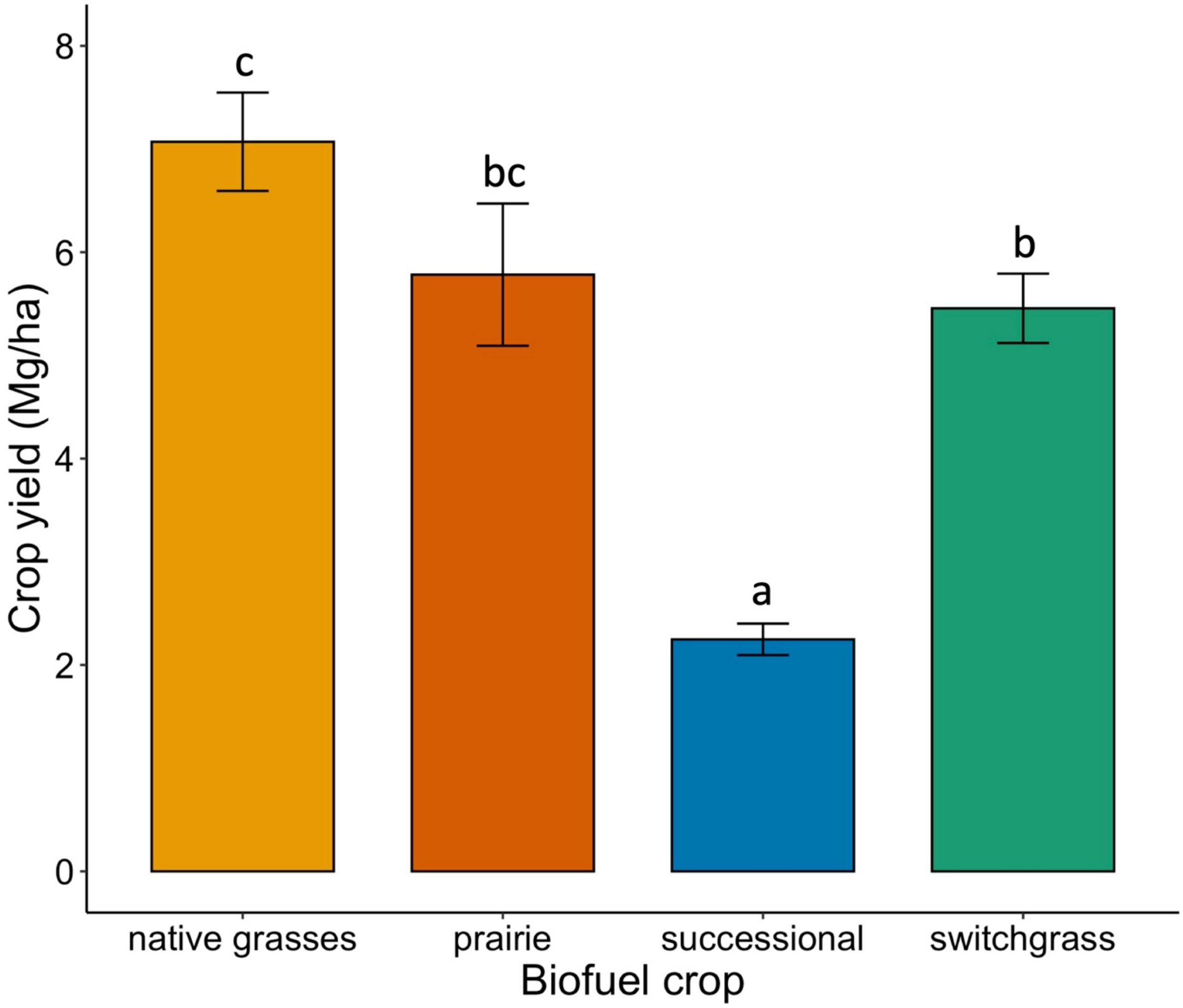
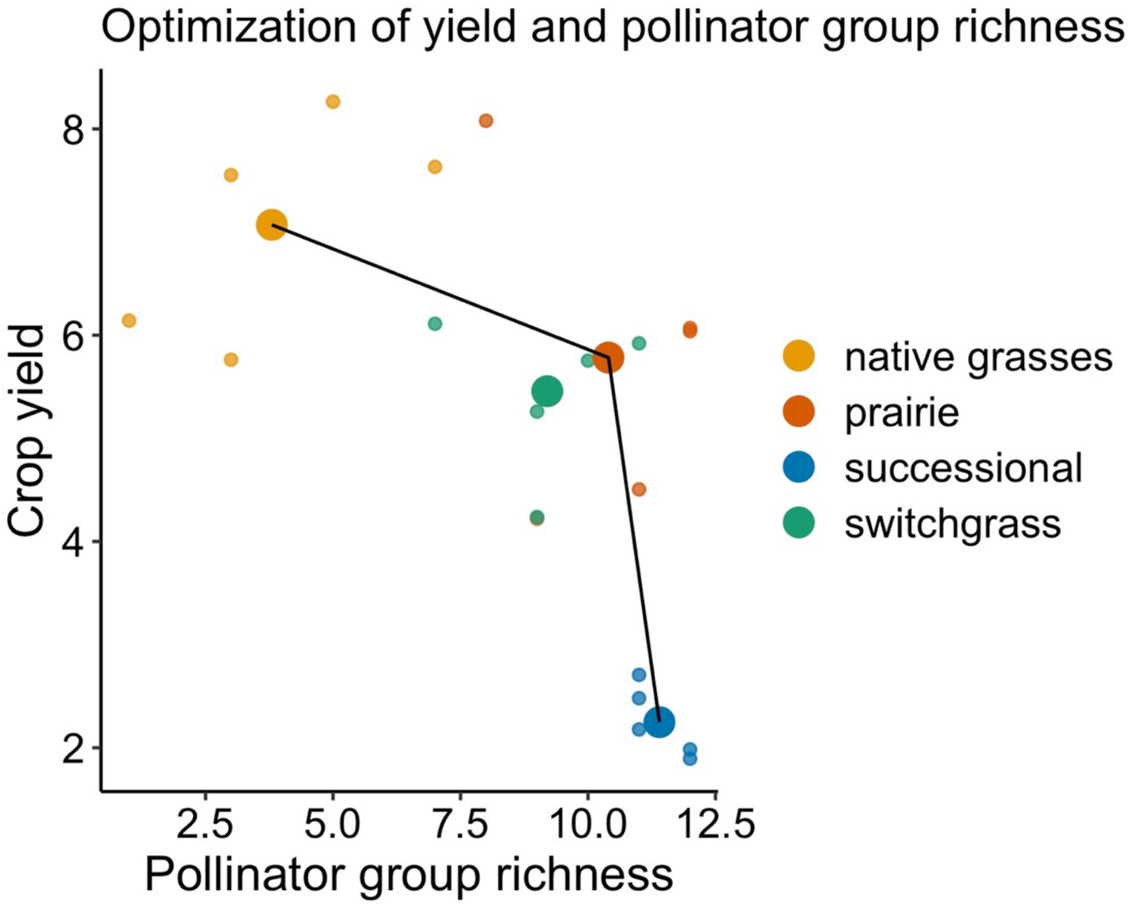


Figure 1.5. A Pareto frontier for mean crop yield (Mg/ha) and mean pollinator group richness across biofuel crop treatments. The Pareto frontier is shown as a solid black line; this describes the optimal values for crop yield and pollinator group richness over a range of preferences. The means for each treatment are the larger, bolded points and the data points for each plot are the smaller points.



LITERATURE CITED

LITERATURE CITED

Albrecht, M., Kleijn, D., Williams, N. M., Tschumi, M., Blaauw, B. R., Bommarco, R., Campbell, A. J., Dainese, M., Drummond, F. A., Entling, M. H., Ganser, D., Arjen de Groot, G., Goulson, D., Grab, H., Hamilton, H., Herzog, F., Isaacs, R., Jacot, K., Jeanneret, P., Jonsson, M., Knop, E., Kremen, C., Landis, D. A., Loeb, G. M., Marini, L., McKerchar, M., Morandin, L., Pfister, S. C., Potts, S. G., Rundlöf, M., Sardiñas, H., Sciligo, A., Thies, C., Tscharntke, T., Venturini, E., Veromann, E., Vollhardt, I. M. G., Wäckers, F., Ward, K., Wilby, A., Woltz, M., Wratten, S., and Sutter, L. (2020). The effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield: A quantitative synthesis. *Ecology Letters*, *23*(10), 1488–1498. https://doi.org/10.1111/ele.13576

Basso, B., Shuai, G., Zhang, J., and Robertson, G. P. (2019). Yield stability analysis reveals sources of large-scale nitrogen loss from the US Midwest. *Scientific Reports*, *9*(1), 5774. https://doi.org/10.1038/s41598-019-42271-1

Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1). https://doi.org/10.18637/jss.v067.i01

Bennett, A. B. and Isaacs, R. (2014). Landscape composition influences pollinators and pollination services in perennial biofuel plantings. *Agriculture, Ecosystems & Environment*, *193*, 1–8. https://doi.org/10.1016/j.agee.2014.04.016

Bennett, A. B., Meehan, T. D., Gratton, C., and Isaacs, R. (2014). Modeling Pollinator Community Response to Contrasting Bioenergy Scenarios. *PLoS ONE*, *9*(11), e110676. https://doi.org/10.1371/journal.pone.0110676

Bennett, E. M., Baird, J., Baulch, H., Chaplin-Kramer, R., Fraser, E., Loring, P., Morrison, P., Parrott, L., Sherren, K., Winkler, K. J., Cimon-Morin, J., Fortin, M.-J., Kurylyk, B. L., Lundholm, J., Poulin, M., Rieb, J. T., Gonzalez, A., Hickey, G. M., Humphries, M., Krishna, K. C., and Lapen, D. (2021). Ecosystem services and the resilience of agricultural landscapes. In *Advances in Ecological Research* (p. S0065250421000015). Elsevier. https://doi.org/10.1016/bs.aecr.2021.01.001

Brandes, E., Plastina, A., and Heaton, E. A. (2018). Where can switchgrass production be more profitable than corn and soybean? An integrated subfield assessment in Iowa, USA. *GCB Bioenergy*, *10*(7), 473–488. https://doi.org/10.1111/gcbb.12516

Cai, X., Zhang, X., and Wang, D. (2011). Land Availability for Biofuel Production. *Environmental Science & Technology*, *45*(1), 334–339. https://doi.org/10.1021/es103338e

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., and Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs*, *84*(1), 45–67. https://doi.org/10.1890/13-0133.1

Dale, B. E., Anderson, J. E., Brown, R. C., Csonka, S., Dale, V. H., Herwick, G., Jackson, R. D., Jordan, N., Kaffka, S., Kline, K. L., Lynd, L. R., Malmstrom, C., Ong, R. G., Richard, T. L., Taylor, C., and Wang, M. Q. (2014). Take a Closer Look: Biofuels Can Support Environmental, Economic and Social Goals. *Environmental Science & Technology*, *48*(13), 7200–7203. https://doi.org/10.1021/es5025433

Díaz, S., Settele, J., Brondízio, E. S., Ngo, H. T., Agard, J., Arneth, A., Balvanera, P., Brauman, K. A., Butchart, S. H. M., Chan, K. M. A., Garibaldi, L. A., Ichii, K., Liu, J., Subramanian, S. M., Midgley, G. F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., Polasky, S., Purvis, A., Razzaque, J., Reyers, B., Chowdhury, R. R., Shin, Y. J., Visseren-Hamakers, I., Willis, K. J., and Zayas, C. N. (2019). Pervasive human-driven decline of life on Earth points to the need for transformative change. *Science*, *366*(6471), eaax3100. https://doi.org/10.1126/science.aax3100

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., and Collen, B. (2014). Defaunation in the Anthropocene. *Science*, *345*(6195), 401–406. https://doi.org/10.1126/science.1251817

Ebeling, A., Klein, A.-M., Schumacher, J., Weisser, W. W., and Tscharntke, T. (2008). How does plant richness affect pollinator richness and temporal stability of flower visits? *Oikos*, *117*(12), 1808–1815. https://doi.org/10.1111/j.1600-0706.2008.16819.x

Fargione, J. E., Cooper, T. R., Flaspohler, D. J., Hill, J., Lehman, C., Tilman, D., McCoy, T., McLeod, S., Nelson, E. J., and Oberhauser, K. S. (2009). Bioenergy and Wildlife: Threats and Opportunities for Grassland Conservation. *BioScience*, *59*(9), 767–777. https://doi.org/10.1525/bio.2009.59.9.8

Fischer, J., Lindenmayer, D. B., and Manning, A. D. (2006). Biodiversity, ecosystem function, and resilience: Ten guiding principles for commodity production landscapes. *Frontiers in Ecology and the Environment*, *4*(2), 80–86. https://doi.org/10.1890/1540-9295(2006)004[0080:BEFART]2.0.CO;2

Foley, J. A., Ramankutty, N., Brauman, K. A., Cassidy, E. S., Gerber, J. S., Johnston, M., Mueller, N. D., O'Connell, C., Ray, D. K., West, P. C., Balzer, C., Bennett, E. M., Carpenter, S. R., Hill, J., Monfreda, C., Polasky, S., Rockström, J., Sheehan, J., Siebert, S., Tilman, D., and Zaks, D. P. M. (2011). Solutions for a cultivated planet. *Nature*, *478*(7369), 337–342. https://doi.org/10.1038/nature10452

Fournier, D. A., Skaug, H. J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M. N., Nielsen, A., and Sibert, J. (2012). AD Model Builder: Using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods and Software*, *27*(2), 233–249. https://doi.org/10.1080/10556788.2011.597854

Gardiner, M. A., Tuell, J. K., Isaacs, R., Gibbs, J., Ascher, J. S., and Landis, D. A. (2010). Implications of Three Biofuel Crops for Beneficial Arthropods in Agricultural Landscapes. *BioEnergy Research*, *3*(1), 6–19. https://doi.org/10.1007/s12155-009-9065-7

Garibaldi, L. A., Carvalheiro, L. G., Leonhardt, S. D., Aizen, M. A., Blaauw, B. R., Isaacs, R., Kuhlmann, M., Kleijn, D., Klein, A. M., Kremen, C., Morandin, L., Scheper, J., and Winfree, R. (2014). From research to action: Enhancing crop yield through wild pollinators. *Frontiers in Ecology and the Environment*, *12*(8), 439–447. https://doi.org/10.1890/130330

Gelfand, I., Hamilton, S. K., Kravchenko, A. N., Jackson, R. D., Thelen, K. D., and Robertson, G. P. (2020). Empirical Evidence for the Potential Climate Benefits of Decarbonizing Light Vehicle Transport in the U.S. with Bioenergy from Purpose-Grown Biomass with and without BECCS. *Environmental Science & Technology*, *54*(5), 2961–2974. https://doi.org/10.1021/acs.est.9b07019

Goldstein, J. H., Caldarone, G., Duarte, T. K., Ennaanay, D., Hannahs, N., Mendoza, G., Polasky, S., Wolny, S., and Daily, G. C. (2012). Integrating ecosystem-service tradeoffs into land-use decisions. *Proceedings of the National Academy of Sciences*, *109*(19), 7565–7570. https://doi.org/10.1073/pnas.1201040109

Graham, J. B., Nassauer, J. I., Currie, W. S., Ssegane, H., and Negri, M. C. (2017). Assessing wild bees in perennial bioenergy landscapes: Effects of bioenergy crop composition, landscape configuration, and bioenergy crop area. *Landscape Ecology*, *32*(5), 1023–1037. https://doi.org/10.1007/s10980-017-0506-y

Harrison, T. and Berenbaum, M. R. (2013). Moth diversity in three biofuel crops and native prairie in Illinois: Moth diversity in biofuel crops and prairie. *Insect Science*, *20*(3), 407–419. https://doi.org/10.1111/j.1744-7917.2012.01530.x

Helms, J. A., Ijelu, S. E., Wills, B. D., Landis, D. A., and Haddad, N. M. (2020). Ant biodiversity and ecosystem services in bioenergy landscapes. *Agriculture, Ecosystems & Environment*, *290*, 106780. https://doi.org/10.1016/j.agee.2019.106780

Hill, J., Nelson, E., Tilman, D., Polasky, S., and Tiffany, D. (2006). Environmental, economic, and energetic costs and benefits of biodiesel and ethanol biofuels. *Proceedings of the National Academy of Sciences*, *103*(30), 11206–11210. https://doi.org/10.1073/pnas.0604600103

Hill, J. (2009). Opportunities and challenges of transitioning to sustainable next-generation transportation biofuels. *International Journal of Biotechnology*, *11*(1/2), 5-13. https://doi.org/10.1504/IJBT.2009.028098

Hope, R. M. (2013). Rmisc: Ryan Miscellaneous. R package version 1.5. https://CRAN.R-project.org/package=Rmisc

Hothorn, T., Bretz, F., and Westfall, P. (2008). Simultaneous Inference in General Parametric Models. *Biometrical Journal*, *50*(3), 346–363. https://doi.org/10.1002/bimj.200810425

Hsieh, T. C., Ma, K. H., and Chao, A. (2016). iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, *7*(12), 1451–1456. https://doi.org/10.1111/2041-210X.12613

Intergovernmental Platform on Biodiversity and Ecosystem Services. (2019). Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Díaz, S., Settele, J., Brondízio, E.S., Ngo, H. T., Guèze, M., Agard, J., Arneth, A., Balvanera, P., Brauman, K. A., Butchart, S. H. M., Chan, K. M. A., Garibaldi, L. A., Ichii, K., Liu, J., Subramanian, S. M., Midgley, G. F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., Polasky, S., Purvis, A., Razzaque, J., Reyers, B., Chowdhury, R. R., Shin, Y. J., Visseren-Hamakers, I. J., Willis, K. J., and Zayas, C. N., (editors). IPBES secretariat, Bonn, Germany. 56 pages. https://doi.org/10.5281/zenodo.3553579

Isbell, F., Adler, P. R., Eisenhauer, N., Fornara, D., Kimmel, K., Kremen, C., Letourneau, D. K., Liebman, M., Polley, H. W., Quijas, S., and Scherer-Lorenzen, M. (2017). Benefits of increasing plant diversity in sustainable agroecosystems. *Journal of Ecology*, *105*(4), 871–879. https://doi.org/10.1111/1365-2745.12789

Jarchow, M. E., Liebman, M., Rawat, V., and Anex, R. P. (2012). Functional group and fertilization affect the composition and bioenergy yields of prairie plants. *GCB Bioenergy*, *4*(6), 671–679. https://doi.org/10.1111/j.1757-1707.2012.01184.x

Jordan, N. and Warner, K. D. (2010). Enhancing the Multifunctionality of US Agriculture. *BioScience*, *60*(1), 60–66. https://doi.org/10.1525/bio.2010.60.1.10

Kempski, C. (2013). *The Abundance and biodiversity of arthropods in biofuel crops: Insects and arachnids in corn, switchgrass and native mixed grass prairie fields* [Thesis]. Rochester Institute of Technology. Accessed from https://scholarworks.rit.edu/theses/4090

Kennedy, C. M., Lonsdorf, E., Neel, M. C., Williams, N. M., Ricketts, T. H., Winfree, R., Bommarco, R., Brittain, C., Burley, A. L., Cariveau, D., Carvalheiro, L. G., Chacoff, N. P., Cunningham, S. A., Danforth, B. N., Dudenhöffer, J.-H., Elle, E., Gaines, H. R., Garibaldi, L. A., Gratton, C., Holzchuh, A., Isaacs, R., Javorek, S. K., Jha, S., Klein, A. M., Krewenka, K., Mandelik, Y., Mayfield, M. M., Morandin, L., Neame, L. A., Otieno, M., Park, M., Potts, S. G., Rundlöf, M., Saez, A., Steffan-Dewenter, I., Taki, H., Viana, B. F., Westphal, C., Wilson, J. K., Greenleaf, S. S., and Kremen, C. (2013). A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters*, *16*(5), 584–599. https://doi.org/10.1111/ele.12082

Kennedy, M. C., Ford, E. D., Singleton, P., Finney, M., and Agee, J. K. (2008). Informed multi-objective decision-making in environmental management using Pareto optimality: Multi-objective optimization. *Journal of Applied Ecology*, *45*(1), 181–192. https://doi.org/10.1111/j.1365-2664.2007.01367.x

Klein, A.-M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., and Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1608), 303–313. https://doi.org/10.1098/rspb.2006.3721

Kremen, C. and Merenlender, A. M. (2018). Landscapes that work for biodiversity and people. *Science*, *362*(6412), eaau6020. https://doi.org/10.1126/science.aau6020

Kremen, Claire, M'Gonigle, L. K., and Ponisio, L. C. (2018). Pollinator Community Assembly Tracks Changes in Floral Resources as Restored Hedgerows Mature in Agricultural Landscapes. *Frontiers in Ecology and Evolution*, *6*, 170. https://doi.org/10.3389/fevo.2018.00170

Kremen, C. and Miles, A. (2012). Ecosystem Services in Biologically Diversified versus Conventional Farming Systems: Benefits, Externalities, and Trade-Offs. *Ecology and Society*, *17*(4), art40. https://doi.org/10.5751/ES-05035-170440

Landis, D. A., Gratton, C., Jackson, R. D., Gross, K. L., Duncan, D. S., Liang, C., Meehan, T. D., Robertson, B. A., Schmidt, T. M., Stahlheber, K. A., Tiedje, J. M., and Werling, B. P. (2018). Biomass and biofuel crop effects on biodiversity and ecosystem services in the North Central US. *Biomass and Bioenergy*, *114*, 18–29. https://doi.org/10.1016/j.biombioe.2017.02.003

Landis, D. A. and Werling, B. P. (2010). Arthropods and biofuel production systems in North America: Arthropods and biofuel crops. *Insect Science*, *17*(3), 220–236. https://doi.org/10.1111/j.1744-7917.2009.01310.x

Mallinger, R. E., Gibbs, J., and Gratton, C. (2016). Diverse landscapes have a higher abundance and species richness of spring wild bees by providing complementary floral resources over bees' foraging periods. *Landscape Ecology*, *31*(7), 1523–1535. https://doi.org/10.1007/s10980-015-0332-z

McGuire, B. and Rupp, S. (2013). Perennial Herbaceous Biomass Production and Harvest in the Prairie Pothole Region of the Northern Great Plains. National Wildlife Federation. http://www.nwf.org/~/media/PDFs/Wildlife/BiomassBMGPPR.pdf

Meehan, T. D., Gratton, C., Diehl, E., Hunt, N. D., Mooney, D. F., Ventura, S. J., Barham, B. L., and Jackson, R. D. (2013). Ecosystem-Service Tradeoffs Associated with Switching from Annual to Perennial Energy Crops in Riparian Zones of the US Midwest. *PLoS ONE*, *8*(11), e80093. https://doi.org/10.1371/journal.pone.0080093

Mishra, S. K., Negri, M. C., Kozak, J., Cacho, J. F., Quinn, J., Secchi, S., and Ssegane, H. (2019). Valuation of ecosystem services in alternative bioenergy landscape scenarios. *GCB Bioenergy*, *11*(6), 748–762. https://doi.org/10.1111/gcbb.12602

Mitchell, R., Vogel, K. P., and Uden, D. R. (2012). The feasibility of switchgrass for biofuel production. *Biofuels*, *3*(1), 47–59. https://doi.org/10.4155/bfs.11.153

Morandin, L. A. and Kremen, C. (2013). Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecological Applications*, *23*(4), 829–839. https://doi.org/10.1890/12-1051.1

Nelson, E., Mendoza, G., Regetz, J., Polasky, S., Tallis, H., Cameron, Dr., Chan, K. M., Daily, G. C., Goldstein, J., Kareiva, P. M., Lonsdorf, E., Naidoo, R., Ricketts, T. H., and Shaw, M. (2009). Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. *Frontiers in Ecology and the Environment*, *7*(1), 4–11. https://doi.org/10.1890/080023

Nicholls, C. I. and Altieri, M. A. (2013). Plant biodiversity enhances bees and other insect pollinators in agroecosystems. A review. *Agronomy for Sustainable Development*, *33*(2), 257–274. https://doi.org/10.1007/s13593-012-0092-y

Núñez-Regueiro, M. M., Siddiqui, S. F., and Fletcher, R. J. (2019). Effects of bioenergy on biodiversity arising from land-use change and crop type. *Conservation Biology*, *35*(1), 77–87. https://doi.org/10.1111/cobi.13452

Polasky, S., Nelson, E., Lonsdorf, E., Fackler, P., and Starfield, A. (2005). Conserving Species in a Working Landscape: Land Use with Biological and Economic Objectives. *Ecological Applications, 15*(4), 16.

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., and Kunin, W. E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology & Evolution*, *25*(6), 345–353. https://doi.org/10.1016/j.tree.2010.01.007

Potts, S. G., Vulliamy, B., Dafni, A., Ne'eman, G., and Willmer, P. (2003). Linking bees and flowers: How do floral communities structure pollinator communities? *Ecology*, *84*(10), 2628–2642. https://doi.org/10.1890/02-0136

Power, A. G. (2010). Ecosystem services and agriculture: Tradeoffs and synergies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1554), 2959–2971. https://doi.org/10.1098/rstb.2010.0143

Ramankutty, N., Mehrabi, Z., Waha, K., Jarvis, L., Kremen, C., Herrero, M., and Rieseberg, L. H. (2018). Trends in Global Agricultural Land Use: Implications for Environmental Health and Food Security. *Annual Review of Plant Biology*, *69*(1), 789–815. https://doi.org/10.1146/annurev-arplant-042817-040256

Raudsepp-Hearne, C., Peterson, G. D., and Bennett, E. M. (2010). Ecosystem service bundles for analyzing tradeoffs in diverse landscapes. *Proceedings of the National Academy of Sciences*, *107*(11), 5242–5247. https://doi.org/10.1073/pnas.0907284107

Ridgway, A. J. (2016). Density and diversity of bees in the Midwestern agricultural landscape: Influence of surrounding agricultural land use and local plant community characteristics. Dissertations and Theses at University of Northern Iowa. 282.

Robertson, G. P., Dale, V. H., Doering, O. C., Hamburg, S. P., Melillo, J. M., Wander, M. M., Parton, W. J., Adler, P. R., Barney, J. N., Cruse, R. M., Duke, C. S., Fearnside, P. M., Follett, R. F., Gibbs, H. K., Goldemberg, J., Mladenoff, D. J., Ojima, D., Palmer, M. W., Sharpley, A., Wallace, L., Weathers, K. C., Wiens, J. A, and Wilhelm, W. W. (2008). Sustainable Biofuels Redux. *Science*, *322*(5898), 49–50. https://doi.org/10.1126/science.1161525

Robertson, G. P., Hamilton, S. K., Barham, B. L., Dale, B. E., Izaurralde, R. C., Jackson, R. D., Landis, D. A., Swinton, S. M., Thelen, K. D., and Tiedje, J. M. (2017). Cellulosic biofuel contributions to a sustainable energy future: Choices and outcomes. *Science*, *356*(6345), eaal2324. https://doi.org/10.1126/science.aal2324

Rogelj, J., Shindell, D., Jiang, K., Fifita, S., Forster, P., Ginzburg, V., Handa, C., Kheshgi, H., Kobayashi, S., Kriegler, E., Mundaca, L., Séférian, R., and Vilariño, M. V. (2018). Mitigation Pathways Compatible with 1.5°C in the Context of Sustainable Development. In: *Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty* Masson-Delmotte, V., Zhai, P., Pörtner, H.-O., Roberts, D., Skea, J., Shukla, P. R., Pirani, A., Moufouma-Okia, W., Péan, R. Pidcock, S. Connors, J.B.R. Matthews, Y. Chen, X. Zhou, M.I. Gomis, E. Lonnoy, C., Maycock, T., Tignor, M., and Waterfield, T., (editors.). In Press.

Romero, M. J. and Quezada-Euán, J. J. G. (2013). Pollinators in biofuel agricultural systems: The diversity and performance of bees (Hymenoptera: Apoidea) on Jatropha curcas in Mexico. *Apidologie*, *44*(4), 419–429. https://doi.org/10.1007/s13592-013-0193-x

Roocks, P. (2016). Computing Pareto Frontiers and Database Preferences with the rPref Package. *The R Journal*, *8*(2), 393. https://doi.org/10.32614/RJ-2016-054

Roozeboom, K. L., Wang, D., McGowan, A. R., Propheter, J. L., Staggenborg, S. A., and Rice, C. W. (2019). Long-term Biomass and Potential Ethanol Yields of Annual and Perennial Biofuel Crops. *Agronomy Journal*, *111*(1), 74–83. https://doi.org/10.2134/agronj2018.03.0172

Samson, F. and Knopf, F. (1994). Prairie Conservation in North America. *BioScience*, *44*(6), 418–421. https://doi.org/10.2307/1312365

Sanford, G. R., Oates, L. G., Jasrotia, P., Thelen, K. D., Robertson, G. P., and Jackson, R. D. (2016). Comparative productivity of alternative cellulosic bioenergy cropping systems in the North Central USA. *Agriculture, Ecosystems & Environment*, *216*, 344–355. https://doi.org/10.1016/j.agee.2015.10.018

Schulte, L. A., Niemi, J., Helmers, M. J., Liebman, M., Arbuckle, J. G., James, D. E., Kolka, R. K., O'Neal, M. E., Tomer, M. D., Tyndall, J. C., Asbjornsen, H., Drobney, P., Neal, J., Van Ryswyk, G., and Witte, C. (2017). Prairie strips improve biodiversity and the delivery of multiple ecosystem services from corn–soybean croplands. *Proceedings of the National Academy of Sciences*, *114*(42), 11247–11252. https://doi.org/10.1073/pnas.1620229114

Senapathi, D., Biesmeijer, J. C., Breeze, T. D., Kleijn, D., Potts, S. G., and Carvalheiro, L. G. (2015). Pollinator conservation—The difference between managing for pollination services and preserving pollinator diversity. *Current Opinion in Insect Science*, *12*, 93–101. https://doi.org/10.1016/j.cois.2015.11.002

Skaug H., Fournier D., Nielsen A., Magnusson A., and Bolker B. (2013). Generalized Linear Mixed Models using AD Model Builder. R package version 0.7.5.

Stahlheber, K. A., Watson, B., Dickson, T. L., Disney, R., and Gross, K. L. (2016). Balancing biofuel production and biodiversity: Harvesting frequency effects on production and community composition in planted tallgrass prairie. *Biomass and Bioenergy*, *92*, 98–105. https://doi.org/10.1016/j.biombioe.2016.06.012

Stanley, D. A. and Stout, J. C. (2013). Quantifying the impacts of bioenergy crops on pollinating insect abundance and diversity: A field-scale evaluation reveals taxon-specific responses. *Journal of Applied Ecology*, *50*(2), 335–344. https://doi.org/10.1111/1365-2664.12060

Tendler, A., Mayo, A., and Alon, U. (2015). Evolutionary tradeoffs, Pareto optimality and the morphology of ammonite shells. *BMC Systems Biology*, *9*(1), 12. https://doi.org/10.1186/s12918-015-0149-z

Tilman, D., Balzer, C., Hill, J., and Befort, B. L. (2011). Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Sciences*, *108*(50), 20260–20264. https://doi.org/10.1073/pnas.1116437108

Tilman, D., Hill, J., and Lehman, C. (2006). Carbon-Negative Biofuels from Low-Input High-Diversity Grassland Biomass. *Science*, *314*(5805), 1598–1600. https://doi.org/10.1126/science.1133306

Tilman, D., Socolow, R., Foley, J. A., Hill, J., Larson, E., Lynd, L., Pacala, S., Reilly, J., Searchinger, T., Somerville, C., and Williams, R. (2009). Beneficial Biofuels—The Food, Energy, and Environment Trilemma. *Science*, *325*(5938), 270–271. https://doi.org/10.1126/science.1177970

U.S. Environmental Protection Agency. (2018). Biofuels and the Environment: The Second Triennial Report to Congress. U.S. Environmental Protection Agency, Washington, DC, EPA/600/R-18/195.

van Klink, R., Bowler, D. E., Gongalsky, K. B., Swengel, A. B., Gentile, A., and Chase, J. M. (2020). Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science*, *368*(6489), 417–420. https://doi.org/10.1126/science.aax9931

Wagner, D. L., Grames, E. M., Forister, M. L., Berenbaum, M. R., and Stopak, D. (2021). Insect decline in the Anthropocene: Death by a thousand cuts. *Proceedings of the National Academy of Sciences*, *118*(2), e2023989118. https://doi.org/10.1073/pnas.2023989118

Waldron, A., Justicia, R., Smith, L., and Sanchez, M. (2012). Conservation through Chocolate: A win-win for biodiversity and farmers in Ecuador's lowland tropics: Win-win in cocoa farms. *Conservation Letters*, *5*(3), 213–221. https://doi.org/10.1111/j.1755-263X.2012.00230.x

Wepprich, T., Adrion, J. R., Ries, L., Wiedmann, J., and Haddad, N. M. (2019). Butterfly abundance declines over 20 years of systematic monitoring in Ohio, USA. *PLOS ONE*, *14*(7), e0216270. https://doi.org/10.1371/journal.pone.0216270

Werling, B. P., Dickson, T. L., Isaacs, R., Gaines, H., Gratton, C., Gross, K. L., Liere, H., Malmstrom, C. M., Meehan, T. D., Ruan, L., Robertson, B. A., Robertson, G. P., Schmidt, T. M., Schrotenboer, A. C., Teal, T. K., Wilson, J. K., and Landis, D. A. (2014). Perennial grasslands enhance biodiversity and multiple ecosystem services in bioenergy landscapes. *Proceedings of the National Academy of Sciences*, *111*(4), 1652–1657. https://doi.org/10.1073/pnas.1309492111

Wickham H (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York. ISBN 978-3-319-24277-4. https://ggplot2.tidyverse.org.

Wiens, J., Fargione, J., and Hill, J. (2011). Biofuels and biodiversity. *Ecological Applications*, *21*(4), 1085–1095. https://doi.org/10.1890/09-0673.1

Williams, N. M., Ward, K. L., Pope, N., Isaacs, R., Wilson, J., May, E. A., Ellis, J., Daniels, J., Pence, A., Ullmann, K., and Peters, J. (2015). Native wildflower plantings support wild bee abundance and diversity in agricultural landscapes across the United States. *Ecological Applications*, *25*(8), 2119–2131. https://doi.org/10.1890/14-1748.1

World Bank. Agricultural land % of land area (2016). https://data.worldbank.org/indicator/AG.LND.AGRI.ZS

CHAPTER TWO

Prairie strips and lower land use intensity increase biodiversity and ecosystem services[2]

Abstract

Agricultural landscapes can be managed to protect biodiversity and maintain ecosystem services. One approach to achieve this is to restore native perennial vegetation within croplands. Where rowcrops have displaced prairie, as in the US Midwest, restoration of native perennial vegetation can align with crops in so called “prairie strips”. We tested the effect of prairie strips in addition to other management practices on a variety of taxa and on a suite of ecosystem services. To do so, we worked within a 33-year-old experiment that included treatments that varied methods of agricultural management across a gradient of land use intensity. In the two lowest intensity crop management treatments, we introduced prairie strips that occupied 5% of crop area. We addressed three questions: 1) What are the effects of newly established prairie strips on the spillover of biodiversity and ecosystem services into cropland? 2) How does time since prairie strip establishment affect biodiversity and ecosystem services? 3) What are the tradeoffs and synergies among biodiversity conservation, non-provisioning ecosystem services, and provisioning ecosystem services (crop yield) across a land use intensity gradient (which includes prairie strips)? Within prairie strip treatments, where sampling effort occurred within and at increasing distance from strips, dung beetle abundance, spider abundance and richness, active

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carbon, decomposition, and pollination decreased with distance from prairie strips, and this effect increased between the first and second year. Across the entire land use intensity gradient, treatments with prairie strips and reduced chemical inputs had higher butterfly abundance, spider abundance, and pollination services. In addition, soil organic carbon, butterfly richness, and spider richness increased with a decrease in land use intensity. Crop yield in one treatment with prairie strips was equal to that of the highest intensity management, even while including the area taken out of production. We found no effects of strips on ant biodiversity and greenhouse gas emissions (N_2O and CH_4). Our results show that, even in early establishment, prairie strips and lower land use intensity can contribute to the conservation of biodiversity and ecosystem services without a disproportionate loss of crop yield.

Introduction

Two global challenges of our time are supporting a growing human population and preventing the loss of biodiversity and ecosystem services (Kremen & Merenlander 2018, IPBES 2019). The capacity to address these challenges depends largely on management of agricultural lands that dominate the landscape globally (Campbell et al. 2017, Raven & Wagner 2021). In the US Midwest, for example, 38% of the landscape is planted in principal row crops (USDA 2019). These agroecosystems were designed to maximize the production of food, fuel, and fiber, and they contribute to greenhouse gas emissions, pollution, and the loss of natural ecosystems and biodiversity (Tilman & Clark 2015). To prevent further ecological harm and to sustain food, fuel, and fiber production for future generations, agricultural landscapes must be managed for multifunctionality and biodiversity (Asbjornson et al. 2013, IPBES 2019, Mitchell et al. 2021). Yet, there are few assessments of the tradeoffs and synergies of biodiversity and ecosystem service responses across crop management and conservation practices required to address the two grand challenges (Wittwer et al. 2021).

Diversifying agricultural landscapes can promote biodiversity and non-provisioning ecosystem services without compromising crop yield (Tamburini et al. 2020, Tscharntke et al. 2021). Landscape diversification, an approach to land management rooted in indigenous knowledge, has been experimentally studied by the scientific community for applications in input-intensive cropping systems (IPBES 2016, Nkuba et al. 2020). One method of diversifying agricultural landscapes, as is done in the US Midwest, is to establish prairie strips on row crop farms. This conservation practice consists of retiring areas of farmland and actively restoring them by seeding native perennial vegetation. Supported by the United States Department of Agriculture (USDA) Conservation Reserve Program (CRP), prairie strips are one of many "edge of field" practices–including riparian buffers, hedgerows, and wildflower strips–aimed at incorporating native and diverse habitat into agricultural landscapes (The Nature Conservancy 2021).

Once established, prairie strips in contoured farm landscapes can reduce soil erosion, improve water quality, and support biodiversity. This can provide benefits to the farm and farmer at disproportionately higher levels than the amount of farmland removed from production (Schulte et al. 2017). Prairie strips also have the potential to provide resources and habitat for beneficial insects and increase their spillover into the farm, where they can provide ecosystem services such as biocontrol and pollination (Blitzer et al. 2012, Morandin & Kremen 2013, Kordbacheh et al. 2020). While prairie strips are known to benefit biodiversity and ecosystem services once they have been established for multiple years, these impacts have not been studied during their initial years of establishment. Measuring prairie strips' conservation potential during their early establishment period can address this gap and increase the precision of farmers' expectations of prairie strips.

The conservation potential of prairie strips relative to other agricultural conservation practices such as no tillage is also unknown. Biodiversity and ecosystem services in agroecosystems are driven not only by the presence of natural habitat on or near farms, but also by the agricultural management practices used in row crop areas. Crop rotations and cover crops generally increase biodiversity and enhance nutrient availability (Rusch et al. 2013, de Pedro et al. 2020, Bowers et al. 2021), whereas the use of tillage, pesticides, and fertilizer generally decrease biodiversity and increase greenhouse gas emissions (Syswerda & Robertson 2014, Bowles et al. 2016, Raven & Wagner 2021). But when implemented jointly, landscape diversification and crop management practices can interact to produce unique impacts on on-farm biodiversity and ecosystem services (Schmidt et al. 2005, Tscharntke et al. 2005, Landis 2017). There is some evidence that conventionally managed farm fields with prairie strips increase ecosystem services compared to conventionally managed farm fields without strips, and research has focused on the reduction of nutrient runoff and erosion in contoured agricultural landscapes (Schulte et al. 2017). By directly comparing responses in fields with prairie strips with responses in fields managed with other practices, we can better identify combinations of prairie strips and crop management that may optimize crop yield, biodiversity, and ecosystem services.

We address how targeted conservation can promote multifunctionality including biodiversity, agricultural production, and other ecosystem services. Working in a 33-year-old experiment, we tested the effects of prairie strips and a gradient of crop management strategies across a suite of invertebrate biodiversity metrics and ecosystem services during the first two years of prairie strip establishment. First, we asked: what are the effects of newly established prairie strips on the spillover of biodiversity and ecosystem services into cropland? To test this, we measured how services changed with distance from a prairie strip. Second, we asked: how does time since prairie strip establishment affect biodiversity and ecosystem services in agricultural plots? Third, we asked: what are the tradeoffs and synergies among biodiversity conservation, non-provisioning ecosystem services, and crop yield across a gradient of land use intensity? To answer our third question, we examined all services across a land use gradient (including treatments with prairie strips) in relation to yield changes. Our study includes biodiversity measurements of ants, butterflies, dung beetles, and spiders, all of which can provide ecosystem services to farms. Our study also includes ecosystem service measurements of microbial activity, decomposition, greenhouse gas emissions, pollination, soil carbon, and crop yield.

Materials and Methods

Study sites and sampling locations

We conducted our study at the Kellogg Biological Station Long Term Ecological Research (KBS LTER) site in Hickory Corners, MI USA (occupied Anishinaabe land) that was established in 1987. The KBS LTER is located in a temperate climate with a mean temperature of 10.1°C and mean annual precipitation of 100.5 cm (1981-2011 means) with increasing trends in temperature over the past few decades (Robertson & Hamilton 2015, Liang & Robertson 2021). Surface soils are 17% clay/43% sand Alfisol loams developed on glacial till and outwash (Robertson & Hamilton 2015).

This study occurred in 2019–2020, the first two years after prairie strip planting. We worked in five treatments of KBS-LTER's Main Cropping System Experiment: conventionally managed row crops, no till row crops, reduced input row crops, biologically based (organic) row crops, and conservation land (details of crop management treatments are compared in Figure 2.1 and in Robertson and Hamilton (2015)). The experiment consisted of six replicated plots of each treatment (six experimental blocks; Figure 2.2 a), with each plot having an area of one hectare (87 m x 105 m; Figure 2.2 b). *Conventional* and *no till* treatments received levels of chemical inputs that follow Generally Accepted Agricultural and Management Practices (GAAMP) in Michigan, USA and are typical for the US Midwest (details on the dates and quantities of fertilizer application, pesticide application, weed management, and soil preparation can be found at https://aglog.kbs.msu.edu). The conventional treatment was tilled with a chisel plow, and the no till treatment was managed as the conventional treatment but was left unplowed. The *reduced input* treatment received lower levels of inputs (nitrogen at planting and pesticides) than conventional and no till and had a legume cover crop in the winter. The *biologically based* treatment did not receive any chemical inputs, compost, or manure, and it had a legume cover crop and was rotary hoed five times after planting in 2020 to control weeds. *Conservation land* (referred to as *early successional* in site maps and earlier publications) was unmanaged other than yearly burning in the spring to suppress woody vegetation. This treatment was a grassland with the dominant bloom period in the fall when goldenrods and asters flower. All treatments except conservation land were on a three-year maize (*Zea mays* L.)—winter wheat (*Triticum aestivum* L.)—soybean (*Glycine max* L.) rotation. In the years of our study, wheat was planted in 2019 and maize in 2020.

Prairie strips were introduced in the reduced input and biologically based treatments in April 2019. In five percent of each plot, configured as a strip parallel to row crops down the middle of each plot, we sowed a native prairie plants species mix. The mix consisted of 4 grass species and 18 forb species (Table 2.1) purchased from Native Connections, Kalamazoo, Michigan, USA. The mix was chosen to have species bloom throughout the growing season (Isaacs et al. 2009). The mixes sown in each plot contained the same weight and proportion of each species. The first year's plant community was dominated by agricultural weeds, but with some seeded species flowering. The second year's plant community contained more seeded species, and we expect more seeded species to establish as the prairie strips mature. Prairie strips were mowed three times during the 2019 season to reduce weeds and support establishment of native seeds.

We compared a variety of biodiversity and ecosystem service measures by sampling three sets of sampling locations within the plots (Figure 2.2 b). First, to compare among plot-level treatments, each plot had five sampling locations distributed throughout, all located outside of prairie strips. These sampling locations are referred to as Standard Sampling Stations. Second, also to compare among plot-level treatments, each plot had six sampling stations at the northeast corner for destructive sampling that could not occur at the Standard Sampling Stations. These sampling locations are referred to as Subplot Sampling Stations. Third, reduced input and biologically based treatments had an additional three transects perpendicular to the prairie strips with sampling locations at distances of 0 m, 1 m, 5 m, and 20 m from the prairie strip (the station at 0 m was located within the prairie strip). These sampling stations were used to measure biodiversity and ecosystem services at different distances from the prairie strips and are referred to as Strip Sampling Stations.

Because prairie strips were implemented in all replicates of the reduced input and biologically based treatments, we do not have a fully factorial experiment. Therefore, we cannot isolate the effect of prairie strips from effects of crop management and year on measures of biodiversity and ecosystem services across all crop management treatments. However, we can (i) make conclusions about how treatments with prairie strips, in the context of their associated management strategies (including historical data on these treatments), compare to other crop management strategies without prairie strips, (ii) examine trends of prairie strips with time since establishment, where increases from year to year would suggest prairie strips play a role for processes that stabilized with the background management treatments (though are confounded by crop rotation), and (iii) we can also attribute significant effects of distance from prairie strips on response variables to the presence of the strip, though benefits of prairie strips are not isolated to spillover effects.

Dung beetles

Soil dwelling macroarthropods contribute to decomposition in agricultural landscapes by fragmenting litter, altering soil structure, and feeding on other soil dwelling fauna. Dung beetles break apart manure, mobilize nutrients in the soil (Coleman et al. 2018a), and suppress human and livestock pathogens (Nichols et al. 2008, Jones et al. 2016, Sands & Wall 2017). Dung beetle communities are vulnerable to the effects of crop management and are negatively affected by agricultural intensification (Barbero et al. 1999, Hutton & Giller 2003).

Across management treatments: To compare dung beetle diversity (as well as ants and spiders which are described next) across crop management treatments, we installed pitfall traps at Subplot Sampling Stations within each plot. Pitfall traps consisted of plastic containers (5.1

cm diameter, 120 mL) buried so the container's rim was flush with the soil surface. We partially filled containers with 95% ethanol mixed with a few drops of detergent to break surface tension. To protect the traps from rain and flooding, we mounted clear Plexiglass rain covers (15 x 15 cm) 10 cm above the ground over each trap. We baited traps with approximately 10 g of cow manure per trap that was collected from the Kellogg Pasture Dairy Farm (located approximately 0.4 km from experimental sites) and homogenized by stirring in a bucket. Cows were treated with an ingested larvicide for fly control (unpublished data shows this had no effect on abundance and richness of dung beetles collected or manure decomposition). We deployed pitfall traps at all Subplot Sampling Stations three times during the growing season in 2019, once each in June, July, and August. For each sampling event, traps were collected after 48 h in the field and the samples collected from the traps were stored in ethanol at −20 °C. Dung beetles (Coleoptera: Scarabaeidae of the subfamily Scarabaeinae) were identified to species using a regional guide (Nemes & Price 2015).

Distances from prairie strips: To measure dung beetle richness at distances from prairie strips, baited pitfall traps were deployed at Strip Sampling Stations for each of three sampling rounds each year occurring in June, July, and August of 2019 and 2020.

Ants

Ants comprise half of global insect biomass and perform many ecosystem services (Hölldobler & Wilson 1990, Folgarait 1998, Wills & Landis 2018). Ants are the major predators of agricultural pests at our study site and elsewhere in the US Midwest (Grieshop et al. 2012, Wills et al. 2019, Helms et al. 2020). They also disperse plant material, seeds, and nitrifying bacteria and pool nutrients in the soil (Benckiser 2010, Hölldobler & Wilson 2009, Mueller et al. 2005).

Ants are sensitive to harvesting and management practices that can reduce ant activity (Peck et al. 1998, Agosti et al. 2000, Wodika et al. 2014, Helms et al. 2021, Hussain et al. 2021).

Across management treatments: We collected ants across crop management treatments using baited pitfall traps at Subplot Sampling Stations as described for dung beetles. Captured ants were identified using regional guides (Coovert 2005, Ellison et al. 2012) and vouchers were stored in the senior author's reference collection.

To test effects of treatments on species richness, we first combined species occurrences from all repeated pitfall traps (maximum of 3 traps per each of 6 sampling stations, 16 to 18 total pitfall traps per plot). The occurrence of workers of a given species at least once at any of the 6 sampling stations was conservatively treated as indicating the presence of a single colony of that species (abundance = 1) within a plot during the study year, regardless of how many or how frequently workers were captured (Ellison et al. 2007; Gotelli et al. 2011). In this way, we derived one species list for each of the 30 plots (6 plots per each of 5 treatments).

Distances from prairie strips: To measure ant richness at different distances from prairie strips, ants were collected with non-baited pitfall traps at the Strip Sampling Stations (reduced input and biologically based treatments). Non-baited traps were sampled on a rolling weekly basis (three weeks on, one week off during which baited traps were deployed) from May-September with a total of five sampling rounds per station in 2019 and four in 2020. 2019 prairie strip ant data are modified from those used in Helms et al. (2021).

Spiders

Spiders are generalist predators that can contribute to pest control in agricultural landscapes. Spider communities generally respond positively to agricultural conservation practices, such as cover crops and reduced tillage (Sunderland & Samu 2000, de Pedro et al. 2020). Increased natural habitat in an agricultural landscape can increase spider abundance and richness, but there is little evidence of spillover of spiders from natural habitat into cropland (Sunderland & Samu 2000, Schmidt et al. 2005, but see Hussain et al. 2021).

Across management treatments: We collected spiders across crop management treatments as described for ants. Spiders were identified to family with a key to spiders of North America (Ubick et al. 2017). *Distances from prairie strips:* Pitfall traps were used to collect spiders at distances from the prairie strips as described for ants.

Butterflies

Butterflies are diverse pollinators, herbivores, and indicators of insect response to habitat change, and they hold cultural value (Ghazanfar et al. 2016). Butterflies are declining in abundance at a rate of 2% per year in the US Midwest with agriculture as a main reason for this decline due to habitat loss, pesticides, and fertilizers, which are sources of direct mortality and destroy host plants and food resources (Wepprich et al. 2019, van Klink et al. 2020). Reducing the use of pesticides and fertilizer and restoring habitat on farms helps mitigate the loss of butterfly biodiversity in agricultural landscapes (Reeder et al. 2005, Rundlöf et al. 2008).

Across management treatments: Unlike samples for all the other species and services, we sampled butterfly species richness and abundance using transect counts, modified from Pollard (1977). We conducted surveys along a 12-minute one-way walking transect through each plot. Observers recorded butterflies within 5 m on both sides and above the transect in front of the observer. Transects were surveyed between 10:00am and 4:00pm weekly from June 2019–

September 2019 and May 2020–September 2020. Butterflies were identified to species using a regional guide (Nielsen 1999) and supplementary sources as needed.

Active carbon

Biologically available soil carbon, also termed "active carbon", reflects a fraction of total soil carbon that is readily mineralized by soil microorganisms and serves as an early indicator of longer-term soil carbon accrual (Coleman et al. 2018b, Culman et al. 2012). Conversion of agricultural fields to perennial vegetation has been shown to increase soil active carbon compared to conventionally managed agricultural soils by increasing the production of fine root biomass (Sprunger et al. 2017, Sprunger & Robertson 2018). We expect prairie strips to increase levels of active carbon and for active carbon to spillover from prairie strips into cropland at short distances from prairie strips if roots from perennials extend into cropland, if nitrogen from farming doesn't reach to exactly the edge of the prairie strip, or if litter from prairie strips spills over into cropland.

Across management treatments: Active carbon was determined via a 24-hour assay based on Franzluebbers et al. (2000) that measures CO_2 respired from soils rewetted to a common water holding capacity. We collected soil cores at the Standard Sampling Stations in June, July, and August of 2019. Samples were analyzed individually for active carbon, then data were pooled across June, July and September to form a single dataset for each year in each treatment. We collected field soil with a soil push probe at 0–10 cm depth then sieved to 2 mm. Soil water holding capacity (WHC) and gravimetric soil moisture were determined from fresh sieved soil. We added 5 g of air-dried soil and sterile ultrapure water to a 125 mL Wheaton serum bottle to achieve 70% WHC. Bottles were sealed and incubated at room temperature for 24 hours. We collected gas samples from bottle headspace at two time points following the incubation period (0 and 24 hr). CO_2 samples were collected in overpressurized 6 mL glass vials (Exetainers, Labco Ltd) flushed with N_2. We analyzed samples with a gas chromatograph (Agilent 7890A) coupled to an autosampler (Gerstel MPS2XL) as described in Shcherbak and Robertson (2019).

We calculated short-term mineralizable C as the difference between 0 and 24-hr CO_2 measurements. We report active carbon in micrograms (µg) of CO_2 per day per g of dry soil. *Distances from prairie strips:* Soil cores were collected at Strip Sampling Stations and processed as described above in both 2019 and 2020.

Decomposition

Decomposition is essential for suppressing pathogens, cycling nutrients, and creating soil organic matter (Barrios 2007, Coleman et al. 2018c). Diversified landscapes can increase decomposition by increasing the abundance and richness of beneficial soil fauna (Landis et al. 2000, Karp et al. 2016, Jones et al. 2019). To quantify decomposition services, we measured mass loss of manure over time.

Across management treatments: We placed one patty of fresh cow manure (20 g) at each of the Subplot Sampling Stations (Jones et al. 2019). Manure (fresh) was weighed in the lab and separated into individual packets prior to deployment. We left manure under a rain cover (same rain cover as described for ants) for seven days immediately following pitfall trap collection of dung beetles for all sampling rounds. We then collected manure in an envelope, placed the envelope in a drying oven until moisture evaporated, and then weighed it. The dry weight after deployment was divided by the dry weight of the manure (20 g of fresh manure was equivalent to 6 g dried manure). We defined decomposition as the proportion of manure removed. *Distances* *from prairie strips:* We placed sentinel cow manure patties (20g) at the Strip Sampling Stations and processed samples as described above.

Global warming impact (GWI)

Agriculture produces 10–14% of global anthropogenic greenhouse gas emissions (Barker et al. 2007, Smith et al. 2007). Prairie strips, no till management, and cover crops are among management practices that have the potential to sequester carbon in cropping systems (Robertson et. al 2000, Gelfand & Robertson 2015). We use 100-year global warming impact (GWI) as a measure to convert greenhouse gas emissions (N_2O and CH_4) to units of CO_2 equivalent emissions.

Across management treatments: We sampled greenhouse gas fluxes per Kahmark et al. (2020) approximately biweekly May-September and monthly October-April in both 2019 and 2020 using a stainless-steel gas chamber (14.3 cm radius, 22.8 cm height) with a plastic lid. After placing the lid on the chamber, a needle was inserted into the chamber lid septum to relieve any induced pressure changes. We inserted another individual needle into the septum of a 5.9-mL exetainer sample vial to act as a vent. Then we mixed the chamber headspace three times with a 10-mL sampling syringe. After mixing, we withdrew 10-mL and injected the air into the sample vial with the vent needle in place. After flushing the vial three times, we removed the vent needle, drew a 10-mL sample from the chamber, and injected it into the flushed sample vial (so that it was overpressurized). We collected a sample of ambient air at the same time in each sampling round and also a duplicate chamber sample using the same gas sampling procedure described above. We also recorded soil temperature and moisture next to the gas chamber during the sampling period. We collected four gas samples at 15-minute intervals over each sampling period. Post gas sampling and flux calculations were conducted following the protocol of Holland et al. (1999).

Pollination

Pollinators are necessary for the function of natural and managed ecosystems. Pollinators have experienced a steep decline in abundance and richness, and prairie strips could restore pollinators and their services to agricultural landscapes (IPBES 2016, Wepprich et al. 2019, van Klink et al. 2020, Kordbacheh et al. 2020).

Across management treatments: Pollination was measured with sentinel plants placed at the Standard Sampling Stations in the conventional, no till, and conservation land treatments, as well as at the Strip Sampling Stations in the reduced input and biologically based treatments. We used Black-eyed Susans (*Rudbeckia hirta*) as our sentinel plants, as it is native to southwest Michigan and was also included in the prairie strip seed mix. We propagated plants from seed (purchased from the same location as the prairie strip seed mix) in a greenhouse. Seedlings were transplanted into 16.5 cm pots with a low dose of 12-12-12 N-P-K controlled release organic fertilizer. To avoid pollination prior to receiving experimental treatment, we marked and covered two flower heads on each plant with pollinator exclusion bags just before they started producing pollen. The following day, we deployed plants with exclusion bags on both flowers into the field. Upon placement in the field, we removed one bag to be exposed to pollinators (called open flowers). One bag remained over the flower through the duration in the field (called closed flowers). Closed flowers acted as a measure of potential self-pollination. We deployed plants in experimental treatments for 14 days during each of the three sampling rounds starting on June 18, 2019, August 7, 2019, and July 8, 2020. We bagged all experimental flower heads prior to removal from experimental stations. For analysis of pollination across treatments, we used all plants from Standard Sampling Stations in conventional, no till, and conservation land, and we randomly selected five plants from the Strip Sampling Stations in the reduced input and biologically based treatments to compare consistently among all treatments. For analysis of pollination at distances from prairie strips, we used all plants from the Strip Sampling Stations.

Following experimental deployment, we returned plants to a greenhouse where they senesced and set seed. Seeds were then harvested and stored in a refrigerator from September to January each year. We randomly selected thirty seeds from each flower head for a germination trial. We placed these seeds in petri dishes in a greenhouse, watered them regularly over a 14-day period, and counted the number of individuals that germinated. We calculated seedset as the ratio of not-germinated:germinated seeds for each seed head (two measures per plant). We measured pollination services as the difference between seedset of the open flower and seedset of the closed flower for each plant (one measure per plant). *Distances from prairie strips:* The sentinel plants from the Strip Sampling locations were used to measure pollination services at distances from the prairie strips.

Soil organic carbon (SOC)

SOC is a measure of total carbon in soil organic matter. Agricultural management practices influence SOC accrual and loss. SOC accrual can be stimulated by the addition of high-quality organic inputs like cover crops (Syswerda et al. 2011), as well as the establishment of perennial vegetation (Kravchenko et al. 2019). On the other hand, practices that involve physical soil disturbance, such as tillage, generally reduce SOC by disrupting soil aggregates and releasing organic matter for decomposition (Paul et al. 2015). Whereas active carbon responds quickly to land management changes, SOC generally responds on the order of years to decades, as it is a measure of total carbon across both labile and recalcitrant soil organic matter pools (Culman et al. 2012).

Across management treatments: We collected one soil core with a soil push probe at each Standard Sampling Station in April 2019 and May 2020 at a depth of 0–25 cm. Soil cores within each plot (5 stations per plot) were combined into a pooled sample. We air dried soil samples and then pulverized them to a powder using a Shatterbox grinding mill. We then weighed soil samples (15-20 mg) and packed them into tins. Samples were analyzed for total carbon in triplicate (three soil tins for each sample) on a Costech Elemental Combustion System 4010. Because these soils did not contain carbonates, we express these data as percent SOC.

Crop yield

Across management treatments: Crops were harvested from the entire crop area of each plot across all agronomic treatments. Prairie strips were not harvested, but we area-scaled yields in the reduced input and biologically based treatments by reducing yields 5% to account for area in strips. Wheat was harvested from conventional and no till plots on July 24, 2019 and from reduced input and biologically based plots on July 25, 2019. Maize was harvested from all treatments and plots on October 29, 2020. Crops were harvested with a harvest combine, and yield for the entire crop area of each plot was measured with a weigh wagon. We report yield as kg/ha at crop harvest at standard moisture content (13% for wheat, 15.5% for maize). We did not compare yield with the conservation land treatment, although perennial grasslands have potential to be harvested for bioenergy (Robertson et al. 2017).

In addition to measuring crop yields for 2019 and 2020, we separately compared historical crop yields in the same plots prior to the sowing of prairie strips. We used yield measurements from 2013–2018—two cycles of the crop rotation prior to prairie strips.

Statistical analyses

Across management treatments: We aggregated the individuals of our measures of invertebrate biodiversity (ants, butterflies, dung beetles, and spiders) surveyed over each year within each plot of each treatment (six plots for each of five treatments) by summing. For all measures of biodiversity and ecosystem services, we calculated effect sizes of no till, reduced input, biologically based, and conservation land treatments relative to the conventional treatment. We measured the Hedge's g effect size and 95% confidence intervals using the "compute.es" package in R (Del Re 2013). The conventional treatment served as the baseline, which does not include a confidence interval.

To determine the differences in arthropod richness (ants, butterflies, dung beetles, and spiders) across treatments, we used generalized linear mixed effects models with normal distributions. All model assumptions were met. Richness was used as the response variable; main effects were treatment and year (except for ants which were sampled in only one year), and the random effect was experimental block. We calculated the estimated species richness of butterflies within each replicate of each treatment per year using the R package "iNext" with Chao1 abundance-based rarefaction (Chao et al. 2014, Hsieh et al. 2016). We used measures of raw richness for ants, dung beetles, and spiders; we recognize that abundance affects richness for these measures, but because our abundances were low, rarefaction was not possible.

To determine the differences in arthropod abundances across treatments, we used generalized linear mixed effects models constructed similarly but with negative binomial distributions (except for ants for which we used a normal distribution to meet model assumptions). R package "lme4" was used to construct the models (Bates et al. 2015). An ANOVA followed by a Tukey test was used for post-hoc analyses for all models using R packages "car" (Fox & Weisberg 2019) and "multcomp" respectively (Hothorn et al. 2008). The same method was used for all measured ecosystem services including crop yield (except GWI), but with the measure of the service as the response variable and sampling round included as a fixed effect when multiple sampling rounds occurred within a year (decomposition and pollination). We also modeled crop yield independently for each year using the same method to measure relative yields among treatments for each crop. For GWI, we constructed a generalized linear mixed effects model with log transformed CO_2 as the response variable, treatment, year, sampling round, and temperature as fixed effects, and experimental block as the random effect.

Distances from prairie strips: We aggregated the individuals of our measures of invertebrate biodiversity (ants, dung beetles, and spiders) collected over each year within each distance of each plot of each treatment (four distances for each of six plots for each of two treatments) by summing. To determine the effect of distance from prairie strip and year on measures of arthropod richness (ants, dung beetles, and spiders), we constructed a generalized linear mixed effects model with a normal distribution. Richness was the response variable, crop management treatment, distance from prairie strip, and year were fixed effects with an interaction between distance and year, and experimental block was a random effect. We followed this with an ANOVA. The same method was used for measures of abundance, but with a negative binominal distribution (except ants for which we used a normal distribution). We constructed similar models with normal distributions for measures of ecosystem services but included sampling round as a fixed effect when relevant (decomposition and pollination). Distance was treated as a continuous variable. To test if trends were occurring across distances from the prairie strips, or if they were driven solely by high values within the prairie strips, we also ran analyses for all measures with datapoints at 0 m removed.

Results

Dung beetles

Across management treatments: We collected a total of 553 dung beetles in Standard Sampling Plots (Table 2.2). The effect sizes of dung beetle richness across all treatments did not differ from baseline (Figure 2.3). Species richness did not differ among treatments, however dung beetle abundance was 128–992% higher in conservation land than in all other treatments (Figure 2.4, Table 2.3). *Distances from prairie strips:* We collected a total of 284 dung beetles at Strip Sampling Stations (Table 2.2). There was no relationship between distance and dung beetle richness, but dung beetle richness was higher in 2020 than in 2019 (Figure 2.5, Table 2.4). There was an interaction between year and distance from prairie strip for dung beetle abundance, with 2019 having no relationship with distance from strip and 2020 abundance decreasing with distance from strip (Figure 2.5, Table 2.4). When 0 m samples were removed, there was no effect of distance or year on dung beetle abundance (distance: χ^2=0.6, df=1, p=0.4; year: χ^2=0.5, df=1, p=0.8) or richness (distance: χ^2=0.4, df=1, p=0.53; year: χ^2=1.7, df=1, p=0.2), meaning the linear trend of abundance was driven by high dung beetle abundance in the prairie strips.

Ants

Across management treatments: We collected a total of 1821 worker ants from the Subplot Sampling Stations (Table 2.5). The Hedge's g effect sizes of ant richness in conservation land were higher than the baseline (Figure 2.3). Species richness was higher in conservation land treatments than in all row crop treatments (Figure 2.4, Table 2.3). Ant abundance was the same as ant richness because abundance of any particular species could only be 0 or 1 at a single sampling station, and sampling stations were summed per plot per year (see methods). *Distances from prairie strips:* We collected a total of 3218 ants from the Strip Sampling Stations (Table 2.5). Ant species richness did not vary by year nor with distance from the prairie strip (Figure 2.5, Table 2.4). Ant abundance did not differ by distance from prairie strip, but differed by year, decreasing from 2019 to 2020 (Figure 2.5, Table 2.4).

Spiders

Across management treatments: We collected a total of 1522 spiders from Subplot Sampling Stations (Table 2.6). The effect size of spider richness for treatments with prairie strips and the conservation land treatment were higher than baseline; no till did not differ from the baseline (Figure 2.3). Spider richness increased from conventional to no till and biologically based, to reduced input, to conservation land (Figure 2.4, Table 2.3). Spider abundance was highest in the treatments with prairie strips followed by conservation land and no till, and lowest in conventional (Figure 2.4, Table 2.3). *Distances from prairie strips:* We collected a total of 3626 spiders from Strips Sampling Stations (Table 2.6). There was an interaction between distance from prairie strip and year to explain spider richness and abundance, with 2019 having no change in richness and abundance with increasing distance and 2020 having a decrease in richness with increasing distance (Figure 2.5, Table 2.4).

Butterflies

Across management treatments: We visually identified 5329 butterflies during transect counts (Table 2.7). The effect sizes of butterfly richness were higher than the baseline of conventional in the biologically based and conservation land treatments; no till and reduced input did not differ from baseline (Figure 2.3). Butterfly richness was the highest in the conservation land and biologically based treatments followed by reduced input and no till treatments, and lowest in conventional (Figure 2.4, Table 2.3). Giant Swallowtails, Checkered Skippers, and Red Spotted Purples were species identified in treatments with prairie strips that were never observed in conventional or no till treatments. Butterfly abundance was 134–349% higher in treatments with prairie strips than crop treatments without prairie strips (conventional and no till; Figure 2.4).

Active carbon

Across management treatments: The effect sizes of active carbon in the reduced input and the conservation land treatments were higher than the baseline; no till and biologically based did not differ from the baseline (Figure 2.3). Active carbon was highest in the conservation land treatment, lowest in the no till treatment, and intermediate in the reduced input, biologically based, and conventional (Figure 2.4, Table 2.3). *Distances from prairie strips:* Distance from prairie strip and year had significant effects on active carbon, with 2019 having higher active carbon than 2020, and 2019 having a decrease in active carbon with distance from prairie strip (Figure 2.5, Table 2.4). In the crop area alone, (0 m datapoints removed from analyses), there was a significant interaction between distance and year with a decrease in active carbon with increasing distance from prairie strips in 2019 and no change with distance from prairie strip in 2020 (χ^2=4.9, df=1, $p<0.05$).

Decomposition

Across management treatments: The effect size of decomposition in conservation land was higher than the baseline; no other treatment differed from the baseline (Figure 2.3). Conservation land and no till treatments had the highest rates of decomposition, followed by conventional and reduced input, and then by biologically based (Figure 2.4, Table 2.3). *Distances from prairie strips: There* was an interaction between year and distance from prairie strip, with 2019 having a lower rate of decomposition and no change with distance from prairie strip and 2020 having a higher rate of decomposition with a decreasing trend with increasing distance from prairie strip (Figure 2.5, Table 2.4).

GWI

Across management treatments: The effect size of GWI in conservation land was lower than the baseline; no other treatments differed from the baseline (Figure 2.3). GWI in the conservation land treatment was at least 25x lower than all other treatments (Figure 2.4, Table 2.3). Methane tended to be consumed in the soils rather than emitted to the atmosphere across all land use types. Fluxes in conservation land across 2019 and 2020 were lowest at −2.68 ± 2.46 (mean ± SD) g CH_4-C ha^{-1} day^{-1}, while those in the biologically based treatment were highest at −0.79 ± 1.78 g CH_4-C ha^{-1} day^{-1}. Similarly, N_2O fluxes were lowest in conservation land and highest in the biologically based treatment at 0.34 ± 0.51 and 7.27 ± 17.13 g N_2O-N ha^{-1} day^{-1}, respectively.

Pollination

Across management treatments: The effect size of pollination was higher in reduced input and biologically based treatments than the baseline (Figure 2.3). Pollination rates were 72–222% higher in the treatments with prairie strips than all other treatments (Figure 2.4, Table 2.3).

Distances from prairie strips: Pollination services decreased with distance from prairie strip, and pollination services increased from 2019 to 2020 (Figure 2.5, Table 2.4).

SOC

Across management treatments: SOC was higher than baseline in biologically based and conservation land treatments (Figure 2.3). SOC was lowest in conventional, intermediate in the no till, reduced input, and biologically based treatments, and highest in conservation land treatment (Figure 2.4, Table 2.3).

Crop yield

Across management treatments: The effect size was lower than baseline in the biologically based treatment but did not differ from the baseline for no till and reduced input treatments (Figure 2.3). When including both wheat and maize in analyses, crop yield was highest in the no till treatment, intermediate in the conventional and reduced input treatments, and lowest in the biologically based treatment (Figure 2.4, Table 2.3). Crop yield was scaled to include the land area of prairie strips in analyses (kg/ha measurements include area of the prairie strips). These relative crop yields across treatments were consistent with the previous two crop rotations where, across all the whole crop rotation, crop yields were highest in no till, intermediate in conventional and reduced input (although conventional and no till were not significantly different), and lowest in the biologically based treatment.

When considering the wheat and maize years independently, the pattern among treatments changed from the previous two crop rotations. When measuring just the wheat year (2019), crop yield was lowest in the biologically based, followed by the reduced input treatment, then no till, then conventional (χ^2=1921.2, df=3, p=<0.01). Historically (2013–2017), however, wheat yield was lowest in biologically based but did not differ among other crop treatments. When measuring just the maize year (2020), crop yield was lowest in the biologically based and conventional, intermediate in the reduced input, and highest in no till (χ^2=70.3, df=3, $p<0.01$). This also differs from the previous two crop rotations, where maize yield was lowest in biologically based, intermediate in reduced input and conventional, and highest in no till. Therefore, maize yields in the conventional treatment in 2020 were low compared to the previous two crop rotations. The third crop in the rotation, soy, historically was lowest in conventional and biologically based and highest in no till and reduced input.

Discussion

We show that prairie strips, even early in their establishment, combined with lower land use intensity can promote biodiversity and ecosystem services without compromising crop yield. Within reduced input and biologically based treatments, where sampling effort occurred within prairie strips and at increasing distance from strips, biodiversity and ecosystem services spilled over into agronomic areas for five out of six measures. Among all treatments, using data from the entire plot area (not sampling within prairie strips for treatments with strips), pollination services and the abundance of butterflies and spiders were higher in plots with prairie strips. In addition, soil organic carbon, butterfly richness, and spider richness increased with a decrease in land use intensity. Crop yield in the reduced input treatment was equal to that of conventional management, even while including the area taken out of production. These effects were evident early in strip establishment, during which prairie strip plant communities changed from mostly weeds to a diversity of planted species. We expect the effects of strips to grow over time as native plants establish and become more abundant, and as lagged effects of historic agronomic disturbances abate.

The benefits of prairie strips decreased with distance into cropland for spider abundance and richness, dung beetle abundance, active carbon, decomposition, and pollination (Figure 2.5). Each of these responses decreased with distance from the prairie strip, but did so by different mechanisms. For spiders, the spillover into cropland was delayed one year after the prairie strips were sown. Prairie strips provided new habitat and sources of prey for spiders (Hussain et al. 2021), such that spiders could move into cropland to capture additional prey. The impact on dung beetles and decomposition are likely due to the prairie strips harboring dung beetles in the year after restoration, which in turn caused a higher rate of manure removal near the prairie strips and a decrease in dung beetle abundance and manure removal with increasing distance from the strips (Manning & Cutler 2018). For pollination, prairie strips increased floral resources which attracted pollinators and then exported them into the surrounding habitat (Garibaldi et al. 2011). We were surprised that prairie strips increased pollination as our plot sizes are a fraction of pollinator foraging range (Ricketts et al. 2008), and we suspect that pollinators were attracted to the high concentration of resources that contrasted strongly with crops. For active carbon, the effect of distance from prairie strip may have been driven by high prairie litter inputs. Mowing prairie strips in 2019 may have caused a spillover of prairie litter inputs into cropland that did not occur in 2020, leading to higher levels of active carbon in crop soils immediately adjacent to prairie strips. While the increase of active carbon in nearby sites was subtle, it still highlights the biogeochemical benefits of adjacent prairies for agricultural lands, which are generally underappreciated (Pérez-Suárez et al. 2014).

Our study shows that spillover effects from prairie strips extend across measures of biodiversity and ecosystem services. Pollinators and pollination services have been studied at distances from restorations and habitat edges, often with higher numbers of pollinators and rates of pollination near non-crop habitat (Ricketts 2004, Carvalheiro et al. 2010, Kordbacheh et al. 2020); by also demonstrating this phenomenon in dung beetles, spiders, active carbon, and decomposition, we show that these spatial effects apply to a broader array of organisms and ecosystem services. These results, with detailed attention to mechanism in our controlled experiment, strengthen evidence that suggests that strategic placement and amount of natural habitat in agricultural landscapes can add both conservation value and ecosystem services to an agricultural landscape (Basso et al. 2019, Mitchell et al. 2021). Our study focused on ecosystem services, and we did not measure potential ecosystem disservices from prairie strips that could impact yield, such as herbivory, however such disservices could be addressed in future studies.

Prairie strips require several years after planting to resemble a restored prairie community, over which time diversity and ecosystem services have shown to accrue (Kurtz 2013, Griffin et al. 2017). Supporting this, we found that year since prairie strip establishment affected all responses that we measured at distances from prairie strips except ant richness (Figure 2.5). Lack of response of ant species richness is consistent with other grassland restoration projects where it takes several years for ant communities to turnover (Dauber & Wolters 2005, Menke et al. 2015, Scharnhorst et al. 2021, Hussain et al. 2021). With the exception of active carbon, variables displayed a general progression of the first year having small to no effect of distance from prairie strip, to the second year showing a stronger negative effect of distance. It is important to note that year differences in our experiment are confounded by crop type (wheat or maize). These effects will become easier to separate from effects of prairie strips as measurements are repeated over the next four years (after two full crop rotations) and then in seven years (one full rotation after strip maturation). We expect that as more plant species establish, prairie strips will increase biodiversity even further.

Prairie strips are also likely to continue to increase the provision of soil services; for example, we found higher levels of active carbon and SOC in the prairie strips in this study, with potential for these benefits to extend into the cropland at short distances. Over time, prairie strips could thus be a significant carbon sink, which could provide benefits to agricultural landscapes and may come with economic reward with future carbon pricing. Quantifying the aggregated potential of this sequestration should be a priority, and continued measurement of these variables in our study after the early establishment phase of prairie strips will provide insight to their long-term potential for conservation and impact on crop yield, and more comprehensive opportunities for synergies.

Across all crop management treatments, there was a variable effect of land use intensity on measures of biodiversity (Figure 2.4). Conservation land consistently had the highest level of richness, and often had the highest level of ecosystem services. We found that lower land use intensity treatments with prairie strips increased butterfly abundance and pollination services compared to other crop management schemes. This may be the consequence of pollinators and butterflies being mobile agents with large ranges. They can therefore find and utilize the resources of prairie strips early in strip establishment (Cant et al. 2005, Pasquet et al. 2008). In addition to the prairie strips, reduced input and biologically based treatments have reduced pesticides which likely contributes to increased butterfly richness and pollination services; but the decreasing pollination services with distance from the prairie strips suggests that pollinators are attracted to the strips. Butterflies were most diverse in the conservation land treatment due to the increased floral and habitat diversity throughout the plot (Menéndez et al. 2007). We attribute the low level of pollination services in the conservation land treatment, especially in 2019, to the forager dilution effect, in which pollination services are diluted in an area of mass flowering (Holzschuh et al. 2011). While butterflies and pollination services do not improve the yield of wheat or maize crops, they may improve yield in soy crops (Cunningham-Minnick et al. 2019) or other crops in the landscapes that benefit from pollinators, and the potential of these services remain among the most important to surveyed farmers (Arbuckle 2019, Hevia et al. 2021).

Our hypotheses of increasing biodiversity with a decrease in land use intensity were not supported uniformly. For ground dwelling arthropods, conventional management had surprisingly high species richness. This finding is not without precedent; despite previous findings that organic farms support more biodiversity than conventional farms (Bengtsson et al. 2005, Tuck et al. 2014), ants and dung beetles show mixed results (Hutton & Giller 2003, Jones et al. 2019, Piccini et al. 2019, Helms et al. 2021). In addition, while diversifying farms generally increases spider diversity (Schmidt et al. 2005), prairie strips in our study have not increased spider diversity at the plot level, but have increased spider abundance.

Soil-related ecosystem services (active carbon, decomposition, GWI, and SOC) across the land use intensity gradient were highest in conservation lands, with variable differences among cropping treatments. Decomposition was highest in untilled treatments (no till and conservation land), possibly due to the higher microbial activity and soil moisture maintained by soil aggregates with greater physical protection (Paul et al. 2015), or due to mesofaunal differences that we did not measure, such as earthworms (Smith et al. 2008). As strips develop, we expect decomposition to increase with dung beetle abundance and diversity in prairie strip treatments (Hosler et al. 2021). Conservation land had increased active carbon likely due to the fine root production of diverse perennial vegetation, which we also expect to increase in and near prairie strips as they mature (Sprunger et al. 2017, Sprunger & Robertson 2018). The increased SOC along the land use intensity gradient was likely due to carbon from perennial plants (Syswerda et al. 2011, Mosier et al. 2021). GWI was almost entirely driven by N_2O in our study. The reduced GWI in the conservation land treatment was likely due to reduced fertilizer inputs. Although there was no difference in overall GWI across row crop management treatments, as Gelfand et al. (2016) has also found for N_2O emissions, there was higher GWI in the wheat year, compared to maize. This was likely due to several days of tillage early in the growing season for biologically based maize, management that is different from other treatments that receive alternative methods of weed management. We note that GWI only represents soil emissions and is not a full life cycle analysis.

The potential for prairie strips to enhance biodiversity and ecosystem services at large scales will be most powerful if they do not sacrifice agricultural yield. Historically in our experiment, the no till treatment has the highest yield, followed by the conventional and reduced input treatments with intermediate yields, and the biologically based treatment with the lowest yield. We show that converting 5% of crop area to prairie strips (and using yield measures that include the area taken out of production) does not change differences in yield across treatments beyond differences already induced by existing management. Reduced input management with prairie strips maintained a high yield, equivalent to conventional, while having high levels of pollination, spider abundance, and butterfly richness; biologically based crop management similarly maximized these services, but at the cost of a large cut in yields. This reduction was likely due to limitation of inorganic nitrogen (Robertson et al. 2015), unrelated to prairie strips. While no single method of crop management performed highest or lowest across all measures (e.g., no till treatments had the highest yield but did not have the highest levels of biodiversity or other ecosystem services), there was a synergy among crop yield, biodiversity, and non-provisioning ecosystem services in the reduced input treatment. Prairie strips are an effective conservation practice that can be combined with other techniques—reduced fertilizer and pesticides—to conserve biodiversity and ecosystem services without compromising crop yield.

When considering both 2019 and 2020 yields together, yield in reduced input treatments may have remained equivalent to yield in conventional treatments for at least three reasons. First, converting 5% of cropland to prairie was not enough area to result in significant changes among treatments. Second, ecosystem services generated by strips could increase yield in the remainder of the plot. Several of the responses we measured were higher at the plot scale outside strips. For example, relative to conventional treatments, active carbon was higher in reduced input treatments, and SOC trended toward higher (Figure 2.3). Third, climate or other environmental conditions during the time of our study could have had stronger negative impact in conventional treatments. As the strips mature, and with results through multiple rotations, the mechanism of yield response will become clearer.

Prairie strips were implemented on land that had previously been in crop production in this experiment, but prairie strips could also be implemented on the landscape in a way that does not reduce farm profitability. For instance, prairie strips can be strategically placed on marginal land—land that has consistent low yields relative to nutrient and greenhouse gas inputs. Marginal land occupies 26% of annual cropland land in the US Midwest, resulting in excessive pollution and wasted monetary and nutrient resources (Basso et al. 2019). Converting marginal cropland to prairie strips would reduce inputs without sacrificing crop yield. In addition, prairie strips could be harvested as perennial biofuel for added profitability, and we suggest future studies address how this would impact biodiversity and ecosystem services. Future studies might also examine how the optimal benefits of prairie strips could be achieved with strategic location, particularly cropland that is consistently underperforming and therefore not as profitable, on slopes to prevent soil erosion, or in locations that could increase habitat connectivity in the broader landscape (Basso 2021).

We expect that as prairie strips mature their effects on biodiversity and ecosystem services will grow. We converted just 5% of cropland to prairie, however optimal benefit may be achieved by even larger strips, such as the 10% conversion of cropland to prairie as recommended by Schulte et al. (2017). Our study supports that prairie strips are an effective strategy for conserving biodiversity, and can in some cases be created without impacting crop yield in the US Midwest. More broadly, diversifying agricultural landscapes can help mitigate the loss of biodiversity and ecosystem services while supporting the growing human population.

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APPENDIX

Table 2.1. Native forb and grass species sowed to create prairie strips.

	Species	Common Name	Seeds per m^2	% by weight	% by seed
Grasses	*Andropogon gerardii*	Big Bluestem	9.9	6.3%	3.2%
	Bouteloua curtipendula	Side-oats Grama	20.8	21.9%	6.8%
	Elymus canadensis	Canada Wild Rye	5.2	6.3%	1.7%
	Schizachyrium scoparium	Little Bluestem	37.0	15.6%	12.2%
Forbs	*Achillea millefolium*	Yarrow	22.1	0.8%	7.2%
	Asclepias syriaca	Common Milkweed	3.6	5.6%	1.2%
	Asclepias tuberosa	Butterfly Milkweed	3.2	4.7%	1.1%
	Symphyotrichum novae-angliae	New England Aster	12.3	1.2%	4.0%
	Coreopsis lanceolata	Lance-leaf Coreopsis	19.8	6.3%	6.5%
	Coreopsis tripteris	Tall Coreopsis	2.8	1.3%	0.9%
	Desmodium canadense	Showy Tick Trefoil	2.7	3.1%	0.9%
	Echinacea purpurea	Purple Coneflower	6.6	6.3%	2.1%
	Lespedeza capitata	Round-headed Bush Clover	3.2	2.6%	1.1%
	Monarda fistulosa	Wild Bergamot	13.0	1.2%	4.3%
	Ratibida pinnata	Yellow Coneflower	7.4	1.6%	2.4%
	Rudbeckia hirta	Black-eyed Susan	56.8	3.9%	18.6%
	Silphium perfoliatum	Cupplant	0.4	2.0%	0.2%
	Solidago juncea	Early Goldenrod	28.6	0.6%	9.4%
	Solidago nemoralis	Old-field Goldenrod	29.6	0.6%	9.7%
	Tradescantia ohiensis	Common Spiderwort	1.9	1.6%	0.7%
	Verbena stricta	Hoary Vervain	10.3	2.3%	3.4%
	Zizia aurea	Golden Alexander	7.8	4.5%	2.5%

Table 2.2. Dung beetle abundance per species found in each treatment each year. All distances are combined for strip abundance counts.

2019	Conventional	No till	Reduced input	Bio. based	Conservation land	Strip - Reduced input	Strip - Biologically based
Copris fricator	0	0	0	0	1	0	0
Onthophagus hecate	12	5	3	24	118	27	87
Onthophagus orpheus	1	0	0	0	0	0	0
Onthophagus pennsylvanicus	4	6	9	13	4	4	8
Onthophagus taurus	4	5	3	2	0	1	0
2020							
Copris fricator	1	0	1	0	0	0	0
Copris minutus	0	3	4	1	7	7	3
Onthophagus hecate	21	39	18	15	95	45	31
Onthophagus nuchicornis	1	0	0	0	0	0	0
Onthophagus orpheus	1	0	1	1	1	4	1
Onthophagus pennsylvanicus	23	12	13	19	61	32	33
Onthophagus taurus	0	0	0	1	0	0	1

Table 2.3. Effects of crop management treatments on measures of biodiversity and ecosystem services treatments. Bolded p-values indicate statistically significant measures.

		treatment			year		
measure	unit	χ^2	df	p	χ^2	df	p
ant abundance	number of individuals	42.6	4	**<0.01**	NA	NA	NA
ant richness	number of species	42.6	4	**<0.01**	NA	NA	NA
butterfly abundance	number of individuals	223.9	4	**<0.01**	67.3	1	**<0.01**
butterfly richness	species richness (chao1)	19.3	4	**<0.01**	0.8	1	0.4
dung beetle abundance	number of individuals	95.9	4	**<0.01**	15.2	1	**<0.01**
dung beetle richness	number of species	6.4	4	0.2	12.2	1	**<0.01**
spider abundance	number of individuals	26.9	4	**<0.01**	17.1	1	**<0.01**
spider family richness	number of families	48.0	4	**<0.01**	13.1	1	**<0.01**
active carbon	µg CO_2/day/g	144.4	4	**<0.01**	NA	NA	NA
decomposition	proportion removed	40.8	4	**<0.01**	86.6	1	**<0.01**
GWI	kg CO_2/ha/day	117.5	4	**<0.01**	3.7	1	0.05
pollination	proportion germinated	70.2	4	**<0.01**	32.0	1	**<0.01**
SOC	soil C weight%	102.9	4	**<0.01**	2.7	1	0.1
crop yield	kg/ha	68.3	3	**<0.01**	130.7	1	**<0.01**

Table 2.4. Effects of distance from prairie strips on biodiversity and ecosystem services, including data from both reduced input and biologically based treatments. Bolded p-values indicate statistically significant measures.

	distance			year			distance * year		
measure	χ^2	df	p	χ^2	df	p	χ^2	df	p
ant abundance	2.8	1	0.1	0.004	1	0.9	1.7	1	0.2
ant richness	2.8	1	0.1	0.004	1	0.9	1.7	1	0.2
dung beetle abundance	0.3	1	0.6	5.9	1	**<0.01**	4.6	1	**<0.05**
dung beetle richness	0.2	1	0.7	8.8	1	**<0.01**	0.08	1	0.8
spider abundance	0.06	1	0.8	48.7	1	**<0.01**	13.5	1	**<0.01**
spider family richness	0.03	1	0.86	0.02	1	0.9	6.2	1	**<0.01**
active carbon	8.2	1	**<0.01**	155.1	1	**<0.01**	3.4	1	0.06
decomposition services	1.3	1	0.2	33.3	1	**<0.01**	6.1	1	**<0.01**
pollination services	6.0	1	**<0.01**	40.9	1	**<0.01**	0.4	1	0.5

Table 2.5. Ant abundance per species found in each treatment each year. All distances are combined for strip abundance counts.

2019	Conventional	No Till	Red. input	Bio. based	Conservation land	Strip - Reduced Input	Strip - Biologically Based
Aphaenogaster carolinensis	0	0	0	0	0	1	0
Aphaenogaster rudis	1	0	0	0	6	1	1
Brachymyrmex depilis	0	0	0	0	0	2	0
Crematogaster cerasi	0	0	0	0	0	0	2
Crematogaster lineolata	0	0	0	1	0	0	0
Formica glacialis	2	0	0	2	5	1	3
Formica incerta	0	0	0	0	1	4	2
Formica pallidefulva	0	0	0	0	2	0	0
Formica subsericea	0	0	0	0	0	0	1
Formica vinculans	0	0	0	0	0	0	1
Lasius americanus	1	0	0	0	3	0	0
Lasius latipes	0	0	0	0	1	0	0
Lasius neoniger	6	6	6	6	6	68	59
Myrmica americana	1	0	1	3	4	7	19

Table 2.5 (cont’d)

Myrmica detritinodis	1	0	1	0	3	0	1
Myrmica pinetorum	0	0	0	0	1	0	0
Prenolepis imparis	1	3	5	4	2	56	52
Solenopsis molesta	0	1	0	0	0	1	0
Tapinoma sessile	0	0	0	0	0	0	1
Tetramorium immigrans	3	1	2	2	1	44	49
2020							
Brachymyrmex depilis	-	-	-	-	-	1	1
Formica glacialis	-	-	-	-	-	1	1
Formica incerta	-	-	-	-	-	3	1
Formica subsericea	-	-	-	-	-	1	0
Lasius neoniger	-	-	-	-	-	50	43
Myrmica americana	-	-	-	-	-	2	6
Ponera pennsylvanica	-	-	-	-	-	0	1
Prenolepis imparis	-	-	-	-	-	53	52
Tapinoma sessile	-	-	-	-	-	0	1
Tetramorium immigrans	-	-	-	-	-	47	46

Table 2.6. Spider abundance per family found in each treatment each year. All distances are combined for strip abundance counts.

2019	Conventional	No till	Reduced input	Bio. based	Conservation land	Strip - Reduced input	Strip - Biologically based
Agelenidae	0	0	0	0	0	0	1
Araneidae	0	0	0	0	0	8	3
Clubionidae	0	0	0	0	3	0	0
Corinnidae	0	0	0	0	0	1	0
Dictynidae	0	0	0	0	4	0	0
Gnaphosidae	0	0	0	0	0	2	3
Hahniidae	0	0	1	0	0	0	1
Linyphiidae	16	16	96	45	38	446	492
Lycosidae	10	74	53	159	29	409	868
Salticidae	0	1	0	0	2	0	1
Tetragnathidae	0	1	13	16	3	60	145
Theridiidae	0	1	2	0	11	0	0
Thomisidae	0	1	0	0	19	6	3
2020							
Agelenidae	0	0	1	0	0	0	0

Table 2.6 (cont'd)

Araneidae	0	0	0	0	0	6	4
Clubionidae	0	0	0	1	1	0	0
Corinnidae	0	0	0	0	1	1	2
Dictynidae	0	0	0	0	2	0	0
Gnaphosidae	2	4	5	3	7	2	2
Hahniidae	0	1	1	0	0	0	0
Linyphiidae	28	50	104	96	37	361	275
Lycosidae	133	37	109	83	76	232	243
Pisauridae	0	0	0	0	0	0	1
Salticidae	0	0	0	0	0	1	1
Tetragnathidae	0	0	1	1	2	3	2
Theridiidae	1	9	1	2	3	0	0
Thomisidae	13	33	19	5	36	21	19
Zodariidae	0	0	0	0	0	1	0

Table 2.7. Butterfly abundance per species or morphogroup found in each treatment each year. Unknown butterflies were butterflies that could not be identified in the field, for example if they flew over too quickly; it is likely that these individuals are already included in this table (i.e., not new species).

2019		Conventional	No Till	Reduced input	Biologically based	Conservation land
Baltimore Checkerspot	*Euphydryas phaeton*	0	0	0	0	1
Black Swallowtail	*Papilio polyxenes*	1	4	9	6	3
Blue sp		0	0	0	0	1
Common Buckeye	*Junonia coenia*	1	1	3	3	3
Common Sootywing	*Pholisora catullus*	0	0	0	0	2
Crescent sp		1	2	1	3	34
Eastern Tailed Blue	*Cupido comyntas*	1	1	1	7	14
Fritillary sp		0	0	0	2	0
Giant Swallowtail	*Papilio cresphontes*	0	0	0	1	0
Gray Hairstreak	*Strymon melinus*	2	1	1	4	6
Meadow Fritillary	*Boloria bellona*	0	1	0	0	0
Monarch	*Danaus plexippus*	40	71	70	113	170
Mourning Cloak	*Nymphalis antiopa*	0	0	0	0	1
Peck's Skipper	*Polites peckius*	1	1	0	1	0
Red Admiral	*Vanessa atalanta*	18	20	27	15	11

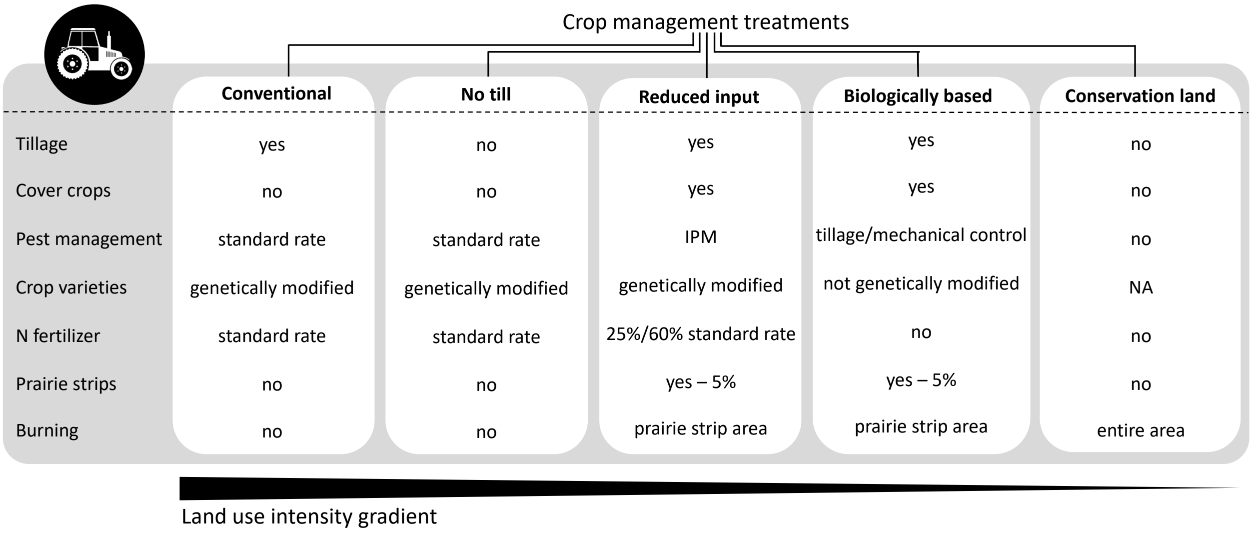
Table 2.7 (cont’d)

Silver Spotted Skipper	*Epargyreus clarus*	25	23	65	51	174
Skipper sp		1	0	0	4	11
Spicebush Swallowtail	*Papilio troilus*	2	1	2	8	0
Sulphur sp		149	210	479	806	580
Tiger Swallowtail	*Papilio glaucus*	3	2	3	4	1
Vanessa sp		15	6	17	38	31
Variegated Fritillary	*Euptoieta claudia*	0	1	0	0	0
Viceroy	*Limenitis archippus*	0	1	0	0	1
unknown butterflies		0	1	0	0	1
2020						
Baltimore Checkerspot	*Euphydryas phaeton*	1	0	0	1	2
Black Swallowtail	*Papilio polyxenes*	2	2	1	3	10
Blue sp		1	0	0	2	2
Checkered Skipper	*Prygus commuis*	0	0	0	1	0
Common Buckeye	*Junonia coenia*	1	1	2	3	11
Crescent sp		2	2	2	5	15
Eastern Tailed Blue	*Cupido comyntas*	1	0	2	5	13
Monarch	*Danaus plexippus*	11	12	12	26	47
Mourning Cloak	*Nymphalis antiopa*	0	0	0	0	1
Peck's Skipper	*Polites peckius*	0	2	1	3	4
Red Admiral	*Vanessa atalanta*	0	0	1	0	2

Table 2.7 (cont'd)

Red Spotted Purple	*Limenitis arthemis*	0	0	1	0	2
Silver Spotted Skipper	*Epargyreus clarus*	15	11	104	134	216
Skipper sp		3	1	9	3	20
Spicebush Swallowtail	*Papilio troilus*	0	0	3	1	3
Sulphur sp		57	47	191	340	523
Swallowtail sp		0	1	1	0	0
Tiger Swallowtail	*Papilio glaucus*	0	4	2	8	4
Vanessa sp		0	1	0	1	2
Variegated Fritillary	*Euptoieta claudia*	0	0	0	0	1
Viceroy	*Limenitis archippus*	0	0	0	0	3
unknown butterflies		3	1	0	0	2

Figure 2.1. Characteristics of experimental crop management treatments. Standard rate refers to Generally Accepted Agricultural and Management Practices. IPM (Integrated Pest Management) in the reduced input treatment refers to a combination of extra tillage (maize years), narrow row spacing (soy years), and reduced herbicide use, mostly related to the number of residual herbicides. Fungicides and pesticides are applied as problems arise and severity is assessed. Also regarding reduced input, N fertilizer is applied at 25% of the standard rate in maize years, and at 60% in wheat years.



Crop management treatments

	Conventional	No till	Reduced input	Biologically based	Conservation land
Tillage	yes	no	yes	yes	no
Cover crops	no	no	yes	yes	no
Pest management	standard rate	standard rate	IPM	tillage/mechanical control	no
Crop varieties	genetically modified	genetically modified	genetically modified	not genetically modified	NA
N fertilizer	standard rate	standard rate	25%/60% standard rate	no	no
Prairie strips	no	no	yes – 5%	yes – 5%	no
Burning	no	no	prairie strip area	prairie strip area	entire area

Land use intensity gradient

Figure 2.2. a. Experimental landscape with six blocks of five crop management treatments. b. Plot layout. Prairie strips and Strip Sampling Stations are only present in the reduced input and biologically based treatments.

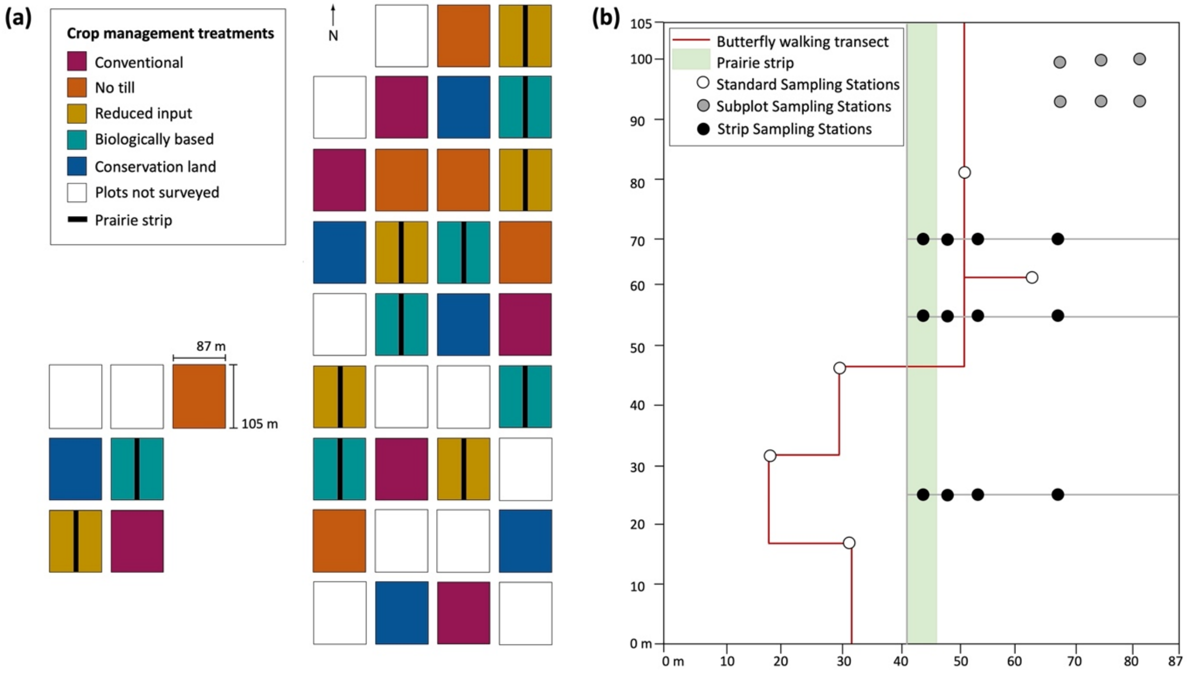


Figure 2.3. Hedge’s g effect size (black and gray dots) with 95% confidence interval. The

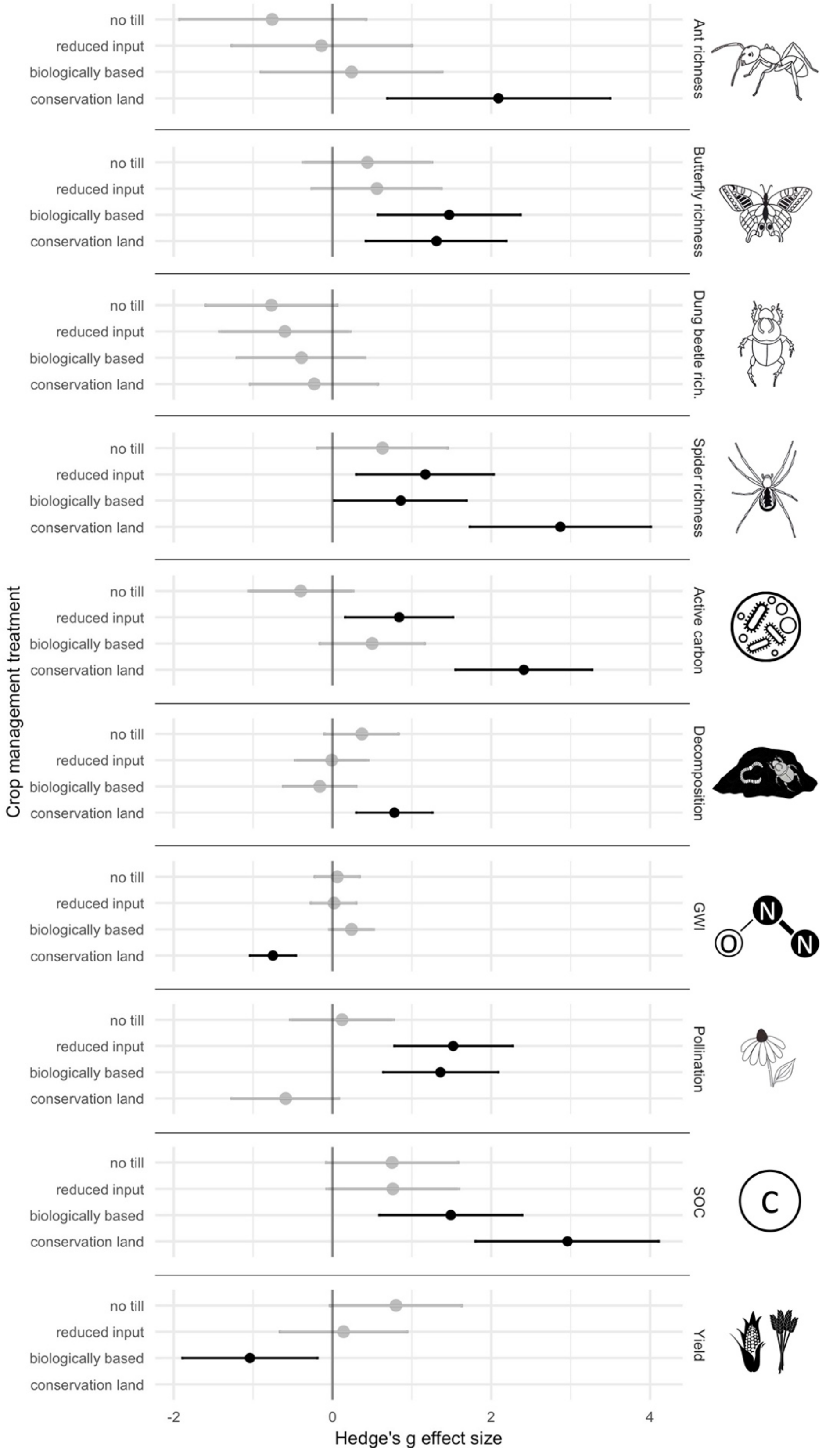


Figure 2.3 (cont'd)

baseline is the conventional management treatment. Negative values are effect sizes lower than that of the baseline, and positive values are effect sizes higher than the baseline. Values that cross zero are shaded gray. Note that lower levels of global warming impact (GWI) would be a more positive ecosystem service. Conservation land was not harvested, therefore crop yield is not applicable for that treatment.

Figure 2.4. Effects of crop management treatment on measures of biodiversity and ecosystem services between years 2019 and 2020. For measures of biodiversity, bars depict means over an entire year; for measures of ecosystem services, bars depict means for each sampling round. Letters denote statistical differences among treatments. Error bars show standard errors. Ants and active carbon were only measured in 2019.

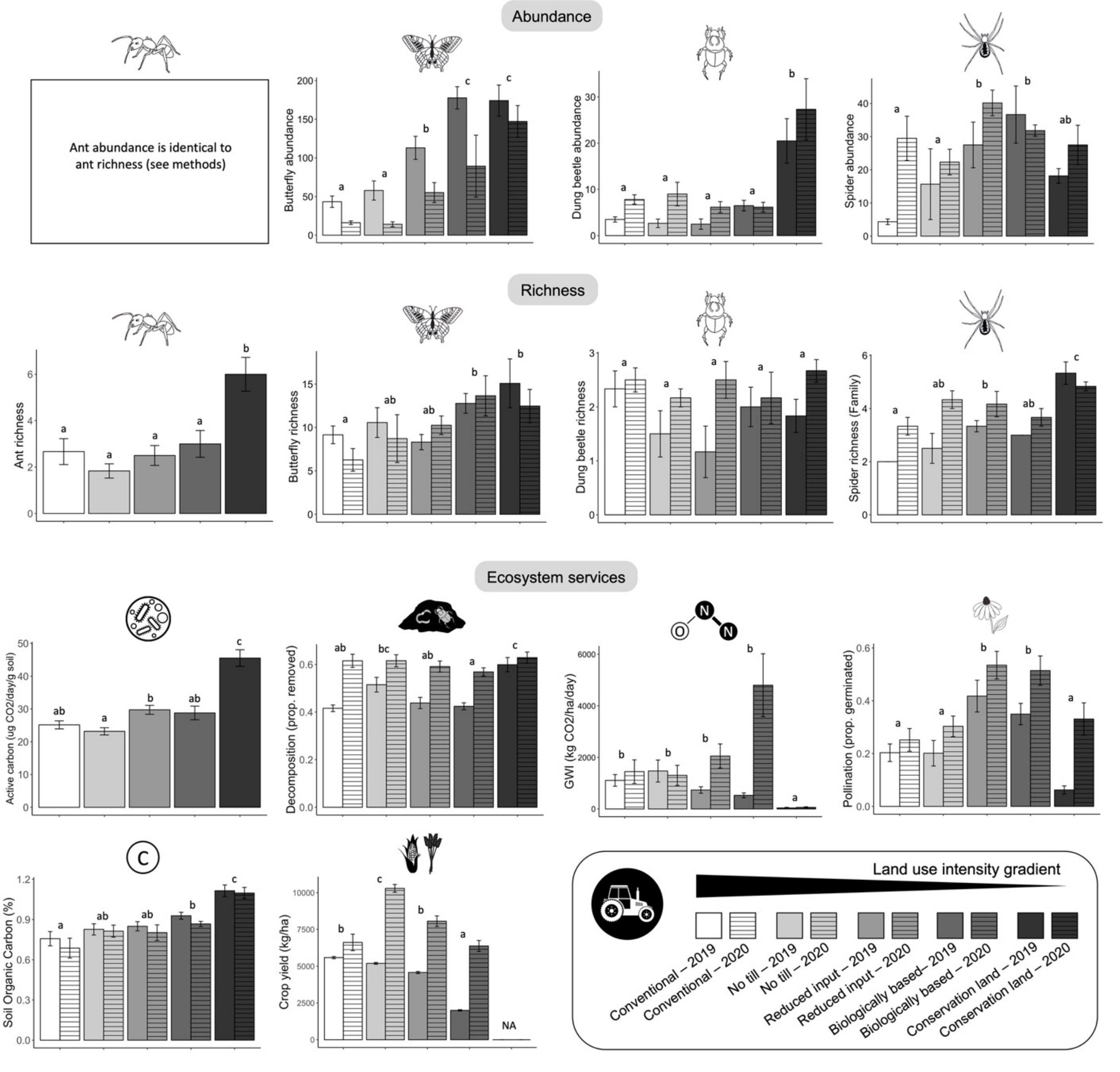


Figure 2.5. Effects of distance from prairie strips on measures of biodiversity and ecosystem

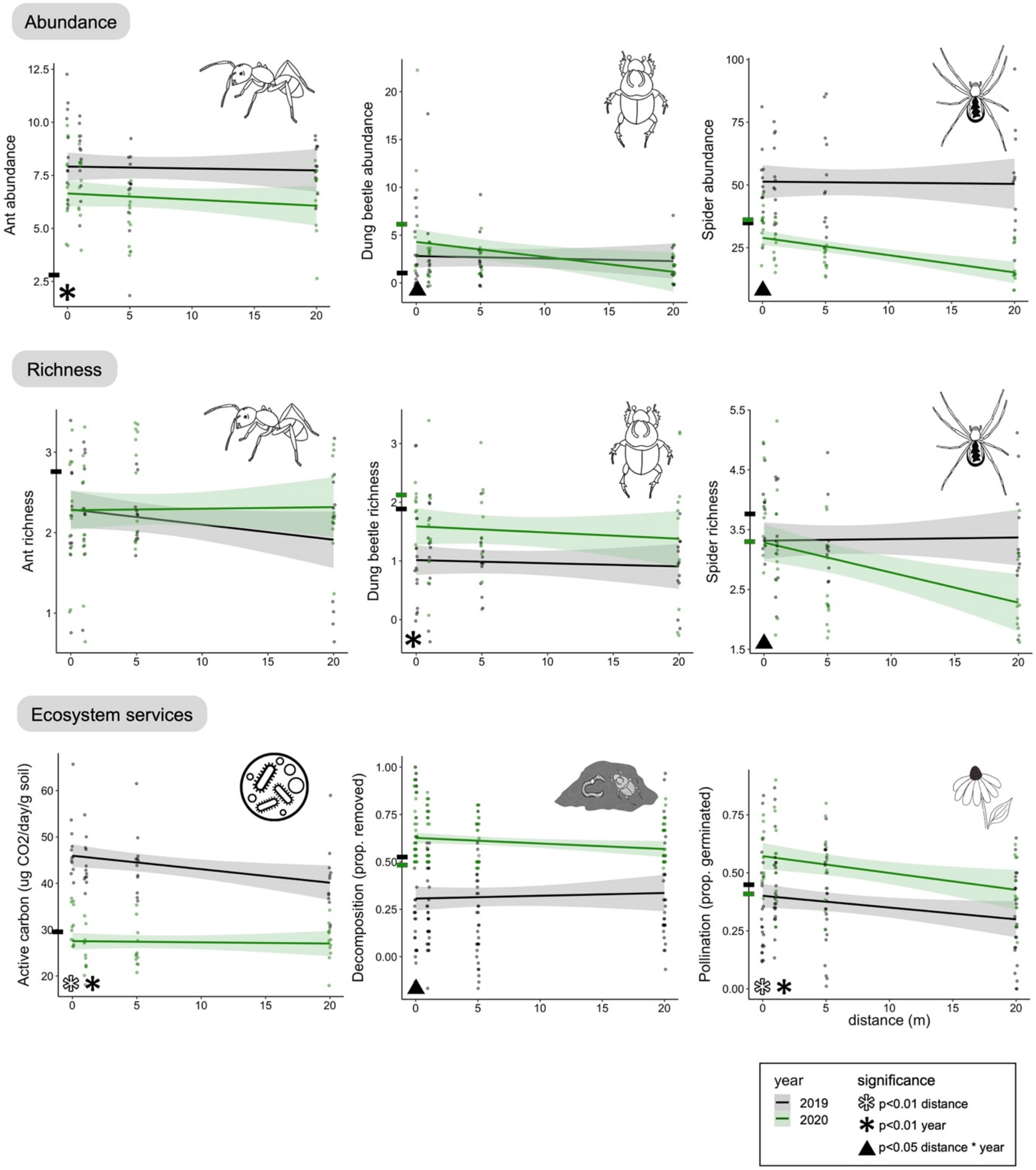


Figure 2.5 (cont'd)

services in both reduced input and biologically based treatments. We considered linear effects of distance from prairie strips. The interaction with year is presented, with 2019 being the first year of prairie strip implementation and a wheat year, and 2020 being the second year and a maize year. Distance 0 m is within the prairie strip. Black dashes on the y-axis represent the mean of the plot level values for reduced input and biologically based for that measure in 2019; green dashes represent 2020. Ant data from 2019 is modified from Helms et al. 2021.

LITERATURE CITED

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Agosti, D., Majer, J. D., Alonso, L. E., and Schultz, T. R. (2000). *Ants: Standard Methods for Measuring and Monitoring Biodiversity.* Smithsonian Institution Press, Washington, D.C.

Arbuckle, J. G. (2019). *STRIPS Cooperator Follow-On Survey: 2018 Results*. Sociology Technical Report No. 1057. Ames, Iowa: Iowa State University Extension Sociology.

Asbjornsen, H., Hernandez-Santana, V., Liebman, M., Bayala, J., Chen, J., Helmers, M., Ong, C. K., and Schulte, L. A. (2013). Targeting perennial vegetation in agricultural landscapes for enhancing ecosystem services. *Renewable Agriculture and Food Systems*, *29*(2), 101–125. https://doi.org/10.1017/S1742170512000385

Barbero, E., Palestrini, C., and Rolando, A. (1999). Dung Beetle Conservation: Effects of Habitat and Resource Selection (Coleoptera: Scarabaeoidea). *Journal of Insect Conservation, 3*, 75-84.

Barker, T., Bashmakov, I., Bernstein, L., Bogner, J. E., Bosch, P. R., Dave, R., Davidson, O. R., Fisher, B. S., Gupta, S., Halsnæs, K., Geij, G. J., Kahn Riveiro, S., Kobayashi, S., Levine, M. D., Martino, D. L., Masera, O., Metz, B., Meyer, L. A., Nabuurs, G. J., Najam, A., Nakicenovic, N., Rogner, H.-H., Roy, J., Sathaye, J., Schock, R., Shukla, P., Sims, R. E. H., Smith, P., Tirpak, D. A., Urge-Vorsatz, D., & Zhou, D. (2007). Technical Summary. Pages 25–93 in Metz, B., Davidson, O. R., Bosch, P. R., Dave, R., and Meyer, L. A., (editors). Climate change 2007: Mitigation. Contribution of Working Group III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York, New York, USA.

Barrios, E. (2007). Soil biota, ecosystem services and land productivity. *Ecological Economics*, *64*(2), 269–285. https://doi.org/10.1016/j.ecolecon.2007.03.004

Basso, B. (2021). Precision conservation for a changing climate. *Nature Food*, *2*(5), 322–323. https://doi.org/10.1038/s43016-021-00283-z

Basso, B., Shuai, G., Zhang, J., and Robertson, G. P. (2019). Yield stability analysis reveals sources of large-scale nitrogen loss from the US Midwest. *Scientific Reports*, *9*(1), 5774. https://doi.org/10.1038/s41598-019-42271-1

Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*(1). https://doi.org/10.18637/jss.v067.i01

Bengtsson, J., Ahnström, J., and Weibull, A. C. (2005). The effects of organic agriculture on biodiversity and abundance: A meta-analysis: Organic agriculture, biodiversity and abundance. *Journal of Applied Ecology*, *42*(2), 261–269. https://doi.org/10.1111/j.1365-2664.2005.01005.x

Blitzer, E. J., Dormann, C. F., Holzschuh, A., Klein, A.-M., Rand, T. A., and Tscharntke, T. (2012). Spillover of functionally important organisms between managed and natural habitats. *Agriculture, Ecosystems & Environment*, *146*(1), 34–43. https://doi.org/10.1016/j.agee.2011.09.005

Bowers, C., Toews, M. D., and Schmidt, J. M. (2021). Winter cover crops shape early-season predator communities and trophic interactions. *Ecosphere*, *12*(7). https://doi.org/10.1002/ecs2.3635

Bowles, T. M., Jackson, L. E., Loeher, M., and Cavagnaro, T. R. (2016). Ecological intensification and arbuscular mycorrhizas: A meta-analysis of tillage and cover crop effects. *Journal of Applied Ecology*, *54*(6), 1785–1793. https://doi.org/10.1111/1365-2664.12815

Campbell, B. M., Beare, D. J., Bennett, E. M., Hall-Spencer, J. M., Ingram, J. S. I., Jaramillo, F., Ortiz, R., Ramankutty, N., Sayer, J. A., and Shindell, D. (2017). Agriculture production as a major driver of the Earth system exceeding planetary boundaries. *Ecology and Society*, *22*(4), art8. https://doi.org/10.5751/ES-09595-220408

Cant, E. T., Smith, A. D., Reynolds, D. R., and Osborne, J. L. (2005). Tracking butterfly flight paths across the landscape with harmonic radar. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1565), 785–790. https://doi.org/10.1098/rspb.2004.3002

Carvalheiro, L. G., Seymour, C. L., Veldtman, R., and Nicolson, S. W. (2010). Pollination services decline with distance from natural habitat even in biodiversity-rich areas: Sub-tropics crop pollination limitation. *Journal of Applied Ecology*, *47*(4), 810–820. https://doi.org/10.1111/j.1365-2664.2010.01829.x

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., and Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs*, *84*(1), 45–67. https://doi.org/10.1890/13-0133.1

Coleman, D. C., Callaham Jr., M. A., and Crossley Jr., D. A. (2018a). Chapter 4 - Secondary Production: Activities of Heterotrophic Organisms—The Soil Fauna - Fundamentals of Soil Ecology. in *Fundamentals of Soil Ecology (Third Edition).* https://doi.org/10.1016/B978-0-12-805251-8.00003-X

Coleman, D. C., Callaham Jr., M. A., and Crossley Jr., D. A. (2018b). Chapter 3 - Secondary Production: Activities of Heterotrophic Organisms—Microbes - Fundamentals of Soil Ecology. in *Fundamentals of Soil Ecology (Third Edition).* https://doi.org/10.1016/B978-0-12-805251-8.00003-X

Coleman, D. C., Callaham Jr., M. A., and Crossley Jr., D. A. (2018c). Chapter 1 – Introduction to Soil: Historical Overview, Soil Science Basics, and the Fitness of the Soil Environment – Fundamentals of Soil Ecology. In *Fundamentals of Soil Ecology (Third Edition).* https://doi.org/10.1016/B978-0-12-805251-8.00001-6

Coovert, G. A. (2005). The Ants of Ohio (Hymenoptera: Formicidae). Bulletin of the Ohio Biological Survey 15.

Culman, S., Snapp, S. S., Freeman, M. A., Schipanski, M. E., Beniston, J., Lal, R., Drinkwater, L. E., Franzluebbers, A. J., Glover, J. D., Grandy, A. S., Lee, J., Six, J., Maul, J. E., Mirsky, S. B., Spargo, J. T., and Wander, M. M. (2012). Permanganate Oxidizable Carbon Reflects a Processed Soil Fraction that is Sensitive to Management. *Soil Science Society of America Journal,* 76, no. 2 494-504. https://doi.org/10.2136/sssaj2011.0286.

Cunningham-Minnick, M. J., Peters, V. E., and Crist, T. O. (2019). Nesting habitat enhancement for wild bees within soybean fields increases crop production. *Apidologie*, *50*(6), 833–844. https://doi.org/10.1007/s13592-019-00691-y

Dauber, J. and Wolters, V. (2005). Colonization of temperate grassland by ants. *Basic and Applied Ecology*, *6*(1), 83–91. https://doi.org/10.1016/j.baae.2004.09.011

de Pedro, L., Perera-Fernández, L. G., López-Gallego, E., Pérez-Marcos, M., and Sanchez, J. A. (2020). The Effect of Cover Crops on the Biodiversity and Abundance of Ground-Dwelling Arthropods in a Mediterranean Pear Orchard. *Agronomy*, *10*(4), 580. https://doi.org/10.3390/agronomy10040580

Del Re, A. C. (2013). compute.es: Compute Effect Sizes. https://cran.r-project.org/web/packages/compute.es/index.html

Ellison, A. M., Gotelli, N. J., Farnsworth, E. J., and Alpert, G. D. (2012). *A Field Guide to the Ants of New England.* Yale University Press, New Haven.

Ellison, A. M., Record, S., Arguello, A., and Gotelli, N. J. (2007). Rapid Inventory of the Ant Assemblage in a Temperate Hardwood Forest: Species Composition and Assessment of Sampling Methods. *Environmental Entomology*, *36*(4), 10.

Folgarait, P. J. (1998). Ant biodiversity and its relationship to ecosystem functioning: A review. *Biodiversity and Conservation*, *7*(9), 1221–1244. https://doi.org/10.1023/A:1008891901953

Fox, J. and Weisberg, S. (2019). An R Companion to Applied Regression, Third edition. Sage, Thousand Oaks CA. https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

Franzluebbers, A. J., Haney, R. L., Honeycutt, C. W., Schomberg, H. H., and Hons, F. M. (2000). Flush of Carbon Dioxide Following Rewetting of Dried Soil Relates to Active Organic Pools. *Soil Science Society of America Journal*, *64*(2), 613–623. https://doi.org/10.2136/sssaj2000.642613x

Garibaldi, L. A., Steffan-Dewenter, I., Kremen, C., Morales, J. M., Bommarco, R., Cunningham, S. A., Carvalheiro, L. G., Chacoff, N. P., Dudenhöffer, J. H., Greenleaf, S. S., Holzschuh, A., Isaacs, R., Krewenka, K., Mandelik, Y., Mayfield, M. M., Morandin, L. A., Potts, S. G., Ricketts, T. H., Szentgyörgyi, H., Viana, B. F., Westphal, C., Winfree, R., and Klein, A. M. (2011). Stability of pollination services decreases with isolation from natural areas despite honey bee visits: Habitat isolation and pollination stability. *Ecology Letters*, *14*(10), 1062–1072. https://doi.org/10.1111/j.1461-0248.2011.01669.x

Gelfand, I., Shcherbak, I., Millar, N., Kravchenko, A. N., and Robertson, G. P. (2016). Long-term nitrous oxide fluxes in annual and perennial agricultural and unmanaged ecosystems in the upper Midwest USA. *Global Change Biology*, *22*(11), 3594–3607. https://doi.org/10.1111/gcb.13426

Gelfand, I. and Robertson, G. P. (2015). Mitigation of greenhouse gas emissions in agricultural ecosystems. Pages 310-339 in Hamilton, S. K., Doll, J. E., & Robertson, G. P., (editors). *The Ecology of Agricultural Landscapes: Long-Term Research on the Path to Sustainability.* Oxford University Press New York, New York, USA.

Ghazanfar, M., Malik, M. F., Hussain, M., Iqbal, R., and Younas, M. (2016). Butterflies and their contribution in ecosystem: A review. *Journal of Entomology and Zoology Studies*, 5.

Gotelli, N. J., Ellison, A. M., Dunn, D. R., and Sanders, N. J. (2011). Counting ants (Hymenoptera: Formicidae): biodiversity sampling and statistical analysis for myrmecologists. Myrmecological News 15:13-19.

Grieshop, M. J., Werling, B., Buehrer, K., Perrone, J., Isaacs, R., and Landis, D. (2012). Big Brother is Watching: Studying Insect Predation in the Age of Digital Surveillance. *American Entomologist*, *58*(3), 172–182. https://doi.org/10.1093/ae/58.3.172

Griffin, S. R., Bruninga-Socolar, B., Kerr, M. A., Gibbs, J., and Winfree, R. (2017). Wild bee community change over a 26-year chronosequence of restored tallgrass prairie: Bee communities of restored tallgrass prairie. *Restoration Ecology*, *25*(4), 650–660. https://doi.org/10.1111/rec.12481

Helms IV, J. A., Smith, J., Clark, S., Knupp, K., and Haddad, N. M. (2021). Ant Communities and Ecosystem Services in Organic Versus Conventional Agriculture in the U.S. Corn Belt. *Environmental Entomology,* 2021: https://doi.org/10.1093/ee/nvab105

Helms IV, J. A., Ijelu, S. E., Wills, B. D., Landis, D. A., and Haddad, N. M. (2020). Ant biodiversity and ecosystem services in bioenergy landscapes. *Agriculture, Ecosystems & Environment*, *290*, 106780. https://doi.org/10.1016/j.agee.2019.106780

Hevia, V., García-Llorente, M., Martínez-Sastre, R., Palomo, S., García, D., Miñarro, M., Pérez-Marcos, M., Sanchez, J. A., and González, J. A. (2021). Do farmers care about pollinators? A cross-site comparison of farmers' perceptions, knowledge, and management practices for pollinator-dependent crops. *International Journal of Agricultural Sustainability*, *19*(1), 1–15. https://doi.org/10.1080/14735903.2020.1807892

Holland, E. A., Robertson, G. P., Greenberg, J., Groffman, P. M., Booner, R. D., and Gosz, J. R. (1999). Soil CO_2, N_2O, and CH_4 exchange. Pages 185-201 in Robertson, G. P., Coleman, D. C., Bledsoe, C. S., Sollins, P., (editors). *Standard Soil Methods for Long-term Ecological Research.* Oxford University Press, New York, New York, USA.

Hölldobler, B. and Wilson, E. O. (2009). The superorganism, W.W. Norton & Company, Inc., New York, New York USA. 522 p.

Hölldobler, B. and Wilson, E. O. (1990). The ants. Springer, Heidelberg, Germany. 732 p.

Holzschuh, A., Dormann, C. F., Tscharntke, T., and Steffan-Dewenter, I. (2011). Expansion of mass-flowering crops leads to transient pollinator dilution and reduced wild plant pollination. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1723), 3444–3451. https://doi.org/10.1098/rspb.2011.0268

Hosler, S. C., Jones, H. P., Nelson, M., and Barber, N. A. (2021). Management actions shape dung beetle community structure and functional traits in restored tallgrass prairie. *Ecological Entomology*, *46*(2), 175–186. https://doi.org/10.1111/een.12950

Hothorn, T., Bretz, F., and Westfall, P. (2008). Simultaneous Inference in General Parametric Models. *Biometrical Journal*, *50*(3), 346–363. https://doi.org/10.1002/bimj.200810425

Hsieh, T. C., Ma, K. H., and Chao, A. (2016). iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, *7*(12), 1451–1456. https://doi.org/10.1111/2041-210X.12613

Hussain, R. I., Brandl, M., Maas, B., Rabl, D., Walcher, R., Krautzer, B., Entling, M. H., Moser, D., and Frank, T. (2021). Re-established grasslands on farmland promote pollinators more than predators. *Agriculture, Ecosystems & Environment*, *319*, 107543. https://doi.org/10.1016/j.agee.2021.107543

Hutton, S. A. and Giller, P. S. (2003). The effects of the intensification of agriculture on northern temperate dung beetle communities. *Journal of Applied Ecology*, *40*(6), 994–1007. https://doi.org/10.1111/j.1365-2664.2003.00863.x

Intergovernmental Platform on Biodiversity and Ecosystem Services. (2019). Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Díaz, S., Settele, J., Brondízio, E.S., Ngo, H. T., Guèze, M., Agard, J., Arneth, A., Balvanera, P., Brauman, K. A., Butchart, S. H. M., Chan, K. M. A., Garibaldi, L. A., Ichii, K., Liu, J., Subramanian, S. M., Midgley, G. F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., Polasky, S., Purvis, A., Razzaque, J., Reyers, B., Chowdhury, R. R., Shin, Y. J., Visseren-Hamakers, I. J., Willis, K. J., and Zayas, C. N., (editors). IPBES secretariat, Bonn, Germany. 56 pages. https://doi.org/10.5281/zenodo.3553579

IPBES (2016): Summary for policymakers of the assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production. Potts, S.G., Imperatriz-Fonseca, V. L., Ngo, H. T., Biesmeijer, J. C., Breeze, T. D., Dicks, L. V., Garibaldi, L. A., Hill, R., Settele, J., Vanbergen, A. J., Aizen, M. A., Cunningham, S. A., Eardley, C., Freitas, B. M., Gallai, N., Kevan, P. G., Kovács-Hostyánszki, A., Kwapong, P. K., Li, J., Li, X., Martins, D. J., Nates-Parra, G., Pettis, J. S., Rader, R., and Viana, B. F., (editors). Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn, Germany. 36 pages.

Isaacs, R., Tuell, J., Fiedler, A., Gardiner, M., and Landis, D. (2009). Maximizing arthropod-mediated ecosystem services in agricultural landscapes: The role of native plants. *Frontiers in Ecology and the Environment*, *7*(4), 196–203. https://doi.org/10.1890/080035

Jones, M. S., Fu, Z., Reganold, J. P., Karp, D. S., Besser, T. E., Tylianakis, J. M., and Snyder, W. E. (2019). Organic farming promotes biotic resistance to foodborne human pathogens. *Journal of Applied Ecology*, *56*(5), 1117–1127. https://doi.org/10.1111/1365-2664.13365

Jones, M. S., Halteman, W. A., and Drummond, F. A. (2016). Predator- and Scavenger-Mediated Ecosystem Services Determined by Distance to Field-Forest Interface in the Maine Lowbush Blueberry Agroecosystem. *Environmental Entomology.* doi:10.1093/ee/nvw082

Kahmark, K., Millar, N., and Robertson, G. P. (2020). Static Chamber Method for Measuring Soil Greenhouse Gas Fluxes. https://doi.org/10.5281/ZENODO.4630396

Karp, D. S., Moses, R., Gennet, S., Jones, M. S., Joseph, S., M'Gonigle, L. K., Ponisio, L. C., Snyder, W. E., and Kremen, C. (2016). Agricultural practices for food safety threaten pest control services for fresh produce. *Journal of Applied Ecology*, *53*(5), 1402–1412. https://doi.org/10.1111/1365-2664.12707

Kordbacheh, F., Liebman, M., and Harris, M. (2020). Strips of prairie vegetation placed within row crops can sustain native bee communities. *PLOS ONE*, *15*(10), e0240354. https://doi.org/10.1371/journal.pone.0240354

Kravchenko, A. N., Guber, A. K., Razavi, B. S., Koestel, J., Quigley, M. Y., Robertson, G. P., and Kuzyakov, Y. (2019). Microbial spatial footprint as a driver of soil carbon stabilization. *Nature Communications,* 10, 3121 https://doi.org/10.1038/s41467-019-11057-4

Kremen, C. and Merenlender, A. M. (2018). Landscapes that work for biodiversity and people. *Science*, *362*(6412), eaau6020. https://doi.org/10.1126/science.aau6020

Kurtz, C. (2013). *A Practical Guide to Prairie Reconstruction: Second Edition.* Page 56. University of Iowa Press, Iowa City, Iowa, USA.

Landis, D. A. (2017). Designing agricultural landscapes for biodiversity-based ecosystem services. *Basic and Applied Ecology*, *18*, 1–12. https://doi.org/10.1016/j.baae.2016.07.005

Landis, D. A., Wratten, S. D., and Gurr, G. M. (2000). Habitat Management to Conserve Natural Enemies of Arthropod Pests in Agriculture. *Annual Review of Entomology*, *45*(1), 175–201. https://doi.org/10.1146/annurev.ento.45.1.175

Liang, D. and Robertson, G. P. (2021). Nitrification is a minor source of nitrous oxide (N_2O) in an agricultural landscape and declines with increasing management intensity. *Global Change Biology*, *27*(21), 5599–5613. https://doi.org/10.1111/gcb.15833

Manning, P. and Cutler, G. C. (2018). Ecosystem functioning is more strongly impaired by reducing dung beetle abundance than by reducing species richness. *Agriculture, Ecosystems & Environment*, *264*, 9–14. https://doi.org/10.1016/j.agee.2018.05.002

Menéndez, R., González-Megías, A., Collingham, Y., Fox, R., Roy, D. B., Ohlemüller, R., and Thomas, C. D. (2007). Direct and indirect effects of climate and habitat factors on butterfly diversity. *Ecology*, *88*(3), 605–611. https://doi.org/10.1890/06-0539

Menke, S. B., Gaulke, E., Hamel, A., and Vachter, N. (2015). The Effects of Restoration Age and Prescribed Burns on Grassland Ant Community Structure. *Environmental Entomology*, *44*(5), 1336–1347. https://doi.org/10.1093/ee/nvv110

Mitchell, M. G. E., Schuster, R., Jacob, A. L., Hanna, D. E. L., Dallaire, C. O., Raudsepp-Hearne, C., Bennett, E. M., Lehner, B., and Chan, K. M. A. (2021). Identifying key ecosystem service providing areas to inform national-scale conservation planning. *Environmental Research Letters*, *16*(1), 014038. https://doi.org/10.1088/1748-9326/abc121

Morandin, L. A. and Kremen, C. (2013). Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecological Applications*, *23*(4), 829–839. https://doi.org/10.1890/12-1051.1

Mosier, S., Córdova, S. C., and Robertson, G. P. (2021). Restoring Soil Fertility on Degraded Lands to Meet Food, Fuel, and Climate Security Needs via Perennialization. *Frontiers in Sustainable Food Systems*, *5*, 706142. https://doi.org/10.3389/fsufs.2021.706142

Mueller, U. G., Gerardo, N. M., Aanen, D. K., Six, D. L., and Schultz, T. R. (2005). The Evolution of Agriculture in Insects. *Annual Review of Ecology, Evolution, and Systematics*, *36*(1), 563–595. https://doi.org/10.1146/annurev.ecolsys.36.102003.152626

Nemes, S. N. and Price, D. L. (2015). Illustrated Keys to the Scarabaeinae (Coleoptera: Scarabaeidae) of Maryland. *Northeastern Naturalist*, *22*(2), 318–344. https://doi.org/10.1656/045.022.0208

Nielsen, M. C. (1999). Michigan Butterflies and Skippers: A Field Guide and Reference. Michigan State University Extension, East Lansing, MI, USA.

Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezquita, S., and Favila, M. E. (2008). Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biological Conservation*, *141*(6), 1461–1474. https://doi.org/10.1016/j.biocon.2008.04.011

Nkuba, M. R., Chanda, R., Mmopelwa, G., Kato, E., Mangheni, M. N., and Lesolle, D. (2020). Influence of Indigenous Knowledge and Scientific Climate Forecasts on Arable Farmers' Climate Adaptation Methods in the Rwenzori region, Western Uganda. *Environmental Management*, *65*(4), 500–516. https://doi.org/10.1007/s00267-020-01264-x

Pasquet, R. S., Peltier, A., Hufford, M. B., Oudin, E., Saulnier, J., Paul, L., Knudsen, J. T., Herren, H. R., and Gepts, P. (2008). Long-distance pollen flow assessment through evaluation of pollinator foraging range suggests transgene escape distances. *Proceedings of* *the National Academy of Sciences*, *105*(36), 13456–13461. https://doi.org/10.1073/pnas.0806040105

Paul, E. A., Kravchenko, A., Grandy, A. S., and Morris, S. (2015). Soil organic matter dynamics: Controls and management for sustainable ecosystem functioning. Pages 104-134 in Hamilton, S. K., Doll, J. E., & Robertson, G. P., (editors). *The Ecology of Agricultural Landscapes: Long-Term Research on the Path to Sustainability.* Oxford University Press, New York, New York, USA.

Peck, S. L., McQuaid, B., and Campbell, C. L. (1998). Using Ant Species (Hymenoptera: Formicidae) as a Biological Indicator of Agroecosystem Condition. *Environmental Entomology,* 27:1102-1110.

Pérez-Suárez, M., Castellano, M. J., Kolka, R., Asbjornsen, H., and Helmers, M. (2014). Nitrogen and carbon dynamics in prairie vegetation strips across topographical gradients in mixed Central Iowa agroecosystems. *Agriculture, Ecosystems & Environment*, *188*, 1–11. https://doi.org/10.1016/j.agee.2014.01.023

Piccini, I., Palestrini, C., Rolando, A., and Roslin, T. (2019). Local management actions override farming systems in determining dung beetle species richness, abundance and biomass and associated ecosystem services. *Basic and Applied Ecology*, *41*, 13–21. https://doi.org/10.1016/j.baae.2019.09.001

Pollard, E. (1977). A method for assessing changes in the abundance of butterflies. *Biological Conservation*, *12*(2), 115–134. https://doi.org/10.1016/0006-3207(77)90065-9

Raven, P. H. and Wagner, D. L. (2021). Agricultural intensification and climate change are rapidly decreasing insect biodiversity. *Proceedings of the National Academy of Sciences*, *118*(2), e2002548117. https://doi.org/10.1073/pnas.2002548117

Reeder, K. F., Debinski, D. M., and Danielson, B. J. (2005). Factors affecting butterfly use of filter strips in Midwestern USA. *Agriculture, Ecosystems & Environment*, *109*(1–2), 40–47. https://doi.org/10.1016/j.agee.2005.02.016

Ricketts, T. H., Regetz, J., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S. S., Klein, A. M., Mayfield, M. M., Morandin, L. A., Ochieng', A., and Viana, B. F. (2008). Landscape effects on crop pollination services: Are there general patterns? *Ecology Letters*, *11*(5), 499–515. https://doi.org/10.1111/j.1461-0248.2008.01157.x

Ricketts, T. H. (2004). Tropical Forest Fragments Enhance Pollinator Activity in Nearby Coffee Crops. *Conservation Biology*, *18*(5), 1262–1271. https://doi.org/10.1111/j.1523-1739.2004.00227.x

Robertson, G. P., Hamilton, S. K., Barham, B. L., Dale, B. E., Izaurralde, R. C., Jackson, R. D., Landis, D. A., Swinton, S. M., Thelen, K. D., and Tiedje, J. M. (2017). Cellulosic biofuel contributions to a sustainable energy future: Choices and outcomes. *Science*, *356*(6345), eaal2324. https://doi.org/10.1126/science.aal2324

Robertson, G. P. and Hamilton, S. K. (2015). Long-term ecological research in agricultural landscapes at the Kellogg Biological Station LTER site: conceptual and experimental framework. Pages 1-32 in Hamilton, S. K., Doll, J. E., & Robertson, G. P., (editors). *The Ecology of Agricultural Landscapes: Long-Term Research on the Path to Sustainability*. Oxford University Press, New York, New York, USA.

Robertson, G. P., Gross, K. L., Hamilton, S. K., Landis, D. A., Schmidt, T. M., Snapp, S. S., and Swinton S. M. (2015). Farming for ecosystem services: An ecological approach to production agriculture. Pages 33-53 in Hamilton, S. K., Doll, J. E., and Robertson, G. P., (editors). *The Ecology of Agricultural Landscapes: Long-Term Research on the Path to Sustainability.* Oxford University Press, New York, New York, USA.

Robertson, G. P., Paul, E. A., and Harwood, R. R. (2000). Greenhouse Gases in Intensive Agriculture: Contributions of Individual Gases to the Radiative Forcing of the Atmosphere. *Science*, *289*(5486), 1922–1925. https://doi.org/10.1126/science.289.5486.1922

Rundlöf, M., Bengtsson, J., and Smith, H. G. (2008). Local and landscape effects of organic farming on butterfly species richness and abundance: Scale-dependent effects of organic farming. *Journal of Applied Ecology*, *45*(3), 813–820. https://doi.org/10.1111/j.1365-2664.2007.01448.x

Rusch, A., Bommarco, R., Jonsson, M., Smith, H. G., and Ekbom, B. (2013). Flow and stability of natural pest control services depend on complexity and crop rotation at the landscape scale. *Journal of Applied Ecology*, *50*(2), 345–354. https://doi.org/10.1111/1365-2664.12055

Sands, B. and Wall, R. (2017). Dung beetles reduce livestock gastrointestinal parasite availability on pasture. *Journal of Applied Ecology*, *54*(4), 1180–1189. https://doi.org/10.1111/1365-2664.12821

Scharnhorst, V. S., Fiedler, K., Frank, T., Moser, D., Rabl, D., Brandl, M., Hussain, R. I., Walcher, R., and Maas, B. (2021). Ant community composition and functional traits in new grassland strips within agricultural landscapes. *Ecology and Evolution*, *11*(12), 8319–8331. https://doi.org/10.1002/ece3.7662

Schmidt, M. H., Roschewitz, I., Thies, C., and Tscharntke, T. (2005). Differential effects of landscape and management on diversity and density of ground-dwelling farmland spiders: Landscape vs. management effects on spiders. *Journal of Applied Ecology*, *42*(2), 281–287. https://doi.org/10.1111/j.1365-2664.2005.01014.x

Schulte, L. A., Niemi, J., Helmers, M. J., Liebman, M., Arbuckle, J. G., James, D. E., Kolka, R. K., O'Neal, M. E., Tomer, M. D., Tyndall, J. C., Asbjornsen, H., Drobney, P., Neal, J., Van Ryswyk, G., and Witte, C. (2017). Prairie strips improve biodiversity and the delivery of multiple ecosystem services from corn–soybean croplands. *Proceedings of the National Academy of Sciences*, *114*(42), 11247–11252. https://doi.org/10.1073/pnas.1620229114

Shcherbak, I. and Robertson, G.P. Nitrous Oxide (N_2O) Emissions from Subsurface Soils of Agricultural Ecosystems. *Ecosystems* **22,** 1650–1663 (2019). https://doi.org/10.1007/s10021-019-00363-z

Smith, R., Mcswiney, C., Grandy, A., Suwanwaree, P., Snider, R., and Robertson, G. P. (2008). Diversity and abundance of earthworms across an agricultural land-use intensity gradient. *Soil and Tillage Research*, *100*(1–2), 83–88. https://doi.org/10.1016/j.still.2008.04.009

Smith, P., Martino, D., Cai, Z., Gwary, D., Janzen, H., Kumar, P., McCarl, B., Ogle, S., O'Mara, F., Rice, C., Scholes, B., and Sirotenko, O. (2007). Agriculture. Pages 498–540 in Metz, B., Davidson, O. R., Bosch, P. R., Dave, R., and Meyer, L. A., (editors). Climate Change 2007: Mitigation. Contribution of Working Group III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK, and New York, New York, USA.

Sprunger, C. D. and Robertson, G. P. (2018). Early accumulation of active fraction soil carbon in newly established cellulosic biofuel systems. *Geoderma*, *318*, 42–51. https://doi.org/10.1016/j.geoderma.2017.11.040

C. D. Sprunger, L. G. Oates, R. D. Jackson, and Robertson, G. P. (2017). Plant community composition influences fine root production and biomass allocation in perennial bioenergy cropping systems of the upper Midwest, USA. *Biomass and Bioenergy*, *105*, 248–258. https://doi.org/10.1016/j.biombioe.2017.07.007

Sunderland, K. and Samu, F. (2000). Effects of agricultural diversification on the abundance, distribution, and pest control potential of spiders: A review. *Entomologia Experimentalis et Applicata*, *95*(1), 1–13. https://doi.org/10.1046/j.1570-7458.2000.00635.x

Syswerda, S. P., and Robertson, G. P. (2014). Ecosystem services along a management gradient in Michigan (USA) cropping systems. *Agriculture, Ecosystems & Environment*, *189*, 28–35. https://doi.org/10.1016/j.agee.2014.03.006

Syswerda, S., Corbin, A., Mokma, D., Kravchenko, A., and Robertson, G. (2011). Agricultural Management and Soil Carbon Storage in Surface vs. Deep Layers. *Soil Science Society of America Journal,* 75: 92-101. https://doi.org/10.2136/sssaj2009.0414

Tamburini, G., Bommarco, R., Wanger, T. C., Kremen, C., van der Heijden, M. G. A., Liebman, M., and Hallin, S. (2020). Agricultural diversification promotes multiple ecosystem services without compromising yield. *Science Advances*, *6*(45). https://doi.org/10.1126/sciadv.aba1715

The Nature Conservancy. (2021). Leading at the Edge: A Roadmap to Advance Edge of Field Practices in Agriculture. Available at https://www.nature.org/content/dam/tnc/nature/en/documents/EOF_Report_LORES_SPREADS.pdf

Tilman, D. and Clark, M. (2015). Food, Agriculture & the Environment: Can We Feed the World & Save the Earth? *Daedalus*, *144*(4), 8–23. https://doi.org/10.1162/DAED_a_00350

Tscharntke, T., Grass, I., Wanger, T. C., Westphal, C., and Batáry, P. (2021). Beyond organic farming – harnessing biodiversity-friendly landscapes. *Trends in Ecology & Evolution*, *36*(10), 919–930. https://doi.org/10.1016/j.tree.2021.06.010

Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., and Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters.* 857-874. doi: 10.1111/j.1461-0248.2005.00782.x

Tuck, S. L., Winqvist, C., Mota, F., Ahnström, J., Turnbull, L. A., and Bengtsson, J. (2014). Land-use intensity and the effects of organic farming on biodiversity: A hierarchical meta-analysis. *Journal of Applied Ecology*, *51*(3), 746–755. https://doi.org/10.1111/1365-2664.12219

Ubick, D., Paquin, P., Cushing, P. E., and Roth, V. (2017). *Spiders of North America: an identification manual.* Second edition. American Arachnological Society.

USDA National Agricultural Statistics Service. (2019). Crop Production 2019 Summary (NASS, Washington, DC). Available at https://www.nass.usda.gov/Publications/Todays_Reports/reports/cropan20.pdf

van Klink, R., Bowler, D. E., Gongalsky, K. B., Swengel, A. B., Gentile, A., and Chase, J. M. (2020). Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science*, *368*(6489), 417–420. https://doi.org/10.1126/science.aax9931

Wepprich, T., Adrion, J. R., Ries, L., Wiedmann, J., and Haddad, N. M. (2019). Butterfly abundance declines over 20 years of systematic monitoring in Ohio, USA. *PLOS ONE*, *14*(7), e0216270. https://doi.org/10.1371/journal.pone.0216270

Wills, B. D., Kim, T. N., Fox, A. F., Gratton, C., and Landis, D. A. (2019). Reducing Native Ant Abundance Decreases Predation Rates in Midwestern Grasslands. *Environmental Entomology*, *48*(6), 1360–1368. https://doi.org/10.1093/ee/nvz127

Wills, B. D. and Landis, D. A. (2018). The role of ants in north temperate grasslands: A review. *Oecologia*, *186*(2), 323–338. https://doi.org/10.1007/s00442-017-4007-0

Wittwer, R. A., Bender, S. F., Hartman, K., Hydbom, S., Lima, R. A. A., Loaiza, V., Nemecek, T., Oehl, F., Olsson, P. A., Petchey, O., Prechsl, U. E., Schlaeppi, K., Scholten, T., Seitz, S., Six, J., and van der Heijden, M. G. A. (2021). Organic and conservation agriculture promote ecosystem multifunctionality. *Science Advances*, *7*(34), eabg6995. https://doi.org/10.1126/sciadv.abg6995

Wodika, B. R., Klopf, R. P., and Baer, S. G. (2014). Colonization and recovery of invertebrate ecosystem engineers during prairie restoration. *Restoration Ecology,* 22(4) 456-464. https://doi.org/10.1111/rec.12084

CHAPTER THREE

Prairie strips and lower land use intensity increase butterfly biodiversity in row crop farms

Abstract

One third of butterfly species are currently declining and butterfly abundance across all species is declining at a rate of 2% per year. Agriculture contributes to butterfly decline through habitat loss, pollution, and climate change. Prairie strips, strips of farmland actively restored to native perennial vegetation, are a conservation practice with potential to mitigate biodiversity loss, but their impact on butterfly biodiversity is not known. Similar to other prairie restorations, the plant community of prairie strips is expected to fluctuate over the first few years after sowing, and therefore higher trophic levels, such as butterflies are also expected to fluctuate. We measured the plant and butterfly community of newly established prairie strips during the first three years of establishment in a row crop agricultural experiment that included a three-year crop rotation of wheat, maize, and soy. We also measured butterfly abundance and richness over across a broader gradient of land use intensity in the same experimental setting including conventional row crops, no till row crops, reduced input row crops with prairie strips, biologically based row crops with prairie strips, and conservation land. Butterfly abundance was higher within prairie strips than in all other treatments. Across the land use intensity gradient and at the plot level (not surveying within prairie strips), treatments with prairie strips had a higher abundance of butterflies than other row crop treatments, and the biologically based treatment which does not use pesticides had a higher abundance than the reduced input treatment. Also across entire plots, butterfly richness increased as land use intensity decreased. Treatments with prairie strips and reduced land use intensity had distinct butterfly communities, as they harbored several butterfly species that were not found in other row crop treatments. We show that prairie strips, in combination

with other crop management practices, can increase overall butterfly biodiversity by supporting unique species and increasing abundance compared to crop management treatments without prairie strips.

Introduction

Biodiversity is declining worldwide, with an estimated one million species threatened with extinction (IPBES 2019). Butterflies alone are decreasing in abundance by 2% per year, with approximately 30% of butterfly species declining (Dirzo et al. 2014, Wepprich et al. 2019, van Klink et al. 2020). In addition to their inherent value as species, butterflies are of particular conservation interest because of their high cultural value and their roles as herbivores and pollinators. Butterflies also have potential to serve as indicators of ecosystem health because they are sensitive to environmental change, they respond to more environmental qualities than vegetation such as chemicals, their ecology is well known, they can be found across the globe, and they can be monitored by scientists and non-scientists alike (Dennis et al. 2003, Thomas 2005, Fleishman & Murphy 2009).

The principal reasons for butterfly decline are habitat loss, chemical pollution, and climate change (Wepprich et al. 2019, Wagner 2021). Agriculture is a leading cause of both habitat loss and chemical pollution from pesticide and fertilizer use, which directly and indirectly result in the destruction of host plants, habitat, and nectar resources for butterflies (Wepprich et al. 2019, van Klink et al. 2020). Mitigating this loss of biodiversity is possible by diversifying monoculture agricultural landscapes into sources of food, shelter, and habitat connectivity (Kremen & Merenlander 2018), which is the focus of this study.

One conservation strategy for diversifying agricultural landscapes in the US Midwest is with prairie strips. Prairie strips are strips of farmland that are retired from production and sown with native, perennial grassland species (Schulte et al. 2017). Prairie strips are multifunctional with their abilities to reduce erosion and nutrient runoff in contoured agricultural landscapes, and support biodiversity on farms. Moreover, prairie strips can promote biodiversity without compromising yield (Kemmerling et al. in review), and farmers can be compensated for implementing prairie strips through the USDA Conservation Reserve Program (Luther et al. 2022). Prairie strips are similar to other management practices such as filter strips and hedgerows that harbor butterflies (Dover & Sparks 2000, Haaland et al. 2011, Dover 2019). While prairie strips are known to increase the prevalence of pollinators and specific species of butterflies like Monarch butterflies (Schulte et al. 2017, Kordbacheh et al. 2020, Murray 2021), the effects of prairie strips on butterfly biodiversity are not known, and is the subject of this study.

One goal of restoring prairie strips, and the approach we take in this study, is to optimize biodiversity, ecosystem services, and yield in agricultural landscapes. This differs from that of typical prairie restorations with the intent to achieve an ecosystem similar to that of reference conditions (Hallett et al. 2013). In management for prairie strips, we can draw on prairie restoration ecology theory to predict how the plant community and higher trophic levels will develop over time. Prairie restorations take several years of management before they resemble a native grassland (Kurtz 2013). During early years of establishment, the plant community and therefore higher trophic levels will fluctuate in biomass, species composition, and diversity (Camill et al. 2004, Griffin et al. 2017). Measuring the impact of prairie strips on biodiversity in their first years of establishment addresses how their structure impacts higher trophic levels and is useful for informing farmers implementing this conservation practice.

Prairie strips are not created in isolation; they are embedded within croplands that are used at different levels of intensity. Treatments in our experiment include other conservation strategies on farms such as cover crops, reduced fertilizer, and integrated pest management including reduced pesticides to mitigate loss of biodiversity. In this study, we measured how prairie strips and crop management impact butterfly biodiversity, addressing three questions. First, how do prairie strips and other agricultural management practices impact butterfly biodiversity? Second, because butterflies are dependent on the plant community for food at larval and adult life stages, how does year since establishment impact prairie strip plant community? And third, how does crop management surrounding the prairie strip impact the plant and butterfly community? We measured butterfly abundance and species richness across a gradient of agricultural management intensity including prairie strips over three years of a wheat, maize, and soy crop rotation.

Methods

Study sites

We conducted this study at the Kellogg Biological Station Long Term Ecological Research (KBS LTER) site, established in 1987, in Hickory Corners, MI USA (occupied Anishinaabe land). The climate of the KBS LTER is temperate with a 100.5 cm average annual precipitation (1981-2011 average) and a 10.1°C average annual temperature (Liang & Robertson 2021). The experiment consisted of five treatments spanning a gradient of land use intensity within the KBS LTER's Main Cropping System Experiment: conventionally managed row crops, no till row crops, reduced input row crops, biologically based row crops, and conservation land. Row crop treatments (all treatments except conservation land) are planted on a three-year rotation of maize (*Zea mays* L.), soy (*Glycine max* L.), and wheat (*Triticum aestivum* L.).

The experiment consists of 6 replicated 1 ha plots of each treatment within the same experimental landscape (plot layout in Figure 3.1 a). *Conventional* management includes tillage, no cover crops, pest management and fertilizer at rates recommended by Generally Accepted Agricultural Management Practices (GAAMP), and genetically modified crop varieties. *No till* management is the same as *conventional* except without mechanical weed management. *Reduced input* management includes tillage, cover crops, integrated pest management, 33% the rate of fertilizer compared to *conventional* and *no till*, and genetically modified crop varieties. *Biologically based* management includes tillage, cover crops, certified organic weed management through mechanical control (cultivation and tillage), no fertilizer or manure, and crop varieties that are not genetically modified. *Conservation land* – unmanaged, with the exception of annual spring burning (this is equivalent to *early successional* in earlier publications and site maps within the same experiment). The conservation land treatment is mainly grassland with peak bloom in the fall of asters and goldenrod. Additional details on management of treatments are detailed in Robertson and Hamilton (2015).

In April 2019, prairie strips were added to reduced input and biologically based treatments. Prairie strips were configured as a 4.5m strip (5% of the plot area) running the entire length through the center of the plot oriented with the rows of crops (Fig. 3.1 a). Prairie strips were implemented by sowing a mix of native prairie plant species consisting of 18 forb species and 4 grass species (Table 2.1). The seed mix is a "pollinator mix", having at least two species per bloom period (spring, summer, and fall; Isaacs et al 2009) plus Common Milkweed and Butterfly Milkweed that combined make up 2.2% of the mix. Annual ryegrass (*Lolium* sp.) and spring oats (*Avena sativa*, also an annual) were added to the seed mix to increase the seeding rate for the seeding machinery. Every prairie strip was sown with the same seed mix—the same weight and proportion of each species sourced from Native Connections in Kalamazoo, MI, USA (Table 2.1). Strips were sprayed with herbicide prior to seeding. In 2019, prairie strips were mowed three times strategically over the growing season to reduce weeds and support establishment of native seeds. In 2021, prairie strips were burned in the spring. Our study occurred in 2019 (initial year of prairie strip planting and a wheat year), 2020 (maize year), and 2021 (soy year).

Plants

We surveyed plants using quadrats counts within the prairie strips (Figure 3.1 a). All plants rooted within five 1x1m quadrats in each plot were identified to species. We measured percent cover for each plant species, and for bare ground, litter, and rocks; percent cover for each quadrat added up to 100% or greater, with a majority greater than 100% as plants overlapped each other. After the five quadrats within a plot were surveyed, we surveyed the entire strip with a single pass walkthrough to record the presence of additional species that were not captured in the quadrats. Plants were surveyed in later summer (July-September) every year.

To visualize the prairie strip plant community changes across years and across treatments, we created an NMDS (nonmetric multidimensional scaling) plot with three dimensions and using Bray-Curtis dissimilarity using data from the plant quadrat surveys. We analyzed the prairie strip plant communities across years using a PERMANOVA (permutational multivariate analysis of variance) with replicate as a blocking factor and also using Bray-Curtis dissimilarity. The NMDS plot and PERMANOVA analysis were created with the “vegan” package in R (Oksanen et al. 2020).

Butterflies

We surveyed butterflies using the Pollard Walk method, which involved weekly transect counts along one-way walking transects (Pollard 1977). Butterflies were identified to species visually, either with use of binoculars or, rarely, after capture with a net. Surveys occurred along two different transects: prairie strip transects and standard transects (Figure 3.1 a). *Prairie strip transects* (105m) were located directly adjacent to the prairie strips in reduced input and biologically based treatments for the whole length of the prairie strips (Figure 3.1 a). Observers visually identified butterflies within and above the prairie strip (4.5m wide) in front of the observer. These surveys were 8 minutes long at a slow and steady pace. *Standard transects* are permanent walking transects replicated in all plots. Standard transects (152m) were located on a walking transect throughout entire plots originally established for other purposes in conventional, no till, reduced input, biologically based, and conservation land treatments (Figure 3.1 a). Observers visually identified butterflies within 5m on both sides and above the transect in front of the observer (Figure 3.1 b). These transects were surveyed at the same walking rate as the Prairie Strip transects and were 12 minutes long. We conducted all surveys between 10:00am and 4:00pm weekly from June 2019-September 2019, June 2020-September 2020, and May-September 2021. Surveys were conducted in conditions without rain and above 15°C.

We identified individuals to species whenever possible (23 species; Table 3.1). Some groups of butterflies are difficult to identify on the wing to species, in which case the species were grouped (7 morphogroups). Spring Azures, Summer Azures, and Eastern-Tailed Blues were categorized as Blue sp. Fritillary sp. are fritillaries that could not be identified on the wing. Skipper sp. can be any skipper species found in this range except Checkered Skippers, Silver Spotted Skippers, Peck's Skippers, and Common Sootywings. Cabbage Whites were identified when possible, and undetermined Cabbage Whites were called Sulpur sp. Sulphur sp. were mainly Orange Sulphurs, Clouded Sulphurs, and Cabbage Whites that are nearly impossible to identify on the wing (we almost never observed Cloudless Sulphurs or Pink-Edged Sulphurs). Swallowtail sp. are swallowtails that could not be identified on the wing, as they tend to fly over quickly (including Black Swallowtails, Eastern Tiger Swallowtails, and Spicebush Swallowtails). Lady sp. includes American Ladies and Painted Ladies. Some individuals could not be identified to any group, for example they flew over quickly before being identified. It is likely that these individuals were of a species that had already been identified. These individuals are referred to as "unknown butterflies" in Table 3.1. These individuals were included for analyses of abundance, but were excluded from analyses of richness.

Butterfly abundance values were summed over each plot for each year. To standardize prairie strip transect surveys and standard transect surveys for comparison, we created an index of butterflies per minute by dividing abundance values per plot per year by eight (minutes) for prairie strip transect surveys and 12 (minutes) for standard transect surveys. We constructed a generalized linear mixed effects model to measure the differences in butterfly abundance among treatments and year. We used a negative binomial distribution with butterfly abundance as the response variable, crop management treatment and year as fixed effects, surveys per plot per year as an offset, and replicate as the random effect.

To measure butterfly richness across treatments, we constructed a similar model as for butterfly abundance, but we used rarefied species richness as the response variable. We rarefied butterfly richness by abundance, treating the species surveyed across a plot each year as a sample using the "iNEXT" package in R (Chao et al. 2014, Hsieh et al. 2016). Models were constructed using the R package "lme4" (Bates et al. 2015). Post-hoc analyses included an ANOVA (R package "car"; Fox & Weisbery 2019) followed by a Tukey test (R package "multcomp"; Hothorn et al. 2008). To visualize butterfly abundance and richness over the year, we plotted butterfly abundance index and butterfly richness using raw values of richness as abundance was too low to rarefy by plot per month.

Results

Plants

All plant species identified in the prairie strips across all years are listed in Table 3.2. All seeded species were present in both treatments by the second year (2020) with the exception of *Tradescantia ohiensis* and potentially *Solidago juncea* and *Solidago nemoralis* as we could not differentiate among *Solidago* species in surveys (Table 3.2). We found distinct communities among plants in prairie strips across years (R^2=0.55, p=<0.01) and across treatments (R^2=0.073, p=<0.01), which are visualized in Figure 3.2. There was also a significant interaction among year and treatment (R^2=0.071, p=<0.01), with reduced input and biologically based treatments becoming more similar to each other over time.

Annual ragweed (*Ambrosia artemisiifolia*) is historically the dominant weed in the biologically based treatment, common throughout entire plots, as that treatment is not treated with herbicides; annual ragweed is uncommon in the reduced input treatment as it is treated with herbicide. Annual ragweed was the dominant plant in the biologically based treatment in 2019, with more than double the coverage of the next most common species—*Anthemis cotula*.

Ryegrass (*Lolium* sp.) and common oat (*Avena sativa*) that were planted with the seed mix in both treatments for weed suppression and thus dominated the reduced input in the first year. By the second year, the three dominant species in the reduced input and biologically based treatments were the same: Black-eyed Susan (*Rudbeckia hirta*), red clover (*Trifolium pratense*), and Lanceleaf Coreopsis (*Coreopsis lanceolata*). Annual ragweed was the fourth most abundant in biologically based and goldenrod (Solidago sp.) was the fourth most abundant in reduced input. By 2021, ten out of twelve most abundant species in reduced input and biologically based were the same with five of them being sown species. The proportion of forbs to grasses in percent cover was 1.6 in 2019, 6.5 in 2020, and 4.1 in 2021.

Butterflies

We observed 6,835 butterflies during prairie strip transect surveys (12 plots) across 24 different species/morphogroups, and we observed 7,145 butterflies during standard transect surveys (30 plots including the 12 that contain prairie strips) across 28 different species/morphogroups. Sulphurs, Silver Spotted Skippers, and Monarchs were the most common species identified across all treatments every year (Table 3.1). Several species were identified in treatments with prairie strips that were not found in conventional or no till treatments, including Coppers (American and Bronze), Checkered Skippers, Checkered Whites, Common Sootywings, and Giant Swallowtails. Mourning Cloaks were only observed in the conservation land treatment. During standard transect surveys across the entire plots, treatments with prairie strips increased the average abundance of Monarchs by 25-222% compared to conventional and no till treatments.

Butterfly richness in the prairie strips did not differ between treatments or years and the three dominant butterfly species in all prairie strips were the same over the three years: Sulphur sp., Silver Spotted Skippers, and Monarchs. However, there was a turnover in the next most abundant species where (in descending order of abundance) Lady sp., Red Admirals, Eastern Tailed Blues, and Skipper sp. were the most common in 2019, Skipper sp., Eastern Tailed Blues, Pearl Crescents, and Tiger Swallowtails were the most common in 2020, and Eastern Tailed Blues, Pearl Crescents, Black Swallowtails, and Tiger Swallowtails were the most common in 2021. Butterfly abundance in the prairie strips also differed among years, with the highest butterfly abundance in 2020.

Butterfly abundance increased as land use intensity of crop management treatments decreased (Figure 3.3); conventional and no till treatments had the lowest abundance (a), reduced input (b), biologically based (bc), and conservation land (c) had an intermediate level of abundance, and strip surveys had the highest abundance (d) (χ^2=325.7, df=6, p<0.01). Butterfly abundance in 2019 and 2020 was higher than butterfly abundance than 2021 (χ^2=37.1, df=2, p<0.01). Butterfly richness also increased as land use intensity decreased, with conventional having the lowest richness (a), followed by no till (ab), reduced input (ac), biologically based (bc), prairie strip in the biologically based treatment (bc), conservation land (c), and prairie strips in the reduced input prairie strip (c) (χ^2=31.5, df=6, p<0.01; Figure 3.3). Butterfly richness did not vary across years (χ^2=4.8, df=2, p=0.09).

Across the growing season, butterfly abundance and richness fluctuated for each crop-year (Figure 3.4). In 2019, wheat was harvested in July, after which crop fields were mostly litter (conventional and no till) or had a red clover cover crop planted in August (reduced input and biologically based). Both richness and abundance of butterflies increased after harvest for all treatments, but treatments with prairie strips, which also have cover crops, increased further in abundance later in the season alongside the conservation land treatment. In 2020, butterfly richness and abundance in the prairie strips peaked in August across all years. This time aligns with the bloom period for the most abundant plants in the prairie strips in 2020, including Lance-leaf Coreopsis and Black-eyed Susan. From August to September 2020, there was a steep decline across all treatments, except conservation land, which is likely a result of obscured visibility as maize grew overhead. The pattern of butterfly richness and abundance across all treatments was relatively consistent across the growing season in 2021.

Discussion

A critical question for butterfly conservation is: how close does a restored patch within a field come to the conservation potential of a whole field of grassland? We asked this question for restored prairie strips in row crop agricultural fields and their effects on the biodiversity of butterflies. Across the entire 1 ha plots, of which prairie strips constituted 5% of the area, butterfly abundance in the biologically based treatment was 72% of that of conservation land (although not statistically different), and butterfly abundance in the reduced input treatment was 52% of that of conservation land. This recovers much of the biodiversity that is lost in conventional agriculture treatments (abundance 20% of the that in conservation land) and no till treatments (abundance 17% of that in conservation land). Butterfly richness did not differ among conventional, no till, and reduced input at the plot scale (Figure 3.3). However, reduced input and biologically based treatments, which both contain prairie strips, attracted several butterfly species that were not found in any other treatment. Although prairie strips did not fully recover biodiversity to levels found in conservation land, reduced input and biologically based treatments shifted strongly toward that level, harboring unique species and a greater abundance of butterflies than row crop treatments without prairie strips.

Within the prairie strips, the richness of butterflies was the same as the conservation land treatments and the entire plots of the reduced input and biologically based treatments, but there was a consistently higher abundance of butterflies in the prairie strips than in the conservation land treatment and all other treatments. This was the result of the intentional sowing of species that flower throughout the growing season in the prairie strips, whereas the conservation land treatment had a peak in bloom in later summer/early fall (Isaacs et al. 2009). Prairie strips can be managed to support particular species or ecosystem services through seed mix selection and other management practices.

The plant community of the prairie strips between the reduced input and biologically based treatments became more similar to each other over time. During the year that strips were seeded, the plant community in prairie strips was largely a result of the agricultural weeds, and these differed among treatments. Over the next two years, sown species emerged in both treatments and the plant communities grew more similar in species composition and plant cover. We expect the prairie strip plant communities to continue to shift over time toward a greater abundance of native species (Carter & Blair 2012, Bach & Kleiman 2021).

Butterfly abundance in prairie strips differed among years, with the highest butterfly abundance in 2020 when the proportion of forbs to grasses was three times higher than in 2019 and 59% higher than in 2021. Butterfly species composition in the prairie strips shifted over the three years as well, and became more similar over time. These changes in butterfly species composition and abundance were the result of local factors (prairie strip floral abundance, crop type within plots, litter cover) and landscape factors among years (crop type in the surrounding landscape) (Davis et al. 2007, Wepprich et al. 2019). As prairie strips are expected to increase in native plant species over time, in turn, butterfly communities in prairie strips are expected to concomitantly become more diverse over time (Davis et al. 2007, Griffin et al. 2017).

Butterfly abundance and richness was likely the result of both prairie strips and other crop management practices across all treatments. Treatments without herbicides and pesticides (biologically based, conservation land, and prairie strips) had the greatest butterfly richness and abundance, likely caused by the increase in floral resources throughout each plot (Rundlöf et al. 2008). The higher levels of butterfly abundance within the prairie strips suggests that the increase in butterfly abundance was not solely due to the other management practices, but also a result of the prairie strips themselves. However, the higher abundance of butterflies in the biologically based treatment than in the reduced input treatment suggests that prairie strips combined with other conservation management strategies can increase butterfly abundance on row crop farms.

Monarchs are of high conservation interest internationally due to their unique life cycle that includes a migration from Mexico to the United States and Canada. Monarchs are a leading example of the cultural value of nature to humans; in Mexico, Monarchs hold significance to indigenous cultures and serve as sources of ecotourism at their overwintering sites, and in the United States, they are the subject of school activities and inspiration for household pollinator gardens. Cultural value is a principal motivator for conservation (Díaz 2018, Doak et al. 2015) and can lead to conservation at the community level (Preston et al. 2021, Caro 2010). The ability of prairie strips to increase the abundance of Monarchs on farms may be of high value to policy or to farmers considering implementing prairie strips. Treatments with prairie strips increased the average abundance of Monarch butterflies by up to two-fold compared to other row crop treatments. This aligns with another study which found a higher abundance of Monarchs and other pollinators in farms with prairie strips than without strips (Murray 2021). Moreover, although there is concern that restoring habitat within croplands sprayed with insecticides can make prairie strips ecological traps for species, a recent study showed that pesticide levels in milkweed within prairie strips are not at harmful levels to Monarchs (Hall et al. 2022).

While prairie strips on individual farms can boost butterfly populations, landscape-scale restoration is crucial for the long-term persistence of butterfly biodiversity. Networks of connected restored grassland enhance butterfly biodiversity more than isolated fragments (Shephard & Debinski 2005). Prairie strips are a conservation practice that can be scaled up and connected across the US Midwest, with potential to increase species richness even on farms embedded in complex landscapes (Kordbacheh et al. 2020). Farmland that is consistently underperforming is of particular interest for restoration to minimize the waste of agricultural inputs (e.g., fertilizer, pesticides, etc.) and the displacement of farmland (Basso 2021). Large, connected strips and patches of prairie on marginal land across agricultural landscapes would benefit butterflies and other species and ecosystem functions with minimal effect on yield (Schulte et al. 2017, Kemmerling et al. in review).

Because of agriculture's pervasive negative effect on biodiversity, it is imperative that strategies are implemented to mitigate the further loss of butterfly biodiversity. Prairie strips are one potential management strategy for supporting butterfly biodiversity in addition to providing benefits for other species and ecosystem services. We suggest future studies examine the ability of prairie strips to support breeding populations of butterflies. And, important for the adoption of this strategy, future studies should assess the role that the presence of butterflies, or of specific species such as Monarchs, serves as motivation for implementing prairie strips on farms. Lastly, future studies should address how much habitat across agricultural landscapes is needed to conserve biodiversity at the level of a grassland while still meeting human resource needs.

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APPENDIX

Table 3.1. Pollard index (sum of the average weekly abundances over the year) of butterflies across crop management treatments. Unknown butterflies were butterflies that could not be identified in the field, for example if they flew over too quickly. These individuals are most likely species already included on this list.

		Conventional	No Till	Red. input	Bio. based	Successional	Strip - Red. Input	Strip - Bio. Based
2019								
Baltimore Checkerspot	*Euphydryas phaeton*	0	0	0	0	1	0	1
Black Swallowtail	*Papilio polyxenes*	1	4	9	6	3	5	6
Blue sp		0	0	0	0	1	0	0
Checkered White	*Pontia protodice*	0	0	0	0	0	0	2
Common Buckeye	*Junonia coenia*	1	1	3	3	3	1	0
Common Sootywing	*Pholisora catullus*	0	0	0	0	2	2	3
Eastern Tailed Blue	*Cupido comyntas*	1	1	1	7	14	7	5
Fritillary sp		0	0	0	2	0	0	0
Giant Swallowtail	*Papilio cresphontes*	0	0	0	1	0	0	1
Gray Hairstreak	*Strymon melinus*	2	1	1	4	6	0	0
Meadow Fritillary	*Boloria bellona*	0	1	0	0	0	0	0
Monarch	*Danaus plexippus*	40	71	70	113	170	56	81
Mourning Cloak	*Nymphalis antiopa*	0	0	0	0	1	0	0
Pearl Crescent	*Phyciodes tharos*	1	2	1	3	34	5	5

Table 3.1 (cont’d)

Peck's Skipper	*Polites peckius*	1	1	0	1	0	4	5
Red Admiral	*Vanessa atalanta*	18	20	27	15	11	18	11
Red Spotted Purple	*Limenitis arthemis*	0	0	0	0	0	0	2
Silver Spotted Skipper	*Epargyreus clarus*	25	23	65	51	174	137	83
Skipper sp		1	0	0	4	11	9	3
Spicebush Swallowtail	*Papilio troilus*	2	1	2	8	0	3	1
Sulphur sp		149	210	479	806	580	478	564
Tiger Swallowtail	*Papilio glaucus*	3	2	3	4	1	5	5
Lady sp		15	6	17	38	31	67	45
Variegated Fritillary	*Euptoieta claudia*	0	1	0	0	0	0	0
unknown butterflies		0	1	0	0	1	2	2
2020								
Baltimore Checkerspot	*Euphydryas phaeton*	1	0	0	1	2	0	1
Black Swallowtail	*Papilio polyxenes*	2	2	1	3	10	12	4
Blue sp		1	0	0	2	2	5	16
Checkered Skipper	*Prygus commuis*	0	0	0	1	0	0	15
Common Buckeye	*Junonia coenia*	1	1	2	3	11	5	6
Common Sootywing	*Pholisora catullus*	0	0	0	0	0	3	3
Eastern Tailed Blue	*Cupido comyntas*	1	0	2	5	13	14	27
Great Spangled Fritillary	*Speyeria cybele*	0	0	0	0	0	1	0
Monarch	*Danaus plexippus*	11	12	12	26	47	60	56
Mourning Cloak	*Nymphalis antiopa*	0	0	0	0	1	0	0

Table 3.1 (cont’d)

Pearl Crescent	*Phyciodes tharos*	2	2	2	5	15	17	13
Peck's Skipper	*Polites peckius*	0	2	1	3	4	13	12
Red Admiral	*Vanessa atalanta*	0	0	1	0	2	5	0
Red Spotted Purple	*Limenitis arthemis*	0	0	1	0	2	1	0
Silver Spotted Skipper	*Epargyreus clarus*	15	11	104	134	216	653	420
Skipper sp		3	1	9	3	20	24	22
Spicebush Swallowtail	*Papilio troilus*	0	0	3	1	3	2	0
Sulphur sp		57	47	191	340	523	1047	989
Swallowtail sp		0	1	1	0	0	1	0
Tiger Swallowtail	*Papilio glaucus*	0	4	2	8	4	18	12
Lady sp		0	1	0	1	2	8	7
Variegated Fritillary	*Euptoieta claudia*	0	0	0	0	1	0	0
Viceroy	*Limenitis archippus*	0	0	0	0	3	0	1
unknown butterflies		3	1	0	0	2	5	1
2021								
American Copper	*Lycaena phlaeas*	0	0	0	0	0	0	1
Baltimore Checkerspot	*Euphydryas phaeton*	0	0	0	0	2	1	4
Black Swallowtail	*Papilio polyxenes*	1	2	4	7	5	9	10
Blue sp		0	0	0	0	4	4	1
Bronze Copper	*Lycaena hyllus*	0	0	0	1	0	0	0
Checkered Skipper	*Prygus commuis*	0	0	4	0	0	0	0
Common Sootywing	*Pholisora catullus*	0	0	3	0	0	2	1

Table 3.1 (cont'd)

Eastern Tailed Blue	*Cupido comyntas*	1	3	7	5	27	21	22
Fritillary sp		0	0	0	0	1	0	0
Gray Hairstreak	*Strymon melinus*	1	0	0	0	1	0	0
Great Spangled Fritillary	*Speyeria cybele*	0	0	1	0	2	0	0
Monarch	*Danaus plexippus*	13	16	42	67	123	112	104
Mourning Cloak	*Nymphalis antiopa*	0	0	0	0	2	0	0
Pearl Crescent	*Phyciodes tharos*	1	0	2	4	16	17	22
Peck's Skipper	*Polites peckius*	0	0	0	0	1	1	0
Red Admiral	*Vanessa atalanta*	0	0	0	0	0	1	0
Red Spotted Purple	*Limenitis arthemis*	0	1	0	0	1	1	0
Silver Spotted Skipper	*Epargyreus clarus*	31	23	123	59	214	275	143
Skipper sp		5	3	2	3	10	5	7
Spicebush Swallowtail	*Papilio troilus*	0	0	1	3	2	3	6
Sulphur sp		51	55	208	203	387	459	440
Swallowtail sp		2	1	0	8	1	1	2
Tiger Swallowtail	*Papilio glaucus*	2	4	1	2	4	8	8
Lady sp		0	0	1	1	1	1	0
Viceroy	*Limenitis archippus*	0	2	1	3	4	10	6
unknown butterflies		3	4	5	5	7	1	3

Table 3.2. Presence/absence of plant species found in the prairie strips of each treatment in each year. A black box indicates that the species was present. * denotes a species seeded into the prairie strips. ** denotes that a species was seeded in that morphogroup and therefore could be a seeded species, but we could not decipher if it was the seeded species.

		2019		2020		2021	
Family	Species	Reduced input	Bio. based	Reduced input	Bio. based	Reduced input	Bio. based
Amaranthaceae	*Amaranthus* sp.			■		■	
	Chenopodium album	■	■	■	■	■	■
Apiaceae	*Daucus carota*		■	■	■	■	■
	*Zizia aurea**	■	■	■	■	■	■
Apocynaceae	*Apocynum cannabinum*	■	■	■	■	■	■
	*Asclepias syriaca**	■	■	■	■	■	■
	*Asclepias tuberosa**	■	■	■	■	■	■
Asteraceae	*Achillea millefolium**	■	■	■	■	■	■
	Ambrosia artemisiifolia	■	■	■	■	■	■
	Anthemis cotula	■	■	■	■	■	■
	Artemisia absinthium			■			
	Aster dumosum					■	
	*Aster novae-angliae**	■	■	■	■	■	■
	Aster sp.			■	■	■	■
	Bidens frondosa	■					

Table 3.2 (cont'd)

	Brickellia eupatorioides				■		
	Centaurea stoebe	■	■		■	■	■
	Cirsium altissimum					■	
	Cirsium arvense	■	■	■	■	■	■
	Cirsium sp.	■		■		■	■
	Cirsium vulgare			■	■	■	■
	Conyza canadensis	■	■	■	■	■	■
	*Coreopsis lanceolata**	■	■	■	■	■	■
	*Coreopsis tripteris**			■	■	■	■
	Crepis capillaris		■			■	
	*Echinacea purpurea**	■	■	■	■	■	■
	Erigeron sp.	■	■	■	■	■	■
	Euthamia graminifolia	■	■	■	■	■	■
	Hieracium sp.	■		■	■		■
	Hypochaeris radicata		■				
	Pseudognaphalium obtusifolium			■			
	*Ratibida pinnata**	■	■	■	■	■	■
	*Rudbeckia hirta**	■	■	■	■	■	■
	Senecio jacobaea					■	
	*Silphium perfoliatum**	■	■	■	■	■	■
	Solidago sp.**	■	■	■	■	■	■
	Sonchus asper		■	■			■

Table 3.2 (cont'd)

	Symphyotrichum pilosum			■	■	■	■
	Symphyotrichum sagittifolium	■	■	■	■	■	■
	Taraxacum officinale	■	■	■	■	■	■
Boraginaceae	*Hackelia virginiana*	■					
Brassicaceae	*Arabidopsis* sp.	■	■				
	Barbarea vulgaris	■	■	■	■	■	■
	Capsella bursa-pastoris	■	■			■	■
	Lepidium sp.	■	■				
Caryophyllaceae	*Dianthus armeria*			■			
	Silene latifolia				■		
	Stellaria sp.	■	■		■		
Fabaceae	*Baptisia alba*			■			
	*Desmodium canadense**	■	■	■	■	■	■
	Desmodium sp.					■	■
	Glycine max	■	■			■	
	*Lespedeza capitata**	■	■	■	■	■	■
	Medicago lupulina					■	
	Securigera varia				■	■	
	Trifolium pratense	■	■	■	■	■	■
	Trifolium repens	■	■	■	■	■	■
	Vicia sp.					■	■
Hypericaceae	*Hypericum* sp.		■	■	■	■	■

Table 3.2 (cont'd)

Juncaceae	*Juncus* sp.					■	■
Lamiaceae	*Monarda citriodora*				■		
	*Monarda fistulosa**	■		■	■	■	■
	Monarda punctata	■					
Malvaceae	*Abutilon theophrasti*	■	■	■	■	■	■
Moraceae	*Morus alba*	■					
Onagraceae	*Circaea lutetiana*	■					
Oxalidaceae	*Oxalis stricta*	■	■	■	■	■	■
Phytolaccaceae	*Phytolacca americana*		■				
Plantaginaceae	*Penstemon digitalis*						■
	Plantago lanceolata	■	■	■	■	■	■
	Plantago major	■	■	■	■	■	■
	Veronica sp.	■	■				
Poaceae	*Andropogon gerardii**	■	■	■	■	■	■
	Avena sativa	■	■				
	*Bouteloua curtipendula**		■	■	■	■	■
	Bromus sp.						■
	Dactylis glomerata	■		■	■	■	■
	Digitaria sp.		■	■	■	■	■
	Echinochloa sp.					■	
	*Elymus canadensis**	■	■	■	■	■	■
	Lolium sp.	■	■	■	■	■	■

Table 3.2 (cont’d)

	Phleum pratense		■		■	■	■
	Poa sp.	■	■	■		■	
	*Schizachyrium scoparium**	■		■	■	■	■
	Setaria sp.	■	■	■	■		■
	Sorghastrum nutans					■	■
	Triticum aestivum	■	■	■	■		■
Polygonaceae	*Fallopia* sp.						■
	Persicaria sp.	■	■	■	■		
	Polygonum aviculare	■	■	■			
	Polygonum convolvulus	■	■				
	Rumex crispus	■	■	■	■	■	■
	Rumex obtusifolius	■	■	■	■	■	■
Rosaceae	*Malus* sp.	■				■	
	Potentilla norvegica	■	■		■	■	■
	Prunus serotina	■		■			
	Prunus sp.	■					
	Pyrus sp.			■			
	Rosa sp.					■	
	Rubus sp.					■	
Sapindaceae	*Acer rubrum*	■			■		
Scrophulariaceae	*Verbascum blattaria*					■	
	Verbascum thapsus						■

Table 3.2 (cont'd)

Solanaceae	*Solanum ptychanthum*	■					
Ulmaceae	*Ulmus* sp.		■				
unknown	Aster-like seedlings	■	■				
	unknown forb 1						■
	unknown forb 2				■		
	unknown forb 3				■		
	unknown forb 4			■			
	unknown forb 5						■
	unknown forb 6					■	
	unknown grasses		■	■	■	■	■
	unknown seedlings		■		■	■	■
Verbenaceae	*Verbena hastata*	■	■		■		
	*Verbena stricta**	■		■	■	■	■
	Verbena urticifolia	■	■				
Vitaceae	*Parthenocissus quinquefolia*	■	■				
	Vitis riparia	■		■			

Figure 3.1. a. A diagram of a plot and survey locations within the plot. The transect and quadrat locations are consistent in every plot. Conventional, no till, and conservation land only have the standard transect. b. Annabelle McCarthy surveys for butterflies along a prairie strip transect. Photo taken by Jamie Smith.

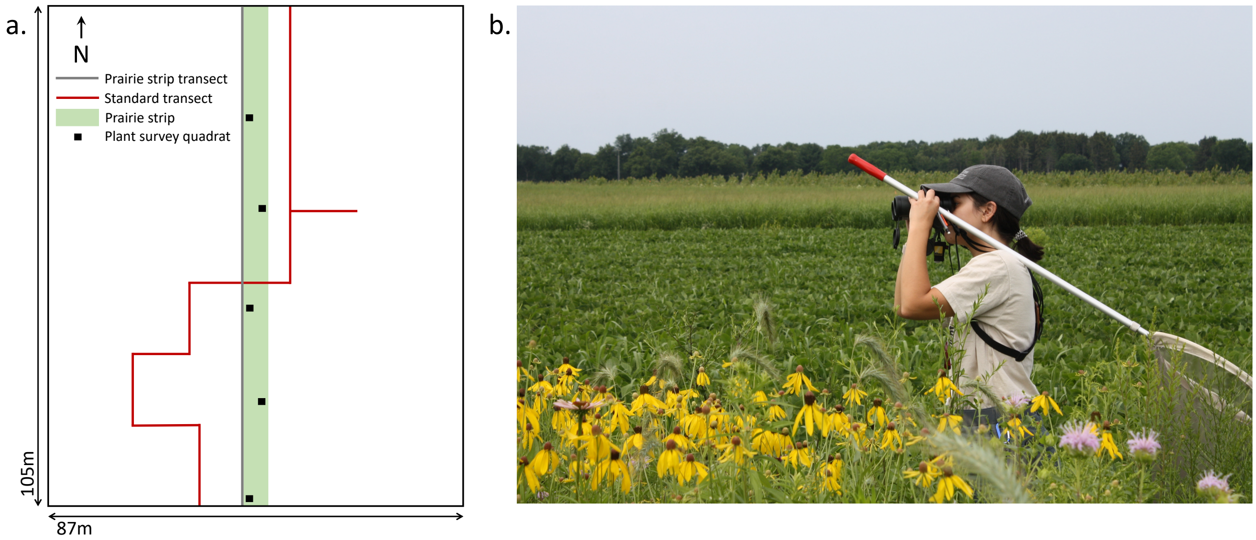


Figure 3.2. NMDS (nonmetric multidimensional scaling) plot of prairie strip plant communities across years and treatments. Each dot represents one plot per year. The ellipses represent a 95% confidence interval around the centroid of each year grouping.

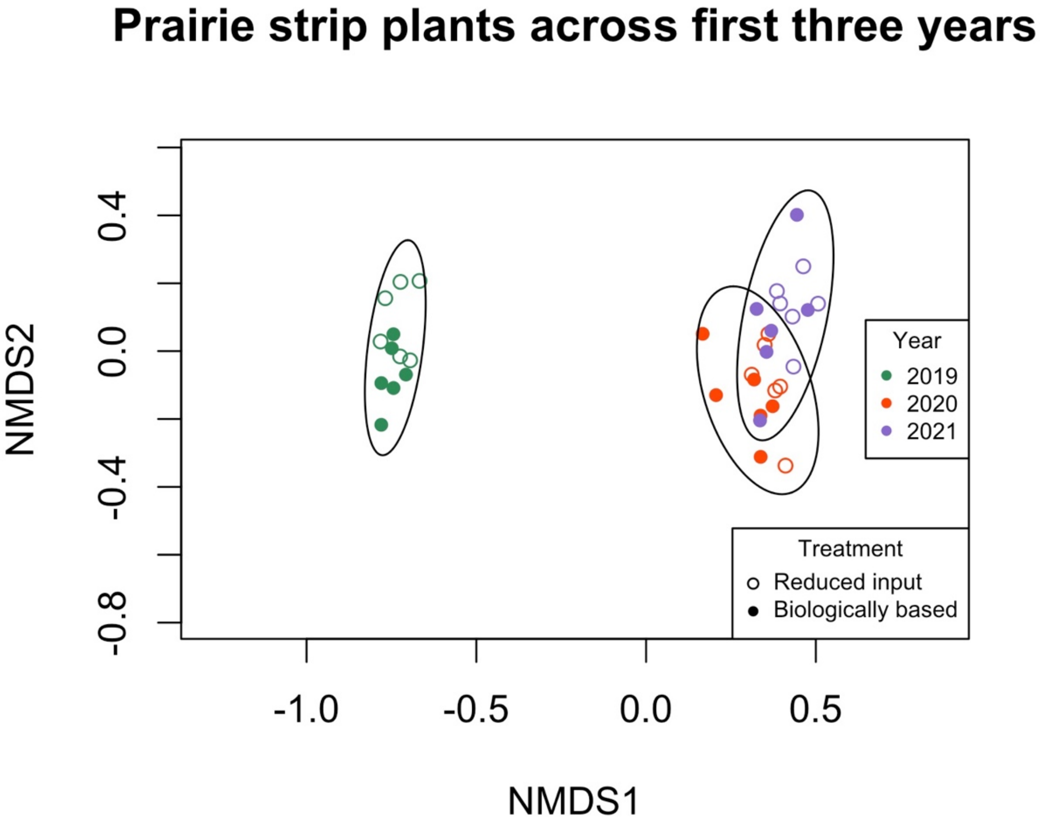


Figure 3.3. Butterfly abundance and richness indices across years for all surveys. Letters indicate significant statistical differences.

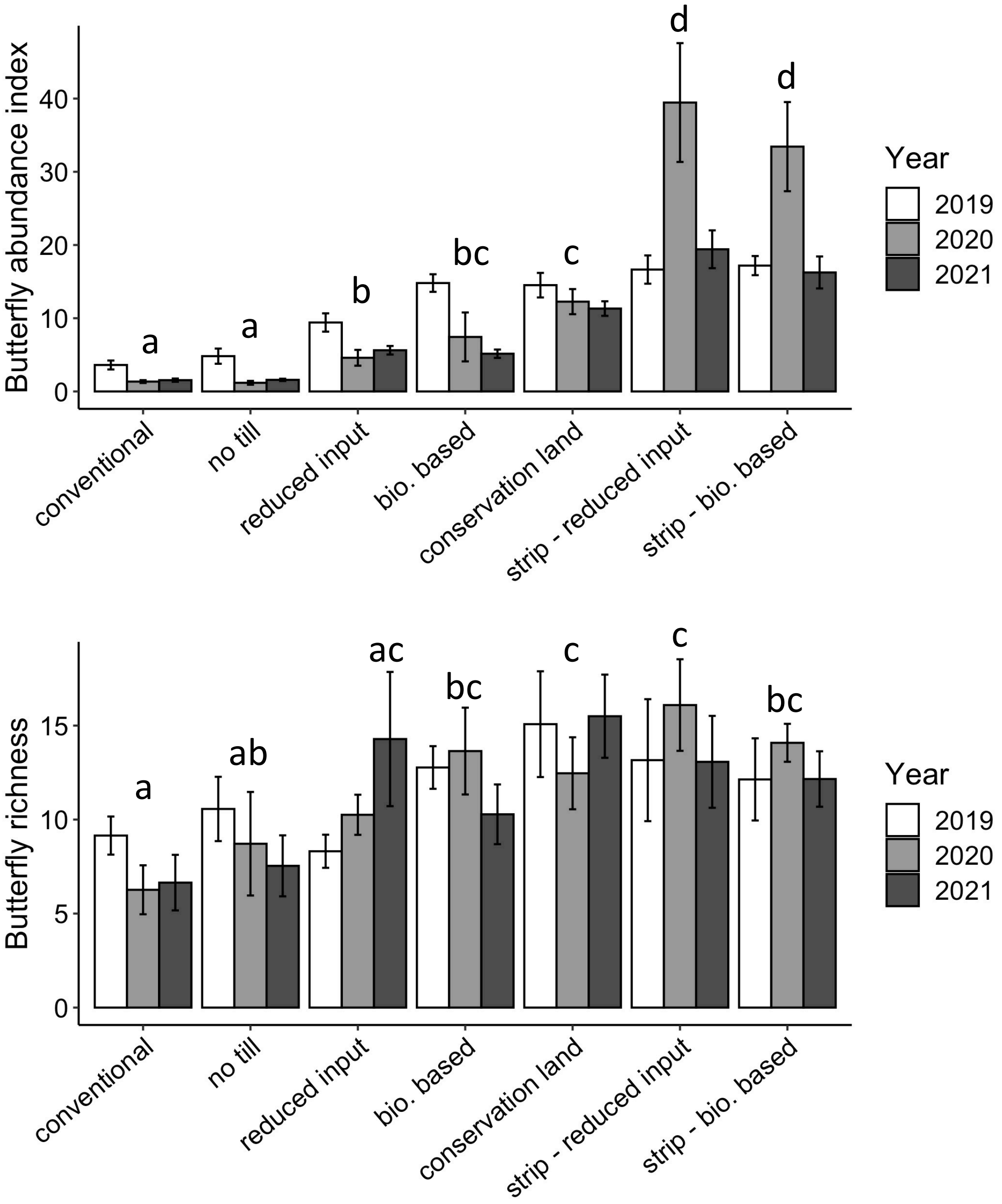
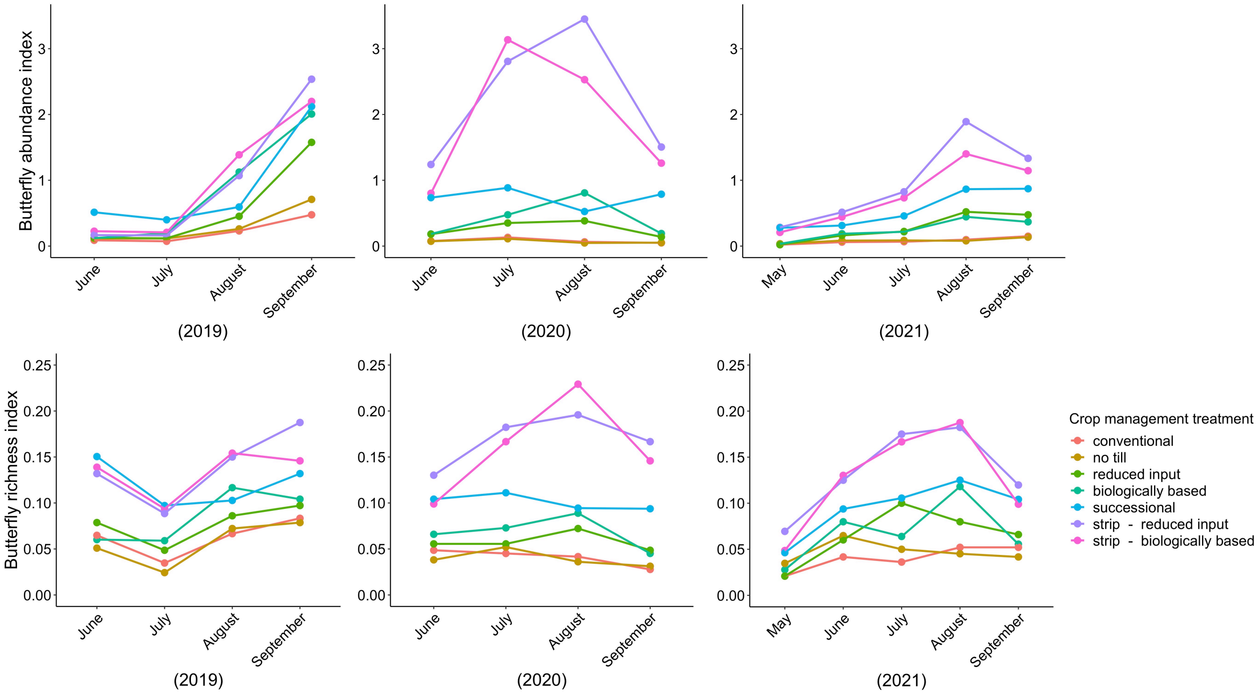


Figure 3.4. Butterfly abundance and richness across treatments each month.



LITERATURE CITED

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Bach, E. M. and Kleiman, B. P. (2021). Twenty years of tallgrass prairie restoration in northern Illinois, USA. *Ecological Solutions and Evidence*, *2*(4). https://doi.org/10.1002/2688-8319.12101

Basso, B. (2021). Precision conservation for a changing climate. *Nature Food*, *2*(5), 322–323. https://doi.org/10.1038/s43016-021-00283-z

Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1). https://doi.org/10.18637/jss.v067.i01

Camill, P., McKone, M. J., Sturges, S. T., Severud, W. J., Ellis, E., Limmer, J., Martin, C. B., Navratil, R. T., Purdie, A. J., Sandel, B. S., Talukder, S., and Trout, A. (2004). Community- and ecosystem-level changes in species-rich tallgrass prairie restoration. *Ecological Applications*, *14*(6), 1680–1694. https://doi.org/10.1890/03-5273

Caro, T. (2010). *Conservation by Proxy: Indicator, Umbrella, Keystone, Flagship, and Other Surrogate Species.* Island Press Washington, DC, USA.

Carter, D. L. and Blair, J. M. (2012). Recovery of Native Plant Community Characteristics on a Chronosequence of Restored Prairies Seeded into Pastures in West-Central Iowa. *Restoration Ecology*, *20*(2), 170–179. https://doi.org/10.1111/j.1526-100X.2010.00760.x

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., and Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs*, *84*(1), 45–67. https://doi.org/10.1890/13-0133.1

Davis, J. D., Debinski, D. M., and Danielson, B. J. (2007). Local and landscape effects on the butterfly community in fragmented Midwest USA prairie habitats. *Landscape Ecology*, *22*(9), 1341–1354. https://doi.org/10.1007/s10980-007-9111-9

Davis, J. D., Hendrix, S. D., Debinski, D. M., and Hemsley, C. J. (2008). Butterfly, bee and forb community composition and cross-taxon incongruence in tallgrass prairie fragments. *Journal of Insect Conservation*, *12*(1), 69–79. https://doi.org/10.1007/s10841-006-9063-4

Dennis, R. L. H., Shreeve, T. G., and Van Dyck, H. (2003). Towards a functional resource-based concept for habitat: a butterfly biology viewpoint. *Oikos*, 102(2), 417-426. https://doi.org/10.1034/j.1600-0579.2003.12492.x

Díaz, S., Pascual, U., Stenseke, M., Martín-López, B., Watson, R. T., Molnár, Z., Hill, R., Chan, K. M. A., Baste, I. A., Brauman, K. A., Polasky, S., Church, A., Lonsdale, M., Larigauderie, A., Leadley, P. W., van Oudenhoven, A. P. E., van der Plaat, F., Schröter, M., Lavorel, S., Aumeeruddy-Thomas, Y., Bukvarera, E., Davies, K., Demissew, S., Erpul, G., Failler, P., Guerra, C. A., Hewitt, C. L., Keune, H., Lindley, S., and Shirayama, Y. (2018). Assessing nature's contributions to people. *Science*, *359*(6373), 270–272. https://doi.org/10.1126/science.aap8826

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., and Collen, B. (2014). Defaunation in the Anthropocene. *Science*, *345*(6195), 401–406. https://doi.org/10.1126/science.1251817

Doak D. F., Bakker V. J., Goldstein B. E., and Hale B. (2015). *What Is the Future of Conservatio*n? In: Wuerthner, G., Crist, E., and Butler, T., (editors). *Protecting the Wild*. Island Press, Washington, DC. https://doi.org/10.5822/978-1-61091-551-9_4

Dover, J. W. 2019. The ecology of butterflies and moths in hedgerows and field margins. Pages 186-209 in Dover, J. W., editor. *The Ecology of Hedgerows and Field Margins*. Routledge, New York, New York, USA.

Dover, J., and Sparks, T. (2000). A review of the ecology of butterflies in British hedgerows. *Journal of Environmental Management*, *60*(1), 51–63. https://doi.org/10.1006/jema.2000.0361

Fleishman, E., and Murphy, D. D. (2009). A Realistic Assessment of the Indicator Potential of Butterflies and Other Charismatic Taxonomic Groups. *Conservation Biology*, *23*(5), 1109–1116. https://doi.org/10.1111/j.1523-1739.2009.01246.x

Fox, J. and Weisberg, S. (2019). *An R Companion to Applied Regression*, Third edition. Sage, Thousand Oaks, CA, USA. https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

Griffin, S. R., Bruninga-Socolar, B., Kerr, M. A., Gibbs, J., and Winfree, R. (2017). Wild bee community change over a 26-year chronosequence of restored tallgrass prairie: Bee communities of restored tallgrass prairie. *Restoration Ecology*, *25*(4), 650–660. https://doi.org/10.1111/rec.12481

Haaland, C., Naisbit, R. E., and Bersier, L.-F. (2011). Sown wildflower strips for insect conservation: A review: Wildflower strips for insect conservation. *Insect Conservation and Diversity*, *4*(1), 60–80. https://doi.org/10.1111/j.1752-4598.2010.00098.x

Habel, J. C., Ulrich, W., Biburger, N., Seibold, S., and Schmitt, T. (2019). Agricultural intensification drives butterfly decline. *Insect Conservation and Diversity*, icad.12343. https://doi.org/10.1111/icad.12343

Hall, M. J., Zhang, G., O'Neal, M. E., Bradbury, S. P., and Coats, J. R. (2022). Quantifying neonicotinoid insecticide residues in milkweed and other forbs sampled from prairie strips established in maize and soybean fields. *Agriculture, Ecosystems and Environment*, *325*, 107723. https://doi.org/10.1016/j.agee.2021.107723

Hallett, L. M., Diver, S., Eitzel, M. V., Olson, J. J., Ramage, B. S., Sardinas, H., Statman-Weil, Z., and Suding, K. N. (2013). Do We Practice What We Preach? Goal Setting for Ecological Restoration: Goal setting for ecological restoration. *Restoration Ecology*, *21*(3), 312–319. https://doi.org/10.1111/rec.12007

Hothorn, T., Bretz, F., and Westfall, P. (2008). Simultaneous Inference in General Parametric Models. *Biometrical Journal*, *50*(3), 346–363. https://doi.org/10.1002/bimj.200810425

Hsieh, T. C., Ma, K. H., and Chao, A. (2016). iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, *7*(12), 1451–1456. https://doi.org/10.1111/2041-210X.12613

Isaacs, R., Tuell, J., Fiedler, A., Gardiner, M., and Landis, D. (2009). Maximizing arthropod-mediated ecosystem services in agricultural landscapes: The role of native plants. *Frontiers in Ecology and the Environment*, *7*(4), 196–203. https://doi.org/10.1890/080035

Kemmerling, L. R., Rutkoski, C. E., Evans, S. E., Helms IV, J. A., Cordova-Ortiz, E., Smith, J. D., Vázquez Custodio, J. A., Vizza, C. and Haddad, N. M. (2022). Prairie strips and lower land use intensity increase biodiversity and ecosystem services. In revision.

Kordbacheh, F., Liebman, M., and Harris, M. (2020). Strips of prairie vegetation placed within row crops can sustain native bee communities. *PLOS ONE*, *15*(10), e0240354. https://doi.org/10.1371/journal.pone.0240354

Kremen, C., and Merenlender, A. M. (2018). Landscapes that work for biodiversity and people. *Science*, *362*(6412), eaau6020. https://doi.org/10.1126/science.aau6020

Kurtz, C. (2013). *A Practical Guide to Prairie Reconstruction: Second Edition.* Page 56. University of Iowa Press, Iowa City, Iowa, USA.

Leston, L., and Koper, N. (2016). Urban Rights-of-Way as Reservoirs for Tall-Grass Prairie Plants and Butterflies. *Environmental Management*, *57*(3), 543–557. https://doi.org/10.1007/s00267-015-0631-9

Liang, D. and Robertson, G. P. (2021). Nitrification is a minor source of nitrous oxide (N_2O) in an agricultural landscape and declines with increasing management intensity. *Global Change Biology*, *27*(21), 5599–5613. https://doi.org/10.1111/gcb.15833

Luther, Z. R., S. M. Swinton, and B. Van Deynze, (2022). "Potential Supply of Midwest Cropland for Conversion to In-Field Prairie Strips." *Land Economics.* (Early access Dec. 28, 2021).

Murray, C. J. (2021). *Pollinator response to prairie strips in the Iowa agricultural landscape* [Master of Science, Iowa State University]. https://doi.org/10.31274/etd-20210609-129

The Nature Conservancy. (2021). Leading at the Edge: A Roadmap to Advance Edge of Field Practices in Agriculture. Available at https://www.nature.org/content/dam/tnc/nature/en/documents/EOF_Report_LORES_SPREADS.pdf

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., and Wagner, H. (2020). vegan: Community Ecology Package. R package version 2.5-7. https://CRAN.R-project.org/package=vegan

Pollard, E. (1977). A method for assessing changes in the abundance of butterflies. *Biological Conservation*, *12*(2), 115–134. https://doi.org/10.1016/0006-3207(77)90065-9

Ries, L., Debinski, D. M., and Wieland, M. L. (2001). Conservation Value of Roadside Prairie Restoration to Butterfly Communities. *Conservation Biology*, *15*(2), 401–411. https://doi.org/10.1046/j.1523-1739.2001.015002401.x

Robertson, G. P. and S. K. Hamilton. 2015. Long-term ecological research in agricultural landscapes at the Kellogg Biological Station LTER site: conceptual and experimental framework. Pages 1-32 in Hamilton, S. K., Doll, J. E., and Robertson, G. P., (editors). *The Ecology of Agricultural Landscapes: Long-Term Research on the Path to Sustainability*. Oxford University Press, New York, New York, USA.

Rundlöf, M., Bengtsson, J., and Smith, H. G. (2008). Local and landscape effects of organic farming on butterfly species richness and abundance: Scale-dependent effects of organic farming. *Journal of Applied Ecology*, *45*(3), 813–820. https://doi.org/10.1111/j.1365-2664.2007.01448.x

Schulte, L. A., Niemi, J., Helmers, M. J., Liebman, M., Arbuckle, J. G., James, D. E., Kolka, R. K., O'Neal, M. E., Tomer, M. D., Tyndall, J. C., Asbjornsen, H., Drobney, P., Neal, J., Van Ryswyk, G., and Witte, C. (2017). Prairie strips improve biodiversity and the delivery of multiple ecosystem services from corn–soybean croplands. *Proceedings of the National Academy of Sciences*, *114*(42), 11247–11252. https://doi.org/10.1073/pnas.1620229114

Shepherd, S. and Debinski, D. M. (2005). Evaluation of isolated and integrated prairie reconstructions as habitat for prairie butterflies. *Biological Conservation*, *126*(1), 51–61. https://doi.org/10.1016/j.biocon.2005.04.021

Stivers, E. K., Wittman, J. T., and Larsen, K. J. (2019). A Comparison of Adult Butterfly Communities on Remnant and Planted Prairies in Northeast Iowa. *The Journal of the Lepidopterists' Society*, *73*(4), 268. https://doi.org/10.18473/lepi.73i4.a2

Thomas, J. A. (2005). Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *360*(1454), 339–357. https://doi.org/10.1098/rstb.2004.1585 van Klink, R., Bowler, D. E., Gongalsky, K. B., Swengel, A. B., Gentile, A., and Chase, J. M. (2020). Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science*, *368*(6489), 417–420. https://doi.org/10.1126/science.aax9931

Wagner, D. L., Grames, E. M., Forister, M. L., Berenbaum, M. R., and Stopak, D. (2021). Insect decline in the Anthropocene: Death by a thousand cuts. *Proceedings of the National Academy of Sciences*, *118*(2), e2023989118. https://doi.org/10.1073/pnas.2023989118

Wepprich, T., Adrion, J. R., Ries, L., Wiedmann, J., and Haddad, N. M. (2019). Butterfly abundance declines over 20 years of systematic monitoring in Ohio, USA. *PLOS ONE*, *14*(7), e0216270. https://doi.org/10.1371/journal.pone.0216270