ORIGINAL ARTICLE

Butterfly biodiversity increases with prairie strips and conservation management in row crop agriculture

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Abstract

1. Butterfly abundances are declining globally, with meta-analysis showing a rate of −2% per year. Agriculture contributes to butterfly decline through habitat loss and degradation. Prairie strips—strips of farmland actively restored to native perennial vegetation—are a conservation practice with the potential to mitigate biodiversity loss, but their impact on butterfly biodiversity is not known.

2. Working within a 30-year-old experiment that varied land use intensity, from natural areas to croplands (maize–soy–wheat rotation), we introduced prairie strips to less intensely managed crop treatments. Treatments included conservation land, biologically based (organic) row crops with prairie strips, reduced input row crops with prairie strips, no-till row crops and conventional row crops. We measured butterfly abundance and richness: (1) within prairie strips and (2) across the gradient of land use intensity at the plot level.

3. Butterfly abundance was higher within prairie strips than in all other treatments. Across the land use intensity gradient at the plot level, the conservation land treatment had the highest abundance, treatments with prairie strips had intermediate levels and no-till and conventional treatments had the lowest abundances. Also across entire plots, butterfly richness increased as land use intensity decreased. Treatments with prairie strips, which also had reduced land use intensity, had distinct butterfly communities as they harboured several butterfly species that were not found in other row crop treatments.

4. In addition to the known effects of prairie strips on ecosystem services including erosion control and increased water quality, prairie strips can increase biodiversity in multifunctional landscapes.

KEYWORDS
conservation, edge-of-field, hedgerows, monarch butterfly, plants, restoration, US Midwest

INTRODUCTION

Biodiversity is declining worldwide, with an estimated 1 million species threatened with extinction (IPBES et al., 2019). Insects make up a majority of species, yet little is known about their loss. Of insects, butterflies are best studied, and they are decreasing in abundance by 2% per year, with approximately 30% of butterfly species declining including both common and rare species (Dirzo et al., 2014; Forister

et al., 2021; Van Klink et al., 2020; Wepprich et al., 2019). Butterflies are best studied because their ecology is well known, they can be found across the globe and they can be monitored by scientists and nonscientists alike (Wepprich et al., 2019). Butterflies are useful indicators of status and trends of abundance and diversity of other insects (Fleishman & Murphy, 2009; Thomas, 2005; Van Klink et al., 2020) and are of conservation interest because of their high cultural value (Duffus et al., 2021) and their roles as herbivores (Ehrlich & Raven, 1964) and pollinators (Cusser et al., 2021; Winfree et al., 2011).

The primary reasons for butterfly decline are habitat loss, chemical pollution and climate change (Wagner et al., 2021; Wepprich et al., 2019). Agriculture is a leading cause of both habitat loss and chemical pollution. Habitat loss occurs directly from the transformation of habitat to agricultural land. Chemical pollution results from pesticide (including herbicide, insecticide, and fungicide) and fertiliser use. Herbicides directly destroy host plants, habitat, and nectar resources for butterflies (Habel et al., 2019; Van Klink et al., 2020; Wepprich et al., 2019). Nitrogen fertiliser indirectly destroys these resources by altering soil and plant chemistry, flora, and fauna, which subsequently decreases plant community richness (Cleland & Harpole, 2010; Haddad et al., 2000), and can also directly impact butterfly physiology and survival (Audusseau et al., 2015; Shephard et al., 2023). Mitigating this loss of biodiversity is possible by diversifying monoculture agricultural landscapes into sources of food, shelter, and habitat connectivity (Kremen & Merenlender, 2018), which is the focus of this study.

A 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), a practice that farmers can be compensated for implementing through the United States Department of Agriculture's Conservation Reserve Program (USDA CRP) practice number CP43 (USDA, 2019). Prairie strips are multifunctional with their ability to reduce erosion and nutrient runoff in contoured agricultural landscapes and support biodiversity on farms. Importantly, prairie strips can increase biodiversity and ecosystem services without disproportionately affecting crop yield (Kemmerling et al., 2022). Prairie strips are similar to other management practices such as filter strips, hedgerows, and wildflower strips that harbour butterflies (Dover, 2019; Dover & Sparks, 2000; Haaland et al., 2011; Wix et al., 2019) and could serve as a promising conservation tool for butterflies of both common and rare species (Kolkman et al., 2022). Although there is concern that restoring habitat within croplands sprayed with insecticides can make prairie strips ecological traps for species they are intended to attract, a recent study showed that pesticide levels in milkweed (Asclepias spp.) within prairie strips are not at harmful levels to monarch butterflies (*Danaus plexippus* L.) (Hall et al., 2022). While prairie strips are known to increase the prevalence of bees and specific species of butterflies like monarchs (Kordbacheh et al., 2020; Murray, 2021; Schulte et al., 2017), the effects of prairie strips on butterfly diversity are not known and are what we address here.

Our work focuses on the early establishment of plant and butterfly communities in prairie strips. Prairie strips attract butterflies through their plant community; introducing flowering plants for nectaring resources and introducing larval host plants are necessary to attract and maintain populations of Lepidoptera (Blumgart et al., 2023; Wix et al., 2019). After seeding, prairie restorations take several years of management before they resemble a native grassland and can take a range of years for seeded species and their associated species to establish and increase in abundance (Grman et al., 2015; Kurtz, 2013). During the early years of establishment, the plant community and, therefore, higher trophic levels fluctuate in biomass, species composition and diversity (Camill et al., 2004; Griffin et al., 2017). Measuring the impact of prairie strip plant communities on biodiversity in their first years of establishment addresses how their structure affects higher trophic levels and is useful for informing farmers about the rate that they can expect conservation gains from this practice.

Prairie strips are not created in isolation; they are embedded within croplands that are used at different levels of intensity. In this experiment, we test the effect of prairie strips on butterflies in the context of other conservation strategies on farms such as cover crops, reduced fertiliser and integrated pest management to mitigate loss of biodiversity. We measured how prairie strips and crop management impact butterfly diversity and address three questions: First, how do prairie strips and other agricultural management practices impact butterfly species richness and abundance? 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 composition? Third, how does management of cropland surrounding a prairie strip impact the plant and butterfly community composition? To address these questions, we measured butterfly abundance and species richness across a gradient of agricultural management intensity including prairie strips over 3 years, which included a rotation of three annual row crops.

METHODS

Study sites

We conducted this study at the Kellogg Biological Station Long Term Ecological Research (KBS LTER) site, in Hickory Corners, MI (occupied Anishinaabe land). The climate of the KBS LTER is temperate with 924 cm average annual precipitation (1988–2021 average) and 9.2°C average annual temperature (https://lter.kbs.msu.edu/datatables/7). Our work took place within an experiment created in 1989. The experiment is embedded within a landscape that includes deciduous and coniferous forests, agricultural land (maize, soy, wheat, and alfalfa), mid-successional communities, and grasslands (Robertson & Hamilton, 2015). The experiment includes five treatments that are the focus of this study, spanning a gradient of land use intensity within the KBS LTER's Main Cropping System Experiment: conventionally managed row crops with tillage, conventionally managed row crops without tillage, reduced input row crops, biologically based row crops, and conservation land. Row crop treatments (all treatments except conservation land) are planted on a 3-year rotation of maize (*Zea mays* L.), soy (*Glycine max* L.) and wheat (*Triticum aestivum* L.).

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The experiment consists of six blocks of replicated 1 ha plots of each treatment within the same experimental landscape, with treatments assigned randomly to plots within blocks (Figure 1a). Plots have received the same treatment since they were established. *Conventional* management includes tillage, no cover crops, pest management, and fertiliser at rates recommended by Generally Accepted Agricultural Management Practices (GAAMP; guidelines for farm management that are scientifically based, supported by policy and annually updated; Michigan Department of Agriculture and Rural Development, 2023) 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, reduced pesticide, herbicide, and fertiliser application compared to conventional and no-till treatments and genetically modified crop varieties. Cover crops vary over the crop rotation; a winter cover crop of red clover (*Trifolium*

pratense L.) is planted before maize; maize is followed by a ryegrass (*Lolium multiflorum* L.) cover crop, which is followed by soy. Soy is followed directly by wheat without a cover crop in between, as wheat is planted in the fall, resulting in ground cover throughout the crop rotation. *Biologically based* management includes tillage and cover crops as described for reduced input, certified organic weed management through mechanical control (cultivation and tillage), no fertiliser or manure, and crop varieties that are not genetically modified. The *conservation land* treatment is unmanaged, with the exception of annual spring burning and additional woody shrub removal (this treatment is also referred to as *early successional* in earlier publications and site maps within the same experiment). The conservation land treatment is mainly grassland with a peak bloom of asters and goldenrod in the fall. Additional details on the management of treatments are detailed in Robertson and Hamilton (2015).
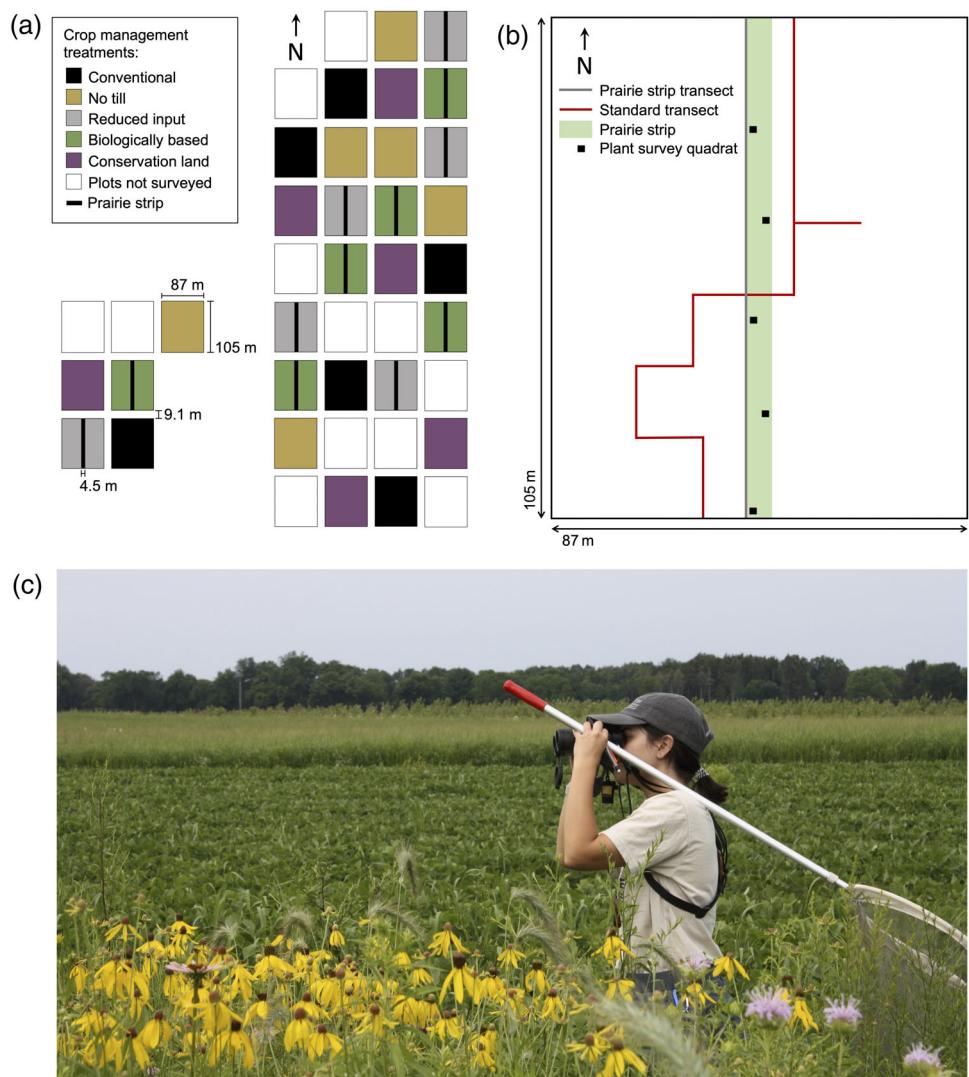
FIGURE 1 (a) A diagram of the crop management treatments within the experimental landscape. Crop rows are oriented north–south. (b) A diagram of a plot and survey locations within the plot. The transect and quadrat locations are consistent in every plot. Conventional, no-till, and conservation land only have the standard transect. (c) Annabelle McCarthy surveys for butterflies along a prairie strip transect. Photo credit: Jamie Smith.

In April 2019, prairie strips were added to reduce input and biologically based treatments. Prairie strips were configured as 4.5 m strips (5% of the plot area) running the entire length through the centre of the plots oriented with the rows of crops (Figure 1b); 4.5 m were of relevant size for our experimental landscape; however, the USDA CRP requires prairie strips to be 30+ ft (9.14 m) to qualify. Prairie strips were implemented by sowing a mix of native prairie plant species consisting of 18 forb species and 4 grass species (Table S1). The seed mix is a 'pollinator mix', having at least two flowering species per bloom period (spring, summer and fall; Isaacs et al., 2009). Annual ryegrass (Lolium sp.) and spring oats (*Avena sativa* L.), both annual species, 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 (Table S1). In July 2019 and June 2020, prairie strips were mowed strategically to reduce weeds and support the 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 within the prairie strips (Figure 1b). All plants rooted within five 1 × 1 m 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. Bare ground, litter, and rocks were removed for our analyses. After the five quadrats within a plot were surveyed, we surveyed the entire strip with a single pass walk-through 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 visualise the prairie strip plant community changes across years and across treatments, we created a nonmetric multidimensional scaling (NMDS) plot with three dimensions and used Bray–Curtis dissimilarity with data from the plant quadrat surveys. We analysed the prairie strip plant communities across years using a permutational multivariate analysis of variance (PERMANOVA) with block as a 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 by sight, with use of binoculars, or, rarely, after capture with a net. We used a local field guide (Nielsen, 1999) and supplemental online resources to confirm identification. Surveys occurred along two different transects: prairie strip transects and standard transects (Figure 1b). *Prairie strip transects* (105 m) were located directly adjacent to the prairie strips in reduced input and biologically based treatments for the whole length of a prairie strip, summing to 12 total prairie strip transects (Figure 1b). In 8-min surveys per strip, observers visually identified butterflies in a 5 m radius in front of the observer including within and above the prairie strip (Pollard, 1977). *Standard transects* are permanent walking transects replicated in all plots, summing to 30 total standard transects. Standard transects (152 m) were originally established for other purposes in conventional, no-till, reduced input, biologically based, and conservation land treatments (Figure 1b). These transects were surveyed at the same walking rate as the prairie strip transects and were 12 min long. We conducted all surveys between 10:00 AM and 4:00 PM weekly from June to September in 2019, June to September in 2020, and May to September in 2021. Surveys were conducted in conditions without rain and above 15°C.

We identified individuals to species whenever possible (23 species summed over all surveys; Table S2). Some groups of butterflies are difficult to identify on the wing to species, in which case the species were grouped (seven morphogroups summed over all surveys). Spring azure (*Celastrina ladon* Cramer), summer azure (*Celastrina neglecta* Edwards) and eastern tailed-blue (*Everes comyntas* Godart) were categorised as 'Blue sp.' 'Fritillary sp.' are fritillaries that could not be identified on the wing. 'Skipper sp.' included any skipper species found in this range except checkered-skippers (*Burnsius communis* Grote), silver-spotted skippers (*Epargyreus clarus* Cramer), Peck's skippers (*Polites peckius* Kirby) and common sootywings (*Pholisora catullus* Fabricius). Cabbage whites (*Pieris rapae* L.) were identified when possible, and undetermined cabbage whites were called 'Sulpur sp.' 'Sulphur sp.' were mainly orange sulphurs (*Colias eurytheme* Boisduval) and clouded sulphurs (*Colias philodice* Godart) that are nearly impossible to distinguish on the wing and can hybridise (Brock & Kaufman, 2006). 'Swallowtail sp.' are swallowtails that could not be identified on the wing when they flew over transects quickly, including black swallowtails (*Papilio polyxenes* Fabricius), the black form of eastern tiger swallowtails (*Papilio glaucus* L.) and spicebush swallowtails (*Papilio troilus* L.). 'Lady sp.' includes American ladies (*Vanessa virginiensis* Drury) and painted ladies (*Vanessa cardui* L.). 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 S2. These individuals were included for analyses of abundance but were excluded from analyses of richness.

Consistent with Pollard Walk methods, butterfly abundance values were summed over each transect for each year. To standardise 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 8 (min) for prairie strip transect surveys and 12 (min) for standard transect surveys. We constructed a generalised linear mixed effects model to measure the differences in

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Prairie strip plant communities across first three years

(a)

Year:
$R^2 = 0.55$
$p < 0.01$

Treatment:
$R^2 = 0.073$
$p < 0.01$

Treatment * Year:
$R^2 = 0.071$
$p < 0.01$

Year
2019
2020
2021

Treatment
○ Reduced input
● Biologically based

Prairie strip butterfly communities across first three years

(b)

Year:
$R^2 = 0.37$
$p < 0.01$

Treatment:
$R^2 = 0.03$
$p = 0.11$
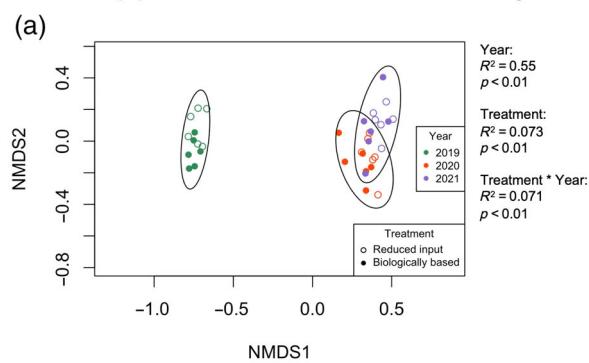
Year
2019
2020
2021

Treatment
○ Reduced input
● Biologically based
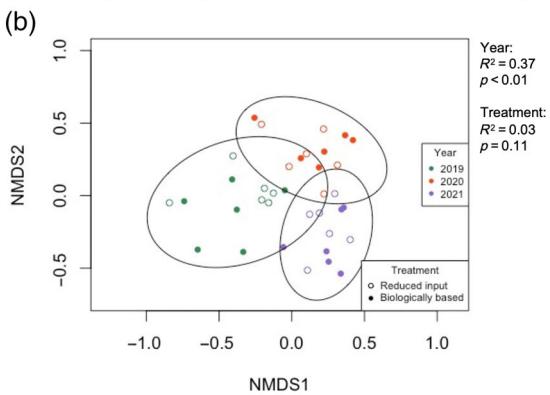
FIGURE 2 Nonmetric multidimensional scaling (NMDS) plots of (a) prairie strip plant communities and (b) prairie strip butterfly communities across years and treatments. Each dot represents one plot per year. The ellipses represent a 95% confidence interval around the centroid of each year.

butterfly abundance among treatments and years. We used a negative binomial distribution with butterfly abundance as the response variable, crop management treatment, year, and their interaction as fixed effects, surveys per plot per year as an offset, and plot within block as the random effect.

To determine butterfly richness across treatments, we constructed a similar model as for butterfly abundance, but we used rarefied species richness as the response variable and removed the interaction of the fixed effects as it was not statistically significant. 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 analysis of variance (R package 'car'; Fox & Weisberg, 2019) followed by a Tukey test (R package 'emmeans'; Lenth, 2021). Separately, we plotted the butterfly abundance index and butterfly richness using raw values of richness, as abundance was too low to rarefy by plot per month (Figure S1). We did not conclude statistical inferences from this figure but included the figure to visualise butterfly abundance and richness over the growing seasons. All plots were created using package 'ggplot' (Wickham, 2016).

To visualise the prairie strip butterfly community changes across years and treatments, we created an NMDS plot, as we did for the prairie strip plants, using the prairie strip transect survey data. We similarly analysed the prairie strip butterfly communities across years using a PERMANOVA as we did for the plants.

RESULTS

Plants

We found distinct plant communities in prairie strips across years ($R^2 = 0.55$, $p < 0.01$) and across treatments ($R^2 = 0.073$, $p < 0.01$), as visualised in Figure 2a. There was also a significant interaction between 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. All seeded species were present in both treatments by the second year (2020), with the exception of *Tradescantia ohiensis* Raf. and potentially *Solidago juncea* Aiton and *Solidago nemoralis* Aiton as we could not differentiate among Solidago species in surveys (Table S3). All plant species identified in the prairie strips across all years are listed in Table S3, as well as the butterfly species for which they serve as a larval host.

Annual ragweed (*Ambrosia artemisiifolia* L.) was the dominant plant in the biologically based treatment in 2019, with more than double the coverage of the next most common species—stinking chamomile (*Anthemis cotula* L.). Annual ragweed 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. Ryegrass (Lolium sp.) and common oat (*A. sativa* L.) that were planted with the seed mix in both treatments for weed suppression dominated the reduced input treatment in the first year, but not the biologically based treatment, likely due to the aforementioned agricultural weeds. By the second year, the three dominant species in the reduced input and biologically based treatments were the same: black-eyed Susan (*Rudbeckia hirta* L.), red clover (*T. pratense* L.) and lanceleaf coreopsis (*Coreopsis lanceolata* L.). The fourth most abundant species in the biologically based treatment was annual ragweed and in the reduced input treatment was goldenrod (Solidago sp.). By 2021, 10 out of the 12 most abundant species in reduced input and biologically based treatments 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

In the 12 plots with prairie strip transect surveys, we observed 6835 butterflies that included 24 different species/morphogroups. In the 30 plots with standard transect surveys (12 of which have prairie strips), we observed 7145 butterflies across 28 different species/morphogroups. Every year, and across all treatments, sulphurs, silver-
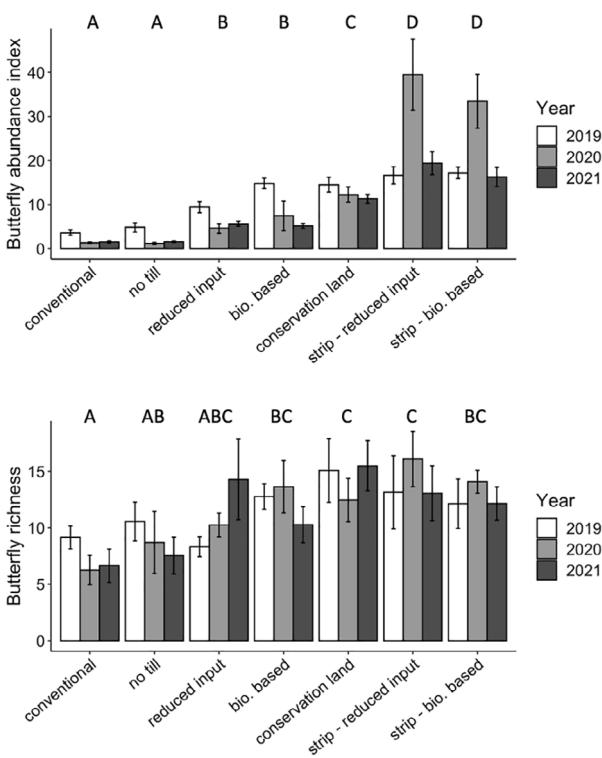
FIGURE 3 Butterfly abundance and richness indices across years for all surveys. Letters indicate significant statistical differences. Error bars represent SE.

spotted skippers and monarchs were the most common species identified (Table S2). Several species were identified in treatments with prairie strips that were not found in conventional or no-till treatments, including an American copper (*Lycaena phlaeas* L.) and a bronze copper (*Lycaena hyllus* Cramer), checkered-skippers (*Pyrgus communis* Grote), checkered whites (*Pontia protodice* Boisduval & Le Conte), common sootywings, and giant swallowtails (*Papilio cresphontes* Cramer). Mourning cloaks (*Nymphalis antiopa* L.) 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 with 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 3 years: sulphur sp., silver-spotted skippers, and monarchs. However, there was turnover in the next most abundant species (in descending order of abundance); in 2019, lady sp., red admirals, eastern tailed-blues, and skipper sp. were the most common; in 2020, skipper sp., eastern tailed-blues, pearl crescents (*Phyciodes tharos* Drury), and eastern tiger swallowtails were the most common; and in 2021, eastern tailed-blues, pearl crescents, black swallowtails and eastern tiger swallowtails were the most common. Butterfly abundance in the prairie strips differed among years, with the highest butterfly abundance in 2020. We found distinct communities among butterflies in prairie strips across years ($R^2 = 0.37$, $p < 0.01$) but not across treatments ($R^2 = 0.03$, $p = 0.11$; Figure 2b).

Butterfly abundance increased as land use intensity of plot-level treatments decreased (Figure 3); conventional and no-till treatments had the lowest abundance, followed by reduced input and biologically based, then conservation land. The prairie strip surveys had the highest abundance ($\chi^2 = 91.6$, df = 6, $p < 0.01$). Butterfly abundances in 2019 and 2020 were higher than butterfly abundance in 2021 ($\chi^2 = 81.8$, df = 2, $p < 0.01$). There was a significant interaction between butterfly abundance and year ($\chi^2 = 158.7$, df = 12, $p < 0.01$; Figure S2). In the standard transects, butterfly abundance was highest in 2019. In the prairie strip transects, butterfly abundance peaked in 2020. Butterfly richness also generally increased as land use intensity decreased, with conventional and no-till having the lowest richness, and higher levels in all other treatments ($\chi^2 = 31.5$, df = 6, $p < 0.01$; Figure 3). Butterfly richness did not vary across years ($\chi^2 = 4.9$, df = 2, $p = 0.09$). We note that due to visual identification, we had to lump some species together for accuracy, which could affect the estimates of richness. However, we do not expect our groupings to affect richness differences among treatments.

Butterfly abundance and richness fluctuated across the growing season each year (Figure S1). 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; treatments with prairie strips, which also have red clover cover crops, increased further in abundance later in the season as did 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 lanceleaf coreopsis and black-eyed Susan. From August to September 2020, there was a decline in abundance and richness across all treatments, except conservation land, which was likely a result of obscured visibility as maize grew overhead. The temporal patterns of butterfly richness and abundance across all treatments were relatively consistent across the growing season in 2021.

DISCUSSION

We found that prairie strips attracted much of the butterfly community that is otherwise lost when conservation areas are converted to agriculture. We found that when 5% of plots were converted from row crops to prairie strips, butterfly abundance in the biologically based treatment was 83% of that of the conservation land treatment, and butterfly abundance in the reduced input treatment was 72% of that of the conservation land treatment. This recovers much of the biodiversity that is lost in conventional agriculture treatments (where abundance is 26% of that in conservation land) and no-till treatments (where abundance is 30% of that in conservation land). 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 species richness at the plot level to levels found in conservation land, reduced

input and biologically based treatments shifted strongly towards that level, harbouring unique species and a greater abundance of butterflies than row crop treatments without prairie strips.

Within the prairie strips, butterfly richness was the same as the conservation land treatment and the entire plots of the reduced input and biologically based treatments. In addition, butterfly abundance was consistently higher in the prairie strips than in the conservation land treatment and all other treatments. This was the result of intentionally sowing species in the prairie strips that flower throughout the growing season, 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. Whereas typical prairie restorations have the intent to achieve an ecosystem similar to that of reference conditions (Hallett et al., 2013), a goal of restoring prairie strips, and the approach we take in this study, is to optimise biodiversity, ecosystem services, and yield in agricultural landscapes.

The plant communities of the prairie strips in the reduced input and biologically based treatments became more similar to each other over the 3 years of our study. During the year that strips were seeded, the plant community in prairie strips was largely determined by the agricultural weeds, and these differed among treatments. Over the next 2 years, sown species emerged in both treatments, and the plant communities grew more similar in species composition and plant cover. Flowering plant cover peaked in the second year when the showy, large, flowering forbs black-eyed Susan and lanceleaf coreopsis became dominant. We expect the prairie strip plant communities to continue to shift over time towards a greater abundance of native species (Bach & Kleiman, 2021; Carter & Blair, 2012).

Butterfly abundance in prairie strips differed among years, with the highest butterfly abundance in 2020 when the proportion of forbs to grasses within the prairie strips was three times higher than in 2019 and 59% higher than in 2021. Butterfly species composition in the prairie strips shifted over the 3 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, and litter cover), landscape factors among years (crop type in the surrounding landscape), and annual variation (precipitation, temperature; Davis et al., 2007; Wepprich et al., 2019; Wix et al., 2019). As prairie strips are expected to increase in native plant species over time and as seeded species mature and flower, the butterfly communities in the prairie strips are expected to concomitantly become more diverse (Davis et al., 2007; Griffin et al., 2017). Such was the case in decade old strips in Wallonia, Belgium, signifying the importance of maintaining these conservation practices in agricultural landscapes over the long term (Kolkman et al., 2022). We will be able to measure this in our experiment as we continue to survey plants and butterflies in these plots.

The values of butterfly abundance and richness we measured were likely the result of both prairie strips and other crop management practices across all treatments. Treatments with reduced or no pesticides (reduced input, biologically based, conservation land, and

prairie strips) had increased butterfly richness and abundance, likely caused by the increase in floral resources throughout each survey area (Rundlöf et al., 2008). However, the higher levels of butterfly abundance within the prairie strips suggest that the increase in butterfly abundance at the plot level was not solely due to the other management practices but also a result of the prairie strips themselves. Prairie strips combined with other conservation management strategies can be implemented to increase butterfly biodiversity on row crop farms.

More than one third of plant species present in these prairie strips have the ability to serve as the larval host for one or more butterfly species that we observed in the prairie strips, in addition to the abundance of general nectaring resources the flowering plants provide. There were also instances of plant species present that are larval host plants for butterflies, but of which the butterfly species that they host were not observed. For example, Digitaria sp. was present, but we did not observe any little wood satyrs (Megisto cymela Cramer), which feed on Digitaria sp. (Scott, 1986). If the species is not limited by patch size or other environmental characteristics, there is potential for those butterfly species to establish in the future. The butterfly species we observed were relatively common and highly mobile (Burke et al., 2011), which can seek out new resources more easily and at greater distances than less mobile species. Longer term surveys should assess if rarer butterfly species or prairie specialists can establish in prairie strips.

Most individual butterflies we observed were not just flying over, but interacting with the prairie strips in some way, for example, nectaring or sunning. With many of their host plants present in the prairie strips, there is potential for observed individuals to have carried out their life cycle in the prairie strips; however, the extent of their interaction with the prairie strips was not tested. While we assessed prairie strips impact on adult butterflies, the intentional addition of host plants may better support other life stages and breeding populations of butterflies. We suggest that future studies examine the ability of prairie strips to support host plants of both common and rare butterflies, as butterfly host plants could be selected for inclusion in seed mixes to better support particular species. In addition, while there is currently no evidence that prairie strips act as ecological traps, this potential should also be considered.

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 that found a higher abundance of monarchs and other pollinators in farms with prairie strips than without strips (Murray, 2021). Beyond its biological significance, the increased abundance of monarchs has cultural and aesthetic values, which can support prairie strip adoption. Monarchs are the butterfly species with possibly the highest conservation value internationally due to their unique life cycle that includes migration from Mexico to the United States and Canada. Monarchs are a leading example of the cultural value of nature to humans; monarchs hold significance to indigenous cultures, serve as sources of ecotourism, are the subject of learning and creative activities, and are the inspiration for pollinator restorations. Cultural value is a principal motivator for conservation (Díaz et al., 2018; Doak et al., 2015) and can lead to

conservation at the community level (Caro, 2010; Preston et al., 2021). 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.

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 (Shepherd & Debinski, 2005). Prairie strips are a conservation practice that can be scaled up and connected across the US Midwest, with the potential to increase species richness even on farms embedded in complex landscapes (complex landscapes are defined as those having greater than 20% non-crop area; Kordbacheh et al., 2020). Farmland that is consistently underperforming—marginal land—is of particular interest for restoration to minimise the waste of agricultural inputs (e.g., fertiliser, pesticides, etc.) and the displacement of farmland (Basso, 2021). 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 (Kemmerling et al., 2022; Schulte et al., 2017) and should be the focus of future research and policy. Considering other landscape features such as connectivity and proximity to source populations will maximise the potential for prairie strips to benefit biodiversity (Hussain et al., 2023).

Furthermore, important for the adoption of this strategy, future studies should assess the role that the presence of butterflies, or specific species such as monarchs, serves as motivation for implementing prairie strips on farms. Several federally administered programs in the United States (e.g., USDA CRP, the Clean Lakes, Estuaries and Rivers Initiative [CLEAR], the Conservation Reserve Enhancement Program [CREP] and the Environmental Quality Incentives Program [EQIP]) and non-governmental organisations (e.g., Tallgrass Prairie Center, IA; Sand County Foundation, WI; Missouri Prairie Foundation, MO; University of Nebraska-Lincoln, NE; and MiSTIRIPS, MI) already recognise prairie strips as an eligible conservation practice and provide pathways for prairie strip implementation. We recommend the continued support of farmers in implementing prairie strips as a conservation practice, providing new evidence for their benefits to butterflies.

Because of agriculture's pervasive negative effects on biodiversity, it is imperative that conservation strategies are implemented on farms to mitigate further biodiversity loss. Prairie strips are one management strategy to support butterfly biodiversity in addition to providing benefits for other species and ecosystem services. Although large, connected landscapes are the gold standard for conservation, we show that small amounts of farmland restoration can have outsized effects on butterfly conservation without disrupting food production.

AUTHOR CONTRIBUTIONS

Lindsey R. Kemmerling: Conceptualization; investigation; funding acquisition; writing – original draft; methodology; validation; visualization; writing – review and editing; formal analysis; data curation; supervision. **Annabelle C. McCarthy:** Investigation; writing – review and editing; visualization; formal analysis. **Cameron S. Brown:** Investigation; writing – review and editing. **Nick M. Haddad:** Conceptualization; investigation; funding acquisition; writing – review and editing; validation; methodology; project administration; supervision; resources; formal analysis; visualization.

ACKNOWLEDGEMENTS

CONFLICT OF INTEREST STATEMENT

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be considered a potential conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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PRAIRIE STRIPS INCREASE BUTTERFLY BIODIVERSITY IN ROW CROP FARMS

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Butterfly abundance and richness across treatments each month.

Figure S2. Butterfly abundance index across years for all surveys. Letters indicate significant statistical differences for the interaction between treatment and year effects. Error bars represent SE.

Table S1. Native plant species sowed to create prairie strips (modified from Kemmerling et al., 2022). * indicates potential butterfly host plant for species in the area of this study (Brock & Kaufman, 2006; Scott, 1986, supplementary searches on iNaturalist). All seeded forb species are potential nectaring sources for butterflies.

Table S2. 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.

Table S3. Plant species found in the prairie strips of each treatment in each year, and the butterfly species for which they can serve as a larval host. 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.

How to cite this article: Kemmerling, L.R., McCarthy, A.C., Brown, C.S. & Haddad, N.M. (2023) Butterfly biodiversity increases with prairie strips and conservation management in row crop agriculture. *Insect Conservation and Diversity*, 1–10. Available from: https://doi.org/10.1111/icad.12675