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Research paper

Contour prairie strips alter microbial communities and functioning both below and in adjacent cropland soils

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ABSTRACT

Prairie strips are narrow strips of native, perennial vegetation (10–40 m width) integrated within cropped fields to provide benefits for water quality and biodiversity. However, the impact of prairie strips on soil microbial communities and function, both underneath the prairie strips and in the adjacent cropland, is not known. We assessed the effect of restoring native perennial vegetation on soil C and N, potential enzyme activities (PEA), and microbial community composition in the soil directly underneath and cropland adjacent (0.1 to 9 m) to 12-year-old prairie strips integrated within row crop fields. We found that prairie strips consistently increased soil microbial biomass carbon (>56 %) and altered PEA in complex ways. Generally, prairie strips increased hydrolase and decreased oxidoreductase PEA. Prairie strips also changed the soil microbial community directly under prairie vegetation, and, contrary to the expectation that greater plant diversity leads to greater soil microbial diversity, prairie strips reduced bacterial and fungal diversity. The prairie strip's effect on adjacent cropland soils depended on year, but it was strong when it occurred and was typically independent of distance from the prairie strip. Prairie strips increased PEA in adjacent soils (<9 m) by as much as 38 % and shifted bacterial and fungal beta diversity, but neither showed patterns with distance from the prairie strip, indicating that prairie strips cause field-scale shifts in soil biota and functioning, and these effects are not mediated by proximity to the prairie strip. Understanding the mechanisms underlying prairie strips' impact on soil biota, both underneath and adjacent to the prairie, is key to optimize their agroecosystem benefits.

1. Introduction

While intensive agriculture has steadily increased the per-hectare productivity of most grain crops (Cassman and Grassini, 2020), it has come with consequences, including the degradation of soil ecosystem services (SESs) regulated by soil biota (Baldwin-Kordick et al., 2022; Gerla, 2007). To restore biota-driven SESs and maintain economic viability of agroecosystems, we must find ways to regenerate soil health while maintaining or increasing crop productivity. In the Midwest US, restoring native, perennial vegetation is one effective approach to regenerate SESs (Bach and Hofmockel, 2015; Baer et al., 2002; De et al., 2020; McLauchlan et al., 2006). Despite the known improvement in SESs, converting entire fields from annual cropland to perennial grassland is often not economically feasible for individual growers, nor can it meet the global demand for agricultural products.

Integrating prairie strips into cropland is a new conservation practice that offers both the environmental benefits of grassland restoration and the economic benefits of crop production. Instead of taking an entire field out of production, prairie strips are narrow strips of diverse perennial grasses and forbs (10–40 m width and <25 % of the field) integrated into agricultural fields to slow overland water flow and minimize sediment and nutrient losses from fields (Fig. 1). Prairie strips disproportionately benefit ecological function at the catchment scale (Schulte et al., 2017). For example, prairie strips occupying as little as 10 % of a given catchment can: reduce sediment export by up to 95 % (Helmers et al., 2012; Schulte et al., 2017), reduce total water runoff by up to 29–44 % (Gutierrez-Lopez et al., 2014; Hernandez-Santana et al., 2013), increase plant diversity up to 380 % and increase wildlife abundance and activity by up to 150–288 % (Hirsh et al., 2013; Schulte et al., 2016).

In addition to these catchment-scale benefits, prairie strips should also enhance SESs in the soil directly underneath, similar to large swaths of native, perennial vegetation. Specifically, restoring perennial grasslands increases microbial biomass (Bach and Hofmockel, 2015; Li et al.,

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2018), increases microbial activity measured as respiration or potential enzyme activities (PEA; Bach and Hofmockel, 2015; Raiesi and Salek-Gilani, 2018), reduces mobile nitrate-nitrogen (N; Baer et al., 2002; Karlen et al., 1999), increases labile C (De et al., 2020; Hurisso et al., 2014), and increases soil organic C (Li et al., 2017; Munson et al., 2012; Pérez-Suárez et al., 2014). These biochemical measurements often coincide with measures of larger and more stable aggregates (Jastrow, 1996), reduced nutrient leaching (Daigh et al., 2015), and lower greenhouse gas emissions (Oates et al., 2016).

Like larger prairie or grassland restoration studies, prairie strips will also alter the soil microbial community composition under the perennial, native vegetation. Over time, the soil microbial communities in restored prairies increasingly resemble those of remnant prairie during the first several years of establishment, and prairie strip communities may follow a similar trajectory (Barber et al., 2017). Restoring prairie vegetation has been shown to increase bacterial diversity in some cases (Bach et al., 2018; Upton et al., 2018), but in other cases, soil bacterial diversity declines as perennial restorations become older and more established (Barber et al., 2017).

While the effects of restored perennial vegetation might be strongest on the underlying soil, the benefits of prairie strips may also extend beyond, causing a “spillover effect” into the adjacent cropland. Indeed, more motile organisms like insects can move between habitats when prairie is integrated into cropland (Kemmerling et al., 2022), but the extent to which this may apply to other, less-motile soil biota is unclear. One line of reasoning is that a landscape comprised of varied habitat types can serve as an important source for microbial colonizers that would otherwise be absent from a disturbed, simplified landscape of annual crops (Mony et al., 2022; Bell and Tylianakis, 2016). Prairie strips could provide a habitat source or refuge by providing a reservoir of novel prairie taxa, especially closer to the strip. In addition, prairie strips have already been shown to alter the adjacent cropland soil environment (Dutter et al., 2023; Fig. S1). More specifically, prairie strips have been shown to decrease soil water content, decrease nitrate, and accumulate plant-available phosphorus and potassium in cropland soils up to 9 m distance from the native, perennial vegetation (Dutter et al., 2023). And this, in turn, would likely impact soil biota in the adjacent cropland (Senaviratne et al., 2012); especially cropland soil closer to the prairie strip (Hargreaves et al., 2015).

Alternatively, prairie strips may not affect adjacent cropland soil biota because the intensity of cropland management as an “environmental filter,” and may preclude any influence of the prairie strip on cropland soil biota. Many soil microbes are limited in movement, or rely on the movement of air, water, fungal hyphae, and microbivores to migrate (Choudoir et al., 2018; Chaudhary et al., 2020; van Elsas et al., 1991; Warmink et al., 2011; Coleman and Wall, 2015). Cropland management is also likely to prevent soil biota from growing and surviving, even if dispersed from the prairie strip. Tillage, agrochemical applications, harvest, and other management practices are known to have strong effects on soil microbial community composition, alter SESs (Manzoni et al., 2012; West and Whitman, 2022; Fierer and Jackson, 2006; Schmidt et al., 2018), and be stronger drivers than dispersal limitation (Jones et al., 2022). This management-induced environmental filter may generate two distinct soil habitats - prairie and cropland - rather than a gradual integration of prairie and cropland soil biota at the habitat edges.

Fig. 1. Overhead photograph of prairie strip planted in a soybean field in Eastern Iowa, USA.
Photo Credit: Iowa State University.

Our primary research objectives were to quantify prairie strips' effect on soil microbial biomass, PEA, and microbial community composition and diversity under the prairie strips and in the adjacent cropland (< 9 m). We hypothesize that prairie strips will 1) increase microbial biomass, PEA, and bacterial and fungal diversity under the prairie strip as has been observed in larger grassland and prairie restorations (Bach and Hofmockel, 2015; Bach et al., 2018; Upton et al., 2018); and 2) have little-to-no effect on adjacent cropland soil microbial biomass, PEA, and bacterial and fungal diversity because cropland management will be a strong environmental filter of the microbial community (Manzoni et al., 2012; West and Whitman, 2022; Fierer and Jackson, 2006; Schmidt et al., 2018; Jones et al., 2022), and because of previous inconsistent effects of prairie strips on cropland soil moisture and plant-available nutrients (Dutter et al., 2023). Measuring the direct and indirect effects of prairie strips on soil biota and SESs is critical for understanding how the practice impacts long-term agroecosystem sustainability.

2. Materials and methods

2.1. Site description and experimental design

The study was located on the Neal Smith National Wildlife Refuge (NSNWR; 41° 33′ N;93°16′ W), a 3000-ha mosaic of forest, remnant prairie, restored prairie, and cropland managed by the U.S. National Fish and Wildlife Service. NSNWR is in the Walnut Creek watershed in Jasper County, Iowa, which lies on the Iowa southern drift plain (Major Land Resource Area 108C; USDA Natural Resources Conservation Service, 2006). This area consists of steep rolling hills of Wisconsinan loess on pre-Illinoian till (Prior, 1991). The soils within the catchments which we are studying prairie strips are classified as Ladoga (Mollic Hapludalf) or Otley (Oxyaquic Argiudolls) soil series with 5 to 14 % slopes and are highly erodible (Nestrud and Worster, 1979; Soil Survey Staff, 2003). The 50-year mean (± standard deviation) annual precipitation is 876 ± 205 mm, and the mean annual temperature is 9.6 ± 0.9 °C.

In 2007, a catchment-scale prairie strip experiment was established within NSNWR. Prairie strip and control catchments were arranged in a randomized, balanced, incomplete block design on 12 catchments ranging in size from 0.47 to 3.2 ha. Prairie strips were planted such that the prairie covered 0 % (control), 10 %, and 20 % of the catchment area, and the prairie was established within the cropland (usually shoulder or backslope contour position) and at the foot slope of the catchments (Zhou et al., 2010). Before 2007, these fields were in smooth brome (*Bromus inermis* L) cover for at least ten years. Prairie strips were seeded with a tallgrass prairie seed mix containing 32 species in 2007. The seed mix consisted of 27 % grasses, 24 % forbs, 5 % weedy forbs and weedy grasses, and 44 % inert material by weight. Since 2007, after the prairie strip establishment, the adjacent cropland was planted in a soybean (*Glycine* max (L.) Merr.) and maize (*Zea mays* L.) rotation with no-till

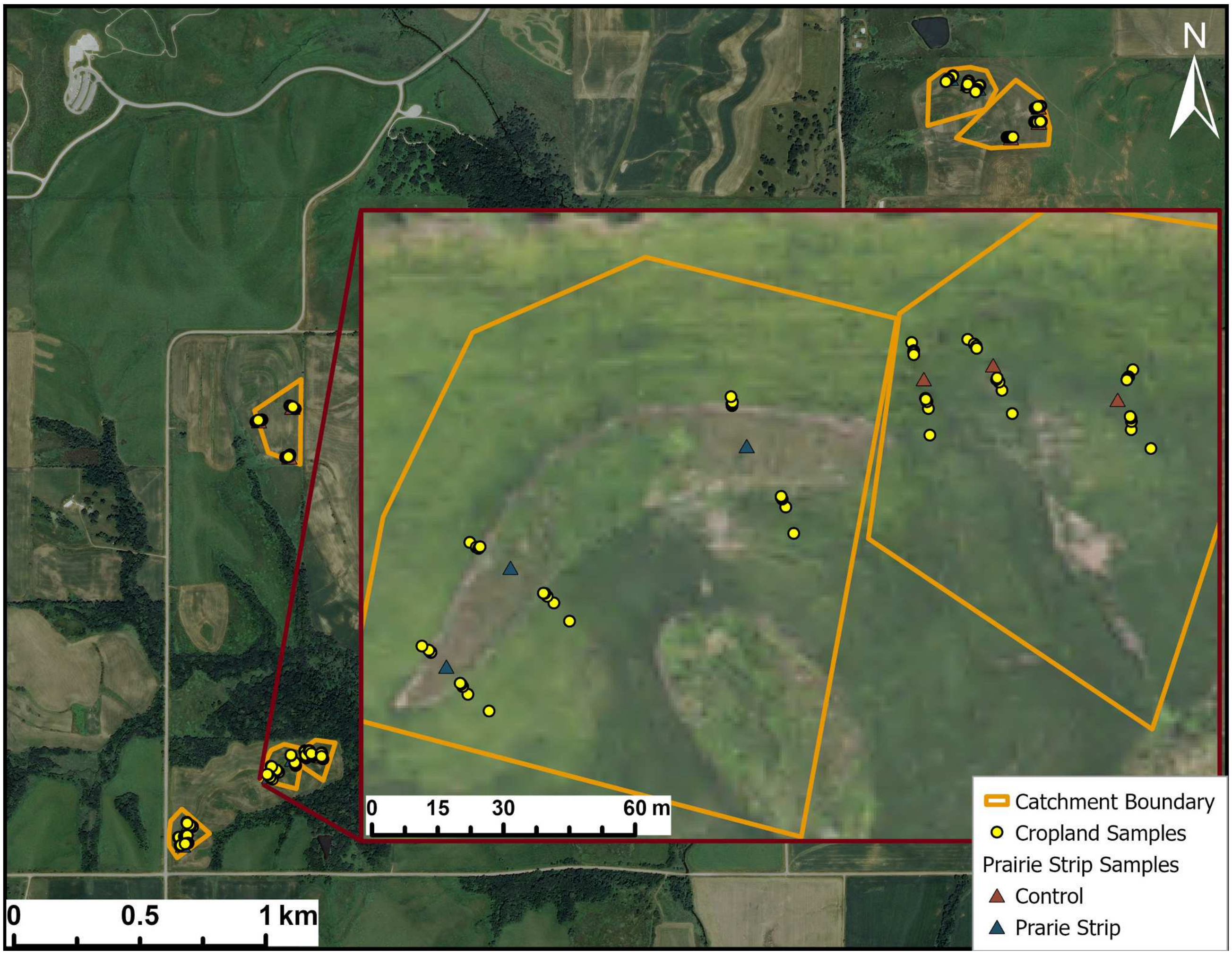

Fig. 2. Map of prairie strip ($n = 3$) and control catchments ($n = 3$) and transects ($n = 3$) with measurements at −3, −1, −0.3, −0.1, 0.1, 0.3, 1, 3, and 9 m (yellow dots). Inset: close-up of prairie strip and control catchment showing transects used for soil sampling. Paired sampling locations for prairie strips (blue) and control (red) 0 m locations are indicated by triangles. Map Credit: Dr. Haliegh Summers. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

management. During the initial two years, the prairie strips were mowed periodically. In 2019, no fertilizer was added to the cropland before planting soybeans. In 2020, cropland was fertilized with 211 kg N ha^{-1}, 136 kg P ha^{-1}, and 185 kg K ha^{-1} before planting maize. This N rate is typical for maize years, but these P and K rates are applied on a 3–4 year basis depending on soil fertility tests.

For this study, we compared only the paired 10 % prairie strip catchments ($n = 3$) to those with 0 % prairie ($n = 3$), hereafter referred to as '*control*' (Fig. 2). We chose to sample the 10 % prairie strip catchments because previous research showed that converting 10 % of a catchment to prairie was sufficient for environmental benefits (Schulte et al., 2017). Three transects perpendicularly bisecting prairie strips and paired positions in control catchments were chosen based on a digital elevation model, plan curvature and flow accumulation (see Dutter et al., 2023 for more details). Soil samples were collected along transects at ten distances with respect to the prairie strip and paired location in the control catchments: 3, 1, 0.3, 0.1 m upslope; and 0,0.1, 0.3, 1, 3, and 9 m downslope. The 0 m distance is in the center of the prairie strips or the equivalent, paired position in the control catchments (Fig. 2). Transects and sampling locations were marked using the Arrow 100 GNSS® receiver. For more experimental details, see Dutter et al. (2023).

2.2. *Soil sampling and analysis*

Ten soil cores (0–15 cm depth) were taken with a 2-cm-diameter probe from each of the ten transect sampling points and composited (10 distances from strips × 3 transects × 3 catchments × 2 treatments). Soil cores were taken on July 1st in both 2019 and 2020. Samples were sieved to <2 mm for analysis. A 15 g subsample of soil was weighed and dried at 105 °C for 24 h for gravimetric water content (GWC) measurement. To measure microbial biomass C and N, twin replicates from each soil were weighed to ~5 g. One replicate was fumigated for 24 h with ethanol-free chloroform and both replicates were extracted with 25 ml of 0.5 M K_2SO_4. Non-purgeable organic carbon and total salt-extractable nitrogen were measured in all samples with a Shimadzu TOC-L analyzer with TN capabilities (Shimadzu Corporation, Kyoto, Japan). Readings were corrected with extraction coefficients (0.45 for C, 0.54 for N) and compared between each replicate (Brookes et al., 1985; Vance et al., 1987; Jenkinson, 1988; Joergensen and Mueller, 1996). Total salt-extractable N values were corrected for inorganic N. The C and N in salt-extracted but unfumigated samples are hereafter referred to as salt-extractable organic C (SEOC) and organic N (SEON). The non-fumigated extracts were also measured for ammonium-N and nitrate-N, hereafter referred to as salt-extractable inorganic N (SEIN), using a SynergyTM HTX Multi-Mode Microplate Reader (BioTek Instruments, Winooski, VT, USA) with Gen5TM software (Doane and Horwáth, 2003; Sinsabaugh et al., 2000). Ammonium-N was measured using absorbance at 595 nm wavelength and nitrate-N was measured using absorbance at 540 nm wavelength. The remainder of the soil was air dried at 24 °C until stable weight (~1 month). Soil organic matter (SOM) was measured using loss on ignition for 2 h at 360 °C using a Blue M oven and TSI weighing system. Soil pH was measured using a 1:1 (w:w) soil water slurry and measured with a meter (Lignin Probes, Albuquerque, NM, USA). Cation exchange capacity was estimated from ammonium acetate equivalent values of the Mehlich 3 extracted cations.

2.3. *Potential enzyme activity assays*

Five g soil was immediately frozen after sieving and lyophilized within 2–3 months and stored at −20 °C before measuring PEA. Freezing soils has been shown to affect potential enzyme activity (Abellan et al., 2011; Peoples and Koide, 2012), but logistical constraints precluded analysis on fresh soils, and any storage effects are consistent for all samples. The potential activities of both hydrolytic and oxidative enzymes were measured according to standard protocols (DeForest, 2009; Deng et al., 2011; German et al., 2011a). Hydrolytic enzymes – arylsulfatase (ARSase), β-glucosidase (BGase), cellobiohydrolase (CBHase), β-*N*-acetylglucosaminidase (NAGase), leucine aminopeptidase (LAPase), phosphatase (PHOSase) (Table 1) – were assayed following Deng et al.'s (2011) protocol for fluorescence measured via methylumbelliferyl - or methyl-coumarin-linked substrates in 96-well microplates with some modifications. One gram of freeze-dried soil was weighed and placed in a 200 ml beaker, with 150 ml of distilled (DI) water and stirred for 30 min. Afterward, 200 μl aliquots of soil suspension were incubated for 1 h at 37 °C with 50 μl of the substrate. After the incubation, 50 μl of the substrate was added to the control columns, and 50 μl of THAM was added to all columns to terminate enzyme activities. Then pre-incubation and post-incubation suspensions were compared. Autohydrolysis controls were also used for each enzyme, and standard curves for each catchment were prepared. Enzyme activity was calculated from fluorescence with excitement at 360 nm and emission at 460 nm.

Oxidative enzyme activities – polyphenol oxidase (PPOase) and peroxidase (PERase) – were quantified using the colorimetric assay method in clear 96-well plates (Saiya-Cork et al., 2002). One gram of freeze-dried soil was weighed, put into suspension with 125 ml of Acetate buffer, and incubated with L-DOPA for 18 h at 25 °C. Activities were calculated from an absorbance of 450 nm, and the standard extinction coefficient of 7.9 was used for these equations (DeForest, 2009). All enzyme activities, both fluorometric and colorimetric, were measured using a SynergyTM HTX Multi-Mode Microplate Reader (BioTek Instruments, Winooski, VT, USA) with Gen5TM software. Potential enzyme activity was calculated as measured substrate activity in nmol divided by g SOM and time in hours. We normalized for SOM due to known influence of SOM on PEA and increased SOM under the prairie strip (German et al., 2011b; Zhang et al., 2015).

2.4. *Microbial community analysis*

A 5 g subsample from each original composite sample was sieved to <2 mm and frozen at −80 °C for 4 months before DNA extraction. We characterized microbial communities in all prairie strip and cropland soil samples using a high-throughput amplicon sequencing Illumina MiSeq platform (Illumina, CA, USA). For each soil sample (360 samples total), we extracted genomic DNA using the Qiagen MagAttract KF PowerSoil DNA extraction kit with a Thermo Fisher KingFisher Flex automated extraction instrument (Thermo Fisher, U.S.A.) following all manufacturer protocols. DNA concentration was determined for all samples via fluorometry with the Invitrogen Qubit dsDNA HS Assay Kit (Thermo Fisher, U.S.A.).

Extracted DNA template was submitted to the Michigan State University Core Genomics Facility for Illumina bacterial 16S V4 and fungal ITS1 library construction using the Illumina TruSeq Nano DNA library preparation kit and sequencing, and reads were quality filtered and merged using the USEARCH pipeline (https://drive5.com/usearch). Libraries of the bacterial 16S V4 region were prepared using Illumina-compatible, dual-indexed 515Ff/806rf primers (Kozich et al., 2013). Libraries of the fungal ITS1 region were prepared using ITS1f/ITS2 primer sequences (Martin and Rygiewicz, 2005) in an initial PCR followed by the addition of dual indexed Illumina library adapters in a subsequent PCR. Libraries were batch normalized using Norgen Biotek NGS Normalization Kits, pooled, cleaned up, and concentrated using AmpureXP magnetic beads. The pool was quality checked and quantified using a combination of Qubit dsDNA HS, Agilent 4200 TapeStation HS DNA1000 and Kapa Illumina Library Quantification qPCR assays. 16S and ITS1 amplicons were sequenced independently in a 2x250bp paired end format using independent v2 500 cycle MiSeq reagent cartridges.

Reads were quality filtered and merged using the USEARCH pipeline (https://drive5.com/usearch). Primers and adapter bases were removed using cutadapt. Bacterial reads were filtered and truncated to 250 bp, clustered into actual sequence variants (ASVs, hereafter referred to as

Table 1
Extracellular enzymes assayed in this study and the corresponding substrates for potential enzyme activity (PEA) measurements.

Enzyme	Enzyme commission number	Abbreviation	Substrate
Arylsufatase	EC 3.1.6.1	ARSase	4-MUF-sulfate
β-1,4-glucosidase	EC 3.2.1.21	BGase	4-MUF-β-D-glucoside
Cellobiohydrolase	EC 3.2.1.91	CBHase	4-MUF-β-D-cellobioside
β-*N*-acetylglucosaminidase	EC 3.2.1.14	NAGase	4-MUF-*N*-acetyl-β-D-glucosaminise
Leucyl aminopeptidase	EC 3.4.11.1	LAPase	L-Leucine-7-amido-4-methylcoumarin
Acid (alkaline) Phosphatase	EC 3.1.3.1	PHOSase	4-MUF-phosphate
Polyphenol oxidase	EC 1.10.3.2	PPOase	L-3,4-dihydroxyphenylalanine
Peroxidase	EC 1.11.1.7	PERase	L-3,4-dihydroxyphenylalanine and H_2O_2

Abbreviation: MUF = methylumbelliferyl.

ZOTUs) at 100 % sequence similarity then classified against SILVAv138 rRNA database (https://arb-silva.de). ZOTUs classified to Chloroplast, Mitochondria, or with less than two reads across all samples were removed (Thiéry et al., 2012) and samples were rarefied to 6984 reads (all samples included), resulting in 68,703 bacterial ZOTUs and 2,507,256 bacterial reads. Fungal sequences were filtered to 250 bp. Fungal reads were clustered into ZOTUs at 100 % sequence similarity and classified against the UNITE 8.3 reference database (https://unite.ut.ee). Non-fungal ZOTUs and ZOTUs with fewer than two reads were removed and samples were rarefied to 5803 reads, resulting in 12,716 fungal ZOTUs and 2,060,065 fungal reads.

2.5. Statistical analysis

First, we divided the data into two groups to be analyzed separately: i) under the prairie strip and paired control catchment locations (0 m), and ii) adjacent cropland locations (−3, −1, −0.3, −0.1, 0.1, 0.3, 0.1, 3, 9). The data were checked for normality and heterogeneity of variances, and if not found, data were log transformed to meet assumptions and/or outliers removed. The two groups of data were then analyzed via separate mixed-effect linear models. Both linear models used the following response variables on the log scale: microbial biomass C and N, salt-extractable inorganic N, salt-extractable organic C and N, ARSase, BGase, CBHase, LAPase, NAGase, PHOSase, PPOase, and PERase. Data were analyzed for normalcy and homoscedasticity using ggResidpanel (version 0.3.0) (Goode and Rey, 2019). The fixed effect for the prairie strip samples was treatment and the random effects were catchment (six levels) and transect within the catchment (3 per catchment). The model equation is given by:

$$log(\text{response}) \sim \text{treatment} + (\text{transect} \mid \text{catchment}).$$

The fixed effects for adjacent cropland samples were treatment (control vs. prairie strip), distance (9-level categorical variable) from the prairie strip, and treatment-distance interaction. The random effects were catchment (six levels) and transect within the catchment (3 per catchment). The model equation is given by:

$$log(\text{response}) \sim \text{treatment} + \text{distance} + \text{treatment} \times \text{distance} + (\text{transect} \mid \text{catchment}).$$

All variables were analyzed separately within years, i.e., the model was fit independently for a given response and year. We chose to separate years because the year variable was confounded with crop type (soybean vs. maize), land management decisions (fertilizer vs. none), and weather conditions in 2019 and 2020. The unknowns were estimated via residual maximum likelihood (REML) using the software defaults in lme4 (version 1.1.31) (Bates et al., 2015) and emmeans (version 1.8.3) (Lenth, 2021) packages in the statistical software R (version 4.2.2) (R Core Team, 2022).

Univariate microbial diversity measurements - observed richness, Shannon diversity and evenness - were analyzed using two-factor ANOVA. Prairie strip treatment was the sole predictor variable for modeling soil communities under the prairie strip. Treatment, distance, and their interaction were predictors for modeling soil communities in surrounding cropland. Microbial community structure was analyzed using PERMANOVA on Bray–Curtis distance matrices for rarefied bacterial and fungal communities using *phyloseq* (version 1.42.0) (McMurdie and Holmes, 2013) and *vegan* (version 2.6.4) (Oksanen et al., 2022) in R (version 4.2.2) (R Core Team, 2022). Two extreme outliers were removed from Bray-Curtis distance matrices - one prairie strips treatment 9 m downslope sample from the 2019 surrounding cropland dataset and one Control treatment 3 m downslope sample from the 2020 surrounding cropland dataset. We used distance-based redundancy analysis (dbRDA function in *vegan,* Legendre and Anderson, 1999) to determine the correlation of PEA and soil physiochemical properties to bacterial and fungal community structure under the prairie strip and in surrounding cropland (Oksanen et al., 2022). Our dbRDA model included watershed as a conditional factor. We identified phyla with differential abundance among prairie strip treatments and distances from prairie strips using the ‘manyglm’ and ‘anova’ functions in the *MVabund* (version 4.2.1) R package (Wang et al., 2012a).

3. Results

3.1. Microbial biomass, functioning, and community composition directly under the prairie strip

Overall, prairie strips did influence soil physiochemical properties under the prairie strip (Fig. S2). Prairie strips increased SOM by 12 %, pH by 7 %, and also 17 % in soil moisture content but in just 2020 ($p < 0.05$; Fig. S2). Prairie strips strongly affected C and N pools under the prairie strip in both years (Fig. 3, Table S1). Prairie strips, on average, increased microbial biomass C (MBC) and microbial biomass N (MBN) by 56 % and 133 % across 2019 and 2020. Prairie strips did not affect SEOC or SEON. Prairie strips lowered SEIN by 66 % across 2019 and 2020 (Fig. 3) – and, on average, SEIN was composed of about 50 % nitrate-N and 50 % ammonium-N.

Prairie strips had inconsistent effects on the soil PEA underneath the prairie strips when expressed per gram of SOM (Fig. 4, Table S1). Generally, prairie strips tended to increase hydrolase and decrease oxidoreductase enzymes. Prairie strips had the most consistent positive effects on PEA in 2019, when the early growing season was relatively wet, with 233 more mm in the 2019 growing season than 2020 (Fig. S3; Dutter et al., 2023). Prairie strips significantly increased hydrolytic PEA of CBHase by 77 %, NAGase by 108 %, and PHOSase by 46 % compared

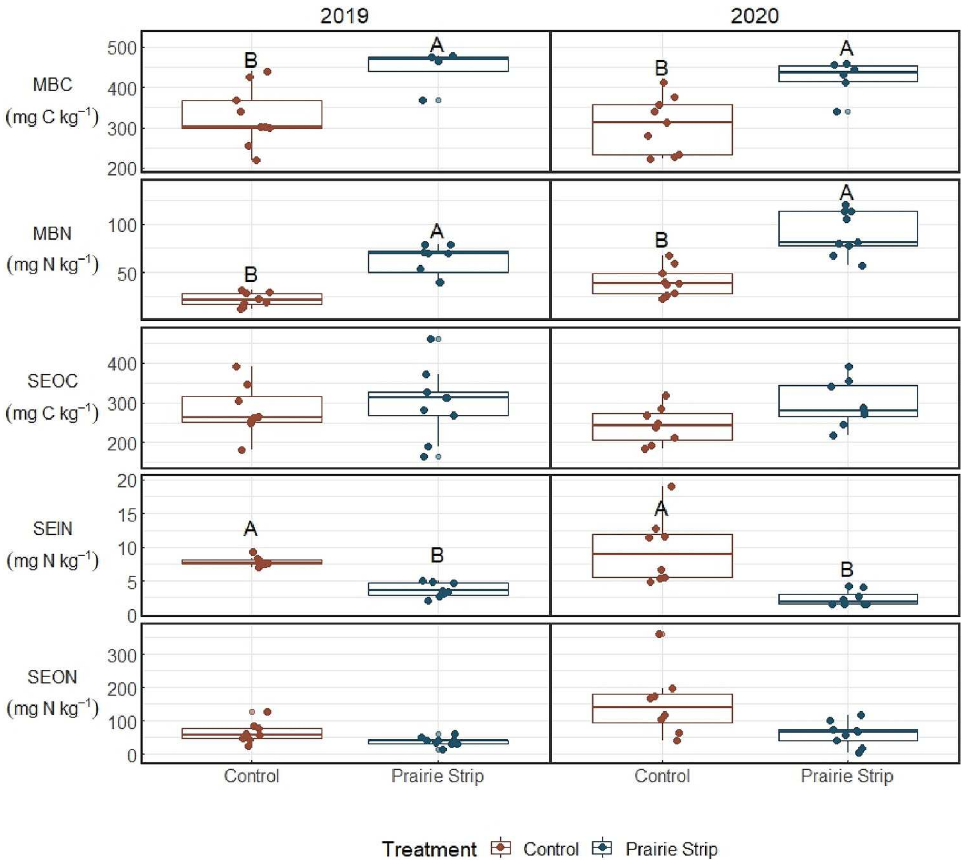

Fig. 3. Soil carbon (C) and nitrogen (N) pools under prairie strips and paired control locations in 2019 and 2020. Boxplots of prairie strip and paired control catchment samples ($n = 9$) sampled across three treatment catchments. Letters indicate significance of p-value <0.05. Abbreviations: MBC = microbial biomass C, MBN = microbial biomass N, SEOC = salt-extractable organic C, SEIN = salt-extractable inorganic N, SEON = salt-extractable organic N.

to the control when expressed per gram of SOM. Unlike hydrolytic PEA, however, prairie strips had a negative effect on oxidative PEA. For instance, prairie strips decreased PERase by 28 % in 2019 and PPOase by 33 % in 2020 (Fig. 4; Table S1).

Prairie strips shifted bacterial and fungal beta diversity compared to cropland control soils in both 2019 and 2020 (Table S1). The extent to which prairie strips affected bacterial and fungal alpha diversity measures varied by year, but in general, prairie strips either reduced or had no effect on fungal and bacterial alpha diversity (Table S1, Fig. 5). Prairie strips reduced bacterial and fungal alpha diversity up to 12 % compared to the cropland control ($p < 0.085$; Table S1, Fig. 5). Prairie strips also changed the relative abundance of specific microbial phyla (Fig. S2, Table S4). Gemmatimonadetes bacteria ($p = 0.018$ in 2019; $p = 0.012$ in 2020; Table S4), Elusimicrobia bacteria (p = 0.01 in 2019), Armatimonadetes bacteria ($p = 0.026$ in 2019), and Basidiomycota fungi ($p = 0.003$ in 2019 and p = 0.003 in 2020) were more abundant in prairie strip soils. On the other hand, Chytridiomycota fungi ($p = 0.028$ in 2019 and $p = 0.029$ in 2020), Mortierellomycota fungi ($p = 0.04$ in 2019), and Ascomycota fungi ($p = 0.037$ in 2020) were more abundant in cropland soils (Fig. S2, Table S4).

3.2. Microbial biomass, functioning, and microbial communities in adjacent cropland soil

In general, prairie strips did not affect soil physiochemical properties in adjacent cropland soils (Fig. S1). Across both study years, cropland soils in prairie strip and control catchments showed similar SOM, pH, and CEC. Cropland soils in prairie strip catchments showed marginally lower GWC in 2019 but not 2020 (Fig. S1; Dutter et al., 2023). Prairie strips also had negligible effects on adjacent soils' C and N pools. There were no significant prairie strip effects on the C and N pools besides SEIN. Salt-extractable inorganic N, comprised mostly of nitrate-N (85 %), was 33 % lower in the soil <1 m from the prairie strip but only in 2019 under soybean (Fig. 6; Dutter et al., 2023).

Prairie strips more clearly affected PEA in the adjacent cropland, but these effects were highly inconsistent among enzymes and dependent on the year (Fig. 7, Table S2). The effects of prairie strips on adjacent cropland PEA, when they occurred, were largely independent of distance from the prairie strips. In other words, prairie strips affected adjacent soil PEA equally at all distances up to 9 m away from the prairie strip.

Prairie strips had more positive effects in 2019 when cropland was under soybean, mirroring the predominantly positive effects seen directly under the prairie strip (Fig. 7). Prairie strips significantly increased three hydrolytic PEA in adjacent crop – BGase by 27 %, NAGase by 31 %, and PHOSase by 38 % – in 2019 soybeans, across all distances when expressed per gram of SOM. In 2020 under maize, however, there was a prairie strips Treatment × Distance interaction on LAPase, whereby the prairie strips increased LAPase PEA by 164 % but only 0.3 m downslope from the prairie strips (Fig. 7). In 2020 maize, there was also a significant positive main effect of prairie strips on PERase, where prairie strips increased adjacent cropland PERase by 29 % compared to the control across all distances.

Prairie strips affected bacterial and fungal community composition in surrounding cropland soils in both 2019 soybean and 2020 maize (Fig. S4, Table S2), but neither distance from the prairie strips nor the interaction between distance and prairie strip treatment were significant drivers of bacterial and fungal community composition in either crop year (Table S2). Prairie strips only affected microbial alpha diversity measurements in surrounding cropland soils in 2019 soybean (Shannon

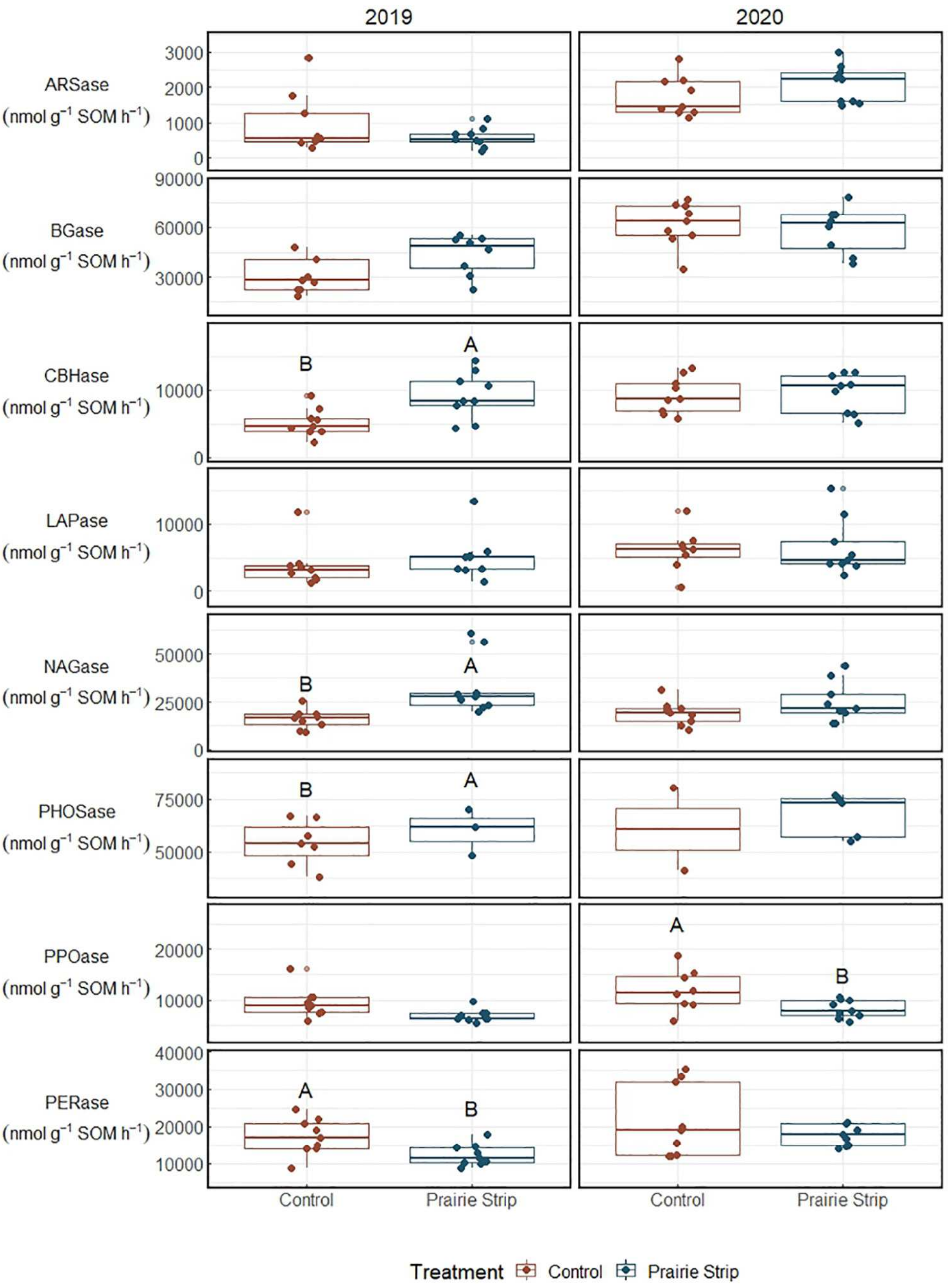

Fig. 4. Potential enzyme activities, expressed per g of soil organic matter (SOM), under the prairie strips and paired control locations in 2019 and 2020. Boxplots of *prairie strip and paired control catchment samples* (n = 9) sampled across three treatment catchments. Letters indicate significance at p-value <0.05. Abbreviations: ARSase = arylsulfatase, BGase = β-glucosidase, CBHase = cellobiohydrolase, LAPase = leucine aminopeptidase, NAGase = *N*-acetyl-glucosiminidase, PHOSase = phosphatase, PPOase = polyphenol oxidase, PERase = peroxidase.

diversity $p = 0.023$, observed richness $p = 0.032$, evenness $p = 0.033$) and showed no effect on bacterial and fungal alpha diversity measurements in 2020 maize (Fig. S5, Table S2). In 2019 soybean, bacterial and fungal observed richness was 2.85 % and 4.87 % lower, respectively, in the adjacent cropland soils of prairie strip catchments (Fig. S5). Distance from the prairie strip correlated with changes in microbial community richness, Shannon diversity, and evenness, but the direction and magnitude of this effect varied among upslope and downslope distances (Fig. S5). Prairie strips also shifted the relative abundance of several bacterial and fungal phyla in adjacent cropland soils (Fig. S4, Table S3).

Prairie strips explained some, but not all, correlations between soil properties, PEA, and microbial community composition in surrounding cropland soils. Soil microbial biomass C correlated with fungal community composition in both years, likely driven by high microbial biomass C in soils under the prairie strip ($p < 0.002$; Fig. 8, Table S5). Marginally higher soil nitrate in cropland control soils was a significant predictor of bacterial (Table S5, $p = 0.029$ in 2019 soybean, $p = 0.003$ in 2020 maize) and fungal (Table S5, $p = 0.001$ in 2019 soybean, $p = 0.001$ in 2020 maize) community composition across both years. Several other soil properties and one PEA were consistent correlates of bacterial and fungal community composition across both years: GWC, soil pH, clay, SEOC, nitrate, and PERase (Fig. 8, Table S5); however, in this study, only half of these variables in surrounding cropland soils were affected by prairie strips (GWC in 2019, SEIN in 2019 as Treatment × Distance interaction and PERase in 2020, Tables S2 & S4; Figs. 5 & S5). In other words, because prairie strips did not significantly affect all of these soil properties and PEAs in surrounding cropland, we can attribute some - but not all - correlations to the presence of prairie strips.

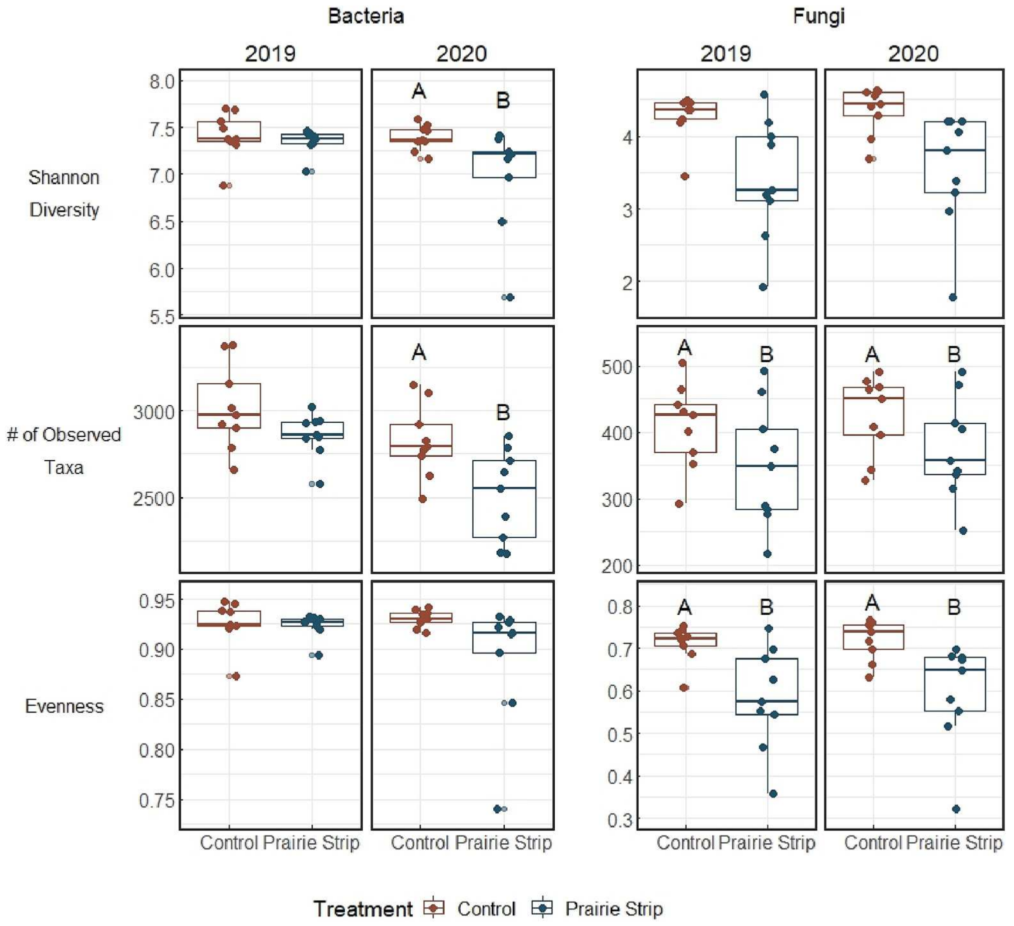

Fig. 5. Bacterial and fungal alpha diversity under prairie strips and paired control locations in 2019 and 2020. Boxplots of prairie strip and paired control catchment samples (n = 9) sampled across three catchments. Letters indicate significance at p-value <0.05.

4. Discussion

Prairie strips had strong effects on soil microbial community composition and function, both underneath the prairie strips and in adjacent cropland, though effects can be highly dependent on the cropping year. These inconsistent effects could be driven by crop and/or weather (Fig. S3, Smith et al., 2015). This discussion is separated into the effects of prairie strips on soils underneath the prairie strip (Sections 4.1 and 4.2) – which are more analogous to traditional land-use change studies converting cropland to restored grasslands – and the effects of prairie strips on adjacent cropland soil (Sections 4.3 and 4.4) – which draw from studies on ecotone and edge effects at the interface of habitat types.

4.1. Prairie strips increased soil microbial biomass and hydrolytic enzyme activity but decreased oxidoreductase enzymes under the prairie strip

In partial support of our 1st hypothesis, prairie strips had positive effects on soil microbial biomass and hydrolytic enzyme activities. More specifically, 12 years of prairie strips increased soil microbial biomass but not salt-extractable organic C and N, and decreased plant-available inorganic N, suggesting that prairie strips tighten C and N cycling. This supports findings from larger prairie and grassland restoration studies, which show a 100 % to 500 % increase in microbial biomass following restoration (Bach and Hofmockel, 2015; Purakayastha et al., 2009; Rosenzweig et al., 2016). Greater microbial biomass and less leachable, bioavailable N (i.e., SEIN) under the prairie strip is likely due to greater density and duration of living plant roots and greater rhizodeposition rate (Dietzel et al., 2017; Leptin et al., 2021). Prairie strips even increased more static soil properties like soil organic matter (+12 %) and pH (+7 %) (Fig. S2). These findings, in support of our first hypothesis, show that narrow strips of prairie have similar impacts on underlying soil inorganic C and N as have been observed in larger prairie restoration studies. Potential enzyme activities, however, were not as consistent.

Generally, prairie strips had positive effects on hydrolytic PEA and negative effects on oxidoreductase PEA but depended on the crop year (Fig. 4). This incongruence between the consistent increase in microbial biomass and yet inconsistent effect of prairie strips on PEA implies that PEA are not merely increasing or decreasing due to changes in the microbial biomass, but because of year-to-year shifts in bioavailable soil resources. PEA can also be temporally variable within a year, so it is possible that our sampling captured only a snapshot of potential activity amid fluctuations throughout the growing season (Bach and Hofmockel, 2015).

Perennial, diverse plant communities often increase hydrolase PEA compared to monoculture cropland (Li et al., 2023; Wallenius et al., 2011; Yu et al., 2017). CBHase degrades cellulose and may increase in the presence of increased substrate availability (i.e., plant residue; Ljungdahl and Eriksson, 1985). NAGase degrades chitin and our finding is consistent with other studies that found grasslands increase NAGase activities compared to cropland (Shahariar et al., 2021; Xu et al., 2019). The elevated NAGase activity may be due to the decrease in bioavailable N (i.e., SEIN, Fig. 3). In combination with increased microbial biomass C, this may reflect a shift toward mining fungal necromass for C and N acquisition from under prairie strips (Guggenberger et al., 1999; Kallenbach et al., 2015; Manzoni et al., 2008). Prairie strips also increased phosphatase activity in 2019 (Fig. 4). Phosphatase cleaves phosphate

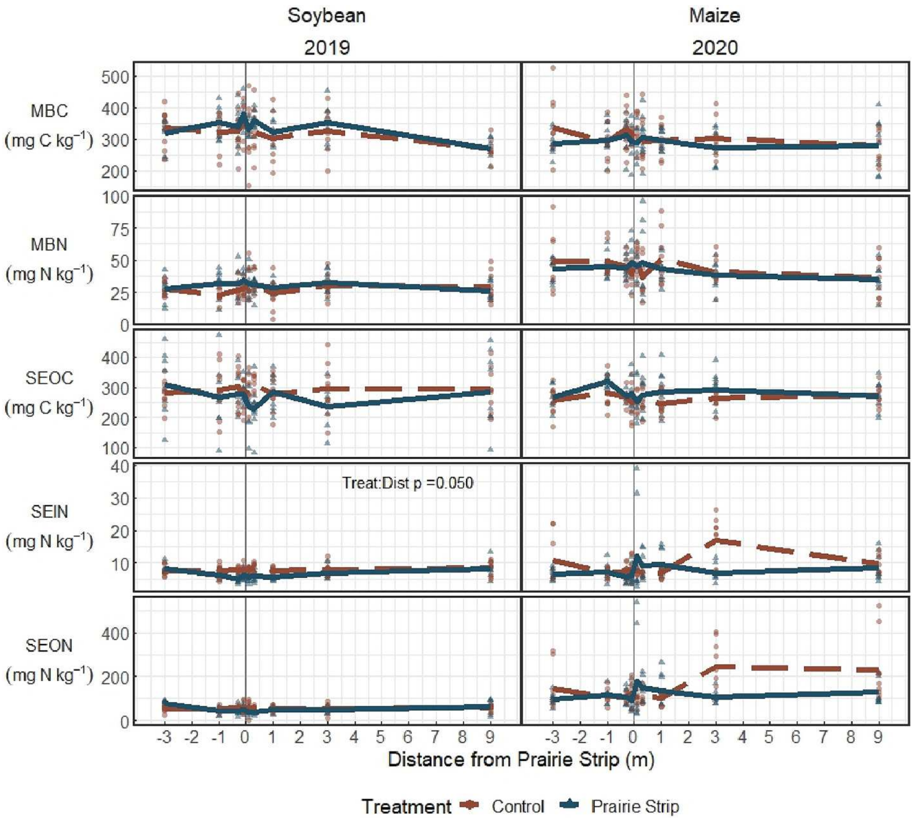

Fig. 6. Soil carbon (C) and nitrogen (N) pools within cropland adjacent to the prairie strip and paired control locations in 2019 and 2020. Significant treatment or treatment × distance interaction and *p*-values shown within graph panels ($p < 0.1$). Individual samples shown and lines drawn through mean ($n = 9$) at each distance soil samples were collected from the prairie strip, prairie strip samples (0 m) not included. Thin vertical line indicates the placement of the prairie strip. Abbreviations: MBC = microbial biomass C, MBN = microbial biomass N, SEOC = salt-extractable organic C, SEIN = salt-extractable inorganic N, SEON = salt-extractable organic N.

from organic sources and can be secreted by plants and microbes (Utobo and Tewari, 2015). Elevated PHOSase activity could be due to increased plant root competition for organic P in the prairie strips as P fertilizer is not added to the prairie strips since planting (Curtright and Tiemann, 2021; Margalef et al., 2017).

Prairie strips generally reduced oxidoreductase PEA (PPOase and PERase; Fig. 4). PPOase can degrade lignin, detoxify phenolic compounds, and metal ions, and be used as an antimicrobial defense (Sinsabaugh, 2010). PERase activity can also indicate lignin degradation, detoxification, and oxidative stress (Sinsabaugh, 2010). Both oxidoreductase enzymes are thought to be used by fungi for mining N from SOM (Jian et al., 2016; Sinsabaugh, 2010). Our study confirms many previous studies that show agricultural management practices that reduce residual inorganic N, increase labile SOM and general microbial activity also decrease oxidoreductase PEA (Bowles et al., 2022; McDaniel and Grandy, 2016; Wickings et al., 2011). More specifically, our findings align with cropland restoration studies that report decreased oxidoreductase PEA (Sciubba et al., 2021; Wang et al., 2011, 2012b).

4.2. *Prairie strips decreased microbial community richness and shifted community composition underneath the prairie strip*

Contrary to our 1st hypothesis, prairie strips did not increase but instead decreased soil bacterial and fungal diversity (Fig. 5, Table S1). This decrease was more or less consistent across years and multiple diversity metrics. Previous studies have shown inconsistent findings, where converting agricultural land to prairie has been shown to both increase (Bach et al., 2018; Upton et al., 2018) and decrease (Barber et al., 2017) soil microbial diversity. Our findings challenge the more generally accepted paradigm that restoring physical habitat and restoring diverse plant community will increase microbial diversity (Hilderbrand et al., 2005; Lange et al., 2015). Our contrary finding could be due to increased microbial niche space from introducing additional resources (e.g., fertilizer and pesticide inputs) and creating unique soil microhabitat conditions due to soil disturbance (e.g. machinery compaction and minor disturbance from planting equipment; Schmidt et al., 2018). Alternatively, the 12 years of prairie strip establishment may have increased diversity or connectivity among higher-trophic-level primary consumers, like nematodes and invertebrates that feed on fungi and bacteria (not measured here), which then in turn may have suppressed bacterial and fungal diversity (Wang et al., 2022). Because greater soil microbial diversity does not always translate to greater microbial function or resilience, soil microbial diversity in-and-of-itself should not be the ultimate management goal (Shade, 2017). Therefore, it is critical to assess the response of taxa and functions in order to better inform our basic understanding but also for evaluation of different management practices.

Changes in bacterial and fungal community composition underneath the prairie strips corresponded with soil physicochemical properties (Fig. 8). For example, Gemmatimonadetes bacteria were significantly less abundant under prairie strips (Table S4, Fig. 9), and this may be due to the phyla's preference for more acidic conditions under cropland ($<$ 6; Mackelprang et al., 2018). Prairie strips also decreased sporulating fungi and increased filamentous fungi, as is typical under restored prairies (Upton et al., 2018). The reduced soil disturbance and greater plant inputs under perennial prairie likely increased abundance of decomposers like Basidiomycota (Table S4, Fig. 9), while frequent soil disturbance and agrochemicals in cropland increased spore-forming Ascomycota (Fig. 9). While prairie restoration often leads to greater abundance of Glomeromycota (arbuscular mycorrhizal fungi; Allison

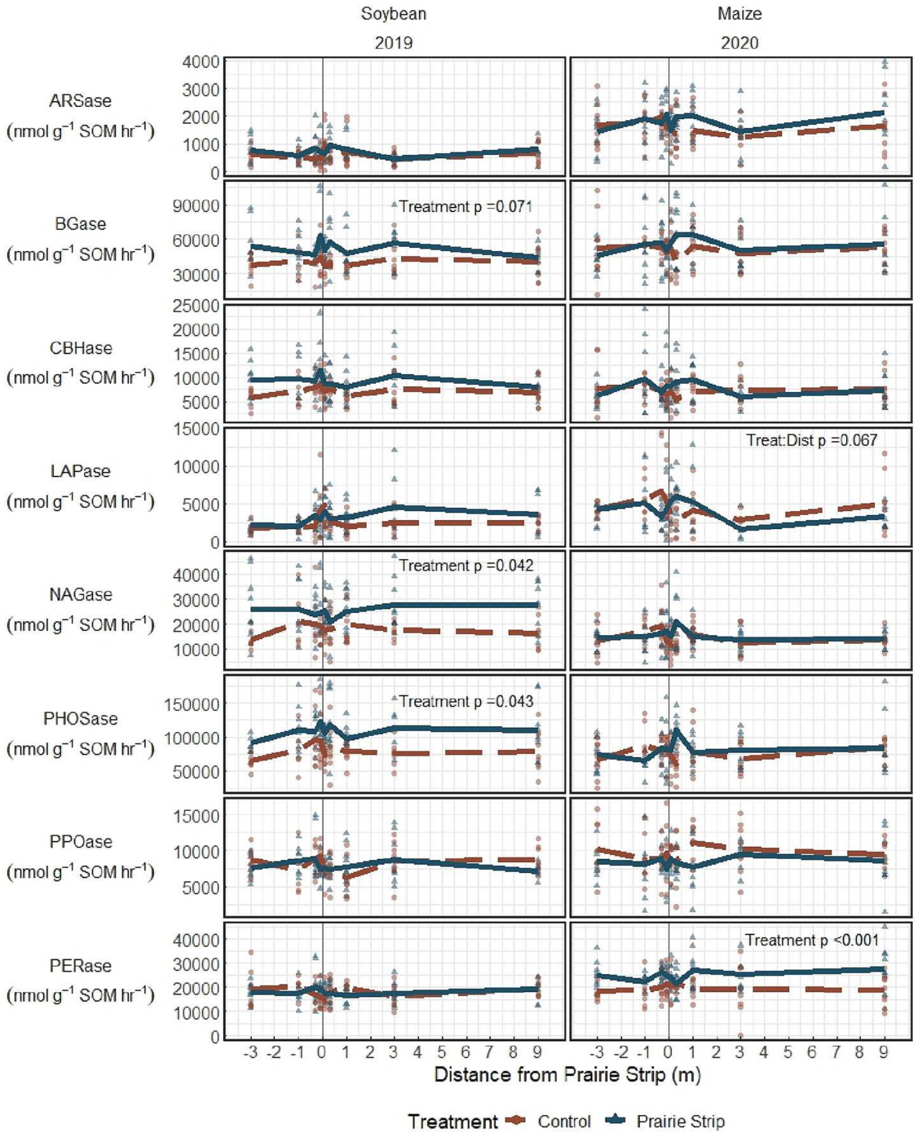

Fig. 7. Potential enzyme activities, expressed per gram of soil organic matter (SOM), in cropland surrounding the prairies strip and paired control locations in 2019 and 2020. Significant treatment or treatment × distance interaction and p-values shown within graph panels ($p < 0.1$). Individual samples shown and lines drawn through mean ($n = 9$) at each distance soil samples were collected from the prairie strip, prairie strip samples (0 m) not included. Thin vertical line indicates the placement of the prairie strip. Abbreviations: ARSase = arylsulfatase, BGase = β-glucosidase, CBHase = cellobiohydrolase, LAPase = leucine aminopeptidase, NAGase = *N*-acetyl-glucosiminidase, PHOSase = phosphatase, PPOase = polyphenol oxidase, PERase = peroxidase.

and Vitousek, 2005; Cook et al., 1988; Herzberger et al., 2014), we did not observe this in prairie strip soils (Table S4, Fig. 9). Low Glomeromycota abundance may be due to the dispersal limitation of some mycorrhizal groups (Chaudhary et al., 2020), to N fertilizer drift from surrounding cropland (Jach-Smith and Jackson, 2018), or to biases in our ITS fungal sequencing method (Lindahl et al., 2013).

4.3. *Prairie strips affected adjacent cropland soil microbial biomass and potential enzyme activities*

Contrary to our 2nd hypothesis, we found prairie strips did affect adjacent cropland soil, but these effects were weaker than on soils directly underneath prairies (Fig. 6). Prairie strips had decreased bioavailable N by 33 % in the adjacent soils, but only in 2019 when cropland was under soybeans (Fig. 6). Prior work showed that prairie strips altered other plant-available nutrients in adjacent cropland; nitrate was reduced by 23 % in soil within 1 m of the prairie strips (Dutter et al., 2023). The change in plant-available nutrients, especially mobile nutrients, might be due to greater uptake of N under prairie strips or prairie strips changing belowground water balance either by increasing evapotranspiration or limiting subsurface flow and transport of nutrients (Zhou et al., 2010, 2014).

Prairie strips had strong effects on some PEA in adjacent croplands depending on the year, and only in one case this effect was dependent on distance from the prairie strip (Fig. 7). Three enzymes – BGase, NAGase, and PHOSase – were all greater in cropland adjacent to the prairie strips than in control catchments, regardless of distance from the prairie strip. The latter two hydrolytic enzymes also had greater activities under the prairie strip, but BGase did not. BGase is a C-acquiring enzyme that tends to be elevated in soils with easily decomposable organic matter (de Almeida et al., 2015). While the specifics of why hydrolytic PEA increases are unclear, it does suggest that prairie strips alter the supply and demand of carbon and nutrients in adjacent soil.

Increased NAGase activity may be due to N scarcity in cropland soils adjacent to prairie strips, or changes in other resources that were not measured in this study (Wang et al., 2013). PHOSase was elevated at all

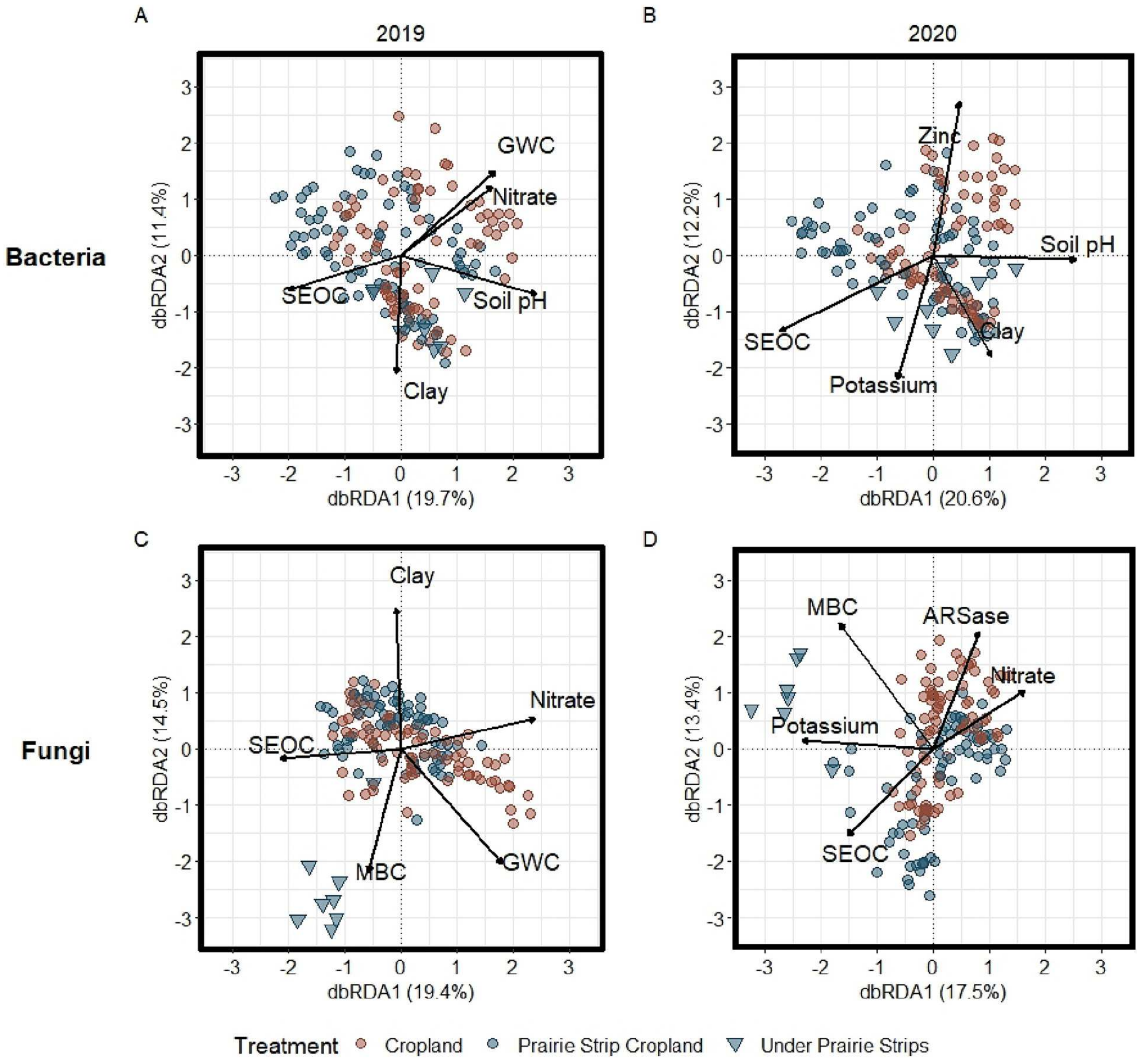

Fig. 8. 1st and 2nd dimensions from distance-based Redundancy Analysis (dbRDA) on soil bacteria communities in 2019 (A) and 2020 (B), and fungal communities in 2019 (C) and 2020 (D). Vectors show the top five strongest predictors of community composition are shown in each panel. All significant predictors of microbial community are in Table S5.

distances in cropland adjacent to prairie strips (Fig. 7). While PHOSase has been shown to negatively correlate to P availability (Allison and Vitousek, 2005; Hernández and Hobbie, 2010), our previous study found that prairie strips increased Mehlich-III extractable $P < 1$ m upslope from the prairie strips (Dutter et al., 2023), but phosphatase activity remained elevated across all distances.

Leucine aminopeptidase, an exclusively N-acquiring enzyme that hydrolyzes leucine amino acid from proteins and peptides, increased by 164 % 30 cm downslope of the prairie strip during 2020 maize. Leucine aminopeptidase was elevated downslope of the prairie strip, at the same locations where maize plants were N-stressed and bioavailable N was depleted in the previous year (Dutter et al., 2023). This provides some evidence that greater plant and microbial demand for bioavailable N downslope of the prairie strip is driving increased LAPase. PERase activity in 2020 was also elevated across the entire prairie strip treatment (Fig. 7). Elevated PERase activity in the cropland adjacent to prairie strips could indicate a labile C or N limitation due to N, P, and K fertilizer addition in 2020.

4.4. Prairie strips decreased microbial richness and enriched C-degrading taxa in adjacent soybean soils, but not maize soils

Another reason we must reject our second hypothesis that prairie strips would have no effect on surround soil microbiota is that prairie strips reduced bacterial and fungal richness under surrounding soils in one out of two years (Fig. S5, Table S2). The difference between years could be because maize and soybean may have different filtering effects on microbial communities, or because cropland fertilization varied across years. N additions in 2020, but not 2019, may have quenched N demand across all distances from the prairie strip, thus homogenizing microbial communities across cropland soils to a greater extent than in 2019. This is also evidenced by the lower NAGase activity in surrounding cropland and was a stronger predictor of fungal community composition in 2019 than in 2020 (Fig. 7, Table S3).

The prairie strip effect seems to have linked structure and function because changes in particular organisms aligned with changes in soil PEA. For example, in 2019 under soybean, prairie strips increased microbial phyla capable of degrading complex C substrates (Fig. S4,

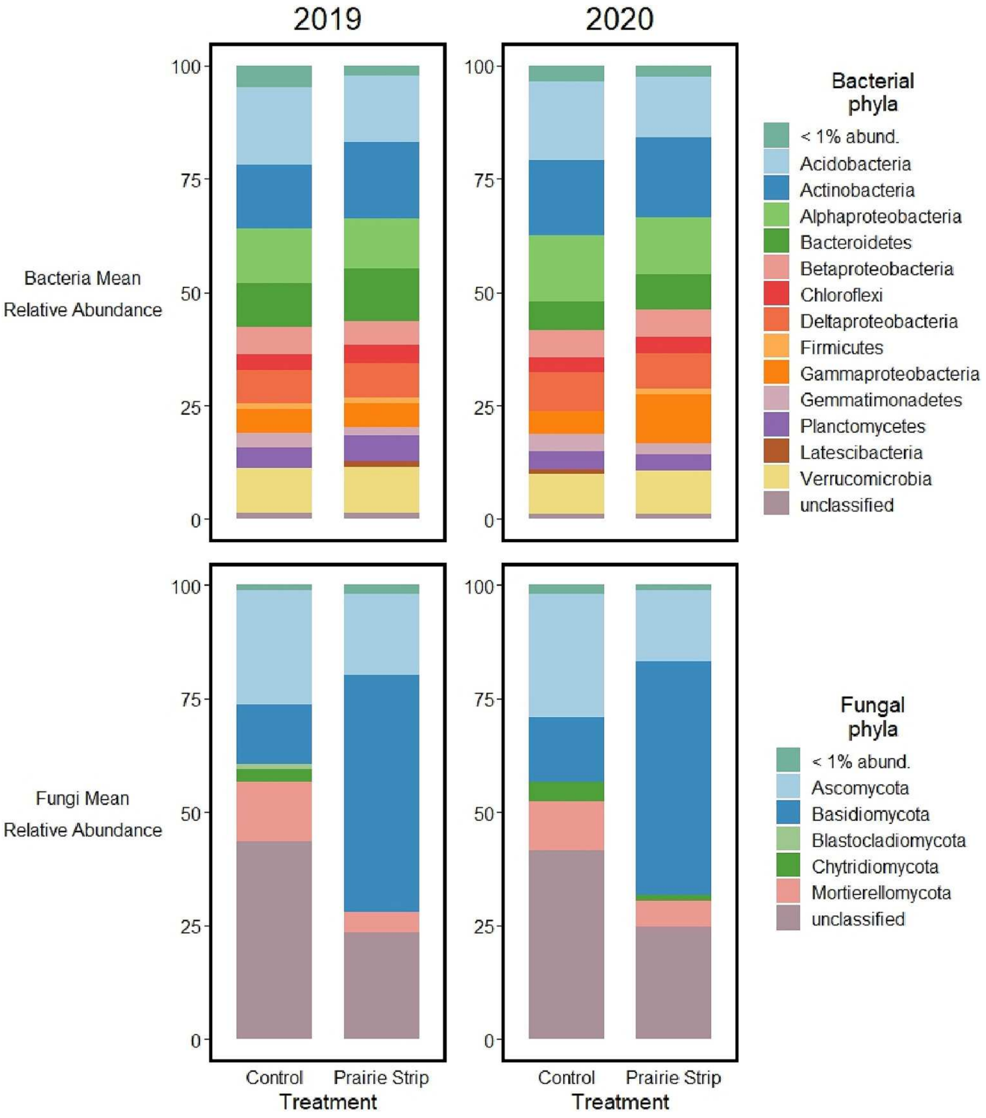

Fig. 9. Relative abundance of bacterial and fungal phyla under prairie strip vegetation and paired control locations in 2019 and 2020. Means shown (n = 9) sampled across three catchments.

Table S4), such as Firmicutes and Planctomycetes (Reguera and Leschine, 2001; Wiegand et al., 2018); and this also corresponded to increases in BGase and NAGase that year. Second, in 2020 under maize, prairie strips enriched decomposer fungi (Basidiomycota; Fig. S4, Table S2) and increased PERase in adjacent cropland soils (Tables S2 & S5). Taken together, these two independent lines of evidence suggests that prairie strips are affecting microbial structure and functioning in subtle, consistent ways but depends on the crop year.

Our findings suggest that environmental filtering is the dominant mechanism shaping soil microbial communities adjacent to prairie strips. Across both years, neither alpha diversity nor beta diversity showed a significant Treatment × Distance interaction, suggesting that bacterial and fungal communities were controlled by the slope position of the soil within the cropland rather than the soil's proximity to the prairie strips (Table S2). The lack of a distance-based spillover effect suggests that either prairie strip microbes are not dispersing outward from the prairie strips, or more likely, dispersal is present, but cropland environmental filtering is shaping community composition at each catchment slope position. Cropland disturbance and fertilization (Fierer and Jackson, 2006; Manzoni et al., 2012; Schmidt et al., 2018; West and Whitman, 2022), in combination with soil physiochemical heterogeneity across the field (Fig. S1; Table S5), appear to be a stronger control on microbial communities than proximity to the prairie strip. These results also indicate that prairie strips do not introduce beneficial microbial taxa to adjacent cropland soils; however, rare taxa that we may not have detected can have a disproportionate effect on function (Shade et al., 2014), so this possibility should not be ruled out.

Microbial community composition was associated with several soil properties and PEA, some as a result of prairie strip establishment, and others as a function of abiotic heterogeneity across the landscape. Inorganic N was a primary driver of differences in bacterial and fungal community composition across treatments, as evidenced by the strong influence of soil nitrate on community composition across years (Table S5, Fig. 8); and specifically evidenced by the enrichment of particular microbial phyla like Planctomycetes which are capable of oxidizing ammonium (Fig. S4, Table S4, Shively et al., 2009). The emergence of microbial biomass C as a significant correlate of fungal, but not bacterial, community composition in surrounding cropland soils may have resulted from the enrichment of Basidiomycota, a filamentous, high C:N fungal group, in cropland soils surrounding prairie strips (Fig. S4, Tables S5 & S3, Zhang and Elser, 2017).

Several soil measurements (nitrate, GWC, soil pH, clay, SEOC, and potassium) and microbial biomass C were consistent correlates with bacterial and fungal community composition (Fig. 8, Table S3). The majority of these variables were not affected by prairie strips (Tables S2 & S5), varied widely across slope positions (Figs. 5 & 6), and did not affect community composition in consistent directions (Fig. 8). The exceptions to this were microbial biomass C and nitrate, variables whose correlations with microbial communities were clearly mediated by the presence of a prairie strip (Fig. 8, Table S3). Our study showed that prairie strips do have some effects (albeit some more consistent than others) on soil biota and SESs in both prairie strip and adjacent cropland soils that may be important for implementation and management.

5. Conclusion

Prairie strips are a conservation practice aimed at increasing biodiversity on the landscape, reducing agricultural runoff, and regenerating soil health. We found that the oldest prairie strips in Iowa (12 years old) had many effects on soil microbial community structure and functioning underneath the prairie strips and even in the adjacent cropland, though effects were more inconsistent and complex in the latter. These prairie strips – like large swaths of restored perennial vegetation – increased soil microbial biomass, hydrolytic PEA, and C-degrading microbial taxa, and decreased salt-extractable inorganic N, oxidative PEA, and bacterial and fungal richness in soils directly underneath the prairie vegetation. In adjacent cropland soils, prairie strips had little effect on C and N pools but did have strong positive effects on several hydrolytic and oxidative PEA (BGase, NAGase, PHOSase, and PERase) and microbial community structure, depending on the crop year. Overall, we find strong evidence for prairie strips' affecting soil biota and SESs both underneath and adjacent to them, but effects are strongly dependent on localized abiotic conditions, crop species, and crop-specific management activities.

Future studies might improve the predictability of prairie strips' effects on adjacent soil biota by monitoring more frequently within one year, exploring the role of prairie plant species composition, and testing the interaction with other cropping systems other than maize-soybean rotation. Doing so will help to understand the complex interactive effects of prairie strips have on shaping soil biota and SESs in adjacent cropland. A greater understanding of these complex interactions between cropland and prairie strips will help improve agriculture management for maximizing ecosystem services.

CRediT authorship contribution statement

Cole R. Dutter: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Corinn E. Rutkoski:** Writing – review & editing, Writing – original draft, Visualization, Validation, Formal analysis, Data curation. **Sarah E. Evans:** Writing – review & editing, Supervision, Project administration. **Marshall D. McDaniel:** Writing – review & editing, Supervision, Project administration.

Declaration of competing interest

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Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2024.105424.

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