PLOS ONE

RESEARCH ARTICLE

Agroecosystem edge effects on vegetation, soil properties, and the soil microbial community in the Canadian prairie

Mariah Aguiar, Alexandra J. Conway, Jennifer K. Bell, Katherine J. Stewart*

Department of Soil Science, University of Saskatchewan, Saskatoon, Saskatchewan, Canada

* Katherine.stewart@usask.ca

Check for updates

OPEN ACCESS

Citation: Aguiar M, Conway AJ, Bell JK, Stewart KJ (2023) Agroecosystem edge effects on vegetation, soil properties, and the soil microbial community in the Canadian prairie. PLoS ONE 18(4): e0283832. https://doi.org/10.1371/journal.pone.0283832

Editor: RunGuo Zang, Chinese Academy of Forestry, CHINA

Received: August 15, 2022

Accepted: March 17, 2023

Published: April 6, 2023

Peer Review History: PLOS recognizes the benefits of transparency in the peer review process; therefore, we enable the publication of all of the content of peer review and author responses alongside final, published articles. The editorial history of this article is available here: https://doi.org/10.1371/journal.pone.0283832

Copyright: © 2023 Aguiar et al. This is an open access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: All soils and vegetation files are available from the Federated Research Data Repository (DOI: https://doi.org/10.20383/103.0623). Raw sequence fasta files and the associated metadata can be found at the National

Abstract

Edge effects resulting from adjacent land uses are poorly understood in agroecosystems yet understanding above and belowground edge effects is crucial for maintaining ecosystem function. The aim of our study was to examine impacts of land management on aboveground and belowground edge effects, measured by changes in plant community, soil properties, and soil microbial communities across agroecosystem edges. We measured plant composition and biomass, soil properties (total carbon, total nitrogen, pH, nitrate, and ammonium), and soil fungal and bacterial community composition across perennial grassland-annual cropland edges. Edge effects due to land management were detected both aboveground and belowground. The plant community at the edge was distinct from the adjacent land uses, where annual, non-native, plant species were abundant. Soil total nitrogen and carbon significantly decreased across the edge ($P < 0.001$), with the highest values in the perennial grasslands. Both bacterial and fungal communities were different across the edge with clear changes in fungal communities driven directly and indirectly by land management. A higher abundance of pathogens in the more heavily managed land uses (i.e. crop and edge) was detected. Changes in plant community composition, along with soil carbon and nitrogen also influenced the soil fungal community across these agroecosystems edges. Characterizing edge effects in agroecosystem, especially those associated with soil microbial communities, is an important first step in ensuring soil health and resilience in these managed landscapes.

1. Introduction

Habitat fragmentation is a leading cause of biodiversity loss [1, 2] and agriculture has caused extensive habitat fragmentation [3, 4]. Highly fragmented landscapes have a high proportion of edges, which affect various ecological aspects [5]. Edges can be high contrast such as a forest abutting a pasture, or a more gradual low contrast edge like a shrub patch adjacent a meadow. Edges have edge effects which are abiotic and biotic changes occurring at the bounds of an ecosystem or habitat patch [5, 6] influencing properties including microclimate, moisture, soils, plant or animal community composition and distribution [7–9]. Some factors that influence

Center for Biotechnology Information (NCBI) under Bioproject PRJNA588061.

Funding: This research was supported by a Natural Sciences and Engineering Research Council of Canada Strategic Partnership Grant entitled "Understanding resilience in agroecosystems: landscapes in transition" with Agriculture and Agri-Food Canada. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

edges are orientation [10, 11], time [12], patch size [13, 14], edge contrast [15] and matrix composition [16, 17]. Ecological dynamics and patterns around edges can be understood through four essential mechanisms, ecological flows across edges, resource distribution, resource mapping, and unique species interactions [6].

Expansion and intensification of agriculture has induced change in nearby habitats, and have been observed in both plant communities and soil properties [18–20]. Agricultural intensification is thought to magnify edge effects [19] further altering vegetation and soil biodiversity in these systems [21]. Commonly, edges in the agroecosystem are inhabited by non-native undesirable plants, here called weeds, or other invasive species [22]. Plant communities at the edge may be of concern to farmers, where weeds can compete with crops [23]. While aboveground vegetation changes at the edge are evident, belowground changes are also occurring. Underlying gradients of soil properties have been found at edges, including soil pH, nitrogen (N), and carbon (C) [24, 25], though these studies are limited to forest edges. Aboveground and belowground interactions are important to consider because those interactions determine ecosystem function, and in particular agroecosystems, where land management has effects beyond the field boundary. However, the extent and characteristics of edges and their effects in agroecosystems remain poorly understood belowground.

Two major land uses in the agroecosystem are cultivated croplands and grasslands; they each have characteristics that affect the soil microbial community. Nutrient dynamics between the two are quite different; for instance, croplands often have lower soil C than grasslands [26, 27] while grasslands have more soil C and are frequently correlated with higher microbial biomass [28]. Various environmental factors affect soil microbial community composition and function [29], but agricultural practices directly alter environmental conditions affecting soil microbes [30]. These agricultural practices include but are not limited to, soil amendments [31, 32], tillage [33, 34], herbicides [35, 36], and crop type [37]. However, the magnitude to which these factors influence the soil microbial community are complex [38–40]; considering edge effects and the interactions with agricultural practices is essential to understand soil microbial community dynamics in these landscapes.

Aboveground edge effects provide insight into belowground conditions and ultimately the soil microbial community. Plant species can have specific microbial associations affecting microbial community composition, such as mycorrhizal associations with plant roots [41]. Additionally, invasive plant species can alter the soil microbial community through changing inputs of litter quality and quantity [42]. Knowing how and what alters the soil microbial community is important, as soil microorganisms are critical in maintaining ecosystem function, especially through nutrient cycling, disease suppression, and plant growth promotion [43, 44].

Understanding how the soil microbial community responds to edge effects is crucial, as the soil microbial community is essential for maintaining ecosystem function, especially with intensification of agricultural lands [44]. To investigate edge effects in agroecosystems above and belowground, we measured vegetation composition and biomass, and soil physicochemical and microbial properties across perennial grassland and annual cropland edges in central Saskatchewan, Canada. Our goal was to determine if changes in land use altered the plant community and soil properties at agricultural edges, and if so, how these changes influenced the microbial community across the edge. Considering the interrelated effects of management on soil properties and plant communities, and their impacts on soil microbial communities, will better our understanding of agroecosystem edges and their ecosystem function.

2. Materials and methods

2.1. Study sites

We examined perennial grassland-annual cropland edges at two locations, St. Denis National Wildlife Area (SDNWA) and the Conservation Learning Centre (CLC), in southern-central Saskatchewan, Canada. SDNWA is located in the Moist Mixed Grassland ecoregion and CLC is in the Boreal Transition ecoregion [45]. Soils at SDNWA are mostly of Dark Brown Chernozemic and CLC are predominantly Black Chernozemic soils [46] and were confirmed by another study that was sampling cores for their study. Authorization to sample at these sites were granted by the St. Denis National Wildlife Area and the Conservation Learning Centre.

Both locations are composed of cropland interspersed with perennial grasslands. Both croplands are no-till, while perennial grasslands are not intensively managed, only being cut for hay and no grazing, fertilizing, or spraying occurs. At SDNWA, in 1977, 97 hectares of cropland were converted to a perennial forage predominately composed of smooth brome (*Bromus inermis* L.), alfalfa (*Medicago sativa* L.), and yellow sweet clover (*Melilotus officinale* L.) [47]. Perennial grasslands at both sites were cut once for hay in 2017 and croplands were planted with flax (*Linuum usitatissiumum* var. CDC Sorrel) in May 2017 at SDNWA. Glyphosate was applied prior to seeding and during seeding granular fertilizer (90 N—36 P– 17 S kg/hectare) was used; herbicides (Buctril M and Centurion mix) were also applied in July 2017 at SDNWA. Canola (*Brassica napus* L., Nexera RR112) was planted in May 2017 at CLC. At the time of seeding, anhydrous fertilizer was applied (112 N– 28 P– 28 S kg/hectare) as well as glyphosate. Fungicides were applied in June (Topnotch/Eclipse) and July (Lance) 2017.

2.2. Field sampling

Two edge sites at each location were sampled; we sampled at SDNWA from June 25–28, 2017 and sampling at CLC took place June 29 –July 6, 2017. At each edge site (n = 2 per location), three transects were laid perpendicular to the grassland-cropland edge and spaced 3 meters apart. Along each transect, samples were taken at the edge (0 m), 25 cm, 50 cm, 1 m, 2 m, 6 m, 8 m, 16 m, and 33 m into each of the two land use types (n = 15 per transect, 90 per location). Each sampling point was randomly assigned a position directly on the transect, or 1 m to either side of the transect (Fig 1). The edge point was visually determined, aided by inspecting the seeding row extent.

At each sampling point, percent cover was assessed for all plant species within a 1 m^2 quadrat and 1 m^2 quadrats were not allowed to overlap between sampling points. We also recorded plant species present within a 1 m radius of the center point; a 1 m radius was chosen to capture plants whose roots may be in the locale of the soil sample. Aboveground biomass was collected in a 20 cm x 50 cm quadrat and separated into three categories: grass, forbs, and plant litter. Biomass samples were dried at 40˚C for four days and weighed to determine dry biomass. During analyses, we combined forbs and grass to encompass all living biomass. To characterize soil properties, we collected a soil core (5 cm diameter x 10 cm depth) from the A horizon at the center of the cover quadrat using a sledge core (AMS Soil Core Sampler, American Falls, ID). A composite sample of three smaller cores (2 cm diameter x 15 cm depth each) was collected for molecular analysis of the soil microbial community. All soil samples were stored at -20˚C and were freshly thawed prior to analysis.

2.3. Soil property analyses

Soil was air-dried and passed through a 5 mm sieve to remove large debris and rocks. Soil nitrate (NO_3) and ammonium (NH_4) extractions were performed using 2.0 M KCl [48] and

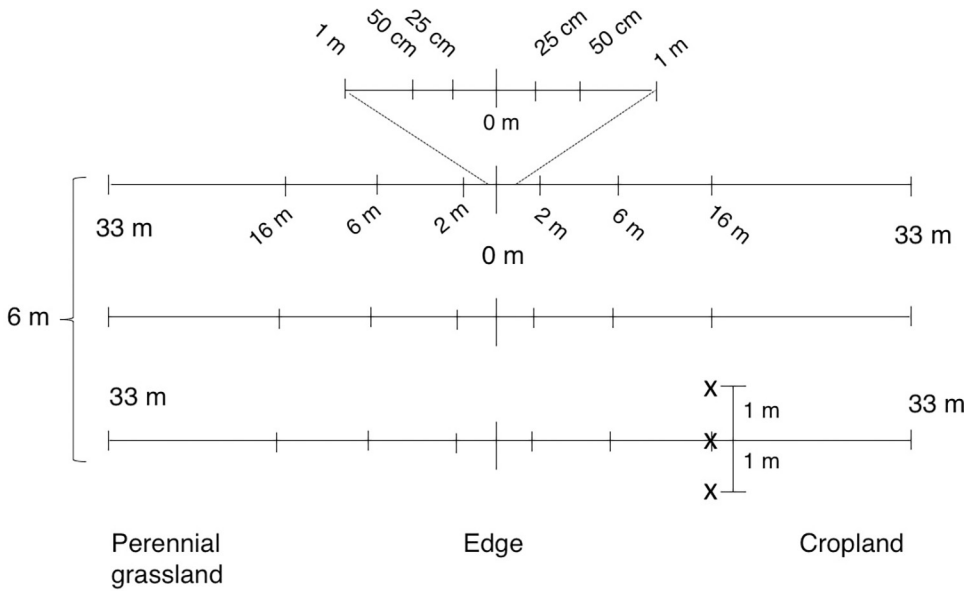

Fig 1. Transect sampling design. Transect sampling design at perennial grassland-annual cropland edges. At each edge site, two per location, three transects (33m from edge into each land use) were spaced 3m apart. Each transect had 15 sampling point locations relative to the edge (25cm-33m). Each sampling point along the transect was randomly assigned to one of three positions (x): 1m left, 1m right or on the transect. At each site, there was a total of 90 sample points (2 sample locations * 3 nested transects * 15 sampling points per transect).

https://doi.org/10.1371/journal.pone.0283832.g001

analyzed on an AutoAnalyzer 3 (SEAL, UK). Soil pH was measured with a pH probe (Mettler Toledo, USA) using a 1:2 soil to 0.1 M $CaCl_2$ solution [49]. Air-dried, sieved soil was ball-ground (Retsch MM-400, Germany) and 0.25 g of soil was used to determine total N and C. Total C was combusted at 1100˚C with a LECO C632 analyzer (LECO, USA) and total N was combusted at 1250˚C with the TruMac CNS analyzer (LECO, USA).

2.4. Soil microbial sequencing and bioinformatics

Composite samples were sub-sampled (5 g) and ball-ground (Retsch MM-400, Germany). DNA was extracted from 1 g of soil using the PowerPlant Pro Kit (Qiagen, Germany) and eluted in 100 μL of EB solution. DNA was quantified using the Qubit 2.0 Fluorometer (Invitrogen, Massachusetts, USA) and all samples were standardized to 1 ng/μL of DNA for downstream amplification.

To target the bacterial community, the 16S rRNA V4 region was amplified using the primers 515F/806R [50]. Reactions were performed at a final volume of 25 μL; 2 μL of template DNA, 12.5 μL of Platinum Green (2X) Master Mix (Thermo Fisher, Massachusetts, USA), and 1.5 μL of each primer (10 μM). PCR conditions followed Caporaso et al., (2011) [50] using 30 cycles. To target the fungal community, the Internal Transcribed Spacer (ITS) region was amplified using the primer pair ITS1-F [51] and ITS2-R [52]. Reactions were performed at a final volume of 25 μL; 2 μL of template DNA, 12.5 μL of Platinum Green (2X) Master Mix (Thermo Fisher, Massachusetts, USA), 1 μL of each primer (10 μM). PCR conditions were 3 minutes 94˚C, 35 cycles: 94˚C 30 s, 52˚C 30 s, 72˚C 45 s, and 72˚C for 7 minutes.

All PCR products were purified using the NucleoMag NGS Clean-up and Size Select magnetic beads (Macherey-Nagel, Germany) following the protocol for single size selection with the exception of reduced drying time after the second ethanol wash (2 minutes). Double size selection purification was performed for the ITS amplicon to ensure that fragments larger than

the target region were removed. Library preparation for Illumina MiSeq followed the Illumina Library Preparation Guide (#15044223 Rev. A) and sequencing was performed at the Toxicology Centre at the University of Saskatchewan (300 cycle v2 kit for 16S, 500 cycle v2 kit for ITS).

Soil microbial sequences were processed through QIIME2 2018.11 [53] using the DADA2 pipeline [54]. DADA2 was used for quality filtering, removal of chimeric variants, and merging forward and reverse ITS reads (only forward reads were used for 16S sequences due to poor overlap). Taxonomy was assigned to Amplicon Sequence Variants (ASVs) using the Greengenes [55] and UNITE [56] databases for 16S and ITS, respectively.

2.5. Statistical analyses

All statistical analyses were conducted in R 3.5.2 [57]. We performed a non-metric multidimensional scaling (NMDS) analysis on plant species cover at each site using the *vegan* package v 2.5–2 [58]. Plant cover data were Hellinger transformed prior to the NMDS [59]. Soil property vectors overlaid on the NMDS were created using the 'envfit' function in *vegan*. From the NMDS, three groups based on sampling point location were apparent. Thus, we split sampling points into three edge locations: perennial grassland, edge, and cropland (n = 5 per transect, n = 30 for each edge location per site). Perennial grassland and cropland included sampling points from 1 m– 33 m on either side of the edge. Edge included samplings points at 0 m, 0.25 m, and 0.5 m into both perennial grassland and cropland. The groupings were examined by permutational multivariate analysis of variance (PERMANOVA) using the adonis function in the *vegan* package. Indicator plant species for each edge location were determined with the *indicspecies* package v 1.7.6 [60].

To examine vegetation biomass and soil properties across the edge, we used linear mixed models (LMM). Fixed effects for all models included edge location, site, and their interaction. Random effects included transect (n = 3) nested within site (n = 2). Total living, grass, forb, and litter biomass, as well as NO_3 and NH_4 were log transformed to meet assumptions of normality. Models were fit with the *lme4* package v 1.1–19 [61] using restricted maximum likelihood (REML) estimation. Model fit was assessed by inspecting residuals to ensure homoscedasticity. We used the *lmerTest* package v 3.0–1 [62] to obtain degrees of freedom and *p*-values. Tukey's HSD post-hoc testing was used to determine significant differences among edge location using the *emmeans* package v 1.3.1 [63].

We conducted an NMDS to examine the bacterial and fungal community of each site. Again, we used a Hellinger transformation on the ASVs, as it places less weight on rare species [64]. The previously established three groups were also examined for the bacterial and fungal communities by PERMANOVA using the adonis function in the *vegan* package.

We used Structural Equation Models (SEMs) to investigate relationships between land management, plants, soil properties, and the soil microbial communities. An advantage of using SEMs is the ability to include multiple complex relationships in an *a priori* theoretical model [65]. Our *a priori* SEM hypothesized that land management had a direct relationship with plants (live plant biomass) (Fig 2). Land management affects plant biomass through direct manipulation of plant community via seeding, harvesting, and mowing. Plant biomass was log-transformed to improve linearity. As land management was included as a categorical variable with three factors (cropland, edge, and perennial grassland), we ran the SEM twice, changing the reference land management category to display all possible comparisons (cropland vs edge, perennial vs edge, cropland vs perennial). We also hypothesized a direct relationship from plant biomass to total C and total N as studies show biomass is an important factor [66, 67]. Lastly, we included an effect of soil properties on the fungal and bacterial communities as soil nutrients may influence soil microbial communities [68, 69].

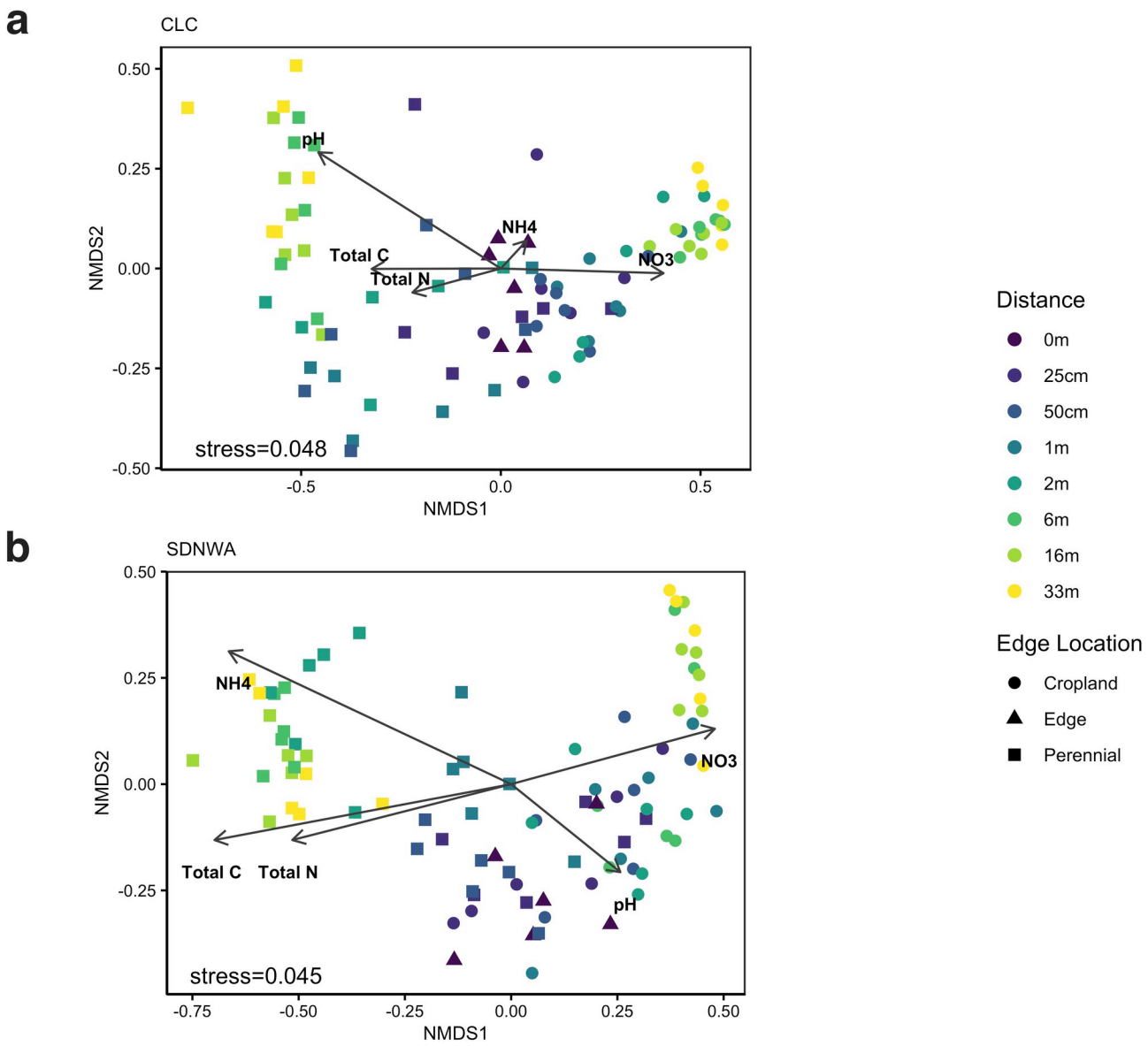

Fig 2. Non-metric multidimensional scaling analysis of vegetation cover. A non-metric multidimensional scaling analysis of vegetation cover at (a) Conservation Learning Centre and (b) St. Denis National Wildlife Area. The colour gradient represents sampling points from 0 m to 33m (into either cropland or perennial grassland), with 0 m being the edge. Shapes represent edge location, triangles are edge points (0m), squares represent points in the perennial grassland and circles represent points in the cropland. Soil property vectors are overlaid on each plot.

https://doi.org/10.1371/journal.pone.0283832.g002

Goodness of fit for SEMs was assessed by the chi-square (p-value > 0.05), Root Mean Square Error of Approximation (RMSEA < 0.08), and Comparative Fit Index (CFI > 0.90) [70, 71]. As our initial *a priori* model was not a good fit (χ^2 p-value < 0.001, RMSEA = 0.299, CFI = 0.692), we evaluated alternative models [72]. As such, our modelling approach was now exploratory and based on modification indices we added pathways with ecological relevance [73]. All models were fit and calculated using the *lavaan* package v 0.6–3 with the maximum likelihood estimation [74].

To further investigate the fungal community, we identified significant fungal genera across the edge at both sites. First, the ASV table was filtered at 20% prevalence across samples to

remove rare species and to prepare data for transformation, zero and NA values in the ASV tables were replaced with an estimate (Count Zero Multiplicative) using the zCompositions package [75]. The centered log-ratio transformation was calculated with the CoDaSeq package v 0.99.4 [76] and these ratios were used for abundance. Genera were aggregated using the *phyloseq* package v 1.24.1 [77] and Welch's *t*-tests used to determine significant differences in genus abundance between each pair of edge location (cropland vs edge, edge vs perennial, perennial vs cropland). *P*-values were adjusted using the p.adjust function in R selecting Bonferroni correction method.

3. Results

3.1. Vegetation community and biomass

Differences in plant community composition were strongly related to edge location (Fig 3). Three distinct clusters were identified: the edge (0.5 m-0.5 m), the cropland (33 m-1 m), and the grassland (1 m-33 m) at both CLC and SDNWA. These plant communities across the edge appear to correlate with soil properties (Fig 2).

The distinct vegetation groupings for edge, perennial grassland, and cropland were driven by abundant non-native annual plant species at the edge, seeded species in the perennial grassland, and the crop in the croplands. Indicator species at the edge included hemp nettle (*Galeopsis tetrahit* L.) and cleaver's (*Galium aparine* L.) at both sites (S1 Table). Non-native annual and some perennial plant species, here called weedy species, were dominant at the edge and comprised 77% ± 8.9% (mean ± SD) of edge plants recorded at CLC and 85% ± 7.4% at SDNWA. In perennial grasslands, *B. inermis* had the highest indicator value of any species at SDNWA, while at CLC, both *B. inermis* and *B. bieberstenii* were strong indicator species. Other indicator species for perennial grassland common to both sites included *M. satvia* and dandelion (*Taraxacum officinale* L.). Indicator species for cropland were the crops planted in 2017, *B. napus* and *L. usitatissimum* for CLC and SDNWA, respectively.

Patterns of aboveground vegetation biomass across the edge differed at each site; as determined by linear mixed modelling, the interaction was significant between site and edge location for each biomass category. At SDNWA, living biomass was greatest in the grassland and significantly decreased across the edge and cropland, however at CLC living biomass was only significantly higher in the perennial grassland compared with the edge (S2A Fig). The greatest forb biomass at CLC was in cropland, due to planted canola, while at SDNWA the greatest forb biomass was at the edge and cropland (S2B Fig). At the edge, forbs consisted of 74% ± 31% and 88% ± 23% (mean ± standard deviation) of living biomass at CLC and SDNWA, respectively. Not surprisingly, the majority of grass biomass was in the perennial grasslands (S2C Fig). Litter biomass was not significantly different across the edge at either site (S2D Fig).

3.2. Soil properties

Overall, soil properties changed across the edge; however, the pattern for total C, NH_4, and pH significantly differed between sites (S2 Table). Total C and N were significantly higher in the perennial grasslands than croplands at both sites. At SDNWA, the edge had intermediate levels of total C and N when compared to grassland and cropland; at CLC, total C and N at the edge were more similar to croplands (S3A and S3B Fig). NO_3 had the opposite trend as total C and N, with significantly higher values in the cropland and edge than the perennial grassland at both sites (S3C Fig). SDNWA had significantly higher NH_4 in perennial grassland compared to edge and cropland, while at CLC, NH_4 was similar across all locations (S2 Table). Soil pH was significantly higher in the perennial grassland at CLC compared to edge and cropland, with pH values ranging across the edge from 4.8–6.9 (S3E Fig). At SDNWA, pH was not

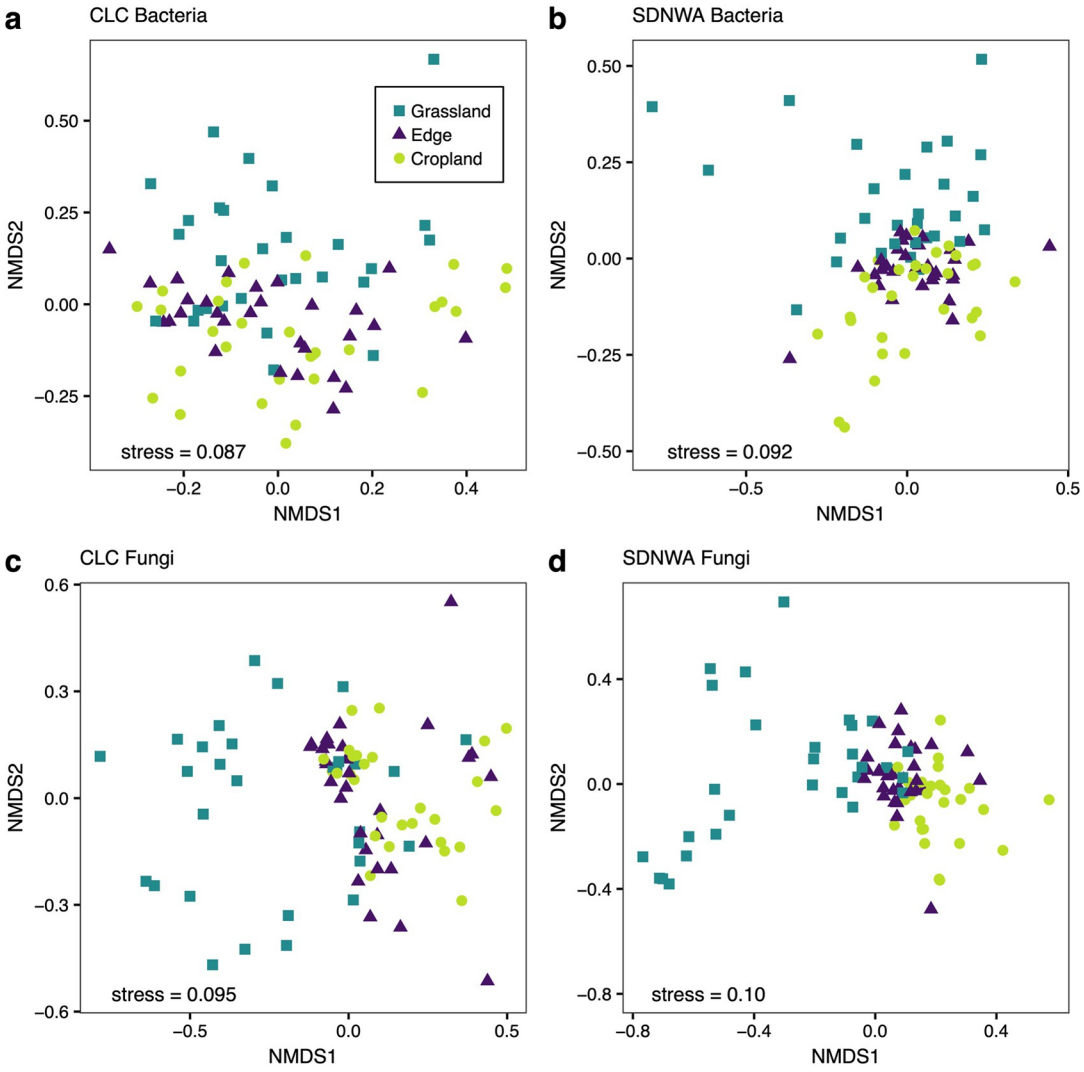

Fig 3. Non-metric multidimensional scaling analysis of microbial community across croplands and perennial grasslands. Non-metric multidimensional scaling analysis for the (a, b) bacterial community and the (c, d) fungal community at the Conservation Learning Centre (CLC) and St. Denis National Wildlife Area (SDNWA). Shape and colour of the points represent location across the edge; perennial grassland (teal squares), edge (purple triangles), and cropland (yellow circles).

https://doi.org/10.1371/journal.pone.0283832.g003

significantly different across the edge, with values that ranged from 6.5–7.5. Overall, soil properties at edge locations were more variable at CLC than at SDNWA.

3.3. Soil microbial community

Both bacterial and fungal communities were different across the edge at CLC and SDNWA (PERMANOVA, S3 Table) (Fig 3). Changes in the bacterial community were less clear, however; at SDNWA, bacterial community composition appears to diverge more with respect to edge location than at CLC (Fig 3A and 3B). Fungal communities at both sites appeared to have a distinct perennial grassland community compared with the edge and cropland (Fig 3C and 3D).

3.4. Structural equation modelling

Our final SEMs, after including direct pathways from land management to both soil properties and microbial communities, were a good fit, with edge as reference (χ^2 p-value = 0.144, RMSEA = 0.074, CFI = 0.996) and perennial grassland as reference (χ^2 p-value = 0.144, RMSEA = 0.074, CFI = 0.996) (S4 Table). We were able to explain 36% of the variation in the fungal community, which was driven primarily by land management (Fig 4). Cropland had a 'positive' relationship and perennial grasslands a 'negative' relationship with the fungal community when compared to the edge, indicating community composition differences (Fig 4A); both cropland and edge had 'positive' relationships with the fungal community, when compared to perennial grasslands (Fig 4B). Therefore, the fungal community was most strongly positively influenced by the cropland, followed by edge, and negatively influenced by perennial grasslands. Bacteria was similarly affected by the cropland and edge (Fig 4A) and had a 'negative' relationship with cropland and edge, compared with perennial grasslands (Fig 4B). Plant biomass had no significant relationships with soil properties but soil properties were significantly influenced by land management (Fig 4A and 4B). Perennial grasslands had 'positive' relationships with both total C and N compared to the edge, while cropland had a 'negative' relationship with total C (Fig 4B). These finding are supported by the significantly higher TC and TN detected in the perennial grassland and the edge having intermediate TC at SDWNA. Similarly, land management relationships with plant biomass follow the same pattern we observed from the linear mixed effect model; the greatest plant biomass was in perennial grasslands (Fig 4A), followed by edge, and then cropland (Fig 4B). While land management had direct impacts on the soil microbial community, soil properties and plant biomass, we did not find any significant pathways from soil properties to the microbial communities. In addition, the interaction between the fungal and bacterial communities was not significant in either model (Fig 4A and 4B).

3.5. Fungal abundance across the edge

Since changes in the fungal community were clearly related to land use (Fig 4) and these differences were more distinct at both of our sites (Fig 3), we further examined shifts in fungal community composition across land uses. After filtering the data set to obtain the most abundant genera (see methods), 50 genera remained (from 392) and six genera were found to be significantly different between at least one location comparison (i.e. cropland vs perennial, edge vs grassland, edge vs cropland). The abundances of five out of the six genera were significantly greater in the cropland than the grassland (Table 1). Two of these genera, *Clonostachys* and *Gibberella*, were also found in greater abundances at the edge compared to the grassland. *Paraphoma* was the only genera that was significantly more abundant at the edge than in the cropland (Table 1).

4. Discussion

We investigated soil properties, vegetation community, and the soil microbial community across edges of perennial grasslands and annual croplands. Land management had direct and indirect influences on the soil microbial community through changes in vegetation and soil properties. Edges acted as an intermediate and unique environment between the two land uses, composed of predominately non-native weedy plants and the edge was more similar to cropland than grassland in both plant and soil.

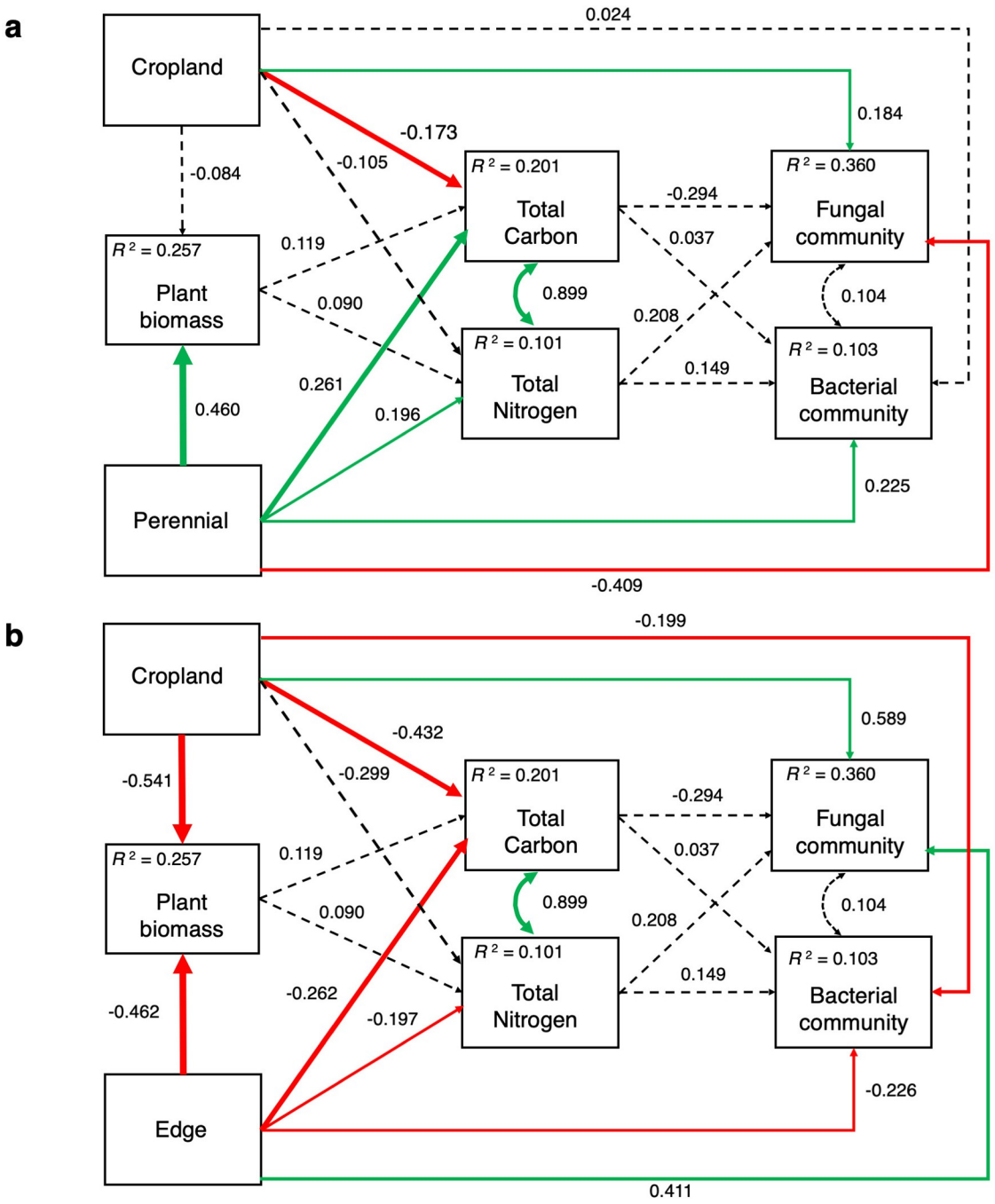

Fig 4. Structural equation model for relationships between land management, microbial communities, soil properties, and vegetation. Final structural equation model (χ^2 p-value = 0.144, RMSEA = 0.074, CFI = 0.996) representing the causal relationships between land management, aboveground plants, soil properties and microbial communities with edge (a) and perennial (b) as the reference category. Data from both SDNWA and CLC are included. Solid arrows are significant ($p < 0.05$) and pathways with dashed arrows are non-significant. Green arrows represent significant positive pathways and red arrows represent significant negative pathways. Standardized partial path coefficients are beside each pathway arrow and R^2 values provided for each dependent variable.

https://doi.org/10.1371/journal.pone.0283832.g004

Table 1. Fungal genera abundance across croplands and perennial grasslands.

Class	Order	Family	Genus (*p*-value)	Abundance
Dothideomycetes	Pleosporales	Phaeosphaeriaceae	*Chalastospora* (0.001[a])	C > E > G
Dothideomycetes	Pleosporales	Phaeosphaeriaceae	*Clonostachys* (0.002[a], <0.001[b])	E > C > G
Sordariomycetes	Hypocreales	Nectriaceae	*Gibberella* (<0.001[a], <0.001[b])	C > E > G
Dothideomycetes	Pleosporales	Phaeosphaeriaceae	*Paraphoma* (0.002[c])	E > G > C
Dothideomycetes	Pleosporales	Phaeosphaeriaceae	*Parastagonospora* (0.001[a])	C > E > G
Sordariomycetes	Hypocreales	Nectriaceae	*Sarocladium* (0.005[a], 0.002[c])	C > E > G

Fungal genera with significantly different ($p < 0.05$) abundances between edge location (at least one significant difference between ([a]) cropland-grassland, ([b]) edge-grassland, ([c]) edge-cropland). Significance was determined by Welch's t-test using abundance values from both sites after centered log-ratio transformation to obtain compositional abundance. All genera were in the Ascomycota phyla and Pezizomycotina subphyla. The order of abundance (greatest to least) is indicated in the abundance column (C = Cropland, E = Edge, G = Grassland).

https://doi.org/10.1371/journal.pone.0283832.t001

4.1. Aboveground changes across the edge

Differences in plant community composition and biomass across the edge was largely determined by land use type. Three different vegetation communities were observed: the perennial grassland, the edge (~1 m in width), and the cropland. Unsurprisingly, cropland vegetation was strongly influenced by the crop seeded; *B. napus* at CLC and *L. usitatissimum* at SDNWA. Living biomass was greatest in grasslands, which were dominated by brome species (*B. inermis* and *B. biebersteinii*) that were seeded in previous years. Both brome species were primary contributors to biomass, as grass constituted 88% of total living biomass.

Plant community composition at the edge was a mixture of grassland plants, crops, and weedy species. Weed population densities are highest near, or at, an edge [78] because these plants are disturbance tolerant [79]. Non-native plant presence in agriculture frequently increases plant species richness in these settings and is driven by agronomic activities [80, 81]. Agronomic activities including general mechanical disturbance such as mowing, crop sowing, and harvesting disturb the edge [82]. While our study sites were no-till systems, croplands still experienced a higher level of disturbance than grasslands throughout the growing season. In-field herbicide and fertilizer application can have unintended effects on adjacent areas [83]. Herbicide and fertilizer drift can reach beyond cropland edges and affect the plant community [84, 85]; for example, fertilizer drift can promote faster growing competitive plant species that outcompete others [84, 86, 87]. In addition to higher nutrient availability, cropland edges have open space allowing undesirable weedy species to establish [82, 88]. These edge effects lend advantages to these plant species that may compete with crops, reducing yields [89] and facilitate invasion of undesirable plants into adjacent, more natural, land use types [90].

Management practices, such as using herbicides or doubling sown crop density are effective in reducing weed populations at edges [91]. However, conventional eradication attempts may bring more detriments to larger agroecosystem, herbicide can drift into non-target areas and weedy species can become herbicide resistant [92]. Field edges can act reservoir for invasive weeds and other undesirable microbial pathogens [93]. However, the reverse is also true, a diverse weed community can provide ecosystem services and habitat to beneficial species [82, 94, 95]. Multiple management strategies are needed to successfully manage edge habitats valuable to many aspects of the agroecosystem.

4.2. Belowground changes across the edge

Land management practices indirectly influenced soil physiochemical properties across perennial grassland-cropland edges through modification of aboveground plant community, and

directly through fertilizer application. We found total C and N were highest in the perennial grasslands and lowest in the cropland; this is common in agroecosystems as soil quality is often poorer in cultivated land compared to non-cultivated land [96–98]. At our sites, perennial grasslands had plant species with relatively high-quality litter that likely influenced soil properties through the deposition of rich C sources. For example, at our sites in the perennial grasslands, *B. inermis* and *M. stavia* produce large amounts of litter that quickly degrades and is high in N content with a low C:N, which can increase soil organic C and rates of soil N cycling [99–101]. In addition, while the cropland is relatively productive, the majority of aboveground biomass is removed, not allowing the plant based C to return to the soil, which is a major source of soil C [102].

Edges are subjected to fertilizer applied to the cropland, evidenced by high spikes of NO_3 in both in cropland and edges. Inorganic N amendments, applied over both long and short time periods, can increase soil total N and NO_3 [103–105]. Nitrate concentrations in edge soils were more similar to croplands, likely due to the close proximity of the edge to the cropland and inputs from surface runoff [106]. However, our observation was only at one time point and may not provide a complete picture of N dynamics and seasonal fluctuations of NO_3 in this system. Regardless, edges in agroecosystems appear to act as a buffer for nutrient movement from managed croplands into adjacent land use types.

4.3. Soil microbial community across the edge

In our study, land management appeared to have a strong influence on soil microbial community composition, as the direct pathways from land management to microbial communities were mostly significant in the SEMs. We chose to focus on community composition rather than a metric like richness, because in cases where richness is not affected, composition can detect more discreet changes [2, 107]. Management practices can directly and indirectly affect soil microbial communities [108–110] and long term practices have selective forces on the soil microbial community, thus changing the microbial community composition as it adapts to these disturbances [111]. Fungal community composition was different in the grassland than cropland, as denoted by a 'negative' impact by the perennial grassland and a 'positive' by the cropland and edge. Fungal community composition was also different between the edge and cropland, though not as pronounced. Bacterial community composition was also different in the perennial grasslands compared to edge or the cropland, however patterns of response across the land uses were not as clear for bacteria as fungi (Fig 3). Bacterial communities may respond less than fungal communities to changes in land use and vegetation, similar patterns were found in no-till cropland and native prairie in Kansas [26] and in comparing native and exotic grasslands [112]. Direct relationships between land management and the microbial community is likely driven by underlying changes of soil and plants associated with land use types.

Plants are an important factor affecting microbial communities, especially at our study sites, land management created three distinct plant communities across the edge. Plant species can influence soil microbes through symbiotic relationships, root exudates, and plant litter inputs [112]. A key difference in plant community across the edge was the dominance of annual plants in the cropland and edge, while the grassland was composed of nearly all perennial plants. *Brassica* species, like the *B. napus* planted at CLC are non-mycorrhizal plants, which would greatly affect both the quantity and quality of AMF hyphae and spores observed [113, 114], thus could be an aspect shaping fungal community composition. The distinction between annual and perennial plants is important as McKenna et al., (2020) [113] found that soil fungal community composition was similar under two different perennial vegetation types

a seeded monoculture of intermediate wheatgrass (*Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey) grassland and a native prairie. However, both perennial fungal communities were different than the fungal community under annual crop rotation. Root architecture and activity may be largely responsible for differences between annual and perennial plants, as perennial grasslands have greater root biomass and more evenly distributed and deeper roots than annual croplands [26]. Annual plants dominated the cropland and edges, which had similar direct effects on fungal community (Fig 4A), suggesting that the life history strategies of dominant plants influence the fungal community.

Although we did not observe significant pathways from soil nutrients to fungi or bacteria, we did observe a strong influence of land use on soil nutrients. The perennial grassland had more total N likely due to more biomass, but high NO_3 and NH_4 were observed in the cropland. Fertilizers containing N can reduce fungal diversity and fungal richness, possibly related to NO_3 [32]. However, others have found no effect of N fertilizers on fungal diversity or richness [114, 115], but differences in fungi community composition [31]. Increased N availability, specifically NO_3, may be disrupting natural plant-soil feedback relationships [31, 116]. By increasing the N available to soil fungi or interrupting available C exudates via N available to plants, NO_3 can alter community composition by promoting or suppressing fungi with different life history strategies based on altered soil conditions [104, 117]. Higher NO_3 levels in the cropland and edge may have been an important driver of microbial community composition, specifically fungi at our study sites. One aspect not considered directly in this analysis, was the soil C to N ratio. The C:N is crucial for microbial functioning [118, 119] and linked to soil microbial community composition [120–122]. Considering the soil C:N explicitly in the future would aid in understanding soil microbial community composition across the edge.

Examining abundant fungal genera revealed further insight into the effect of land management on the fungal community. Plants and soil fungi often develop a stable environment together as their interactions can provide mutual benefits, such as aid in nutrient acquisition for plants and carbon sources for fungi through plant exudates [118]. Different plant species can affect soil fungi differently, likely due to unique soil microbiomes associated with each plant species [119]. For example, plant species with litter high in C:N can promote Basidomycota fungi to aid in decomposition, changing fungal community composition [120, 121]. Fungal genera *Gibberella* and *Paraphoma* were significantly more abundant at the edge and likely reflect the presence of both crop species and grasses. Many *Gibberella* species are plant pathogens that can cause significant crop diseases, such as head blights in grain crops and ear rot in corn (*Zea mays* L.) [122]. *Paraphoma* are common soil fungi and frequently associate with monocots [123]. Furthermore, at the edge we found *P. chrysanthemicola*, a plant pathogen [124, 125] known to affect plants in the Asteraceae and Rosaceae families [126] which were found at the edge. Significant fungal genera abundant in the cropland were mostly pathogenic, including *Sarocladium* [127] and *Parastagonospora*; *P. nodorum*, a major wheat pathogen, which was identified to the species level [128]. Others have hypothesized that edges can act as a reservoir for undesirable microbial pathogens [93]. In our study the difference between fungal communities in cropland and edges, compared to perennial grasslands, was driven by the abundance of pathogens in these more heavily managed land uses supporting this hypothesis.

5. Conclusions

In our study, we saw differences across the edge aboveground and belowground; changes included plant community composition, soil total N and C, and soil microbial community composition. Aboveground, weedy species were most abundant at the edge and appeared to have a positive response to the edge, where conditions from the cropland and grassland made

it ideal for those species [107]. Belowground, soil C and N were lowest in the cropland, but NO_3 was highest in the cropland and edges. Soil microbial community composition across the edge was different, and fungi had more apparent differences in community composition than bacteria. A more in-depth analysis on fungi, showed some genera were more abundant in the cropland, edge, or grassland. For a holistic understanding of agroecosystem impacts, future studies need to consider the interrelated effects of management on soil properties and plant communities as these factors are often driving changes in soil microbial communities [110, 129]. Further knowledge of the interactions between the soil microbial community, soil properties, plants, and edges in the agroecosystem will help to develop more sustainable agricultural practices and build healthier more resilient agroecosystem.

*Raw sequence fasta files and the associated metadata can be found at the National Center for Biotechnology Information (NCBI) under Bioproject PRJNA588061

Supporting information

S1 Fig. *A priori* model used for structural equation models. A priori model used for structural equation modelling. Direct relationships are represented by straight arrows and curved arrows represent unexplained covariate relationships. The first and second axes from non-metric multidimensional scaling analyses was used to represent the fungal and bacterial communities.
(TIF)

S2 Fig. Biomass across croplands and perennial grasslands. Aboveground vegetation biomass (dry weight g/m2) across edge locations (perennial grassland (dark grey), edge (light grey), and cropland (white) at the Conservation Learning Centre (CLC) and St. Denis National Wildlife Area (SDNWA). Boxes encompass 25–75% quantiles of the data, while whiskers encompass 5–95%. The median is indicated by the black horizontal line, and outliers are shown as dots. Different letters indicate a significant difference (p-value < 0.05) between edge locations determined by Tukey-HSD post-hoc tests on linear mixed models.
(TIF)

S3 Fig. Soil properties across croplands and perennial grasslands. Soil properties across edge locations (perennial grassland (dark grey), edge (light grey), and cropland (white) at the Conservation Learning Centre (CLC) and St. Denis National Wildlife Area (SDNWA). Different letters indicate a significant difference (p-value < 0.05) between edge locations determined by Tukey-HSD post-hoc tests on linear mixed models.
(TIF)

S1 Table. Indicator plant species for each edge location (perennial grassland, edge, and cropland) at the Conservation Learning Centre (CLC) and the St. Denis National Wildlife Area (SDNWA). Indicator species are also listed with edge + grassland and edge + cropland. Edge + Grassland is the combination of edge and grassland points on the transect, while Edge + Cropland is the combination of edge and cropland points on the transect.
(DOCX)

S2 Table. F-values (*p*-values) from linear mixed models for biomass (g/m^2) and soil properties (total C and total N (%), NH_4 and NO_3 (μg/g soil), and pH) across edge location (perennial grassland, edge, and cropland), site (Conservation Learning Centre and St. Denis National Wildlife Area), and their interaction. Significant *p*-values are bolded and log transformed data are denoted by †.
(DOCX)

S3 Table. Results from the PERMANOVA for bacteria and fungi at Conservation Learning Centre and St. Denis National Wildlife Area.
(DOCX)

S4 Table. Estimate parameters from both final structural equation models.
(DOCX)

Acknowledgments

Thank you to Alix Schebel for assistance in the laboratory; and Megan Horachek, Raidin Brailsford, Lauren Reynolds, Lukas Smith, and Trang Nguyen for their help with field sampling. Lastly, thank you to Steve Mamet for providing a review of the manuscript.

Author Contributions

Conceptualization: Katherine J. Stewart.

Formal analysis: Mariah Aguiar, Alexandra J. Conway.

Funding acquisition: Katherine J. Stewart.

Investigation: Mariah Aguiar.

Methodology: Jennifer K. Bell.

Supervision: Katherine J. Stewart.

Validation: Jennifer K. Bell.

Writing – original draft: Mariah Aguiar.

Writing – review & editing: Alexandra J. Conway, Jennifer K. Bell.

References

1. Fahrig L. Rethinking patch size and isolation effects: the habitat amount hypothesis. Triantis K, editor. J Biogeogr. 2013 Sep; 40(9):1649–63.
2. Wilson MC, Chen XY, Corlett RT, Didham RK, Ding P, Holt RD, et al. Habitat fragmentation and biodiversity conservation: key findings and future challenges. Landsc Ecol. 2016 Feb; 31(2):219–27.
3. Nagendra H, Munroe DK, Southworth J. From pattern to process: landscape fragmentation and the analysis of land use/land cover change. Agric Ecosyst Environ. 2004 Feb; 101(2–3):111–5.
4. Krauss J, Bommarco R, Guardiola M, Heikkinen RK, Helm A, Kuussaari M, et al. Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels: Immediate and time-delayed biodiversity loss. Ecol Lett. 2010 Apr 16; 13(5):597–605.
5. Fischer J, Lindenmayer DB. Landscape modification and habitat fragmentation: a synthesis. Glob Ecol Biogeogr. 2007 May; 16(3):265–80.
6. Ries L, Fletcher RJ, Battin J, Sisk TD. Ecological responses to habitat edges: mechanisms, models, and variability explained. Annu Rev Ecol Evol Syst. 2004 Dec 15; 35(1):491–522.
7. Dickson BG, Jenness JS, Beier P. Influence of vegetation, topography, and roads on cougar movement in southern California. J Wildl Manag. 2005 Jan; 69(1):264–76.
8. Gieselman TM, Hodges KE, Vellend M. Human-induced edges alter grassland community composition. Biol Conserv. 2013 Feb; 158:384–92.
9. Baker TP, Jordan GJ, Baker SC. Microclimatic edge effects in a recently harvested forest: Do remnant forest patches create the same impact as large forest areas? For Ecol Manag. 2016 Apr; 365:128–36.
10. Honnay O, Verheyen K, Hermy M. Permeability of ancient forest edges for weedy plant species invasion. For Ecol Manag. 2002 May; 161(1–3):109–22.
11. Sarthou JP, Ouin A, Arrignon F, Barreau G, Bouyjou B. Landscape parameters explain the distribution and abundance of Episyrphus balteatus (Diptera: Syrphidae). Eur J Entomol. 2005 Aug 15; 102 (3):539–45.

12. Pohlman CL, Turton SM, Goosem M. Temporal variation in microclimatic edge effects near powerlines, highways and streams in Australian tropical rainforest. Agric For Meteorol. 2009 Jan; 149(1):84–95.

13. Fletcher RJ. Multiple edge effects and their implications in fragmented landscapes. J Anim Ecol. 2005 Mar; 74(2):342–52.

14. Gonzalez M, Ladet S, Deconchat M, Cabanettes A, Alard D, Balent G. Relative contribution of edge and interior zones to patch size effect on species richness: An example for woody plants. For Ecol Manag. 2010 Jan; 259(3):266–74.

15. Watling JI, Orrock JL. Measuring edge contrast using biotic criteria helps define edge effects on the density of an invasive plant. Landsc Ecol. 2010 Jan; 25(1):69–78.

16. Jules ES, Shahani P. A broader ecological context to habitat fragmentation: Why matrix habitat is more important than we thought. J Veg Sci. 2003 Jun; 14(3):459–64.

17. Murphy HT, Lovett-Doust J. Context and connectivity in plant metapopulations and landscape mosaics: does the matrix matter? Oikos. 2004 Apr; 105(1):3–14.

18. Culman SW, Young-Mathews A, Hollander AD, Ferris H, Sánchez-Moreno S, O'Geen AT, et al. Biodiversity is associated with indicators of soil ecosystem functions over a landscape gradient of agricultural intensification. Landsc Ecol. 2010 Nov; 25(9):1333–48.

19. Didham RK, Barker GM, Bartlam S, Deakin EL, Denmead LH, Fisk LM, et al. Agricultural intensification exacerbates spillover effects on soil biogeochemistry in adjacent forest remnants. Lehman RM, editor. PLOS ONE. 2015 Jan 9; 10(1):e0116474.

20. Buhk C, Alt M, Steinbauer MJ, Beierkuhnlein C, Warren SD, Jentsch A. Homogenizing and diversifying effects of intensive agricultural land-use on plant species beta diversity in Central Europe—A call to adapt our conservation measures. Sci Total Environ. 2017 Jan; 576:225–33. https://doi.org/10.1016/j.scitotenv.2016.10.106 PMID: 27788437

21. Lambin EF, Turner BL, Geist HJ, Agbola SB, Angelsen A, Bruce JW, et al. The causes of land-use and land-cover change: moving beyond the myths. Glob Environ Change. 2001 Dec; 11(4):261–9.

22. Wilkerson ML. Invasive plants in conservation linkages: a conceptual model that addresses an underappreciated conservation issue. Ecography. 2013 Dec; 36(12):1319–30.

23. Oerke EC, Dehne HW. Safeguarding production—losses in major crops and the role of crop protection. Crop Prot. 2004 Apr; 23(4):275–85.

24. Pocewicz A, Morgan P, Kavanagh K. The effects of adjacent land use on nitrogen dynamics at forest edges in northern Idaho. Ecosystems. 2007 Jul 17; 10(2):226–38.

25. Bergès L, Pellissier V, Avon C, Verheyen K, Dupouey JL. Unexpected long-range edge-to-forest interior environmental gradients. Landsc Ecol. 2013 Mar; 28(3):439–53.

26. DuPont ST, Culman SW, Ferris H, Buckley DH, Glover JD. No-tillage conversion of harvested perennial grassland to annual cropland reduces root biomass, decreases active carbon stocks, and impacts soil biota. Agric Ecosyst Environ. 2010 Apr 15; 137(1–2):25–32.

27. Zhang Q, Wu J, Yang F, Lei Y, Zhang Q, Cheng X. Alterations in soil microbial community composition and biomass following agricultural land use change. Sci Rep. 2016 Dec; 6(1):36587. https://doi.org/10.1038/srep36587 PMID: 27812029

28. Murphy DV, Cookson WR, Braimbridge M, Marschner P, Jones DL, Stockdale EA, et al. Relationships between soil organic matter and the soil microbial biomass (size, functional diversity, and community structure) in crop and pasture systems in a semi-arid environment. Soil Res. 2011; 49(7):582.

29. Rousk J, Bååth E, Brookes PC, Lauber CL, Lozupone C, Caporaso JG, et al. Soil bacterial and fungal communities across a pH gradient in an arable soil. ISME J. 2010 Oct; 4(10):1340–51. https://doi.org/10.1038/ismej.2010.58 PMID: 20445636

30. Schimel J, Balser TC, Wallenstein M. Microbial stress-response physiology and its implications for ecosystem function. Ecology. 2007 Jun; 88(6):1386–94. https://doi.org/10.1890/06-0219 PMID: 17601131

31. Paungfoo-Lonhienne C, Yeoh YK, Kasinadhuni NRP, Lonhienne TGA, Robinson N, Hugenholtz P, et al. Nitrogen fertilizer dose alters fungal communities in sugarcane soil and rhizosphere. Sci Rep. 2015 Aug; 5(1):8678. https://doi.org/10.1038/srep08678 PMID: 25728892

32. Chen C, Zhang J, Lu M, Qin C, Chen Y, Yang L, et al. Microbial communities of an arable soil treated for 8 years with organic and inorganic fertilizers. Biol Fertil Soils. 2016 May; 52(4):455–67.

33. Lupwayi NZ, Rice WA, Clayton GW. Soil microbial diversity and community structure under wheat as influenced by tillage and crop rotation. Soil Biol Biochem. 1998 Nov; 30(13):1733–41.

34. Brussaard L, de Ruiter PC, Brown GG. Soil biodiversity for agricultural sustainability. Agric Ecosyst Environ. 2007 Jul; 121(3):233–44.

35. Van Bruggen AHC, He MM, Shin K, Mai V, Jeong KC, Finckh MR, et al. Environmental and health effects of the herbicide glyphosate. Sci Total Environ. 2018 Mar;616–617:255–68. https://doi.org/10.1016/j.scitotenv.2017.10.309 PMID: 29117584

36. Guijarro KH, Aparicio V, De Gerónimo E, Castellote M, Figuerola EL, Costa JL, et al. Soil microbial communities and glyphosate decay in soils with different herbicide application history. Sci Total Environ. 2018 Sep; 634:974–82. https://doi.org/10.1016/j.scitotenv.2018.03.393 PMID: 29660891

37. Postma-Blaauw MB, de Goede RGM, Bloem J, Faber JH, Brussaard L. Soil biota community structure and abundance under agricultural intensification and extensification. Ecology. 2010 Feb; 91(2):460–73. https://doi.org/10.1890/09-0666.1 PMID: 20392011

38. Boer W de Folman LB, Summerbell RC, Boddy L. Living in a fungal world: impact of fungi on soil bacterial niche development. FEMS Microbiol Rev. 2005 Sep; 29(4):795–811. https://doi.org/10.1016/j.femsre.2004.11.005 PMID: 16102603

39. Sayer EJ, Oliver AE, Fridley JD, Askew AP, Mills RTE, Grime JP. Links between soil microbial communities and plant traits in a species-rich grassland under long-term climate change. Ecol Evol. 2017 Feb; 7(3):855–62. https://doi.org/10.1002/ece3.2700 PMID: 28168022

40. Sun R, Li W, Dong W, Tian Y, Hu C, Liu B. Tillage changes vertical distribution of soil bacterial and fungal communities. Front Microbiol [Internet]. 2018 Apr 9 [cited 2019 Apr 2];9. Available from: http://journal.frontiersin.org/article/10.3389/fmicb.2018.00699 PMID: 29686662

41. Berg G, Smalla K. Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere: Plant species, soil type and rhizosphere communities. FEMS Microbiol Ecol. 2009 Apr; 68(1):1–13.

42. Callaway RM, Thelen GC, Rodriguez A, Holben WE. Soil biota and exotic plant invasion. Nature. 2004 Feb; 427(6976):731–3. https://doi.org/10.1038/nature02322 PMID: 14973484

43. Zak DR, Holmes WE, White DC, Peacock AD, Tilman D. Plant diveristy, soil microbial communities and ecosystem function: are there any links? Ecology. 2003 Aug; 84(8):2042–50.

44. van der Heijden MGA, Bardgett RD, van Straalen NM. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecol Lett. 2008 Mar; 11(3):296–310. https://doi.org/10.1111/j.1461-0248.2007.01139.x PMID: 18047587

45. Shorthouse JD. Ecoregions of Canada's prairie grasslands. In: Arthropods of Canadian Grasslands: Ecology and Interactions in Grassland Habitats. Biological Survey of Canada; 2010.

46. Pennock D, Bedard-Haughn A, Viaud V. Chernozemic soils of Canada: genesis, distribution, and classification. Can J Soil Sci. 2011 Oct; 91(5):719–47.

47. Henderson DC, Canada, Environment Canada, Canadian Wildlife Service. St. Denis National Wildlife Area management plan. [Internet]. 2013 [cited 2021 Jan 20]. Available from: http://epe.lac-bac.gc.ca/100/201/301/weekly_checklist/2014/internet/w14-10-U-E.html/collections/collection_2014/ec/CW66-325-2013-eng.pdf

48. Carter M, Gregorich E, editors. Soil sampling and methods of analysis, second edition [Internet]. CRC Press; 2007 [cited 2019 Apr 11]. Available from: https://www.taylorfrancis.com/books/9781420005271

49. Thomas GW. Soil pH and soil acidity. In: Methods of Soil Analysis Part 3: Chemical Methods. Madison, Wisconsin: Soil Science Society of America; 1996. p. 475–90. (SSSA Book).

50. Caporaso JG, Lauber CL, Walters WA, Berg-Lyons D, Lozupone CA, Turnbaugh PJ, et al. Global patterns of 16S rRNA diversity at a depth of millions of sequences per sample. Proc Natl Acad Sci. 2011 Mar 15; 108(Supplement_ 1):4516–22. https://doi.org/10.1073/pnas.1000080107 PMID: 20534432

51. Gardes M, Bruns TD. ITS primers with enhanced specificity for basidiomycetes—application to the identification of mycorrhizae and rusts. Mol Ecol. 1993 Apr; 2(2):113–8. https://doi.org/10.1111/j.1365-294x.1993.tb00005.x PMID: 8180733

52. White TJ, Bruns T, Lee S, Taylor J. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: In PCR protocols: a guide to methods and applications. New York: Academic Press; 1990. p. 315–22.

53. Caporaso JG, Kuczynski J, Stombaugh J, Bittinger K, Bushman FD, Costello EK, et al. QIIME allows analysis of high-throughput community sequencing data. Nat Methods. 2010 May; 7(5):335–6. https://doi.org/10.1038/nmeth.f.303 PMID: 20383131

54. Callahan BJ, McMurdie PJ, Rosen MJ, Han AW, Johnson AJA, Holmes SP. DADA2: high-resolution sample inference from Illumina amplicon data. Nat Methods. 2016 Jul; 13(7):581–3. https://doi.org/10.1038/nmeth.3869 PMID: 27214047

55. DeSantis TZ, Hugenholtz P, Larsen N, Rojas M, Brodie EL, Keller K, et al. Greengenes, a chimera-checked 16S rRNA gene database and workbench compatible with ARB. Appl Environ Microbiol. 2006 Jul 1; 72(7):5069–72. https://doi.org/10.1128/AEM.03006-05 PMID: 16820507

56. Nilsson RH, Larsson KH, Taylor AFS, Bengtsson-Palme J, Jeppesen TS, Schigel D, et al. The UNITE database for molecular identification of fungi: handling dark taxa and parallel taxonomic classifications. Nucleic Acids Res. 2019 Jan 8; 47(D1):D259–64.

57. R Core Team. R: A language and environment for statistical computing [Internet]. Vienna, Austria; 2018. (R Foundation for Statistical Computing). Available from: https://www.R-project.org/

58. Oksanen J, Guillaume Blanchet F, Friendly M, Kindt R, Legendre P, McGlinn D, et al. vegan: community ecology package. R package version 2.5–3 [Internet]. 2018. Available from: https://CRAN.R-project.org/package=vegan

59. Legendre P, Legendre L. Numerical ecology. Third English edition. Amsterdam: Elsevier; 2012. 990 p. (Developments in environmental modelling).

60. Cáceres MD, Legendre P. Associations between species and groups of sites: indices and statistical inference. Ecology. 2009 Dec; 90(12):3566–74. https://doi.org/10.1890/08-1823.1 PMID: 20120823

61. Bates D, Mächler M, Bolker B, Walker S. Fitting linear mixed-effects models using lme4. J Stat Softw [Internet]. 2015 [cited 2019 Apr 8];67(1). Available from: http://www.jstatsoft.org/v67/i01/

62. Kuznetsova A, Brockhoff PB, Christensen RHB. lmerTest package: tests in linear mixed effects models. J Stat Softw [Internet]. 2017 [cited 2019 Apr 8];82(13). Available from: http://www.jstatsoft.org/v82/i13/

63. Lenth R. emmeans: estimated marginal means, aka least-squares means. R package version 1.3.2. [Internet]. 2019 Mar. Available from: https://CRAN.R-project.org/package=emmeans

64. Legendre P, Gallagher ED. Ecologically meaningful transformations for ordination of species data. Oecologia. 2001 Oct; 129(2):271–80. https://doi.org/10.1007/s004420100716 PMID: 28547606

65. Grace JB. Structural equation modeling and natural systems [Internet]. Cambridge, UK; New York: Cambridge University Press; 2006 [cited 2019 Apr 4]. Available from: https://doi.org/http%3A//dx.doi.org/10.1017/CBO9780511617799

66. Li W, Xiao Y, Wang C, Dang J, Chen C, Gao L, et al. A new species of Devriesia causing sooty blotch and flyspeck on rubber trees in China. Mycol Prog. 2013 Nov; 12(4):733–8.

67. Bansal S, Sheley RL, Blank B, Vasquez EA. Plant litter effects on soil nutrient availability and vegetation dynamics: changes that occur when annual grasses invade shrub-steppe communities. Plant Ecol. 2014 Mar; 215(3):367–78.

68. Bulluck LR, Brosius M, Evanylo GK, Ristaino JB. Organic and synthetic fertility amendments influence soil microbial, physical and chemical properties on organic and conventional farms. Appl Soil Ecol. 2002 Feb; 19(2):147–60.

69. Koorem K, Gazol A, Öpik M, Moora M, Saks Ü, Uibopuu A, et al. Soil Nutrient Content Influences the Abundance of Soil Microbes but Not Plant Biomass at the Small-Scale. Reinhart KO, editor. PLoS ONE. 2014 Mar 17; 9(3):e91998.

70. Hooper DU, Coughlan J, Mullen MR. Structural Equation Modelling: Guidelines for Determining Model Fit. Electron J Bus Res Methods. 2008; 6(1):53–60.

71. Grace JB, Schoolmaster DR, Guntenspergen GR, Little AM, Mitchell BR, Miller KM, et al. Guidelines for a graph-theoretic implementation of structural equation modeling. Ecosphere. 2012 Aug; 3(8):art73.

72. Grace JB, Anderson TM, Olff H, Scheiner SM. On the specification of structural equation models for ecological systems. Ecol Monogr. 2010 Feb; 80(1):67–87.

73. Lamb E, Shirtliffe S, May W. Structural equation modeling in the plant sciences: An example using yield components in oat. Can J Plant Sci. 2011 Jul; 91(4):603–19.

74. Rosseel Y. lavaan: an R package for structural equation modeling. J Stat Softw [Internet]. 2012 [cited 2019 Apr 4];48(2). Available from: http://www.jstatsoft.org/v48/i02/

75. Palarea-Albaladejo J, Martín-Fernández JA. zCompositions—R package for multivariate imputation of left-censored data under a compositional approach. Chemom Intell Lab Syst. 2015 Apr; 143:85–96.

76. Gloor GB, Reid G. Compositional analysis: a valid approach to analyze microbiome high-throughput sequencing data. Can J Microbiol. 2016 Aug; 62(8):692–703. https://doi.org/10.1139/cjm-2015-0821 PMID: 27314511

77. McMurdie PJ, Holmes S. phyloseq: an R package for reproducible interactive analysis and graphics of microbiome census data. Watson M, editor. PLoS ONE. 2013 Apr 22; 8(4):e61217.

78. Cardina J, Johnson GA, Sparrow DH. The nature and consequence of weed spatial distribution. Weed Sci. 1997 Jun; 45(3):364–73.

79. Owen MD, Zelaya IA. Herbicide-resistant crops and weed resistance to herbicides. Pest Manag Sci. 2005 Mar; 61(3):301–11. https://doi.org/10.1002/ps.1015 PMID: 15668920

80. Benvenuti S. Weed seed movement and dispersal strategies in the agricultural environment. Weed Biol Manag. 2007 Sep; 7(3):141–57.

81. Boscutti F, Sigura M, De Simone S, Marini L. Exotic plant invasion in agricultural landscapes: A matter of dispersal mode and disturbance intensity. Ohlemuller R, editor. Appl Veg Sci. 2018 Apr; 21(2):250–7.

82. Gaba S, Perronne R, Fried G, Gardarin A, Bretagnolle F, Biju-Duval L, et al. Response and effect traits of arable weeds in agro-ecosystems: a review of current knowledge. Storkey J, editor. Weed Res. 2017 Jun; 57(3):123–47.

83. Fried G, Villers A, Porcher E. Assessing non-intended effects of farming practices on field margin vegetation with a functional approach. Agric Ecosyst Environ. 2018 Jul; 261:33–44.

84. Schmitz J, Hahn M, Brühl CA. Agrochemicals in field margins–An experimental field study to assess the impacts of pesticides and fertilizers on a natural plant community. Agric Ecosyst Environ. 2014 Aug; 193:60–9.

85. Metcalfe H, Hassall KL, Boinot S, Storkey J. The contribution of spatial mass effects to plant diversity in arable fields. Manning P, editor. J Appl Ecol. 2019 Jul; 56(7):1560–74.

86. Bassa M, Boutin C, Chamorro L, Sans FX. Effects of farming management and landscape heterogeneity on plant species composition of Mediterranean field boundaries. Agric Ecosyst Environ. 2011 May; 141(3–4):455–60.

87. Pellissier L, Wisz MS, Strandberg B, Damgaard C. Herbicide and fertilizers promote analogous phylogenetic responses but opposite functional responses in plant communities. Environ Res Lett. 2014 Jan 1; 9(2):024016.

88. Radosevich SR, Holt JS, Ghersa C, Radosevich SR. Ecology of weeds and invasive plants: relationship to agriculture and natural resource management. 3rd ed. Hoboken N.J: Wiley-Interscience; 2007. 454 p.

89. Mack RN, Simberloff D, Mark Lonsdale W, Evans H, Clout M, Bazzaz FA. Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl. 2000 Jun; 10(3):689–710.

90. With KA. The Landscape Ecology of Invasive Spread. Conserv Biol. 2002 Oct; 16(5):1192–203.

91. Poggio SL, Chaneton EJ, Ghersa CM. The arable plant diversity of intensively managed farmland: Effects of field position and crop type at local and landscape scales. Agric Ecosyst Environ. 2013 Feb; 166:55–64.

92. MacLaren C, Storkey J, Menegat A, Metcalfe H, Dehnen-Schmutz K. An ecological future for weed science to sustain crop production and the environment. A review. Agron Sustain Dev. 2020 Aug; 40 (4):24.

93. Boutin C, Jobin B. Intensity of agricultural practices and effects on adjacent habitats. Ecol Appl. 1998 May; 8(2):544–57.

94. Tscharntke T, Tylianakis JM, Rand TA, Didham RK, Fahrig L, Batáry P, et al. Landscape moderation of biodiversity patterns and processes—eight hypotheses. Biol Rev. 2012 Aug; 87(3):661–85. https://doi.org/10.1111/j.1469-185X.2011.00216.x PMID: 22272640

95. Magura T, Lövei GL, Tóthmérész B. Edge responses are different in edges under natural versus anthropogenic influence: a meta-analysis using ground beetles. Ecol Evol. 2017 Feb; 7(3):1009–17. https://doi.org/10.1002/ece3.2722 PMID: 28168036

96. Hebb C, Schoderbek D, Hernandez-Ramirez G, Hewins D, Carlyle CN, Bork E. Soil physical quality varies among contrasting land uses in Northern Prairie regions. Agric Ecosyst Environ. 2017 Mar; 240:14–23.

97. Cade-Menun B, Bainard L, LaForge K, Schellenberg M, Houston B, Hamel C. Long-term agricultural land use affects chemical and physical properties of soils from Southwest Saskatchewan. Can J Soil Sci [Internet]. 2017 Jul 13 [cited 2019 Apr 5]; Available from: http://www.nrcresearchpress.com/doi/https://doi.org/10.1139/CJSS-2016-0153

98. Panico SC, Memoli V, Esposito F, Maisto G, De Marco A. Plant cover and management practices as drivers of soil quality. Appl Soil Ecol. 2018 Aug; 129:34–42.

99. Redin M, Recous S, Aita C, Dietrich G, Skolaude AC, Ludke WH, et al. How the chemical composition and heterogeneity of crop residue mixtures decomposing at the soil surface affects C and N mineralization. Soil Biol Biochem. 2014 Nov; 78:65–75.

100. Lardner HA, Damiran D, McKinnon JJ. Evaluation of 3 bromegrass species as pasture: Herbage nutritive value, estimated grass dry matter intake and steer performance. Livest Sci. 2015 May; 175:77–82.

101. Piper CL, Lamb EG, Siciliano SD. Smooth brome changes gross soil nitrogen cycling processes during invasion of a rough fescue grassland. Plant Ecol. 2015 Feb; 216(2):235–46.

102. Berti A, Morari F, Dal Ferro N, Simonetti G, Polese R. Organic input quality is more important than its quantity: C turnover coefficients in different cropping systems. Eur J Agron. 2016 Jul; 77:138–45.

103. Malhi SS, Lemke R, Wang ZH, Chhabra BS. Tillage, nitrogen and crop residue effects on crop yield, nutrient uptake, soil quality, and greenhouse gas emissions. Soil Tillage Res. 2006 Nov; 90(1–2):171–83.

104. Zhou J, Jiang X, Zhou B, Zhao B, Ma M, Guan D, et al. Thirty four years of nitrogen fertilization decreases fungal diversity and alters fungal community composition in black soil in northeast China. Soil Biol Biochem. 2016 Apr; 95:135–43.

105. Huang R, McGrath SP, Hirsch PR, Clark IM, Storkey J, Wu L, et al. Plant–microbe networks in soil are weakened by century-long use of inorganic fertilizers. Microb Biotechnol. 2019 Nov; 12(6):1464–75. https://doi.org/10.1111/1751-7915.13487 PMID: 31536680

106. Tsiouris SE, Mamolos AP, Kalburtji KL, Alifrangis D. The quality of runoff water collected from a wheat field margin in Greece. Agric Ecosyst Environ. 2002 Apr; 89(1–2):117–25.

107. Ries L, Murphy SM, Wimp GM, Fletcher RJ. Closing Persistent Gaps in Knowledge About Edge Ecology. Curr Landsc Ecol Rep. 2017 Mar; 2(1):30–41.

108. Papiernick SK, Lindstrom MJ, Schumacher JA, Farenhorst A, Stephens KD, Schumacher TE, et al. Variation in soil properties and crop yield across an eroded prairie landscape. J Soil Water Conserv. 2005 Nov; 60(6).

109. Helgason BL, Konschuh HJ, Bedard-Haughn A, VandenBygaart AJ. Microbial distribution in an eroded landscape: Buried A horizons support abundant and unique communities. Agric Ecosyst Environ. 2014 Oct; 196:94–102.

110. Tosi M, Mitter EK, Gaiero J, Dunfield K. It takes three to tango: the importance of microbes, host plant, and soil management to elucidate manipulation strategies for the plant microbiome. Can J Microbiol. 2020 May 12;1–21. https://doi.org/10.1139/cjm-2020-0085 PMID: 32396748

111. Checinska Sielaff A, Upton RN, Hofmockel KS, Xu X, Polley HW, Wilsey BJ. Microbial community structure and functions differ between native and novel (exotic-dominated) grassland ecosystems in an 8-year experiment. Plant Soil. 2018 Nov; 432(1–2):359–72.

112. van der Putten WH, Bardgett RD, Bever JD, Bezemer TM, Casper BB, Fukami T, et al. Plant-soil feedbacks: the past, the present and future challenges. Hutchings M, editor. J Ecol. 2013 Mar; 101(2):265–76.

113. McKenna TP, Crews TE, Kemp L, Sikes BA. Community structure of soil fungi in a novel perennial crop monoculture, annual agriculture, and native prairie reconstruction. Bhadauria T, editor. PLOS ONE. 2020 Jan 30; 15(1):e0228202.

114. Mueller RC, Belnap J, Kuske CR. Soil bacterial and fungal community responses to nitrogen addition across soil depth and microhabitat in an arid shrubland. Front Microbiol [Internet]. 2015 Sep 4 [cited 2019 Apr 2];6. Available from: http://journal.frontiersin.org/Article/10.3389/fmicb.2015.00891/abstract

115. Katulanda PM, Walley FL, Janzen HH, Helgason BL. Land use legacy regulates microbial community composition in transplanted Chernozems. Appl Soil Ecol. 2018 Aug; 129:13–23.

116. in 't Zandt D, van den Brink A, de Kroon H, Visser EJW. Plant-soil feedback is shut down when nutrients come to town. Plant Soil. 2019 Jun; 439(1–2):541–51.

117. Chen D, Xing W, Lan Z, Saleem M, Wu Y, Hu S, et al. Direct and indirect effects of nitrogen enrichment on soil organisms and carbon and nitrogen mineralization in a semi-arid grassland. Wang F, editor. Funct Ecol. 2019 Jan; 33(1):175–87.

118. Mooshammer M, Wanek W, Hämmerle I, Fuchslueger L, Hofhansl F, Knoltsch A, et al. Adjustment of microbial nitrogen use efficiency to carbon:nitrogen imbalances regulates soil nitrogen cycling. Nat Commun. 2014 Sep; 5(1):3694. https://doi.org/10.1038/ncomms4694 PMID: 24739236

119. Spohn M. Microbial respiration per unit microbial biomass depends on litter layer carbon-to-nitrogen ratio. Biogeosciences. 2015 Feb 10; 12(3):817–23.

120. Ni Y, Yang T, Zhang K, Shen C, Chu H. Fungal Communities Along a Small-Scale Elevational Gradient in an Alpine Tundra Are Determined by Soil Carbon Nitrogen Ratios. Front Microbiol. 2018 Aug 7; 9:1815. https://doi.org/10.3389/fmicb.2018.01815 PMID: 30131790

121. Wan X, Huang Z, He Z, Yu Z, Wang M, Davis MR, et al. Soil C:N ratio is the major determinant of soil microbial community structure in subtropical coniferous and broadleaf forest plantations. Plant Soil. 2015 Feb; 387(1–2):103–16.

122. Shen C, Xiong J, Zhang H, Feng Y, Lin X, Li X, et al. Soil pH drives the spatial distribution of bacterial communities along elevation on Changbai Mountain. Soil Biol Biochem. 2013 Feb; 57:204–11.

123. Zeilinger S, Gupta VK, Dahms TES, Silva RN, Singh HB, Upadhyay RS, et al. Friends or foes? Emerging insights from fungal interactions with plants. van der Meer JR, editor. FEMS Microbiol Rev. 2016 Mar; 40(2):182–207.

124. Hannula SE, Ma H, Pérez-Jaramillo JE, Pineda A, Bezemer TM. Structure and ecological function of the soil microbiome affecting plant–soil feedbacks in the presence of a soil-borne pathogen. Environ Microbiol. 2020 Feb; 22(2):660–76. https://doi.org/10.1111/1462-2920.14882 PMID: 31788934

125. Lauber CL, Strickland MS, Bradford MA, Fierer N. The influence of soil properties on the structure of bacterial and fungal communities across land-use types. Soil Biol Biochem. 2008 Sep; 40(9):2407–15.

126. Tian Q, Taniguchi T, Shi WY, Li G, Yamanaka N, Du S. Land-use types and soil chemical properties influence soil microbial communities in the semiarid Loess Plateau region in China. Sci Rep. 2017 May; 7(1):45289. https://doi.org/10.1038/srep45289 PMID: 28349918

127. Desjardins AE. Gibberella from a (venaceae) to z (eae). Annu Rev Phytopathol. 2003 Sep; 41 (1):177–98.

128. Boerema GH, editor. Phoma identification manual: differentiation of specific and infra-specific taxa in culture. Wallingford: CABI Publ; 2004. 470 p.

129. Hay FS, Gent DH, Pilkington SJ, Pearce TL, Scott JB, Pethybridge SJ. Changes in distribution and frequency of fungi associated with a foliar disease complex of Pyrethrum in Australia. Plant Dis. 2015 Sep; 99(9):1227–35. https://doi.org/10.1094/PDIS-12-14-1357-RE PMID: 30695926