Received: 7 October 2023 | Revised: 12 April 2025 | Accepted: 9 June 2025

DOI: 10.1002/ecs2.70375

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

ARTICLE

Agroecosystems

Reduction in nitrification during the early transition from conventional to organic farming practices

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Funding information
Stroud Water Research Center, Endowment Fund; William Penn Foundation, Grant/Award Number: 188-17

Handling Editor: Jacob M. Jungers

Abstract

Little is known about the nitrogen transformation dynamics during the early transition phase from conventional to organic farming. We investigated changes in microbial N-cycling in agricultural fields transitioning from conventional to organic farming practices by quantifying nitrification/mineralization rates, extracellular enzyme activity (EEA), and nitrogen transformation genes (nitrification and denitrification). The farming practices we investigated contained three binary treatments: Management System (denoting both general approach and fertility source), Tillage, and Cover Crop. Four years after the transition, we found that the process of converting conventionally managed fields to organic agricultural practices significantly reduced net nitrification rates, likely as a result of lower abundances of ammonia-oxidizing archaea (AOA) and ammonia-oxidizing bacteria (AOB). In addition to terms pertaining to the experimental treatments, we included a term, Year, in our models to control for noise due to the cash/cover crop rotation and weather-related differences. We found that the Year covariate to have highly significant variation related to net nitrification, soil NH_4^+-N concentration, the EEA ratio of NAG:BG, and the abundances of AOA, AOB, and the denitrifying gene *nosZ*. In contrast to much of the published literature, our results showed the absence of a significant response to the Tillage and Cover Crop treatments after four years of conversion. Combined with year-to-year variation being generally more important of an influence than the Tillage and Cover Crop treatments, our results suggest that nutrient processes change gradually in response to farming practices. Therefore, incorporating research about the inter-year variations may yield predictive models that would be useful not just to researchers but also to guide farmers engaged in conventional-to-organic conversion projects.

KEYWORDS
climate change, conventional and organic farming, tillage, cover crops, early transition, extracellular enzyme, N functional genes, nitrification and mineralization

INTRODUCTION

Conventional agricultural practices, often characterized by the use of synthetic fertilizers, herbicides, pesticides, and intensive monocropping, have greatly increased agricultural yields, but at great cost to soil health, soil stability, and water quality (Baumhardt et al., 2015; McLeman et al., 2014; Poore & Nemecek, 2018; Zhang et al., 2015). For example, tilling not only increases soil fertility by facilitating the degradation of soil organic matter (SOM) and increasing the amount of bioavailable nutrients for crops but also simultaneously leads to the depletion of soil nutrients, organic matter, and physical soil properties, leading soils to be more susceptible to wind and water erosion (Baumhardt et al., 2015; Johnson & Hoyt, 1999; McLeman et al., 2014). In unamended soils, SOM is the major nutrient source, including nitrogen (N) (Nieder et al., 2011), but the degradation of SOM from over-tilling often necessitates the use of fertilizers as supplements, particularly for some grain crops such as corn, which require large amounts of N. Fertilizers have at least three major negative impacts: (1) changing the microbiome structure within agricultural soils (Kim et al., 2022), (2) contributing to the eutrophication of waterbodies (Zhang et al., 2015), and (3) directly or indirectly contributing to global warming (Bowles et al., 2018; Fagodiya et al., 2017). It is the goal of minimizing these costs that has motivated researchers to study a number of agricultural approaches such as reducing tillage requirements or intensity; eliminating pesticides, herbicides, and fungicides; and implementing cover crops and crop rotations (Aune, 2011; Palm et al., 2014; Tittonell, 2014).

Efforts to reduce some of the deleterious effects agriculture has on the natural environment have contributed to the emergence of two new classes of agricultural approaches: conservation agriculture and organic agriculture (Aune, 2011). Conservation agriculture builds off the conventional approaches of utilizing mineral/synthetic fertilizers and pesticides by implementing the use of cover crops, rotating crops seasonally, retaining crop residues, and reducing or eliminating tillage altogether. Organic agricultural approaches, on the other hand, are generally characterized by the absence of any mineral fertilizers and pesticides, instead relying on crop rotations or the application of composted manure to replenish nutrients in the soil and cover crops to suppress weed growth. Both of these approaches attempt to address problems associated with conventional farming: providing a source of fertility and maintaining the physical stability of the soil itself, which, from an organic farming practices approach in particular, has largely centered around reducing the number of tillage events, reducing the tillage intensity, maintaining plant cover over the full course of the year via cover cropping, and leveraging crop rotations (Baumhardt et al., 2015; Cambardella & Elliott, 1993; Palm et al., 2014; Peterson et al., 1998).

Within agricultural soils, organic matter decomposition and nutrient cycling are largely facilitated by microbial communities as they break down complex soil organic matter. The rate and efficiency of this process can be highly variable depending upon land use, vegetation type, agricultural activity, and physical and chemical soil properties such as soil moisture content (Baldrian, 2014; Bauke et al., 2022; Nguyen, Osanai, Anderson, Bange, Braunack, et al., 2018; Panettieri et al., 2014). Understanding how farming practices, environmental and soil conditions, and cycling and crop production are all interlinked is essential to achieving optimal anthropogenic and environmental outcomes (Cassman et al., 2002; van der Werf et al., 2020). Several methods exist to measure the rates and patterns of nutrient cycling within soils. One approach measures the activities or rates of extracellular enzymes secreted by microbial cells which carry out catabolic functions, enabling bacterial cells to access otherwise inaccessible nutrients. Microbial extracellular enzymes play a crucial role in soil organic matter transformation and nutrient cycling (Sinsabaugh & Shah, 2012). Measurements of potential extracellular enzyme activity (EEA) are often used as a reliable index of changes in soil status as affected by differentiated natural and anthropogenic factors since they are more sensitive to any changes than many other soil variables (Caldwell et al., 2014; Panettieri et al., 2014). Quantifying the activities of extracellular enzymes such as C-acquiring enzyme β-1,4-glucosidase (BG), N-acquiring enzyme β-1,4-N-acetylglucosaminidase (NAG), and P-acquiring enzyme alkaline phosphatase (AP), as well as the ratios between them, provides vital information about C, N, and P pathways from sources of organic matter to crops.

Soil incubations provide another, complementary, approach to quantifying the state of nutrient transformation within soils (Abril et al., 2001; Mariano et al., 2013). These incubations can provide information about the magnitudes of nitrate removal/uptake, nitrification, organic N mineralization, and ammonia uptake/removal. By measuring N transformation rates in aggregate, this soil incubation method provides information that is complementary to EEA data, which is primarily focused on the activity of individual enzymes. Using soil incubation methods, it has been found that net N processing rates are responsive not just to the properties of a given soil but also to the climatic context including immediately antecedent wetting and drying patterns (Dessureault-Rompré et al., 2010; Guo et al., 2014).

Quantitative polymerase chain reaction (qPCR) provides a third approach to characterizing nutrient transformation in soils. Instead of measuring the potential for microbial nutrient demand, as in EEA, or the potential rates of nitrification and N mineralization, as with soil incubations, qPCR provides the quantification of copy number, or abundance, of target genes. Gene quantification of N-transformation processes via qPCR is useful for approximating the relative rate at which N is being shunted through a particular pathway, particularly when multiple qPCR targets are simultaneously assessed for a given sample. Combining data from multiple targets has allowed researchers to demonstrate that organic fertilizers can more strongly influence the abundance of nitrifiers in agricultural soils (Ouyang et al., 2018) and that the implementation of cover cropping practices does not result in immediate responses in N-cycling microbe abundances (Kim et al., 2022).

The impact of weather-related influences on nutrient cycling within agricultural soils is often overlooked (Frindte et al., 2019; Leyrer et al., 2022; Parker & Schimel, 2011; Wallenstein & Weintraub, 2008). Temperature and moisture are very influential factors in determining microorganism structure and activities such as nutrient cycling within soils (Frindte et al., 2019; Leyrer et al., 2022; Wallenstein & Weintraub, 2008). Soil moisture, in particular, has a substantial influence on nutrient cycling within natural (Lewis et al., 2021; Nguyen, Osanai, Anderson, Bange, Braunack, et al., 2018; Nguyen, Osanai, Anderson, Bange, Tissue, & Singh, 2018; Petrakis et al., 2017; Poblador et al., 2017) and agricultural contexts (Bauke et al., 2022; Bowles et al., 2018) by changing the redox environment, facilitating nutrient transport via advection and diffusion, nutrient availability in the soil (Bauke et al., 2022), and the microbial taxa that live within them (Bauke et al., 2022; Blazewicz et al., 2020; Heděnec et al., 2018; van Rijssel et al., 2022). Microbial access to insoluble nutrients within soil pore spaces is constrained to pores and cavities larger than themselves (Bauke et al., 2022). During dry conditions, entrained soil organic matter (SOM) and associated nutrients are effectively inaccessible (Nunan et al., 2003, 2020), but higher soil moisture levels induce reducing conditions, destabilize soil aggregates, and enhance mineralization of SOM (Huang & Hall, 2017). Slight variations in water content (Barnard et al., 2020; Gomez et al., 2020; Kivlin & Treseder, 2014) and temperature (Kivlin & Treseder, 2014) or even a soil's environmental history (Leyrer et al., 2022; Nguyen, Osanai, Anderson, Bange, Tissue, & Singh, 2018) can dramatically affect the behavior of soil microbial communities (Cuddington, 2011). The tight linkage between soil nutrient content, soil moisture, and microbial community composition necessitates that these interactions be taken into account when research into the effects of other perturbations, such as agricultural practices, is being performed.

Previous research on the effects of different agricultural approaches is predominantly comparative and relies on data obtained from fields with long histories of continuous and consistent agricultural approaches. Much less attention has been focused on how soil nutrient cycling changes during transitional phases (Tu et al., 2006), despite the common challenges of reduced yield, changing physical and biological soil properties, and increased pest pressures that are commonly experienced within that time frame (Zinati, 2002). The goal for this study was to evaluate how N cycling within agricultural fields responds in the understudied early phases of the conventional-to-organic conversion process. Specifically, we were interested in the effects of implementing cover cropping and reduced tillage practices within otherwise conventionally managed fields and making comparisons with fields that were in the process of being converted from conventional to organic farming methods. We investigated N mineralization and nitrification rates, EEA rates, and nitrifying and denitrifying gene abundances within agricultural soils during the early transition of farming practices, and we assessed these responses in relation to year-to-year variations.

METHODS

Site description

This study was carried out in conserved farmland within the Stroud Preserve in West Chester, Pennsylvania, USA (39°56′46.90″ N, 75°39′10.05″ W). The study site contains multiple agricultural fields and has a humid continental (Dfa) climate. We selected eight crop fields of approximately 0.5 hectares each. All the selected fields have a similar underlying geology and soil composition, as well as their shared agricultural history (Figure 1). All fields have northerly exposures, and their close proximity ensures that they experience identical environmental conditions (Figure 1). The study site's soil type is a Gladstone gravelly loam with a taxonomic class of fine-loamy, mixed, active, mesic Typic Hapludults. A Riparian Forest Buffer System (RFBS) was constructed on the site in 1992, and further context about the watershed and the RFBS is described by Newbold et al. (2010).

Experimental design

Each of the three farming practices we investigated consisted of two treatments (Figure 2). Two Management

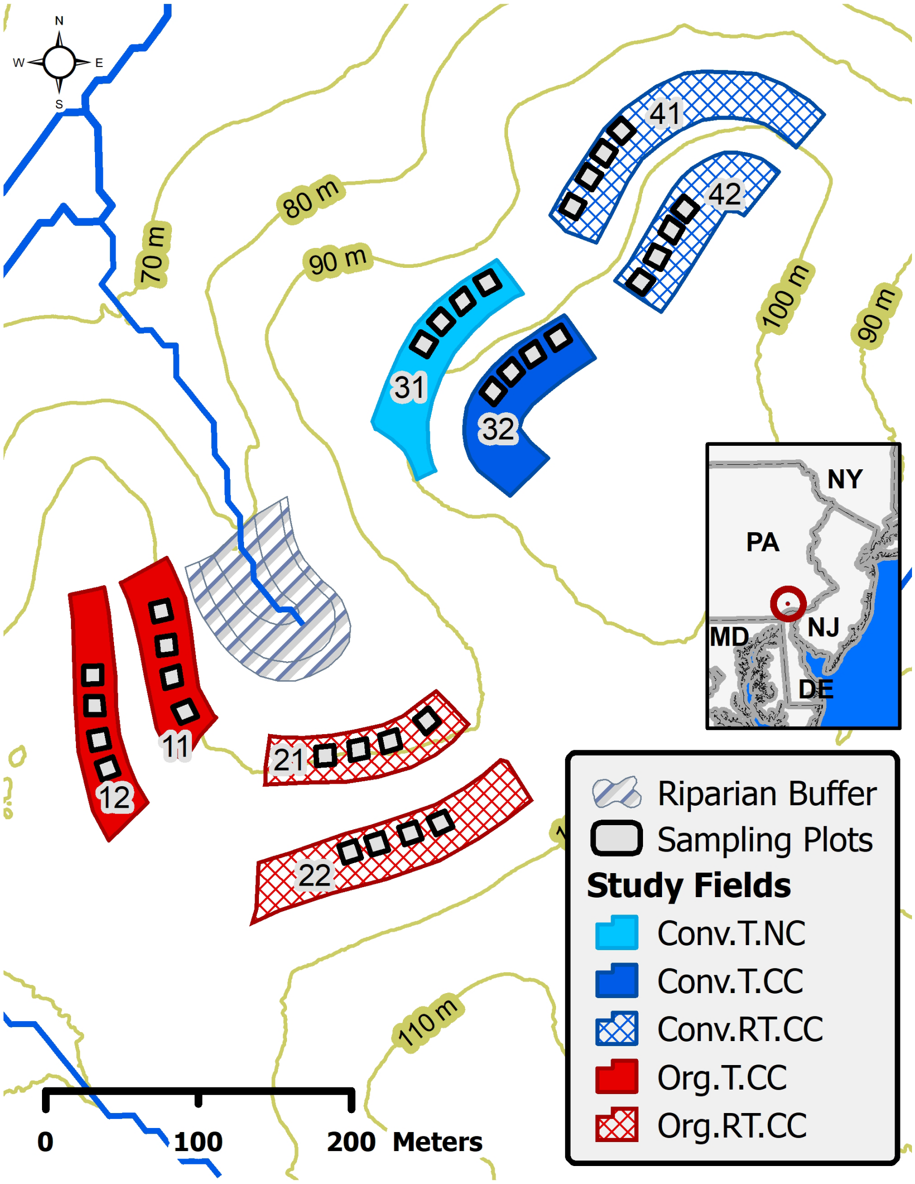

FIGURE 1 Plan view of the study site. A total of eight fields were utilized in this study. Four of the fields were subjected to Organic farming management practices (Org), while the remaining four were Conventionally managed (Conv). All fields except the Conventionally managed field (Conv.T.NC) were cover cropped (CC) in the offseason. Half of the fields were subjected to standard tilling treatments (T, solid colors), and the remaining half received a reduced till treatment (RT, indicated by hatching).

Systems, Conventional and Organic, were defined to delimit the overall farming methodology applied to a given field as well as the fertility source. Conventional (Conv) fields received applications of mineral fertilizer, herbicides, and pesticides consistent with typical regional conventional agricultural practices, while organic (Org) fields did not receive any mineral fertilizer, herbicides, or pesticides and were cover cropped. A Tillage treatment was also applied, where some fields (Till, T) were tilled in a way consistent with standard farming practices, and others (Reduced Till, RT) were subjected to fewer tilling passes and less vigorous tilling methods. Lastly, cover cropping (CC) was applied to seven of the eight fields to allow us to draw conclusions about the impact of adding cover crops to the fields, while the eighth field remained without cover crops (NC). Further details on the applied farming practices are provided below.

Three constraints influenced the experimental design, replication strategy, and statistical models to be tested (Figure 2). Many organic farming systems, such as the system used herein, require the use of cover crops to reduce weed growth and provide nutrient additions for cash crops to utilize. This requirement implicitly invalidates the Organic treatments that

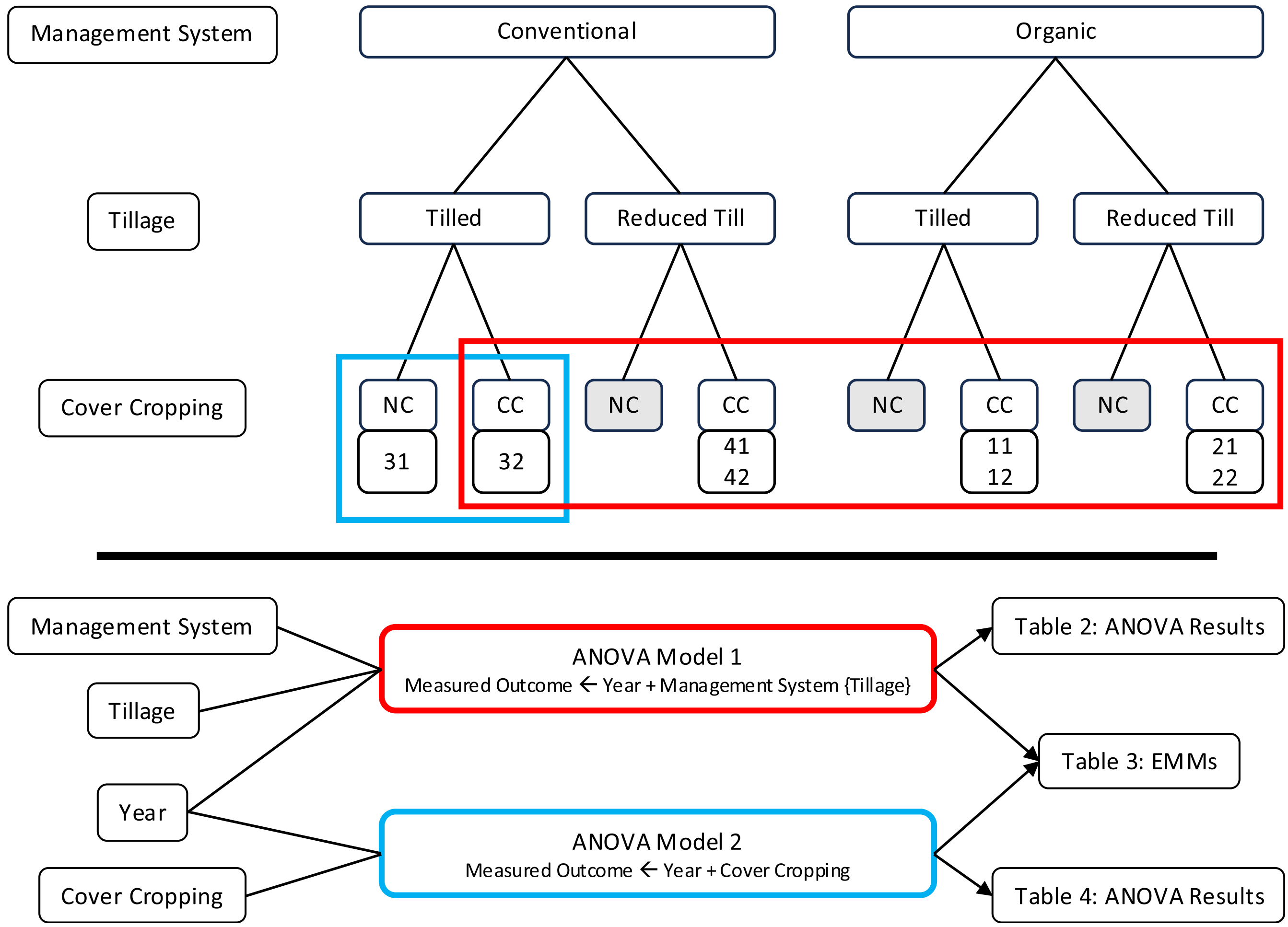

FIGURE 2 The top panel depicts a diagram of the experimental design structure, in which the two Tillage treatments (Till [T] and Reduced Till [RT]) were nested under their respective Management Systems (either Conventional [Conv] or Organic [Org]), while the Cover Cropping treatment (No Cover Crop [NC] and Cover Crop [CC]) was considered to be independent from the two other treatments. Field numbers corresponding to each treatment combination are noted in the boxes under the Cover Cropping treatment specification. Two treatment combinations falling under the Organic Management System were invalid (Org.T.NC and Org.RT.NC), and a third treatment combination (Conv.RT.NC) was not tested; these treatment combinations are indicated by gray fill in the diagram. The bottom panel shows two ANOVA statistical models: The first model (treatments and samples indicated with a red box in both the top and bottom panels) was used to test how Management System and Tillage impacted each of the measured outcomes; and the second model (indicated with a blue box in both the top and bottom panels) tested the impact of the Cover Cropping treatment.

would receive no cover crops in a truly crossed experimental design (Org.T.NC and Org.RT.NC) in this study. Furthermore, Conventional and Organic farming methods require different numbers of tillage passes, tillage methods, and tillage intensity even for the same cash crop, necessitating that the Tillage treatment be nested under each Management System treatment. Lastly, being limited to the eight fields meant that we were not able to have equal numbers of replicate fields for all six valid treatment combinations, necessitating both a reduction in replicates and an unbalanced design. We prioritized the comparison of Management Systems (Conv vs. Org) and Tillage (Till vs. Reduced Till) by not testing the Conv.RT.NC treatment and having one replicate field each for the Conv.T.NC and Conv.T.CC treatments (Figure 2).

Farming practices

Prior to the start of experimentation, all eight experimental fields were managed according to conventional practices, including being continuously farmed with corn (*Zea mays*) as a cash crop; the application of fertilizer, herbicides, and pesticides; and the absence of cover cropping. N-containing fertilizer ($(NH_4)_2SO_4$) and dry chicken manure, to the effect of 48.5 kg N ha^{-1} and 4480 kg dry chicken manure ha^{-1} (or 5.5 kg N ha^{-1}), respectively, were applied annually to facilitate crop growth.

Changes to each field's farming practices were implemented at the beginning of the 2018 planting season. For 2018, cash and cover crops were changed from the previously continuous corn cropping system, and in 2019, cash and cover crop rotations were implemented for each of the fields (Table 1). The fully conventional (Conv.T.NC, Field 31) rotation was altered to a 3-year corn, corn, soybean rotation. This field was partially paired with the Conv.T.CC field (32), which was placed on the same 3-year cash crop rotation, with the addition of a cover cropping and being offset by one year. The Conv.RT.CC treatment, which is consistent with conservation agricultural practices, was applied to two fields (41 and 42), with the cash/cover crop matching between Fields 31/41 and 32/42. The mixed cover applied to Field 41 was a blend of hay, orchard grass (*Dactylis glomerata*) and fescue (*Festuca* sp.), and either vetch (*Vicia villosa*) or clover (*Trifolium pratense*) for all years. The cash/cover crop rotations of the Org.T.CC and Org.RT.CC fields were paired (Fields 11/21 and 12/22, respectively) and placed on 4-year crop rotations of corn/rye (*Secale cereale*), oats (*Avena sativa*)/rye, soybeans (*Glycine max*)/wheat (*Triticum aestivum*), and wheat/vetch (wheat being overwintered in the fourth year) (Table 1). While the organic fields have been managed according to standard legume-based crop rotations, composted manure was applied at a rate of 49.42 ton per hectare in March 2019 to Fields 11 and 21 to provide the N necessary for the corn cash later that spring.

Tillage treatments (T, RT) were implemented by the prompt adoption of those practices. In the Org.T treated fields, a moldboard plow, set to 25.4 cm (10 in.) deep, was used to carry out tilling; disking was performed with a packer hooked behind the plow to level at 15.24 cm (6 in.) deep; two to three passes of tine weeding were performed per season, and one pass of cultivation between rows was performed in fields growing corn. The moldboard plowing process left little to no residue on the soil surface. The Org.RT fields were not tilled, disked, or tine weeded. The differences in Tillage treatments between the conventional fields were that a chisel plow was used to carry out tilling in the Conv.T fields while that process was omitted in the Conv.RT fields. The chisel plow left roughly 20%–30% residue on the soil surface. A roller crimper was used to terminate cover crops for all of the Org fields, while herbicide was used to terminate cover crops in the Conv fields.

Weather and soil moisture data

Weather conditions at the study site were continuously monitored and logged using an ONSET HOBO RX3000 Outdoor Remote Monitoring Station. The monitoring station had sensors to measure temperature, pressure, dew point, precipitation, relative humidity, solar radiation, wind direction, wind speed, and gust speed. Observations for each sensor were recorded every 5 min. Starting in May 2020, two GrowPoint Profile Soil Moisture and Temperature Sensors (GrowPoint, North Saanich, BC, Canada) were installed in each field to continuously monitor moisture and temperature profiles within the soils; values were recorded every 10 min. As the soil moisture sensors were installed within the fields themselves, some farming activities, such as tilling or cultivation, required removal of the sensors, followed by reinstallation. The sensors were removed in November 2021 to prevent frost damage.

TABLE 1 Enumeration of the cash and cover crops from the beginning of experimentation through the data collection period for this manuscript.

		2018		2019		2020		2021	
Field	**Treatment**	**Cash**	**Cover**	**Cash**	**Cover**	**Cash**	**Cover**	**Cash**	**Cover**
11	Org.T.CC	Oats	Vetch	Corn	Rye	Oats	Rye	Soybeans	Wheat
12	Org.T.CC	Oats	Rye	Soybeans	Wheat	Wheat	Vetch	Corn	Rye
21	Org.RT.CC	Oats	Vetch	Corn	Rye	Oats	Rye	Soybeans	Wheat
22	Org.RT.CC	Oats	Rye	Soybeans	Wheat	Wheat	Vetch	Corn	Rye
31	Conv.T.NC	Soybeans	...	Corn	...	Corn	...	Soybeans	...
32	Conv.T.CC	Corn	Rye	Corn	Rye	Soybeans	Wheat	Wheat	Rye
41	Conv.RT.CC	Soybeans	Mix cover	Corn	Mix cover	Corn	Mix cover	Soybeans	Mix cover
42	Conv.RT.CC	Corn	Rye	Corn	Rye	Soybeans	Wheat	Wheat	Rye

Note: The Treatment column designates the experimental treatment each field received; see Figure 2 for a diagram of the experimental treatments.

Sample collection and processing

Topsoil samples were collected 14 times over the course of 2020 and 2021 during the active growing seasons of spring, summer, and autumn. During sampling events, topsoil samples (0–20 cm in depth) were collected from each of four sub-plots delineated within each field and transported on ice to the laboratory prior to analysis (Appendix S1: Table S1). Aliquots were taken from each of the 32 physical samples (four sub-plots for each of the eight fields) to assess nitrification and mineralization rates. Each field's sub-plot samples were then composited and homogenized to create a single bulk sample for each field. This bulk sample was then used to carry out the EEA assays and qPCR analyses. Please see Appendix S1: Figure S1 for a diagram and description of sample handling and processing.

Nitrification and mineralization rates in soil

We performed soil incubations to characterize net nitrification and net mineralization rates (in milligrams of Nitrogen per kilogram per day) in each field following similar procedures to those described by Drury et al. (1991). Specifically, four 8-g subsamples were separated from each topsoil sample within each field and incubated in the laboratory at a constant temperature of 26°C and under dark conditions for 0, 7, 14, and 28 days, respectively. At the end of each incubation period, we extracted both ammonium and nitrate from each soil subsample using a 2-M KCl solution. Each subsample was first stirred for 90 min after adding the KCl solution and then centrifuged for 15 min at 3200 rpm prior to collecting a liquid sample from the top to analyze NO_3^- (EPA-126-D) and NH_4^+ (EPA-148-D) concentrations using an AQ300 discrete analyzer (SEAL Analytical, Wisconsin, US). The initial NO_3^--N and NH_4^+-N concentrations indicate soil N concentrations at each sampling time, while net nitrification and net mineralization rates can be calculated as the increase in NO_3^--N and NH_4^+-N concentrations over time using linear regression. Net nitrification rates are the result of both accumulation (from nitrification) and removal (from uptake) of NO_3^--N. When negative, net nitrification values indicate greater uptake rates than nitrification, although the contribution of assimilatory and dissimilatory (denitrification) uptake processes is not determined. Similarly, positive values of net mineralization rates indicate greater NH_4^+-N accumulation (from ammonification) than removal (uptake).

Extracellular enzyme activity

The potential activities of C-acquiring enzyme β-1,4-glucosidase (BG), N-acquiring enzyme β-1,-N-acetylglucosaminidase (NAG), and P-acquiring enzyme alkaline phosphatase (AP) were measured following standardized protocols (Bell et al., 2013; Wallenstein & Weintraub, 2008). In brief, soil samples were combined with a pH buffer and homogenized on a stirring plate. The slurries were then transferred to deep 96-well plates where they were inoculated with a non-limiting amount of fluorescently labeled substrate (4-methylumbelliferone-phosphate for AP, 4-methylumbelliferone-β-D-glucose for BG, and 4-methylumbelliferone-acetylglucosamine for NAG) and incubated for 0, 0.5, and 1 h. When the incubation period ended, the sealed deep 96-well plates were centrifuged and the supernatant was transferred to a black 96-well microplate that was read at an excitation wavelength of 365 nm and emission wavelength of 450 nm using a multimode plate reader (Synergy LX, BioTek). Potential EEA was determined as the change in fluorescence through time in response to the cleavage of the substrate by the enzymatic activity and was expressed as micromoles of substrate released per hour per gram of soil organic matter (μmol gOM^{-1} h^{-1}).

Absolute quantification of nitrifying and denitrifying genes via qPCR

Total DNA was extracted from 0.25 g of soil using Qiagen Dneasy Powersoil Pro Kits with 100-μL elution volumes according to the manufacturer's protocols. qPCR was applied to estimate nitrification and denitrification genes. Ammonia-oxidizing archaea (AOA) and bacteria (AOB) were quantified with ammonia monooxygenase genes (*amo*A) (Kuypers et al., 2018): Arch-*amo*AF and Arch-*amo*AR for AOA (Francis et al., 2005) and *amo*A-1F and *amo*A-2R (Rotthauwe et al., 1997) for AOB. Primers *nos*ZF (Kloos et al., 2001) and *nos*Z1622R (Throbäck et al., 2004) were used to quantify nitrous oxide reductase (denitrification). All qPCR reactions were set up in triplicate with SYBR Green chemistry by using an Applied Biosystems QuantStudio 3 (ThermoFisher Scientific, Waltham, MA). All qPCR reactions were 20 μL in volume, with 2 μL of DNA template, 0.5 μM forward and reverse primer concentrations, 0.5 mg mL^{-1} BSA (Invitrogen, 50 mg mL^{-1} stock), and 1× PowerUp SYBR Green Master Mix (Applied Biosystems). qPCR standards were consensus sequences confirmed from NCBI GenBank and purchased from Integrated Data Technologies (IDT) in the form of synthetic custom oligonucleotides. Sequences for the synthetic standards and the RefSeq IDs used to generate them are presented in Appendix S1. Serial dilutions of these standards were carried out to create standard curves enabling absolute quantification of all three target genes. The thermocycler program contained the following steps: preincubation and initial denaturation, 50°C for 2 min, 95°C for 2 min, and followed by 45 cycles of 95°C for 15 s, 55°C for 15 s, and 72°C for 1 min. Melt curves were performed at the end of each run and analyzed to ensure product purity and specificity. The copy numbers of each gene were calculated and reported per gram of soil based on the concentration of template DNA and amplicon size (Einen et al., 2008).

Data processing and statistical analysis

Data collected by the weather station were compared between years to identify any major differences in the overall climate that may influence the outcomes. Average daily temperature was computed, as was daily precipitation and cumulative precipitation. Nine of the 14 sampling dates had corresponding soil moisture data available. For each of those dates, individual in-field estimates of soil moisture were generated by averaging the soil moisture values recorded between the times of 8:00 a.m. and 12:00 p.m. (noon); the selection of these times corresponds to when physical samples were collected.

As to the laboratory generated results, technical replicate values for each sample were averaged to obtain the final values used in the analysis. qPCR results (gene copy number counts) and EEA were $\log_{10}$ and natural log transformed, respectively, prior to statistical testing to enforce normality. We assessed the effects of the conventional-to-organic conversion process and the impact of reducing tillage using two-way ANOVA with Type II Sum of Squares. Type II Sum of Squares were selected because we were primarily interested in the main effects of the experimental variables and not their interactions.

For each measured outcome (e.g., net nitrification, soil NH_4^+-N), ANOVA was applied to two statistical models (Figure 2). The first model was intended to explore how the Management System and Tillage treatments affected each of the measured outcomes. Management System was the primary (experimental) fixed effect with Tillage being nested within the Management System. While not part of the experimental process, Year was included in the model to account for the potential influences from the cash crop/cover-crop rotation or weather-related differences between the two years; interaction terms were not included in the model. When testing this model, observations from the fully conventional field (Conv.T.NC) were removed from the dataset to avoid any error induced by it not being cover cropped. The second model we investigated was intended to determine how Cover Cropping affects each of the outcomes. For this model, the dataset was limited to include only the Conv.T.NC and Conv.T.CC fields (Fields 31 and 32, respectively). Cover Cropping was the main experimental effect being tested and, as with the first model, Year was included without an interaction term.

Because multiple hypothesis testing was performed, false discovery rate (FDR) adjustment was applied to p-values obtained from ANOVA to control the false discovery rate (Benjamini & Hochberg, 1995). FDR adjustment was applied simultaneously on all p-values obtained for a single model. A $p = 0.10$ significance heuristic (after FDR adjustment) was utilized for all statistical tests. Post hoc tests were not performed because each term in the model was binary in nature and no interaction terms were present. Estimated marginal means (EMMs) were calculated after each ANOVA model as assessed. Lastly, Spearman's (rho) and Pearson's (r) correlation coefficients were computed, and their significance was tested between observed soil moisture data and each of the measured outcomes. Even though we were primarily interested in the Spearman's rho results due to its relative insensitivity to non-normal data and its non-parametric nature, both correlation coefficients were calculated in order to provide an indication as to the robustness of the results.

All statistical analyses and visualizations were performed within R (R Core Team, 2020). Testing the significance of each overall model with Type II Sum of Squares was carried out using the "car" package (Fox & Weisberg, 2019). The "emmeans" package was used to generate the EMM for each outcome (Lenth, 2022). Visualizations were created using the "ggplot2" package (Wickham, 2016). The raw data for this study as well as the R scripts used to generate the results, including data processing, statistical analyses, and visualizations, are available from Zenodo (Price et al., 2023).

RESULTS

Year-to-year variations in weather conditions

Daily average temperature was very similar between 2020 and 2021 (Figure 3). Similarly, total annual precipitation

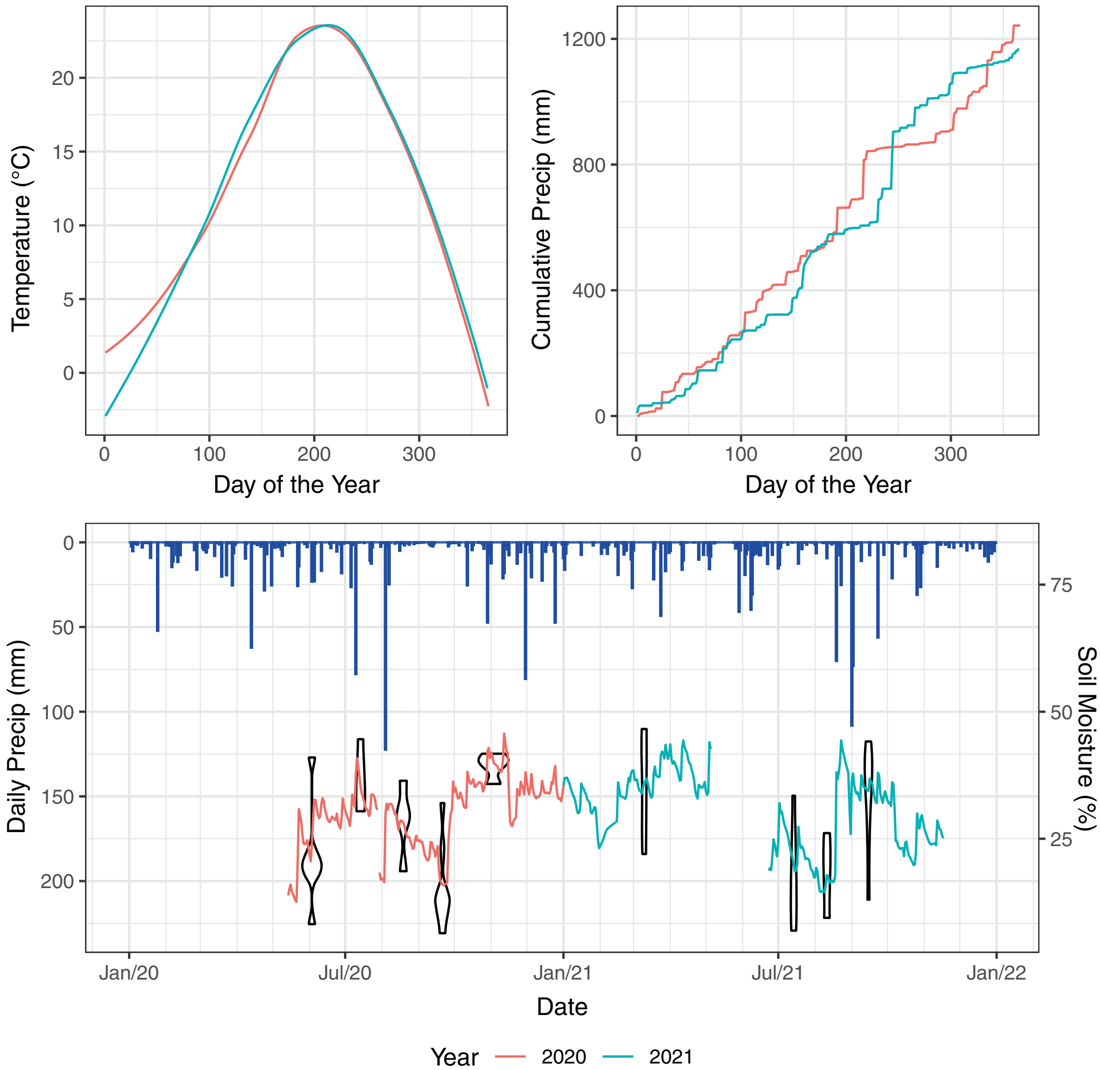

FIGURE 3 Temperature, precipitation, and soil moisture conditions in 2020 and 2021 at the study site. Average daily temperature values were calculated for each day of the year, and locally estimated scatterplot smoothing (LOESS) regression was used to generate smoothed curves to ease interpretation. Daily precipitation (blue bars, left *y*-axis) and soil moisture content (colored lines and violin plots, right *y*-axis) are shown in the bottom panel. The daily values of soil moisture were calculated by taking average of all observations from all fields on that date. Soil moisture data were available for 9 of the 14 sampling dates; the soil moisture values on those dates are depicted using violin plots to convey the variance in observations for those dates.

varied little between 2020 and 2021 with values of 1240 and 1170 mm respectively. However, daily precipitation was much more uniformly distributed in 2020 than it was in 2021, with an initial peak in late June and early July corresponding with the local onset of the 2020 hurricane season and the arrival of Hurricanes Fay (Day 192) and Isaias (Day 217) (Figure 3). A number of late fall and winter storms, including Hurricane Zeta (Day 303), generated a total of 338 mm of precipitation in the last 69 days of 2020. In 2021, three named storms, Tropical Storm Fred and Hurricanes Henri and Ida occurred within 15 days of each other (between August 19 and September 2, 2021, days 231 and 245, respectively); these storms generated a combined 286 mm of precipitation or 25% of the total 2021 precipitation.

Effects of changes to farming practices

Six of the twelve parameters we investigated had a significant response to Year: net nitrification, soil NH_4^+-N, NAG:BG, AOA, AOB, and *nosZ* (Table 2, Figure 4). All six of these parameters had higher estimated marginal means in 2021 than in 2020 (Table 3). Three of the parameters, net nitrification, AOA, and AOB, were found to also vary significantly between Management Systems (Table 2). All three of these variables were found to have

TABLE 2 Summary of the ANOVA results for each of the measured parameters across Year (2020 vs. 2021), Management Systems (Conv vs. Org), and Tillage treatments (Till vs. Reduced Till, nested within Management System).

		Year			Management system			Tillage (within management)		
Parameter	dfd	dfn	*F*	*p*	dfn	*F*	*p*	dfn	*F*	*p*
Net Nit.	86	1	15.43	**<0.01**	1	6.28	**0.063**	2	0.01	0.995
Soil NH_4^+-N	86	1	7.07	**0.049**	1	0.41	0.704	2	0.28	0.871
Net Min.	86	1	2.63	0.3	1	0.10	0.871	2	0.14	0.95
Soil NO_3^--N	86	1	2.44	0.313	1	3.79	0.18	2	0.10	0.962
BG	93	1	4.28	0.149	1	0.26	0.765	2	0.04	0.993
NAG	93	1	0.48	0.703	1	0.68	0.669	2	0.49	0.765
AP	93	1	3.58	0.185	1	0.71	0.669	2	0.26	0.871
NAG:BG	93	1	7.00	**0.049**	1	0.63	0.669	2	1.62	0.453
NAG:AP	93	1	1.37	0.486	1	0.54	0.697	2	1.38	0.486
AOA	36	1	138.89	**<0.001**	1	7.91	**0.049**	2	1.61	0.453
AOB	36	1	41.05	**<0.001**	1	6.39	**0.064**	2	0.91	0.669
*nos*Z	36	1	59.67	**<0.001**	1	0.41	0.704	2	1.68	0.453

Note: Statistically significant *p* values appear in boldface.

Abbreviations: AOA, ammonia-oxidizing archaea; AOB, ammonia-oxidizing bacteria; AP, alkaline phosphatase; BG, β-1,4-glucosidase; dfd, denominator degrees of freedom; dfn, numerator degrees of freedom; NAG, N-acetylglucosaminidase; Net Min., net mineralization; Net Nit., net nitrification; *nos*Z, nitrous oxide reductase.

higher values in the conventional fields than in the organic fields (Table 3, Figure 4). None of the measured outcomes responded in a statistically significant manner to the Tillage treatment (Table 2).

Analysis of our second model did not find any significant effects due to the Cover Cropping treatment (Table 4). However, the NAG:BG ratio and AOA abundances had significantly higher values in 2021 than those in 2020 by roughly the same amounts in the previous model, described above (Table 3). As only data from the Conv.T.NC and Conv.T.CC fields (31 and 32) were included in this analysis, the lack of significant responses could be due to under sampling (too few observations) or high variation within the observed values themselves; more data may help resolve this point.

Impact of weather variations (e.g., precipitation and soil moisture) on nitrogen cycling across years

Each of the twelve measured parameters was tested for correlation with soil moisture; four displayed statistically significant correlations with soil moisture (Appendix S1: Table S2). Net nitrification ($\rho = 0.33$, $n = 53$, S statistic $= 16{,}526$, $p = 0.015$) and soil NH_4^+-N ($\rho = 0.27$, $n = 53$, S statistic $= 18{,}056$, $p = 0.049$) increased with soil moisture, while net mineralization ($\rho = -0.27$, $n = 53$, S statistic $= 31{,}568$, $p = 0.049$) and soil NO_3^--N ($\rho = -0.33$, $n = 53$, S statistic $= 33{,}030$, $p = 0.016$) were found to have negative correlations with soil moisture; the Pearson correlations and statistical test outcomes were consistent with those of the Spearman correlations (Appendix S1: Table S2).

Seasonal and year-to-year variability

Seasonal patterns of microbial composition and processes in the soils were substantially different between the two years (Figure 5; Appendix S1: Figure S2). Concentrations of soil NH_4^+-N appear to be temporally shifted between the two years, with the highest concentrations in January and July in 2020 and May and August in 2021. A similar, but less severe, shift was also observed for net mineralization rates. In 2020, mineralization rates were positive and highest in May and June, while the rest of the year were generally negative. In comparison, mineralization rates peaked in June and July and a second high at the end of November in 2021.

EEA data indicated that the patterns in enzyme activities in 2021 strongly diverged from those observed in 2020 (Figure 5). GLU, NAG, and PHO activities all peaked in June, July, and August 2020, while in 2021, activities were nearly constant from January through August and then rose in September, staying at elevated levels through the end of November 2021. The ratios between NAG:BG, and to a lesser extent NAG:AP, appeared to follow the general patterns for their individual components; in addition, their ranges were smaller in 2021 than in 2020 (Appendix S1: Figure S3).

Higher abundances of nitrifying and denitrifying genes were observed in 2021 than in 2020 (Figures 4 and 5). Moreover, within the 2021 data, the abundances of all three genes decreased drastically in the fully conventional field (Conv.T.NC) in comparison with all of the other treatments for

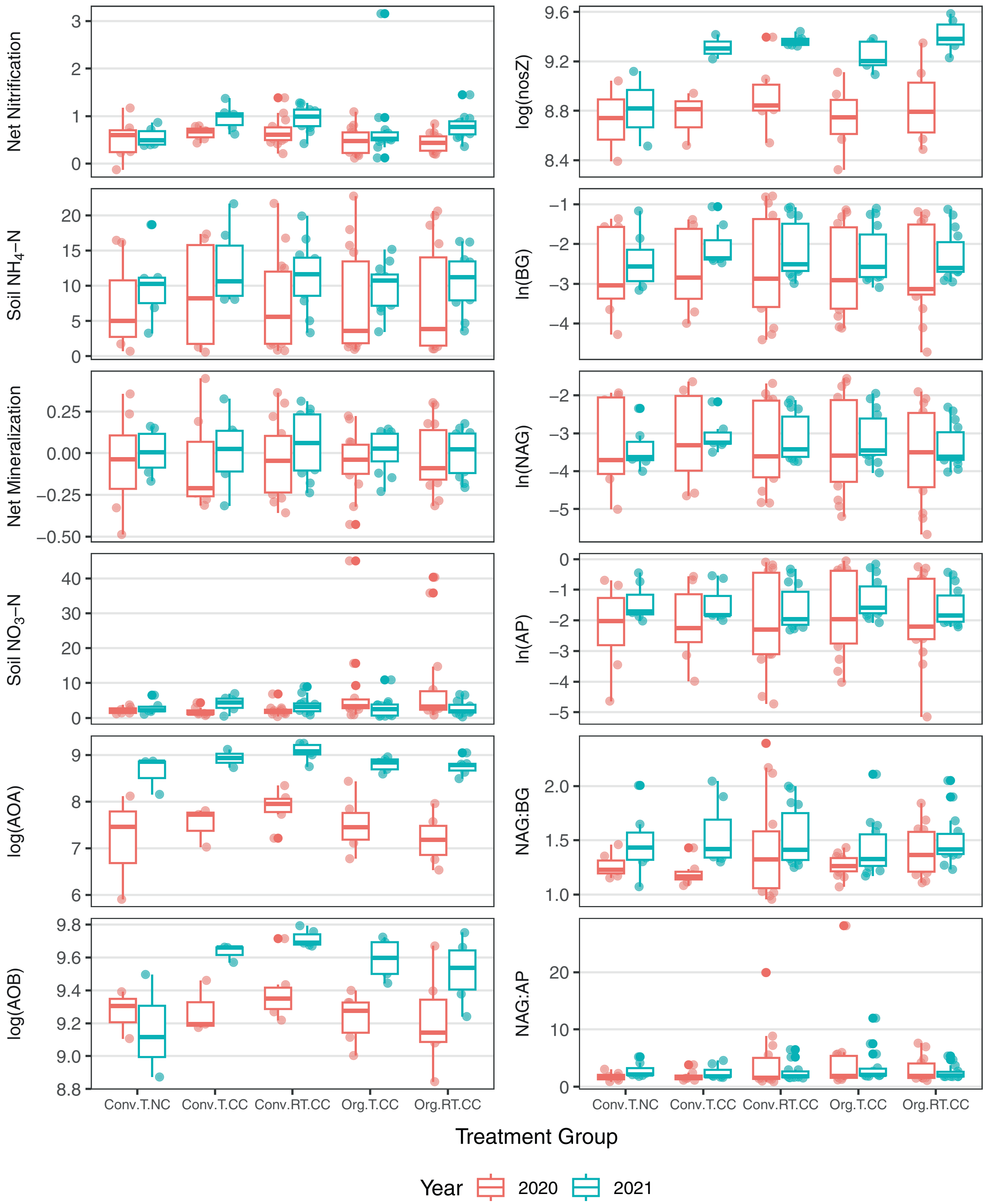

FIGURE 4 Legend on next page.

TABLE 3 Estimated marginal means (EMM) for the treatments found to significantly influence the measured outcomes.

	Model 1[a]				Model 2[b]	
	Year		Management system		Year	
Parameter	2020	2021	Conventional	Organic	2020	2021
Net Nit.	0.559	0.862	0.808	0.614		
Soil NH_4^+-N	7.782	11.142				
NAG:BG	1.335	1.482			1.230	1.508
AOA	3.37E+07	7.66E+08	2.22E+08	1.16E+08	2.17E+07	5.95E+08
AOB	1.90E+09	4.08E+09	3.18E+09	2.44E+09		
*nos*Z	6.57E+08	2.14E+09				

Abbreviations: AOA, ammonia-oxidizing archaea; AOB, ammonia-oxidizing bacteria; BG, β-1,4-glucosidase; NAG, N-acetylglucosaminidase; Net Nit., net nitrification; *nos*Z, nitrous oxide reductase.

[a]Model 1: Parameter ~ Year + Management System + Tillage (nested within Management System).

[b]Model 2: Parameter ~ Year + Cover Crop.

the July 14, 2021, sampling event (Appendix S1: Figure S2).

DISCUSSION

Nutrient cycling responds gradually to farming practices

Our statistical analysis indicates that, for the parameters that had significant responses to the models, year-to-year variation was generally more influential than the experimental agricultural practice treatments (Table 2, Table 4). Each of the parameters determined to covary with Year (net nitrification, soil NH_4^+-N, NAG:BG, AOA, AOB, and *nosZ*) had higher values (EMMs) in 2021 than in 2020 (Table 3). The increase in net nitrification was likely driven by the increase in NH_4^+-N within the soil and facilitated by the large increases in nitrifiers within the soil. Abundances of the denitrifying gene *nos*Z also increased. While increasing abundances of both nitrifying and denitrifying genes indicate an overall intensification in N cycling for the purposes of energy conservation (i.e., dissimilatory nitrate reduction), the moderate (~11%), but still significant, elevation observed in NAG:BG, the rate of enzymatic scavenging of N in relation to C, also suggests that shifts in N:C availability or metabolic requirements may have occurred between years. Of the three experimental treatments, only Management System had a statistically significant impact on the response variables net nitrification, AOA, and AOB (Table 2, Table 4). The dominance of the Management System term is likely due to it encompassing many differences between conventional and organic agricultural methods, whereas tillage intensity and cover crop are restricted to specific manipulations of agricultural practice.

The lack of response to the Tillage and Cover Crop treatments was unexpected and, at first, appears to stand in contrast to the current body of knowledge describing how different farming practices, to varying degrees, impact nutrient cycling, nutrient utilization, and crop yields within agricultural soils (Coskun et al., 2017; Kim et al., 2020; Ouyang et al., 2018; Tu et al., 2006; Zuber & Villamil, 2016). In the current study, changes in Management System induced a detectable change in the measured outcomes, while the Tillage and Cover Crop treatments did not. Three possible explanations are that

FIGURE 4 Boxplots of the measured and calculated parameters partitioned by treatment group (the combination of Management System, Tillage, and Cover Crop treatments) and Year. In each boxplot, the midline represents the median, the box limits indicate the 1st and 3rd quartiles, and the whiskers extend 1.5 times the length of the interquartile range; data that falls outside of the whisker range are presented as points. Extracellular enzyme activity (EEA) and quantitative polymerase chain reaction (qPCR) results were natural log transformed and $\log_{10}$ transformed, respectively, prior to plotting. The values of net nitrification and net mineralization are presented in milligram N per kilogram soil per day; soil NH_4^+-N and NO_3^--N have units of milligram N per kilogram soil; the qPCR assays ammonia-oxidizing archaea (AOA), ammonia-oxidizing bacteria (AOB), and nitrous oxide reductase (*nos*Z) are measured in $\log_{10}$-transformed copy number per gram of soil; the EEA parameters β-1,4-glucosidase (BG), N-acetylglucosaminidase (NAG), and AP have units of μmol of substrate per gram of OM per hour; the ratios NAG:BG and NAG:AP are unitless. Due to the nested treatment design and the testing of marginal effects, the data are presented at the most granular level—that of the treatment group—and ordered to facilitate comparisons among years. The statistical results for the testing of marginal effects are presented in Tables 2–4.

TABLE 4 Summary of ANOVA results for each of the measured parameters across Year (2020 vs. 2021) and cover crop (No Cover Crop [NC] vs. Cover Crop [CC]).

	Year				Cover crop			
Parameter	**dfn**	**dfd**	***F***	***p***	**dfn**	**dfd**	***F***	***p***
Net Nit.	1	23	2.99	0.264	1	23	5.68	0.206
Soil NH_4^+-N	1	23	2.08	0.355	1	23	0.77	0.621
Net Min.	1	23	0.53	0.669	1	23	0.00	0.977
Soil NO_3^--N	1	23	4.83	0.23	1	23	0.28	0.764
BG	1	25	1.24	0.553	1	25	0.38	0.724
NAG	1	25	0.02	0.977	1	25	0.57	0.669
AP	1	25	3.11	0.264	1	25	0.02	0.977
NAG:BG	1	25	10.77	**0.037**	1	25	0.00	0.977
NAG:AP	1	25	4.19	0.246	1	25	0.11	0.894
AOA	1	9	16.61	**0.037**	1	9	0.87	0.621
AOB	1	9	0.91	0.621	1	9	3.39	0.264
*nos*Z	1	9	4.23	0.264	1	9	2.83	0.304

Note: Statistically significant *p* values appear in boldface.
Abbreviations: AOA, ammonia-oxidizing archaea; AOB, ammonia-oxidizing bacteria; AP, alkaline phosphatase; BG, β-1,4-glucosidase; dfd, denominator degrees of freedom; dfn, numerator degrees of freedom; NAG, N-acetylglucosaminidase; Net Min., net mineralization; Net Nit., net nitrification; *nos*Z, nitrous oxide reductase.

(1) the effects due to Management System treatment are large enough to mask effects of the other two treatments, (2) the effects of the Tillage and Cover Crop treatments have not yet emerged or are not yet detectable, or (3) the changes in agricultural practices have not, and possibly will not, created changes in the parameters we are monitoring. Ongoing and longer term monitoring is needed to test or validate these potential explanations.

The absence of a response to the Tillage and Cover Cropping treatments, as we describe herein, has been reported before, principally in studies concentrating on the effects of transition. For example, Kim et al. (2022) did not observe a detectable difference in N-cycling microbes after two years of implementing cover cropping in fields previously subjected to corn monoculture without cover cropping. They hypothesized that the lack of response was due to changes in soil acidification and excess N availability caused by long-term fertilizer application. Hinson et al. (2022), while studying the conversion of conventionally managed dual-purpose wheat fields to an organic system, demonstrated that although the initial crop yields were substantially lower in the transitioning organic fields, there were no differences in yield by the third year. The effects of tillage can also take an extended period of time to normalize. Cavigelli et al. (2008) reported that it took nine years for corn grain yields to be comparable between conventionally tilled and reduced tilled systems. Similarly, while studying the changes in crop yields resulting from the conversion of conventional systems to both low-input composted cattle manure organic and low-input legume-based organic systems, despite yields being up to 25% lower in the initial years after conversion, Liebhardt et al. (1989) did not observe a significant difference in crop yield after 5 years had elapsed. These studies indicate that drastic changes in nutrient cycling and crop productivity are induced during the process of conventional-to-organic transitioning; however, some of the effects are not visible early on. This lack of treatment effects within the first 4 years of transition to organic is, at least in part, indicative of the time that the microbial population requires to react to the new farming treatments and establish a new equilibrium (Coskun et al., 2017; Ouyang et al., 2018; Tu et al., 2006; Zuber & Villamil, 2016). The absence of a response to the Tillage and Cover Crop treatments that we observed in this study may be due to the microbial communities still being within this transitional state.

Conventional-to-organic conversion suppresses nitrification during the early transitional phases

We observed that organic fields had significantly lower net nitrification rates (−24%) and abundances of AOA (−48%) and AOB (−23%) than those observed in the conventional fields (Tables 2 and 3), signifying that nitrification processes are slower in fields transitioning to organic agricultural practices. We did not find a significant difference in soil NH_4^+-N concentrations. We believe that the differences in net nitrification rates are due to the facilitation of the nitrification process by a more abundant nitrifier community in the conventional systems. Furthermore, the source of nutrients and how they are distributed between the conventionally and organically managed fields/soils differentiates nutrient-cycling

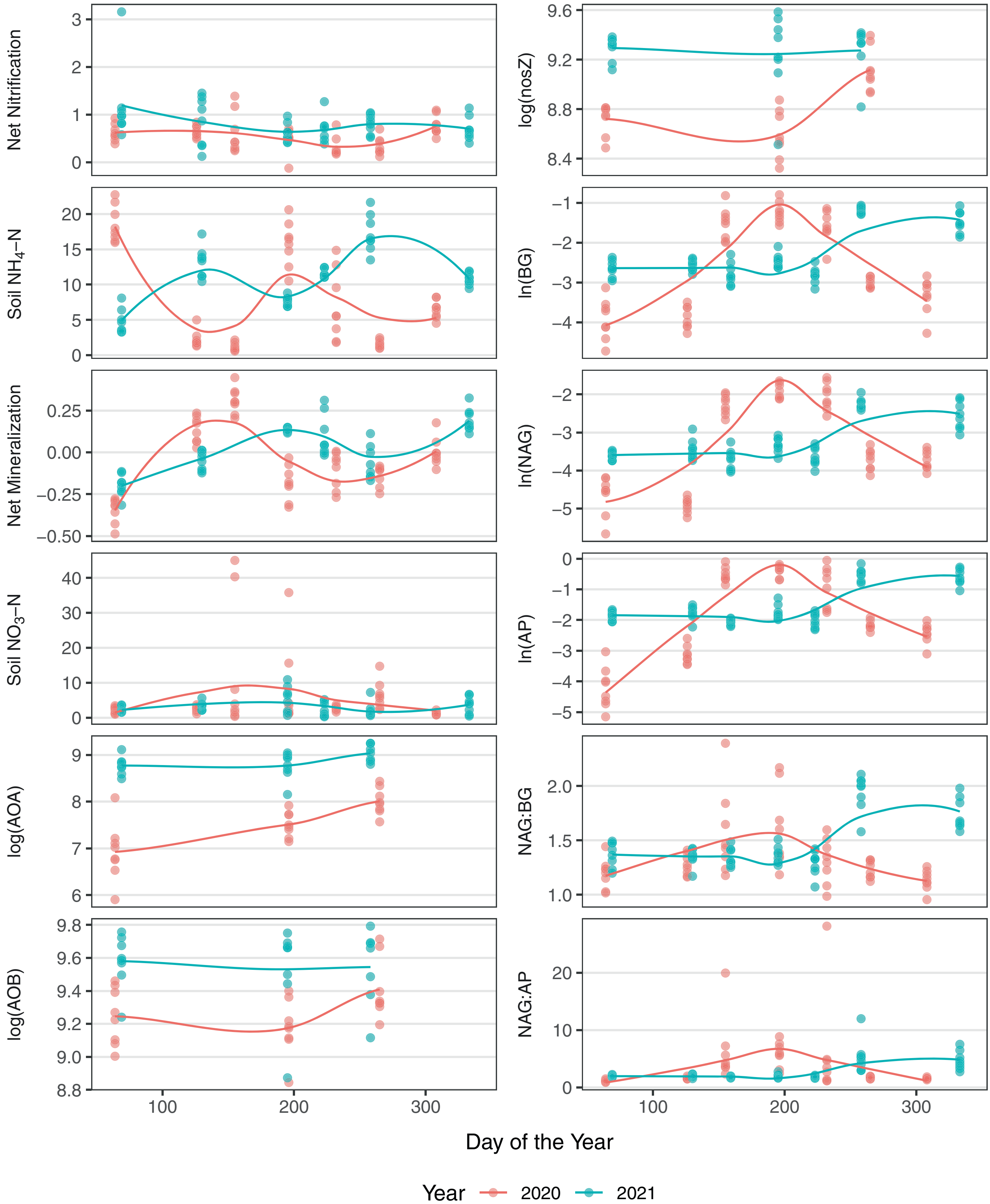

FIGURE 5 Legend on next page.

performance (Stockdale et al., 2002). The fertilizer added to the conventional fields over the course of this study to facilitate crop growth is ammonium sulfate, $(NH_4)_2SO_4$, which provides a readily oxidizable ammonium source for nitrifiers to leverage, while the organic system crops rely on soil fertility created through crop rotations (e.g., legumes) and the occasional addition of supplementary nutrient sources (Watson et al., 2002). While legume-based organic systems are capable of matching the productivity of conventionally managed systems, it is often reported that supplemental N additions are required, particularly for N-demanding crops such as corn (Archer et al., 2007; Cavigelli et al., 2008; Hinson et al., 2022; Liebhardt et al., 1989). The absence of a significant difference in soil NH_4^+-N may be due to (1) the interaction term between Year and Management System not being included in the model, (2) the specific cash/cover crop combinations for the two years of data under investigation, or (3) differences in soil physical/chemical characteristics such as soil pore-space distributions skewed toward scales that make NH_4^+-N unavailable to nitrifiers (Bauke et al., 2022; Gomez et al., 2020), potentially as a result of pore size exclusion (Nunan et al., 2003) or through the fractionation and subsequent reduction in accessible microbial organism habitat during soil drying (Tecon & Or, 2016, 2017).

Year-to-year variations in weather conditions and their impact on nutrient cycling during the transition

Weather conditions and year-to-year changes (e.g., total annual precipitation) were observed in our study and closely related to measured nitrogen processes. For instance, our correlation analysis indicates that soil moisture was significantly related to the rates of nitrification and N mineralization, as well as the availability of NH_4^+-N and NO_3^--N (Appendix S1: Table S2). The rewetting of a soil after dry periods often induces both increased C and N mineralization by making SOM more available (the Birch Effect) (Birch, 1958; Orchard & Cook, 1983; Rudaz et al., 1991), which corresponds with our elevated observed mineralization rates in mid-2020 and at the end of 2021. This effect may explain why the net mineralization rates and soil NH_4^+-N concentrations move in opposite directions for both years, to a striking degree (Figure 5). Nitrate accumulates in dry soils, often resulting in large N_2O emissions following rewetting (Liu et al., 2018), and may explain why the highest abundances of *nos*Z were observed in 2021. While variations in soil moisture and precipitation have demonstrated a sometimes-outsized effect on enzyme activity due to their effects on substrate concentrations, diffusion rates, and soil pH (Gomez et al., 2020; Sinsabaugh et al., 2008; Sinsabaugh & Shah, 2012), we did not find any statistically significant correlations between the EEA data and soil moisture. Bell et al. (2010) hypothesized that inorganic N additions may have caused suppression of genes related to the acquisition of organic N, although such interactions are unlikely in this study due to both the conventional and organic fields behaving similarly. Perhaps most relevantly, it has been determined that EEA can respond more strongly to contextual influences, such as elevation, topography, or, of particular interest, seasonality, than farming methods or soil treatments (Bell et al., 2010; Wickings et al., 2016). The substantial differences in precipitation patterns between 2020 and 2021 and consequent differences in soil moisture levels, when further compounded by crop rotations, may have introduced too much variation in external boundary conditions to detect variations in EEA. Nevertheless, year-to-year variations and changes in weather conditions need to be carefully considered when studying nutrient dynamics during conversion and transition in farming practices.

CONCLUSION

In this study, mineralization and nitrification assays, EEA, and qPCR were used to investigate how N cycling changed in response to the recent implementation of three attributes of organic farming methodologies, namely, organic fertility sources, reduced tillage, and cover cropping. Results indicate that only 3 of the

FIGURE 5 Seasonal patterns observed in the measured and calculated parameters. Extracellular enzyme activity (EEA) and quantitative polymerase chain reaction (qPCR) results were natural log transformed and log_{10} transformed, respectively, prior to plotting. The values of net nitrification and net mineralization are presented in milligram N per kilogram soil per d; soil NH_4^+-N and NO_3^--N have units of milligram N per kilogram soil; the qPCR assays ammonia-oxidizing archaea (AOA), ammonia-oxidizing bacteria (AOB), and nitrous oxide reductase (*nos*Z) are measured in log_{10}-transformed copy number per gram of soil; the EEA parameters BG, NAG, and AP have units of μmol of substrate per gram of OM per h; the ratios NAG:BG and NAG:AP are unitless. Locally estimated scatterplot smoothing (LOESS) regression was used to generate smoother curves to assist in visually interpreting the data. See Appendix S1: Figure S2 for a depiction of the same seasonal pattern visualizations with colors distinguishing between the different treatments and line types distinguishing between years.

12 parameters tested, net nitrification, AOA, and AOB, responded significantly to the experimental treatments, and, furthermore, that those variables only responded to the Management System treatment. We concluded that the conversion of conventionally managed fields to organic agricultural practices reduces nitrification within the soil, not by reducing access to NH_4^+-N within the soil but instead through a reduction in AOA and AOB. As the Tillage and Cover Crop treatments encompass smaller scopes of changes to the agricultural practices being applied, it is possible that these influences have either not emerged yet in a detectable way or that the changes are being masked by the much larger influences attributed to the Management System treatment.

We also found significant year-to-year differences, represented by the Year term in our statistical models, in many of our measured outcomes including net nitrification, soil NH_4^+-N concentration, the EEA ratio of NAG:BG, and the abundances of AOA, AOB, and the denitrifying gene *nos*Z. We suggest that unexpected or unattributed sources of perturbation such as variations in local precipitation leading to different patterns in soil moisture content and temperature, or not considering crop cycling, may interfere with detecting changes in agricultural practices on microbial activity and nutrient dynamics. The data indicate that the fields, from a nutrient and microbial activity perspective, may be still adjusting to the conversion process. This susceptibility implies that longer term and larger scale changes in weather or climate should be accounted for when conventional-to-organic conversion projects are researched or carried out. As the project progresses and more data are collected, we will be able to significantly expand the scope and power of the questions we can answer.

We recognize that our study has limitations, namely, a lack of randomized, replicated treatments distributed over a single contiguous area, and that our findings are based on two years of data. This limitation was kept in mind when designing the analysis, guiding the selection of ANOVA as the statistical test of choice as opposed to more sophisticated approaches which are generally more sensitive to assumption violations. While these limitations exist, this study has a number of strengths including eliminating the need to account for the many between-site differences that should be taken into account including weather patterns, climate, underlying geology and soil type, previous agricultural management practices, and timing differences in planting, cultivating, and harvesting; these types of shared context studies are rare, often due to necessity, but valuable for these reasons (Miller et al., 2008).

ACKNOWLEDGMENTS

This study was supported by the William Penn Foundation under Grant Award No. 188-17 and the Endowment Fund from Stroud Water Research Center. The opinions expressed in this publication are those of the authors and do not necessarily reflect the views of the William Penn Foundation. We would like to acknowledge and thank the Natural Lands' Stroud Preserve for providing access to the study site and their cooperation with this research; Stephanie Bernasconi, Michael Gentile, Kristen McKarthy, David Montgomery, Sherman Roberts, and Laura Zgleszewski for their assistance with field and lab work; Jamie Hicks for his role in carrying out agricultural operations; and Charles Dow and Daniel Myers for providing their feedback on this manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and R scripts (Price et al., 2023) are available from Zenodo: https://doi.org/10.5281/zenodo.8417453.

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SUPPORTING INFORMATION

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

How to cite this article: Price, Jacob R., Diana Oviedo-Vargas, Marc Peipoch, Melinda D. Daniels, and Jinjun Kan. 2025. "Reduction in Nitrification during the Early Transition from Conventional to Organic Farming Practices." *Ecosphere* 16(8): e70375. https://doi.org/10.1002/ecs2.70375