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For arbuscular mycorrhizal fungi in wheat roots and wheat performance in a temperate agricultural setting, distance to semi-natural habitats is important.

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Research Article

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Abstract

There will inevitably be biological, chemical, and physical interactions between semi-natural habitats and agricultural fields in an agricultural landscape. In agricultural regions, fungi may both positively and adversely impact crop development. Thus, in this field investigation, we examined winter wheat performance in relation to semi-natural settings as well as the colonization of arbuscular mycorrhizal (AM) and non-AM fungi in winter wheat roots. We took samples in agricultural transition zones, or 50-meter transects from semi-natural habitats like hedgerows and glacially formed in-field ponds—also known as “kettle holes”—into agricultural fields in an intensively managed agricultural environment in northeastern Germany. To the best of our knowledge, we demonstrate for the first time that, whereas non-AM fungal root colonization remained constant, AM fungal colonization in winter wheat roots declined linearly with increasing distance to semi-natural environments. Grain production and biomass of winter wheat rose marginally as the distance to hedgerows increased, but not to kettle holes. This demonstrates unequivocally that various crop performance metrics vary from one another. The specific significance of distance to semi-natural environments for AM fungal root colonization and winter wheat grain production was validated using random forest machine learning techniques. This trend may be partially explained by less intense agricultural management near semi-natural environments, such as the absence of pesticide and herbicide treatments due to nature preservation laws. However, AM fungi’s spatial response patterns in wheat roots—but not those of non-AM fungi—also suggest altered ecological interactions in semi-natural environments. In agricultural landscapes, semi-natural and natural habitats are becoming acknowledged as being crucial for both sustainable crop production and biodiversity conservation. They may also be a tool for policymakers and farmers to enhance sustainable landscape management. Furthermore, agricultural transition zones are dynamic, geographically and temporally diverse ecosystems that need further research.

KEYWORDS

Boiling holes, hedgerows, random forest analysis, fungal root endophytes, and transition zones

1 | INTRODUCTION

Europe's agricultural landscapes include a patchwork of natural and semi-natural areas as well as agricultural fields. These transition zones are hotspots for biological, chemical, and physical interactions as well as possible land-use disputes and restrictions owing to the close proximity of semi-natural habitats and agricultural fields. An agricultural transition zone is defined as the portion of an agricultural field that is impacted by nearby landscape patches, such as nearby agricultural fields or natural or semi-natural habitats (Kernecker et al., 2022). Since transition zones (ecotones) record an environmental gradient that represents the mixing of the two separate habitats, their biological significance has long been acknowledged (Clements, 1905; Livingstone, 1903; Schmidt et al., 2017). According to meta-ecosystem theory, nearby ecosystems are linked by spatial fluxes of organisms, materials, and energy (Gounand et al., 2018). This interaction would be especially strong in these transition zones. However, since semi-natural habitats may be included in the so-called ecological focal areas (EFA) of the European Common Agricultural Policy (CAP) of the European Union, transition zones in agricultural landscapes can play a significant role in policy concerns. This implies that farmers who use climate-friendly methods in these regions may qualify for compensating incentives. EFAs may be conflict zones of conflicting interests between farming and nature conservation since they are often significant habitats for nature conservation but also occupy a portion of farmland (for example, kettle holes; Kalettka & Rudat, 2006). To improve the sometimes unsuccessful CAP, when EFAs lack management criteria, a thorough ecological knowledge of the conflict zone is required (Pe'er et al., 2017). Agricultural management changes the variety and quantity of organisms at the field size by favoring certain soil microbes and functions (Bowles et al., 2017; Hartmann et al., 2015; Sommermann et al., 2018). As a result, the variety and quantity of microorganisms found in agricultural fields may vary significantly from those found in wild or semi-natural settings. In comparison to more complex areas with a greater quantity and variety of interspersed natural or semi-natural habitats, homogeneous areas with few natural or semi-natural habitats expand the area for agricultural management and, consequently, food production, and are simpler for farmers to manage. But in addition to being a significant factor in the decline of biodiversity (Billeter et al., 2008; Newbold et al., 2015), the shift from complex to simple agricultural landscapes may also lead to the loss of crucial ecosystem services and functions (such as water retention or nutrient cycling) that are derived from semi-natural habitats (Garibaldi et al., 2011; Holden et al., 2019). For instance, Holden et al. (2019) shown that soils under hedgerows may sustain critical ecosystem activities including runoff and carbon storage. Because they develop arbuscular mycorrhizal connections with most vascular plants, arbuscular mycorrhizal (AM) fungi are among the most significant fungi in terrestrial ecosystems (Brundrett & Tedersoo, 2018). AM fungi may have an indirect impact on plant development by altering soil structure (Lehmann et al., 2017; Leifheit et al., 2014) and directly through enhancing plant nutrition (Smith & Read, 2008), pathogen protection (Veresoglou & Rillig, 2012), and stress tolerance (Kakouridis et al. nd; Smith & Read, 2008). AM fungi are useful tools for sustainable agriculture because of their direct and indirect beneficial effects on plant performance (Rillig et al., 2016, 2019). There is a dearth of field research on AM fungus and plant performance at larger spatial scales, particularly the landscape scale, despite the abundance of greenhouse studies on the subject (Lekberg and Helgason, 2018). According to Aguilar-Trigueros et al. (2014) and Geisen et al. (2017), plant roots may have additional endophytic fungi in addition to AM fungi, which can have positive, negative, neutral, or unknown impacts on how plants and plant communities operate. When endophytic fungi interact with AM fungi in plant roots, the effects on plants and plant communities may be either favorable (Andrade-Linares and Franken, 2013; Jia et al., 2016) or varied (Gan et al., 2017). According to some research, agricultural land near certain semi-natural environments may have lower crop yields (Raatz et al., 2019; Van Vooren et al., 2018) and may have altered soil microbial diversity (Dacunto et al., 2014; Holden et al., 2019). Additionally, Holden et al. (2019) discovered that agricultural soil had less AM fungal richness than hedgerow,

field margin, and pasture soil. Battie-Laclau et al. (2020) studied an agroforestry system in France where the quantity of AM fungus in nearby wheat roots was positively impacted by the perennial elements, trees, and herbaceous plants underneath the trees. However, little is known about the geographical patterns of AM and non-AM fungal abundance in crop roots throughout agricultural transition zones and how they relate to various crop performance metrics. In their review, Holland et al. (2017) note that studies of semi-natural settings seldom quantify agricultural productivity. However, agronomic factors must also be considered when evaluating semi-natural habitats for sustainable agricultural landscape management. According to Raatz et al. (2019), yield losses are significant mostly in the vicinity of woody landscape areas. Grain yield was the sole crop performance metric employed in that research, which concentrated on two distinct German agricultural regions across a number of years. Thus, the goal of the current field research was to measure the abundance of AM and non-AM fungi in crop roots along with other crop performance metrics along 50-meter transects from semi-natural habitats into agricultural fields in a North-Eastern German agricultural environment. We discussed the following questions and theories: Does AM and non-AM fungal root colonization in winter wheat agricultural transition zones depend on proximity to semi-natural habitats? We speculate that fungal roots that are AM and non-AM Because semi-natural environments may serve as reservoirs for belowground AM and non-AM fungi and because agricultural management practices like tillage have been proven to reduce AM fungal abundance, colonization declines with increasing distance from semi-natural habitat (Bowles et al., 2017).

(1) Does the distance to semi-natural habitats affect various crop performance metrics, such as grain yield, thousand kernel weight, and biomass during wheat flowering and harvest? We hypothesize that different crop performance parameters are influenced differently by the distance to semi-natural habitats due to changing interactions between agricultural fields and semi-natural habitats during the growing season, given that Raatz et al. (2019) found that grain yield increased with increasing distance from woody landscape patches.

(2) Which biotic and abiotic factors significantly affect crop performance metrics and AM and non-AM fungal root colonization? Because agricultural transition zones are very dynamic, we hypothesize that a number of biotic and abiotic factors influence crop performance indicators and AM and non-AM fungal root colonization.

2 | MATERIALS AND METHODS

2.1 | Site and study design

In 2016, we conducted the research in the agricultural landscape of the "Quillow" river watershed in the State of Brandenburg in northeastern Germany (53° 35' N; 13° 68' E). The research area has a continental climate, with an average annual precipitation of 493 mm and an average temperature of 8.6° C during a 30-year period. The study area, which spans about 290 km², serves as the long-term research platform known as "AgroScapeLab Quillow" (AGRIcultural landSCAPE LABo-ratory) for the Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB) and the Leibniz Center for Agricultural Landscape Research (ZALF). The primary crops farmed on the 62% arable land are cereals for food and energy production, oilseed rape, and maize. Small woodland areas, grasslands, a few tiny communities, and sporadic single-family homes make up the remaining land use. Hedgerows and in-field ponds, sometimes known as "kettle holes," are the two primary semi-natural habitat types found in the "AgroScapeLab Quillow" agricultural environment. In the moraine landscapes of places like northeastern Germany and North America, kettle holes are tiny wetlands formed by glaciers (Euliss & Mushet, 1996; Kalettka & Rudat, 2006). To evaluate the impact of semi-natural habitat distance on several characteristics recorded in agricultural areas, we set up transects from hedgerows (n = 7) and kettle holes (n = 6). We also created "control" transects (n = 4) from the border between cereal fields and the agricultural fields under study in order to differentiate between the effects of edges and semi-natural landscape patches on our response variables. Typically, separate farmers were in charge of the nearby agricultural areas,

which had varied crop rotations, for instance. Along the transects, we chose four sample locations: 1, 5, 20, and 50 meters from one of the two semi-natural habitats' edges. Transect examples from this field investigation. Four sample locations were set up along each transect at 1, 5, 20, and 50 meters from the boundary of an adjacent agricultural field (c: control) and a semi-natural environment (a: kettle hole and b: hedgerow). Due to disparate scales, distance units are not precise values. Since oilseed rape is the most prevalent crop rotation in the study area, we concentrated our research on agricultural fields that were planted with winter wheat during the study year and oilseed rape the year before. We utilized land-use maps from ZALF with geographical and temporal information about crop types in the "AgroScapeLab Quillow" area to choose winter-wheat fields of 2016 with oilseed rape as the primary crop in the prior cropping season. We chose winter wheat fields that contained embedded kettle holes or bordered hedgerows using ArcMap 10.4.1 (ESRI, 2013) and integrated the land-use and natural-habitat maps of Brandenburg (Ministerium für ländliche Entwicklung, 2014). The following criteria were used to choose kettle holes in winter wheat fields: size (up to 1 ha), hydrology (permanently filled with water), plant-community type surrounding the water body (no trees, but shrubs and grassland), transect slope (lowest change of slope possible), and direction of soil management, as plowing (perpendicular to transect) to prevent mixing of soil from two data points of the transect. We chose hedgerows that bordered winter wheat fields and had the following features: width (~8 m), direction of soil management, such as plowing (perpendicular to transect), and plant community (trees up to 14 m tall, shrubs, and grassland with similar vegetation for the various hedgerows).

2.2 | Soil, plant and fungi sampling

2.2.1 | Soil parameters

We collected five soil samples (~15 cm deep) at each sampling location, arranged in a star pattern about 20 cm apart, mixed the samples, and separated them into various aliquots. To determine the physical, chemical, and isotopic features of the soil and plants, fresh soil was chilled and sent to several labs (Supporting Information: Table S1): Wet sieving was used to measure soil aggregation (>250 μm macroaggregates) (Cambardella and Elliott, 1993) and adjusted for sand content (Elliott et al., 1991). Using ceramic pressure plates, available water holding capacity (AWHC) was calculated as the difference between the gravimetric water content at field capacity (-33 kPa) and wilting point (-1500 kPa) (Richards, 1965). Gravimetric measurements of soil moisture were made in accordance with DIN ISO 11465. A TitraMaster85 (HFA D77.1.4.1, -2, DIN EN 27888, DIN ISO 11265) was used to evaluate electrical conductivity using conductometry. A TruSpec CNS (Leco Instruments GmbH; DIN ISO 13878; HFA D58.1.3.1) was used to quantify the nitrogen content of the soil using elemental analysis. Aqua regia extraction was used to assess the phosphorus and potassium content of the soil using an ICP-OES from ThermoFisher SCIENTIFIC GmbH (VDLUFA MB Volume 1 paragraph 2.4.3.1; HFA A3.3.3, HFA Part D, in accordance with DIN ISO 11466 and DIN EN 16274). Following a double lactat extraction, plant-available soil phosphorus was quantified photometrically using a GalleryTM Plus from Microgenics GmbH (VDLUFA MB Volume 1 paragraph 6.2.1.2). Total (TC), organic (TOC), and inorganic (TIC) carbon were determined fractionally simultaneously using an RC 612 from Leco Instruments GmbH (DIN ISO 10694). A TitraMaster85 (HFA D76.1.4.1, -2, -3, DIN 38404-5, DIN ISO 10390) was used to potentiometrically assess the pH of the soil. Using an Elemental Analyzer (EA) Flash 2000 HT (Thermo Fisher Scientific) connected to a Delta Visotope ratio mass spectrometer (IRMS) via a ConFlo IV interface (Thermo Fisher Scientific) and outfitted with a Costech Zero-Blank 50-position autosampler (Costech International), the $^{15}\text{N}/^{14}\text{N}$ ratio was measured to ascertain the isotopic soil N signature. The Bouyoucos hydrometer was used to measure the particle size distribution (Day, 1965), and Hollis et al. (2006) created broad texture groups. Following extraction using CaCl_2 -solution (VDLUFA MB Bd. 1 Volume 6.1.4.1 DIN ISO 14256), the amount of ammonium and nitrate in the soil was determined spectrophotometrically using a CFA-SAN from Skalaranalytic GmbH. Gregorich et al. (1990) improved the chloroform fumigation-extraction technique to assess soil microbial biomass carbon. Using a Carmomat 12D from Wöhhoff Messtechnik GmbH and Scheibler

(VDLUFA MB Bd. 1 Kap. 5.3.1; DIN ISO 10693; HFA D31.3.1.1), the carbonate content of the soil was determined using gas volumetric measurement. Using soil cores (5–15 cm soil depth) and a 100 ml capacity metal corer, the bulk density of the soil was calculated. We weighed the sample and determined the density in g cm⁻³ after the soil had dried to a consistent weight.

2.2.2 | AM fungi and non-AM fungal root colonisation

To identify AM and non-AM fungal colonization in the roots, two winter wheat plants were taken along the transects at 1, 5, 20, and 50 m from the hedgerow, kettle hole, and agricultural field boundary (Figure 1). We cleaned the roots after removing them from the field and refrigerated them for further processing. In the lab, we put roots in test tubes and filled them with a 10% potassium hydroxide (KOH) solution. After that, they were heated to 90° C for 35 minutes in a heating block. After removing the KOH solution, we thoroughly cleaned the roots for ten minutes using a 3.7% hydrochloric acid (HCl) solution. The lactophenol blue solution was then added until the roots were completely coated after the HCl solution was taken out. The lactophenol blue solution was withdrawn after 90 minutes of room temperature incubation, and we then added 50% lactoglycerol to destain the roots and get them ready for storage. At 200x magnification, 200 root segments were examined for each sample (McGonigle et al., 1990). The proportion of AM fungal root colonization was calculated from stained segments containing intraradical AM fungal structures, such as arbuscules, intercellular hyphae, and vesicles (Vierheilig et al., 2005). The other fungal structures were classified as non-AM fungus. Lastly, the proportion of roots colonized by AM and non-AM fungi was determined by dividing the total number of segments by the number of segments colonized by AM and non-AM fungal structures. For further statistical analysis, we determined the average proportion of the two winter wheat plants' roots colonizing each sample location.

2.2.3 | Plant parameters

We collected winter-wheat plant biomass twice to assess crop performance: from May 23 to May 27, 2016, during blooming, and from July 11 to July 20, 2016, when winter-wheat grains were almost ripe. We also measured the thousand kernel weight and grain yield during the second harvest. Thousand kernel weight is a wheat feature that describes the size of a cereal's kernel and is utilized in the agricultural industry, for instance, in breeding projects (Baril, 1992). From the one square meter grain yield harvest, we selected 100 kernels at random, weighed them, and multiplied the result by ten to get the thousand kernel weight. Using the BBCH-scale, which ranges from 00 (dry seed) to 99 (harvested product; Biologische Bundesanstalt, Bundessortenamt und Chemische Industrie), we assessed the phenological development stage of five winter wheat plants on the harvested square meter plot at both harvest times (Meier, 2018). We found that the BBCH-scale for winter-wheat biomass ranged from 45 to 55 during blooming and from 77 to 92 during final harvest. We used a sickle to cut every winter wheat plant inside a square meter, then we dried them till their dry weight remained consistent. Because we had to ensure that we trimmed the plants before the farmer harvested the whole field, some grains were still a little green during the second harvest. As a result, we let them ripen for a few days after harvesting before threshing. Following threshing using a threshing machine, ripe grains (July harvest) were used to calculate grain yield and thousand kernel weight. Additional plant properties are analyzed using the following methods for the random forest analyzes: A TruSpec CNS (Leco Instruments GmbH; DIN ISO 13878; HFA D58.1.3.1) was used to test the nitrogen content of plants by elemental analysis. The isotopic soil N signature was determined by measuring the 15N/14N and 13C/12C ratios using an Elemental Analyzer (EA) Flash 2000 HT (Thermo Fisher Scientific), connected to a Delta V IRMS via a ConFlo IV interface (Thermo Fisher Scientific), and outfitted with a Costech Zero-Blank 50-position autosampler (Costech International). Total carbon (TC) was determined fractionally simultaneously using an RC 612 from Leco Instruments GmbH (DIN ISO 10694). Using a (Braun-Blanquet, 1951) scale, weed cover was assessed in six 1 m² vegetation quadrats near each experimental plot at a wheat growth stage of 37–45, with three quadrats to the left and right of

the plot, parallel to the field boundary. Each experimental plot's single scores were averaged after being translated to percentage values.

2.3 | Data analyses

Important factors that might influence response variables cannot be controlled in field investigations. Because of this, we particularly evaluated for questions 1 and 2 using a linear mixed-effects model analysis. However, we examined the relative significance of a wide range of measurable explanatory factors using a machine learning technique (i.e., question 3).

2.3.1 | Mixed-effects models

For each of the following response variables—AM fungal root colonization, non-AM fungal root colonization, biomass at wheat flowering, biomass at final wheat harvest, wheat grain yield, and thousand kernel weight—we used a linear mixed-effects model in R using the "lme" function from the "nlme" package (Lindstrom & Bates, 1990). Before modeling, we verified that the residual plots from each sample point of the corresponding response variable had a normal distribution. To satisfy the requirements of linear mixed models, AM and non-AM fungal root colonization rates were square root converted. We used the factor "neighboring landscape patch," which included three levels (kettle hole, hedgerow, and agricultural field), distance (1, 5, 20, and 50 m from the semi-natural/agricultural edge), and its interaction term as explanatory variables to see if there was a difference in the effect on the response variables between different types of neighboring landscape patches. We selected "field" as the random factor to account for the variability between agricultural fields (e.g., long-term crop rotation history). Using the geographic coordinates of the sampling points, we used the distance-based Moran's Eigenvector Map (MEM) approach to reduce the possible bias from spatial autocorrelation between sampling points and transects (Blanchet et al., 2008; Borcard & Legendre, 2002; Dray et al., 2006; Legendre & Gauthier, 2014). The distance matrix of the sample locations yielded six orthogonal eigenvectors with a positive eigenvalue that represented potential spatial structure at various spatial scales (MEM1, MEM2,..., MEM6). We used the R statistical computing software program's "dbmem" function from the "adespatial" package (Dray et al., 2017) (R Core Team, 2020).

2.3.2 | Random forest analyses

The Random Forest machine learning algorithm (Breiman, 2001) of Hapfelmeier and Ulm (Hapfelmeier & Ulm, 2013) was used to model each response variable (AM and non-AM fungal root colonization, biomass at wheat flowering and final harvest, grain yield, thousand kernel weight) with all predictors (Supporting Information: Table S2). The technique uses a permutation strategy ($\alpha = 0.05$) to determine each predictor's relative relevance (i.e., how much each predictor contributes to model correctness) and statistical significance (i.e., p-value). A p-value in this test indicates the likelihood that a predictor adds to a model's accuracy by chance (Ryo & Rillig, 2017). In order to quantify variable importance, the method uses a non-parametric modeling technique that resolves the multicollinearity problem (Nicodemus et al., 2010). Furthermore, it can construct a model even if there are more predictors than samples (Breiman, 2001). After establishing that these values are sufficient to stabilize the findings, the hyper-parameters—that is, the numbers of trees and permutations that impact algorithm performance—were set to 1000 and 4000, respectively. We employed 50 explanatory variables for AM and non-AM fungal root colonization and 55 explanatory variables for biomass at flowering, biomass at final harvest, grain yield, and thousand kernel weight (Supporting Information: Table S1) in order to determine the main variables of interest (i.e., the type of neighboring landscape patch and distance from the edge) that explain their variability. In addition to the distance from the edge and the type of nearby landscape patch, the explanatory variables included the chemical, physical, and biological characteristics of plants and soil, the six orthogonal eigenvectors that accounted for the sampling points' spatial distribution, and landscape characteristics that were calculated using Fragstats 4.2 (McGarigal & Marks, 1995), such as the Shannon diversity Index, the percentage of arable land in a 250 m radius landscape surrounding the sampling points, the owners

of the agricultural fields, wheat variety, and weed abundance (Supporting Information: Table S1). $R^2 > 0.05$ variables are the only ones that are reported. The factors that explain random or geographical variation, such "field," "MEM 1-6," and those that have a lot of missing data, like "wheat variety," are not reported since it would be beyond the purview of our research to explain their significance. We used the partial dependency plot technique (Trevor et al., 2009), which shows the relationship between each predictor and the corresponding response variable while taking the impact of the other predictors into consideration. The R packages "party" (Strobl et al., 2009) and "mlr" (Bischl et al., 2016) were used.

3 | RESULTS

3.1 | AM and non-AM fungal wheat root colonisation with increasing distance to semi-natural habitats

Over all sample locations ($n = 68$), arbuscular mycorrhizal root colonization in winter-wheat roots revealed highest values of 20.3%, minimum values of 0.2%, and a mean and standard error of $6.4\% \pm 0.5\%$. The mean and standard error of non-AM fungal root colonization in winter wheat roots were $9.5 \pm 0.8\%$, with highest values of 31.2% and low values of 0.6% across all sample locations ($n = 68$). In contrast to transects bordering another agricultural field (i.e., controls; Figure 2a), AM fungal root colonization of winter-wheat plants reduced linearly with the distance from kettle holes and hedgerows. We discovered an interaction impact of "landscape patch x distance" ($p = 0.01$) and their independent effects (distance: $p < 0.001$ and landscape patch: $p < 0.001$; Table 1) for AM fungal root colonization of winter-wheat plants. For non-AM fungal root colonization, however, we found no such correlations (all $p > 0.05$, Table 1; Figure 2b). Only a few factors account for the variance in the answer variables, according to random forest exploratory analyzes. The type of neighboring landscape patch ($R^2 = 0.16$), the distance to the neighboring landscape patch ($R^2 = 0.10$; Supporting Information: Table S2), and the Shannon-diversity of landscape patches within a 250-m radius landscape area around the sampling points ($R^2 = 0.05$; Table 2 and Supporting Information: Table S2) all contributed significantly to the variation in AM fungal root colonization. Very little of the diversity in non-AM fungal root colonization could be explained by us. The majority of the variance was associated with the kind of nearby landscape patch ($R^2 = 0.06$) and the amount of arable land within a 250-meter radius around the sample spots ($R^2 = 0.05$; Table 2 and Supporting Information: Table S2).

3.2 | Crop performance with increasing distance to semi-natural habitats

Winter-wheat biomass at flowering time had maximum values of 5.295 t ha^{-1} , minimum values of 0.490 t ha^{-1} , and an average and standard error of $3.204 \pm 0.120 \text{ t ha}^{-1}$ for all sampling points ($n = 68$); winter-wheat biomass at final harvest had maximum values of 22.486 t ha^{-1} , minimum values of 6.743 t ha^{-1} , and an average and standard error of $17.036 \pm 0.194 \text{ t ha}^{-1}$; winter-wheat grain yield had maximum values of 9.970 t ha^{-1} , minimum values of 1.615 t ha^{-1} , and an average and standard error of $7.036 \pm 0.194 \text{ t ha}^{-1}$.

FIGURE 1; For transects beginning at kettle holes (circles with a dashed line; $n = 6$), hedgerows (asterisks with a dotted line; $n = 7$), and adjacent agricultural fields (filled circles with a continuous line; $n = 4$), the percentage of arbuscular mycorrhizal (AM) fungal root colonization (a) and non-AM fungal root colonization (b) as a function of distance from the agricultural field border. Because the mixed model analysis for non-AM fungal root colonization was not significant, the regression line for panel how B is not sn.

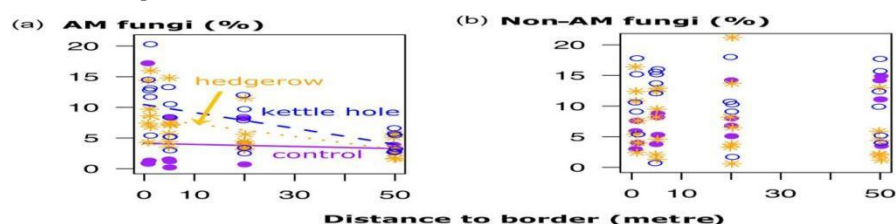


TABLE 1;The percentage of AM fungal (AMF) and non-AM fungal (non-AMF) winter wheat root colonization, winter wheat biomass at flowering time (biomass at flowering) and at final harvest (biomass at final harvest), winter wheat grain yield (grain yield), thousand kernel weight, and the test parameters type of landscape patch (kettle hole, hedgerow, agricultural field; "Landscape patch type") and distance to neighboring landscape patch type;

		12.39	<0.001							3.70	0.033	5.18	0.010
		23.28	<0.001	0.002	0.965	5.74	0.021	12.01	0.001	15.09	<0.001	1.20	0.280
							<0.001	11.10	0.002	4.27	0.045	3.72	0.060
						6.76	0.013	2.53	0.119	10.92	0.002	5.93	0.019
MEM3	1	0.07	0.793	6.44	0.015	5.31	0.027	0.18	0.676	1.84	0.182	0.00	0.978
MEM4	1	0.001	0.971	3.58	0.065	6.90	0.012	0.42	0.520	2.96	0.093	1.55	0.220
						14.79	<0.001	8.34	0.006	4.03	0.051	7.00	0.011
MEM6	1	1.40	0.243	13.60	<0.001	0.98	0.329	0.95	0.336	0.33	0.567	0.28	0.600
			0.010	2.54	0.090	1.34	0.273	1.81	0.176	3.94	0.027	1.57	0.220
		195.65	<0.001	120.47	<0.001	1132.60	<0.001	2893.60	<0.001	1778.68	<0.001	1985.66	<0.001

"distance"), their two-way interactions and Moran's eigenvector maps (MEM1-6) (*p*-values lower than 0.05 are in bold and in grey)

Factor	DF	AMF		Non-AMF		Biomass at flowering		Biomass at final harvest		Grain yield		Thousand kernel weight	
		<i>F</i> -value	<i>p</i> -value	<i>F</i> -value	<i>p</i> -value	<i>F</i> -value	<i>p</i> -value	<i>F</i> -value	<i>p</i> -value	<i>F</i> -value	<i>p</i> -value	<i>F</i> -value	<i>p</i> -value
Landscape patch type	2			0.86	0.431	0.44	0.647	1.12	0.335				
Distance	1												
MEM1	1	1.07	0.307	0.80	0.377	22.61							
MEM2	1	0.48	0.492	0.65	0.423								
MEM5	1	0.19	0.670	0.20	0.661								
Landscape patch type x Distance	2	5.11											
Residuals	1												

TABLE 2; The primary explanatory variables for biomass at flowering and final harvest, grain yield, thousand kernel weight, arbuscular mycorrhizal (AM), and non-AM fungal root colonization were found to have variable importance based on random forest analyzes (see Table S1 for a detailed description of all explanatory variables). "Not incl." refers to variables that were left out of this particular analysis.

	Variable importance (contribution to R ² -fitting)					
	Biomass flowering	Biomass final	Grain yield	1000 kernel weight	AM fungi	non-AM fungi
R ² -fitting	0.797	0.812	0.852	0.846	0.803	0.749
R ² -validation	0.494	0.521	0.597	0.619	0.431	0.448
Weed cover	0.077	0.275	0.337	0.000	0.013	0.000
Distance	0.000	0.152	0.135	0.000	0.101	0.000
Neighboring patch	0.000	0.000	0.013	0.014	0.162	0.060
Soil aggregation	0.035	0.101	0.066	0.000	0.000	0.000
AM fungi	0.000	0.067	0.064	0.000	not included	not included
Shannon Diversity Index	0.005	0.000	0.000	0.031	0.053	0.043
Percentage arable land	0.005	0.000	0.000	0.024	0.025	0.054
Edge density	0.018	0.000	0.000	0.064	0.000	0.014
Patch richness	0.014	0.000	0.000	0.052	0.000	0.000
Soil C/N ratio	0.071	0.000	0.005	0.000	0.000	0.000
AWHC	0.056	0.000	0.000	0.000	0.008	0.000

The thousand kernel weight showed an average and standard error of 45.5 ± 0.07 g, a maximum value of 58.3 g, and a minimum value of 32.6 g. Distance had a significant impact on all crop performance metrics except for household kernel weight, according to the mixed-effects model analyzes (Table 1) (biomass at flowering: $p = 0.021$; biomass at final harvest: $p = 0.001$; grain yield: $p < 0.001$; Figure 3a–d). Grain yield ($p = 0.033$) and thousand kernel weight ($p = 0.01$) were both impacted by the kind of nearby landscape patch. Transects beginning

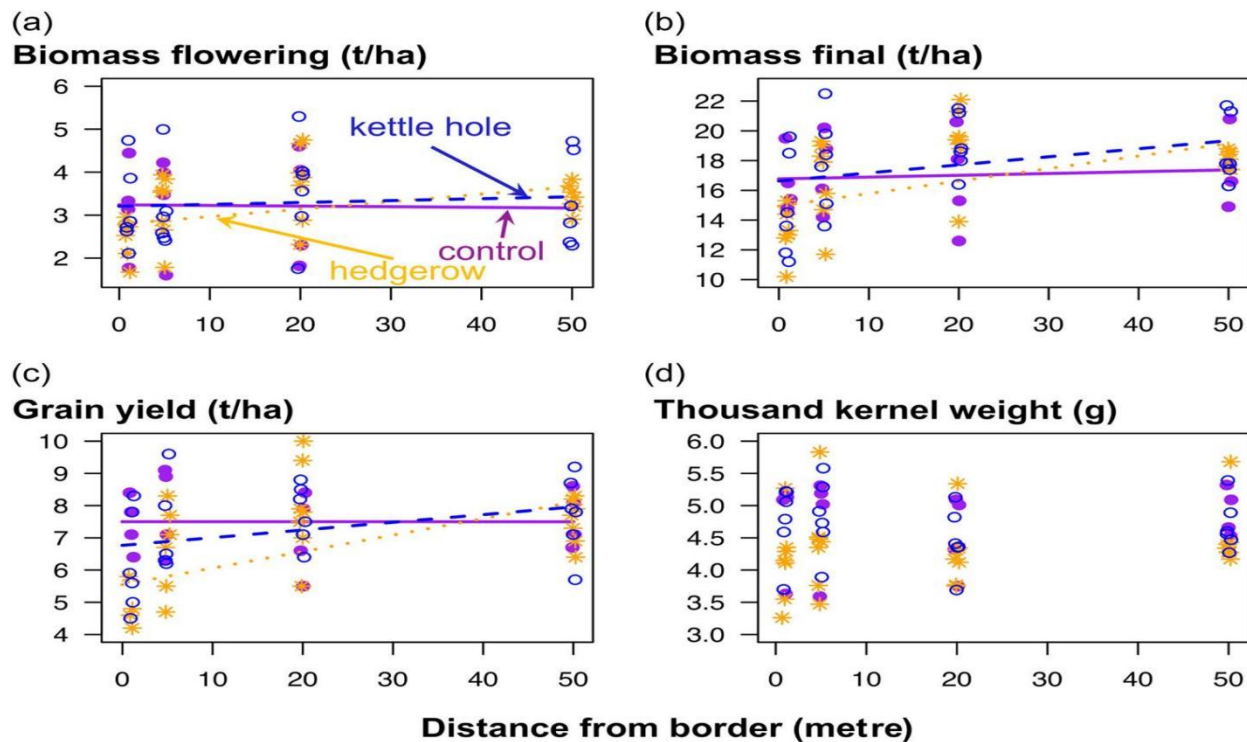


FIGURE 2; Depending on the distance from the agricultural field border for transects beginning at kettle holes (open circles with a dashed line; $n = 6$), hedgerows (asterisks with a dotted line; $n = 7$), and adjacent agricultural fields (filled circles with a continuous line; $n = 4$), winter-wheat biomass at wheat flowering time (a), winter-wheat biomass at final harvest (b), winter-wheat grain yield (c), and thousand kernel weight (d).exhibited lower thousand kernel weight and grain production in hedgerows than those beginning at kettle holes (Table 1; Figure 3c,d). Only grain yield at final harvest showed a significant interaction between “landscape patch $\times$ distance” ($p = 0.027$). This indicates that compared to transects next to other cereal fields, the

drop in grain production in semi-natural landscape sections, particularly hedgerows, was steeper (Figure 3c). Grain yield, however, differed somewhat from controls at a distance of 20 meters or more from the boundary between the semi-natural landscape patches and the agricultural field (Figure 3c). Weed abundance ($R^2 = 0.08$), the June C:N ratio ($R^2 = 0.07$), and the available water holding capacity ($R^2 = 0.06$) all contributed to the explanation of the biomass variability during wheat blooming in the random forest analyzes (Table 2 and Supporting Information: Table S2). The distance to the landscape patch border ($R^2 = 0.15$ and 0.14), weed abundance ($R^2 = 0.28$ and 0.34 , respectively; Table 2 and Supporting Information: Table S2), macroaggregates ($R^2 = 0.10$ and 0.07), and AM fungal root colonization ($R^2 = 0.07$ and 0.06 ; Table 2 and Supporting Information: Table S2) were the primary explanatory factors for wheat biomass and grain yield at harvest. In contrast to the other response variables, edge density ($R^2 = 0.06$) and landscape patch-richness in a 250-meter radius circle ($R^2 = 0.05$) were the only factors that could account for the variability in thousand kernel weight (Table 2 and Supporting Information: Table S2).

DISCUSSION;

To the best of our knowledge, we demonstrate for the first time that wheat AM fungal root colonization declines as one gets further away from semi-natural settings. Even after adding several covariables in a random forest analysis, this association persisted. For fungal root colonization that was not AM, we did not see such a trend. Furthermore, a number of crop performance metrics showed distinct trends in relation to the distance from semi-natural habitats. The greatest impact was shown in grain yield, which mostly increased with distance from hedgerows.

3.3 | AM and non-AM fungal wheat root colonisation with increasing distance to semi-natural habitats

Winter wheat's AM fungal root colonization declined as it got further away from semi-natural areas. This presents a management opportunity because AM fungi are known to improve soil quality, such as soil aggregation, water retention, and soil carbon and nutrient cycling, in addition to helping plants access soil nutrients for plant-derived carbon and strengthening their resistance to biotic and abiotic stress (Bardgett & van der Putten, 2014). The decline in AM fungal root colonization as one moves further away from semi-natural settings might be caused by a number of factors: Perhaps the most important aspect is agricultural management. According to Bowles et al. (2017), Helgason et al. (1998), Manoharan et al. (2017), Pellegrino et al. (2020), and Verbruggen et al. (2010), the conventional methods used by the farmers in our region to manage their winter wheat fields include soil management and plant protection applications. Fungicides against *Alternaria* and *Fusarium* fungi and the spraying of glyphosate, which may have an adverse influence on the AM fungal population, are among the plant protection strategies for winter wheat (Hage-Ahmed et al., 2019; Rivera-Becerril et al., 2017). Furthermore, depending on the crop protection materials, land managers in our research region are required by nature protection legislation to maintain a distance of 5 to 25 meters from semi-natural habitats such as hedgerows and kettle holes (Baer et al., 2018). Thus, we propose that an agricultural management gradient throughout the transects may be the primary cause of the AM fungal root colonization gradient. Raatz et al. (2021) found higher weed abundances around kettle holes and hedgerows at the same transects and in the same year, which they attribute to less pesticide use in the vicinity of semi-natural habitats. AM fungus are found in a variety of weed species (Vatovec et al., 2005). Therefore, decreasing weed richness with distance to semi-natural habitats may potentially contribute to the trend of declining AM fungal root colonization with increasing distance from semi-natural habitats. However, in the random forest analyzes, weed abundance did not significantly predict AM fungal root colonization (Table 2 and Supporting Information: Table S2). To prevent soil mixing across sample locations at different distances, we selected the transects in the field to be perpendicular to the land managers' operating direction (e.g., plowing direction). Our research may have benefited from ecological interactions between semi-natural habitats and agricultural fields, such as light competition (Schmidt et al., 2017) and spatial movements of species, material, and energy (Gounand et al., 2018; Loreau et al., 2003). According to Loreau et al.

(2003), meta-ecosystem theory explains how spatial movements of species, resources, and energy across ecosystem boundaries link various ecosystems. This concept may be useful in comprehending biodiversity-ecosystem functioning in various ecosystems (Scherer-Lorenzen et al., 2022) as well as ecosystem dynamics (Gounand et al., 2018). Although we did not explicitly examine spatial flows along the transects, higher soil moisture, carbon, and nitrogen levels near semi-natural habitats relative to in-field datapoints may be the consequence of such spatial fluxes (Supporting Information: Table S3, Figure S1). For instance, tall kettle hole and hedgerow vegetation can shade the agricultural transition zone, reducing evaporation and increasing soil humidity at field borders; kettle hole water can wet agricultural soil surrounding the pond; and leaves from these vegetation types can fall on agricultural field edges (Schmidt et al., 2017). Field-to-field boundaries do not experience such biotic and abiotic fluxes across landscape patch borders. Additionally, these flows have the potential to affect belowground AM fungus as well as soil biotic properties (Bainard et al., 2014). In the mixed model and random forest, the kind of landscape patch (such as a kettle hole, hedgerow, or agricultural field) was a powerful predictor of AM fungal root colonization (Tables 1 and 2). Therefore, we propose that the AM fungal pattern is influenced by both spatial movements of energy, material, and organisms and agricultural management. AM fungi may spread both actively by extraradical hyphae and passively through biotic (such as small animals and earthworms) and abiotic (such as wind and water) agents (Paz et al., 2021 and references therein). To ascertain how these activities contribute to the observed AM fungal root colonization pattern in agricultural transition zones, further investigation is necessary. There was no correlation between the distance to semi-natural habitats and non-AM fungal root colonization. Our findings, however, show that non-AM fungal root colonization was more common in transects that began near kettle holes than in the other transects. The study's kettle holes were permanently filled with water, and the agricultural soil near the holes had a higher soil-water content than the soil farther away (Supporting Information: Table S3, Figure S1, and Pirhofer Walzl, 2022). This could have had a favorable effect on the presence of fungi (Müller et al., 2016). In contrast to agricultural fields, some investigations revealed higher AM fungal diversity and abundance beneath hedgerows (Holden et al., 2019) or permanent agroforestry vegetation (Battie-Laclau et al., 2020). Consequently, semi-natural environments might be an important source of AM fungus. These AM fungi may be advantageous for agricultural output when they overflow into the field, particularly when crops are subjected to severe disturbances. For instance, AM fungus may make plants more resilient to resource constraint during droughts (Chareesri et al., 2020; Kakouridis et al.; Li et al., 2019), which will occur more often in the future (Masson-Delmotte et al., 2021). Additionally, some management techniques that favor AM fungus, such as no-till and legume cover crops, may enhance AM fungal root colonization and, therefore, soil and plant quality within the agricultural field (Bowles et al., 2017).

3.4 | Crop performance with increasing distance to semi-natural habitats

Several research (e.g., Laura et al., 2017; Raatz et al., 2019) have shown an increase in yield with increasing distance to semi-natural landscape regions, which is consistent with our findings. Raatz et al. (2019) demonstrated that grain yield rose with distance to semi-natural habitats, mostly at wood landscape patches, for two distinct agricultural regions in Germany over a number of years, including the grain yield of our transects during the same year. When assessing semi-natural habitats in agricultural settings, the majority of research have not examined crop production (Holland et al., 2017), however others, like Raatz et al. (2019), have simply looked at one crop performance metric. We give a variety of descriptive and temporal agricultural performance metrics (such as grain yield, thousand kernel weight, and wheat plant biomass at flowering and final harvest) that generate varied outcomes. While thousand kernel weight was unaffected by distance, the impact of distance to nearby landscape areas on crop performance rose from winter-wheat biomass at blooming to final harvest to grain yield. The only variable that changed with distance based on the landscape patch was grain yield, which rose with distance,

particularly at hedgerow transects (Table 1). Crop performance patterns may also be described by a mix of agricultural management, ecological interactions, and nature protection regulations with regard to AM and non-AM fungal wheat root colonization patterns along agricultural transition zones. Furthermore, these elements are often inherently connected to one another. In the random forest analyzes, weed abundance was shown to be a significant explanatory factor for wheat biomass during flowering, final harvest, and grain yield. Raatz et al. (2021), who demonstrate detrimental impacts of weed abundance on grain yields from experimental plots along the identical transects employed for the current investigation at 1 and 5 m distances from semi-natural habitats, are confirmed by our grain yield data. While we gathered wheat plants seeded by the farmers, Raatz et al. (2021) examined wheat plants that they planted in the farmers' fields. Weeds and other incidental plants can effectively reduce crop biomass and grain yield because they compete with crops for space, nutrients, water, and light (Zimdahl, 2004). This is especially true near semi-natural habitats where herbicides cannot be sprayed because of nature protection regulations (Baer et al., 2018). Additionally, a higher abundance of accidental plants in semi-natural environments may be due to seed distribution from hedgerow and kettle hole vegetation into the agricultural field (Lozada-Gobilard et al., 2019). Reduced biomass and productivity at the margins might also be explained by competition between agricultural plants and vegetation from semi-natural habitats. Nutrient and water competition cannot be the reason for yield and crop biomass reduction near the edge in our study because nutrients, such as nitrogen and phosphorus, and soil water were more readily available near semi-natural habitats (Supporting Information: Table S3, Figure S1, and Pirhofer Walzl, 2022). Low crop output in semi-natural environments, such as in agroforestry systems (Dufour et al., 2013) and along hedgerows (Laura et al., 2017; Raatz et al., 2019), has previously been linked to light competition, which may possibly be the reason for our research. However, semi-natural habitats—particularly those with higher vegetation, such hedgerows and forest fragments—can also benefit crops in a number of ways, such as by conserving soil, increasing soil moisture, and shielding them from physical harm (Kort, 1988; Nuberg, 1998). Increased soil water and nutrients around kettle holes and hedgerows in our transects point to a soil protection effect (Supporting Information: Table S3, Figure S1, and Pirhofer Walzl, 2022). To ascertain the impact of semi-natural environments' evapotranspiration on our crop plants, we neglected to assess the wind and the direction of our transects. However, compared to 2017, the shelter impact of semi-natural habitats on yield was more noticeable in our research location during the dry 2016 year (Raatz et al., 2019). Given that climate projections forecast more dry years and more severe weather and climate extremes, this highlights the potential significance of semi-natural habitats as a climate and weather buffer (Masson-Delmotte et al., 2021). Crop performance patterns throughout agricultural transition zones may have been significantly influenced by crop management and nature protection rules (EU and German regulations, No. 1107/2009, Bundestag, 2012). The kind of adjacent landscape patch, the number of natural or semi-natural landscape patches in the surrounding landscape, and the active ingredient all affect these rules (Baer et al., 2018). Increased development of accidental plants near semi-natural environments may have resulted from little or no pesticide use (see above). In addition to pests from nearby semi-natural habitats spilling over into agricultural fields, low or nonexistent application of plant protection measures against pests, such as fungi and herbivores, near semi-natural patches may have led to an increase in pest infestations near hedgerows and kettle holes. However, in the same winter-wheat transects as this research, Raatz et al. (2021) found no impact of fungal seed, fungal leaf diseases, or cereal leaf beetle herbivory on grain production. However, other wheat pests, such aphids, could have contributed to the decreased output near semi-natural settings. Additionally, the yield around kettle holes may have decreased due to poor or nonexistent fertilizer application near bodies of water (Baer et al., 2018). However, our study's two evaluations of soil nutrients throughout the growing season revealed high levels near semi-natural habitats (Supporting Information: Table S3, Figure S1, and Pirhofer Walzl, 2022). The proportion of macroaggregates in the soil had a

favorable impact on biomass at final harvest, whereas grain yield and the C/N ratio had a positive impact on biomass during wheat blooming, according to the random forest analyzes, along with weed abundance and distance to a nearby landscape patch. A crucial aspect of soil quality that affects soil water dynamics, nutrient cycling, and crop output is soil particle aggregation. Additionally, soil biota—particularly bacteria and fungi—have a significant impact on the dynamics of the soil's C/N ratio as well as the quantity of micro- and macro-aggregates in the soil (Lehmann et al., 2017).

4 | CONCLUSION

Our research clarifies trends in wheat plant fungal root colonization and crop performance in relation to semi-natural settings. For the first time, we demonstrate that crop performance, or grain production, rose while AM fungal root colonization decreased increasing distance to semi-natural environments. Additionally, our research demonstrates that several crop performance metrics vary from one another. Consequently, semi-natural environments might be an important source of AM fungus. Our findings may be significantly affected by agricultural management, particularly weed control techniques, which are heavily impacted by laws protecting the environment. Further empirical research in the field is necessary because agricultural transition zones are dynamic, geographically and temporally complex ecosystems. Field research should examine how agricultural management and ecological interactions (such as competition, nutrient fluxes, etc.) affect agronomic parameters and above- and below-ground ecosystem functioning along agricultural transition zones. This information might assist resolve local disputes between farmers and nature preservation organizations as well as CAP restrictions (Kerneck et al., 2022). It is gradually becoming clear that small semi-natural habitats in agricultural landscapes are crucial for both sustainable crop production (Pywell et al., 2015) and biodiversity conservation (Herzon et al., 2022; Tschardt et al., 2021; Wintle et al., 2019). Farmers are under pressure to contribute to sustainable landscape management in addition to producing large crops. Farmers and policy may be able to enhance their contribution to sustainable soil, crop, and landscape management by maintaining and implementing natural or semi-natural landscape areas.

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