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RESEARCH ARTICLE

Effects of crop species on soil functions and soil multifunctionality are species-specific

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Abstract

1. Soil multifunctionality is essential for sustainable agriculture, as soils not only need to support crop growth but also maintain soil biodiversity and sustain other critical ecosystem functions. However, the focus of intensive agriculture on maximizing crop yield has reduced the multifunctional capacity of soil. Here, we examined how crop species can be used to enhance individual soil functions and multifunctionality.
2. We grew 12 common crop species, organized into four groups: legumes (broad bean, green bean and soybean), crucifers (broccoli, Chinese cabbage and cabbage), cereals (wheat, maize and oat), and a vegetable mix (eggplant, chilli pepper and leek) under controlled conditions. We measured how crop species affected individual soil functions (plant biomass production, nutrient cycling, carbon storage and disease suppressiveness), soil multifunctionality and the balance in the performance of these functions, expressed as evenness of functionality.
3. We found that crop species have specific impacts on soil functions and multifunctionality. Broad bean enhanced multifunctionality by enhancing biomass production and nutrient cycling, while Chinese cabbage and broccoli increased multifunctionality via disease suppressiveness and carbon storage functions. There was a positive correlation between multifunctionality and the evenness of functionality, suggesting that crops enhanced multiple soil functions simultaneously.
4. We conclude that no single crop species consistently increased all soil functions. However, most crop species contributed to soil multifunctionality by stimulating either a balanced combination of nutrient and biomass production-related functions or disease and carbon storage-related functions. Therefore, enhancing soil multifunctionality in agricultural systems may require selecting crop species that are complementary in their effects on soil functions. We propose that optimizing the multifunctionality of entire crop rotations instead of focusing only on yield offers a novel perspective for enhancing the sustainability of food production. Such a multifunctional perspective on crop rotations

may also be applicable to intercropping, and both will require attention to keep the agricultural system diversified.

KEYWORDS
agriculture, crop functional complementarity, multifunctional crop rotation, soil function, soil multifunctionality

1 | INTRODUCTION

Soil multifunctionality is crucial for sustainable agriculture, as soils that perform multiple functions optimally will contribute to the provisioning of nutrients to crops, carbon storage, purification and regulation of water, suppression of soil-borne diseases and support of soil biodiversity all at the same time (Larkin, 2015; Schulte et al., 2014). However, in intensive agriculture, many soil functions are bypassed by management practices, such as applying artificial fertilizers and pesticides (Baweja et al., 2020). These and other management practices have maximized yield but have also resulted in a widespread decline in overall soil biodiversity (Tsiafouli et al., 2015) and soil functions (Campbell et al., 2017; Kopittke et al., 2019; Walling & Vaneeckhaute, 2020). Effects of cropland management are not only restricted to the agricultural systems themselves; the spillover of chemicals has also caused a decline in biodiversity in neighbouring natural ecosystems (Didham et al., 2015; Liess et al., 2021; Matson et al., 1997). Hence, there is a major interest in restoring soil functioning in agroecosystems through sustainable practices, such as crop rotation and diversification, which may help to reduce the use of external chemical inputs (Yang et al., 2020; Zwetsloot et al., 2021). However, there is still limited knowledge on how to restore soil functions.

One of the approaches to enhance soil functioning is to choose crop species based on their impact on soil functions. Crop species can affect individual soil functions (Fry et al., 2018; Mathew et al., 2017; Schmid et al., 2021) by influencing abiotic (Fox et al., 2020; Weidenhamer & Callaway, 2010) and biotic soil properties (Bardgett & van der Putten, 2014) through taking up water and minerals, returning organic materials, such as litter and root exudates to the soil, and by interacting with pathogens and mutualists in their rhizosphere (Paterson, 2003; Wardle, 2006). However, the effects of plants on soil functions can be highly species-specific (Bezemer et al., 2006; Hannula et al., 2020; Kardol et al., 2010; Perkins et al., 2011; Singh et al., 2009) as different plants shape soil functions through unique alterations in soil microbiome, nutrient cycling and chemical exudation (Trivedi et al., 2022; Xiong et al., 2021). For example, maize can enhance soil nutrient cycling by recruiting arbuscular mycorrhizal in its rhizosphere, positively impacting plant phosphorus (P) uptake (Xu et al., 2019). Crop species that are phylogenetically closely related may share traits, potentially leading to similar effects on soil properties and functions (Reich, 2014; Wandrag et al., 2020). For example, leguminous species can enhance soil nitrogen (N) availability through their symbiosis with N-fixing rhizobia (Borase et al., 2020; Liu, Ma, et al., 2021), while cruciferous species may reduce soil-borne diseases and weeds by excreting sulphur-containing compounds (Handiseni et al., 2016; Larkin & Lynch, 2018). However, how impacts on soil functions differ among crop species and taxonomic groups remains unclear. Here, we study soil functions within and across taxonomic groups to determine whether generalizable patterns can be used to design cropping systems with enhanced multifunctionality.

Although crop species can impact individual soil functions, it is necessary to consider the impact of crops on multiple soil functions simultaneously, a concept known as multifunctionality (Creamer et al., 2022). Several agricultural practices have already been shown to enhance multifunctionality. For example, organic fertilization was found to enhance multifunctionality (Zheng et al., 2024) by optimizing soil abiotic (Ying et al., 2023) and biotic properties (Luo et al., 2023; Tang et al., 2023). No-tillage or intermittent tillage can also enhance multifunctionality through improved soil fertility, optimized soil enzyme activity and enhanced soil microbial activity (Liu et al., 2025; Zhu et al., 2025). However, little is known about how crop species influence soil multifunctionality. Existing studies are limited and often compare plant species from different functional groups, such as alfalfa versus winter wheat (Liu et al., 2024), or focus on only a few individual functions (Palojärvi et al., 2020). Yet, we do not understand how crop species and taxonomic groups affect soil multifunctionality. Such understanding is crucial for identifying and designing multifunctionally optimized combinations of plants with complementary impacts on soil functions in crop mixtures or rotations (Power, 2010; Schipanski et al., 2014).

Multifunctionality is often studied by combining measurements of individual soil functions into a single index, using either the 'averaging' or the 'threshold' method (Byrnes et al., 2014). The 'averaging method' is quantitative and uses the average of individual soil functions. However, this index does not indicate whether individual functions are performed evenly or if certain functions dominate the outcome, potentially masking imbalances in soil multifunctionality (Greiner et al., 2018). In contrast, the 'threshold method' is based on counting the number of functions meeting predefined benchmarks, indirectly capturing functional evenness. However, selecting benchmarks can be arbitrary and subjective (Manning et al., 2018; Schram et al., 2024). Understanding whether greater multifunctionality results from an extreme increase in one function or a more balanced increase in multiple soil functions is essential. True multifunctionality is achieved only in the latter scenario. Therefore, we propose incorporating the study of 'evenness of multifunctionality' into multifunctionality calculations.

Although rarely applied in multifunctionality research, the multifunctionality evenness calculation can be adapted from the concept of evenness in community ecology research (De Jong, 1975). In this concept, communities with a more even distribution of species abundance are more diverse than those where one species dominates while the others remain subordinate (De Jong, 1975). Applying this concept to multifunctionality research allows us to determine whether crop impacts on multifunctionality are related to an even or uneven performance of individual functions.

The aim of the present study was to investigate the impact of crop species on individual soil functions, soil multifunctionality and the evenness of functionality. We tested two hypotheses: (1) Crop species differ in their capacity to enhance specific soil functions and multifunctionality, and (2) species belonging to the same taxonomic groups are more comparable in their effect on specific soil functions, multifunctionality and evenness of functionality than species among groups. In addition, we explored how multifunctionality correlates with the evenness of functionality. To test our hypotheses, we grew all 12 crop species in a greenhouse under standardized soil and climate conditions. We measured processes related to the four key soil functions of interest and used these to calculate soil multifunctionality. The results are discussed with respect to designing cropping schemes that can enhance soil multifunctionality and thereby promote the environmental sustainability of agricultural food production.

2 | MATERIALS AND METHODS

The experiment was conducted in the greenhouse of the Netherlands Institute of Ecology (NIOO-KNAW, Wageningen, the Netherlands). Twelve major food and vegetable crop species from four different species groups were grown under greenhouse conditions in standardized soil types and climate conditions. Measurements of soil functions were taken after the plants had been harvested (Figure 1).

2.1 | Soil and plant materials

A standard mixture of sterilized background sandy loam soil was inoculated with 15% live soil. Background soil was collected from the layer 20–40 cm below the soil surface of a former agricultural field (52°03′ N, 5°45′ E) that had been abandoned since 1996 (Van der Putten et al., 2000). The background soil was sieved using a 5-mm mesh to remove pebbles and large root fragments, homogenized and sterilized by either gamma irradiation (>25 kGy; Isotron, Ede, the Netherlands) or autoclaving (three consecutive days, for 20 min at 120°C) to obtain sterilized soil. We used two different sterilization methods because the gamma-irradiated soil alone was insufficient, so we supplemented the deficit with autoclaved soil. Recognizing that different sterilization methods might result in variations (McNamara et al., 2003), we used equal proportions of gamma-sterilized and

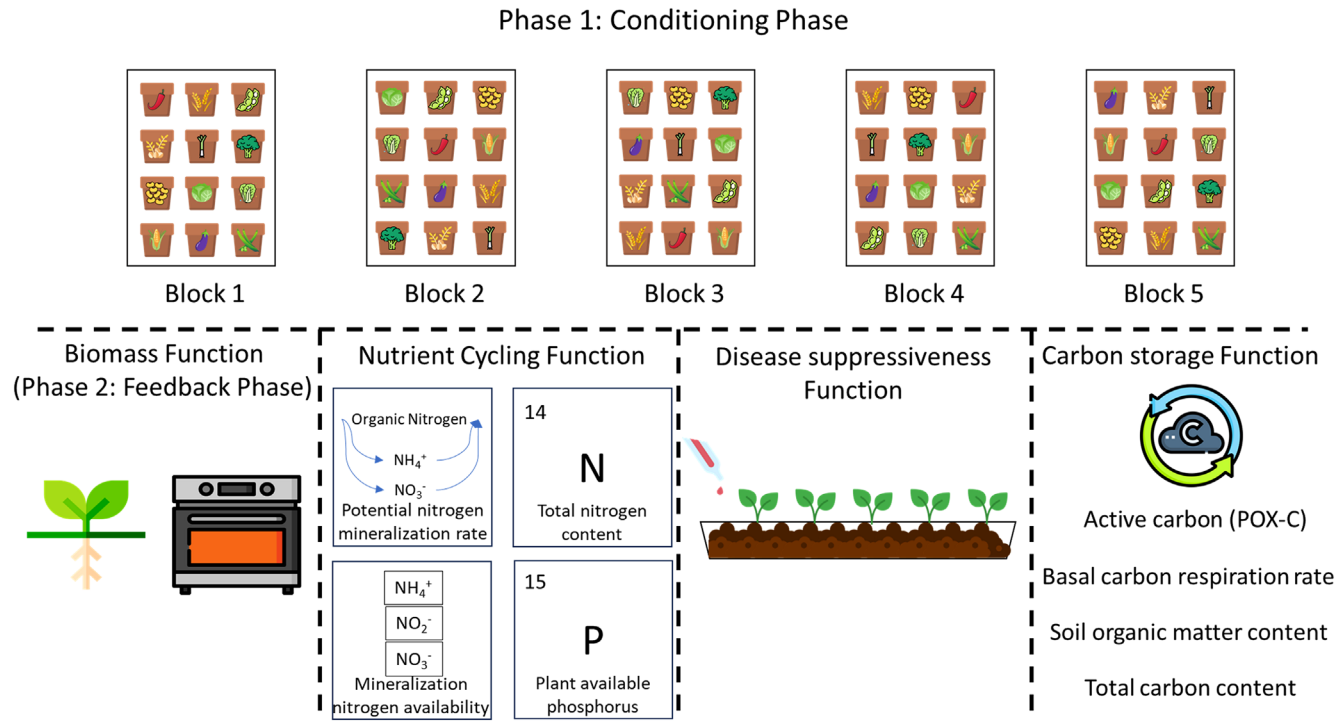

FIGURE 1 Schematic representation of the plant–soil feedback experimental setup used to assess the individual soil functions. Briefly, soil was conditioned first by 12 species for 8 weeks (conditioning phase) to create crop-specific soils. In the feedback phase, all crops were grown in all conditioned soils to measure biomass function. The nutrient cycling function was assessed by measuring the potential N mineralization rate, mineral N availability and plant-available P. The disease suppressiveness function was measured by using a pathosystem of *Rhizoctonia solani*-cress on crop-specific soils. The carbon storage function was assessed by measuring permanganate-oxidizable carbon (POX-C), basal carbon respiration rate, soil organic matter content and total carbon content.

autoclaved soil. Soil from the two sterilization methods was mixed to obtain a homogenous, sterilized background soil. This background soil was then mixed with five independent live soil inocula, each sourced from a separate adjacent agricultural grassland in Wolfheze, the Netherlands, in April 2022. We selected these grassland soils as inocula because they were part of a wider crop rotations scheme. This approach minimized potential legacy effects of the same or related agricultural crop species while working with arable soils. Prior to inoculation, these live soil inocula were sieved at 5 mm to remove coarse fragments and stored at 4°C. For each replicate, sterilized subsoil and live soil inoculum were mixed gently at a ratio of 85/15 (w/w dry weight) (Crawford et al., 2019; Warneke et al., 2023). This mixture of sterilized background soil with live soil helped to minimize the abiotic differences among soil inocula from different grasslands and to avoid creating an artificial soil community from 100% sterilized soil due to accidental contamination and colonization by soil organisms originating from the air or water supply.

The crop species used in this study included legumes (broad bean, green bean and soybean), crucifers (broccoli, Chinese cabbage and cabbage), cereals (wheat, maize and oat) and the three vegetables, hereafter referred to as 'vegcrop' (eggplant, chilli pepper and leek) (Table 1). For each crop species, organic seeds were purchased from Van der Wal B.V. (Hoogeveen, the Netherlands), surface sterilized (for 1 min in a 10% diluted commercially available bleach solution, then rinsed with deionized water), and subsequently germinated on sterile glass beads under a 16/8 h light–dark cycle and a temperature regime of 20/15°C. Due to poor germination on glass beads, soybean and broccoli seeds were germinated in commercial sterilized potting soil under the same light and temperature conditions. Natural daylight was supplemented with 600 W high-pressure sodium lamps (225 mmol $m^{-2} s^{-1}$ PAR, one lamp per 1.5 m^2). After germinating to the two-leaf stage, seedlings were kept at 4°C under a 16/8 light–dark regime (25 µmol $m^{-2} s^{-1}$) until sufficient seedlings of all crop species had been obtained. Subsequently, the seedlings were transplanted into experimental pots.

2.2 | Experimental setup

We used a typical plant–soil feedback experiment (Brinkman et al., 2010), which consisted of two phases, the conditioning phase and the feedback phase. In the conditioning phase, crops were grown to create crop-specific soils. After this phase, the soils were used to measure four functions: biomass production, nutrient cycling, disease suppressiveness and carbon storage. While most functions were directly measured on crop-specific soils, the feedback phase was conducted to determine biomass production as the crop growth responses to all crop-specific soils according to a full-factorial design.

In the conditioning phase, the experimental design included 12 crop species × 5 replicates, resulting in 60 experimental units. Each experimental unit consisted of four identical pots, all treated exactly the same throughout the conditioning phase. These four pots were set up to ensure sufficient soil was available for functional measurements but were considered as one experimental unit. As a result, we had 240 pots in total (60 × 4). Each pot was filled with 4 kg (dry weight) of the inoculated soil. Pots were arranged in the greenhouse in five randomized blocks, one for each replicate. After filling the pots, they were kept in the greenhouse for 1 week to allow the soil to settle without plants. Grass seedlings that emerged from the soil were removed during this period. After 1 week, we transplanted three crop seedlings of similar sizes in each of the pots. Seedlings that died during the first week of the experiment were replaced. To minimize the effects of local differences in microclimate in the greenhouse, pots from the same block were placed together, while pots were placed randomly within blocks. Twice a month, blocks and pots within blocks were redistributed to minimize the impacts of local conditions on plant growth. All pots were watered daily with deionized water. At 2-week intervals, pots also received 50% diluted Hoagland solution based on fixed amounts that were increased every fortnight to keep up with increased plant demands (10 mL in Weeks 2 and 4, 20 mL in Week 6 and 30 mL in Week 8). Eight weeks after transplantation, all above-ground biomass was harvested from each pot, leaving the roots intact in the soil to preserve the plant legacy. Above-ground biomass was dried at 70°C for at least 72 h and then weighed. Soils from the four pots were homogenized to measure biomass production in the feedback phase. Subsamples were collected and sieved for other soil function measurements.

2.3 | Measurements of soil functions

After the conditioning phase, we used crop-specific soils to measure four soil functions: plant biomass production, soil nutrient cycling, disease cycling and carbon storage.

TABLE 1 Twelve crop species used in the experiment.

'Cereal'	'Crucifers'	'Legume'	'Vegcrop'
Wheat (*Triticum aestivum*)	Chinese Cabbage (*Brassica rapa* subsp. *pekinensis*)	Broad Bean (*Vicia faba*)	Chilli Pepper (*Capsicum annuum*)
Maize (*Zea mays*)	Cabbage (*Brassica oleracea* var *capitata*)	Soybean[a] (*Glycine max*)	Eggplant (*Solanum melongena*)
Oat (*Avena sativa*)	Broccoli[a] (*Brassica oleracea* var *italica*)	Green Bean (*Phaseolus vulgaris*)	Leek (*Allium ampeloprasum*)

[a]Seeds were germinated in commercially sterilized potting soil (ZST-D Special Care Zaai/stek).

2.3.1 | Biomass production

To test how the 12 crop species affected subsequent plant biomass production, we grew all crops in all crop-specific soils in the feedback phase experiment (Brinkman et al., 2010). After 8 weeks, both above-ground and below-ground biomass were measured. Broccoli was excluded from the bioassay because it failed to germinate, leaving 11 plant species for the feedback phase. To set up, for each of the 60 experimental units, we distributed soil across 11 pots of 10 × 10 × 11 cm with 1 kg of soil (dry weight). These pots were left in the greenhouse for 2 weeks to stabilise without plants. Soils from the five replicates were kept separate throughout the biomass production bioassay to ensure independent replication, keeping the blocking structure of the conditioning phase intact. After 2 weeks, in each pot, one crop seedling was planted, ensuring similar seedling sizes. All 11 crops were grown in all 12 soils, resulting in (12 × 11 =) 132 combinations and hence in (132 × 5 replicates =) 660 pots. During 8 weeks, plants were grown under the same greenhouse conditions as in the conditioning phase. Pots were randomized within blocks. Twice a month, blocks and pots within blocks were randomized again to avoid local greenhouse conditions impacting plant growth. Starting from the fourth week, pots also received 50% diluted Hoagland solution in fixed amounts that were increased every fortnight to keep up with increased plant demands (2.5 mL in Weeks 4 and 5, 5 mL in Weeks 6 and 7, 7.5 mL in Week 8). At the end of the experiment, above-ground biomass was harvested just above the soil surface, and below-ground biomass was collected after washing the sand from the roots. All biomass was dried at 70°C for at least 72 h, weighed and measured. We calculated the biomass production function using the mean biomass generated per conditioned species.

2.3.2 | Nutrient cycling

Nutrient cycling was quantified by measuring the *soil mineral N availability* (defined as NH_4^+, NO_2^-, NO_3^-), *potential N mineralization rate*, *total soil N content* and *plant-available P content*. The selected indicators for the nutrient cycling function capture different forms of N and plant-available P content (Haney et al., 2018). We used the soils collected at the end of the conditioning phase that were sieved using a 5-mm mesh size to remove larger particles and roots.

Total N content was measured in soil samples that were dried at 40°C for 24 h and then ground. The grounded soil was weighed, placed in 8 × 5 mm tin capsules and analysed with a Flash Elemental Analyzer (Flash EA1112; Thermo Scientific, United States). *Soil mineral N availability* was measured using the potassium chloride extraction method based on Keeney and Nelson (1983). Briefly, 10 g of dry-weight equivalent soil sample was taken and extracted with 50 mL 1 M potassium chloride solution, shaking for 2 h. Then, the extract was filtered by filter paper (Whatman qualitative filter paper Grade 1 85 mm; Sigma-Aldrich, USA) and analysed by an autoanalyser (SAN++ Automated Wet Chemistry Analyzers; Skalar, the Netherlands). The *potential N mineralization rate* was measured by incubating fresh soil for 8 weeks in an incubator at 20°C in the dark. The availability of mineral N was measured at the start and end of the incubation using the same methods described for 'soil mineral N availability'. The mineralization rate was calculated by subtracting the initial from the end mineral N availability and then dividing by the incubation duration: $N_{rate} = (N_{end} - N_{initial}) / \text{time}$. *Plant-available P content* was measured using the Olsen method (Olsen, 1954) and analysed by an autoanalyser. Briefly, 2.5 g of oven-dried soil (dried at 40° for three consecutive days) and 50 mL of 0.5 N sodium bicarbonate ($NaHCO_3$) were applied for the extraction according to the Olsen method. The pH of the extraction solution was 8.5. The extraction time was 30 min, and the extracts were filtered through Whatman 42–110 mm (Whatman products; Little Marlow, Buckinghamshire, United Kingdom). After extraction, the samples were analysed by an autoanalyser (SAN++ Automated Wet Chemistry Analyzers; Skalar, the Netherlands).

2.3.3 | Disease suppressiveness

Disease suppressiveness was measured in a follow-up experiment using the pathogen *Rhizoctonia solani* and the plant *Beta vulgaris* (sugar beet) as a model pathosystem (Kurm et al., 2023; Postma & Schilder, 2015). Sugar beet seeds for the soil disease suppressiveness test were obtained from SESVanderHave Nederland B.V. (Rilland, the Netherlands). Suppressiveness against *R. solani* was analysed by measuring the disease spread of *R. solani* in sugar beet seedlings (cultivar Rhizoc Gevoelig OD0002; SES VanderHave Nederlands B.V.). This fungal pathogen causes damping off, black root rot and crown rot in sugar beet. For each of the 60 conditioned soils from the greenhouse experiment, we filled one plastic container (19.5 cm × 4.5 cm × 3 cm) with 200 g of soil and placed it on trolleys in the greenhouse, and sterilized soil was used as a control. The experiment was performed in a greenhouse at 23/18°C (day/night), 50% humidity, and a photoperiod of 8 h dark and 16 h light.

Sugar beet seeds were first germinated in sterilized potting soil in an incubator until the two-leaf stage and then transplanted into the containers in a row of five seedlings per container. Containers were watered and then covered with plastic foil for 1 week to promote seedling establishment after transplanting. When seedlings died within this period, they were replaced. The pathogen inoculum was prepared using organically grown oat kernels, which were autoclaved (121°C for 20 min) twice at a 24-h interval. The kernels were infested with a plug of a 1-week-old *R. solani* grown on potato dextrose agar medium and incubated in the dark for 2 weeks at 20°C. Then, the soil in each container was inoculated with 0.2 g of oat kernels colonized with *R. solani*. Kernels were placed in front of the first seedling in each container, just beneath the soil surface. Disease spread was determined daily by scoring seedlings displaying damping-off or brown-grey lesions on the stem at the soil level (Postma & Schilder, 2015). Disease spread 16 days after inoculation

was used for data comparison since maximum disease spread was reached in one of the species-conditioned soils.

2.3.4 | Carbon storage

We quantified the carbon storage function using the sieved soil collected at the end of the conditioning phase. We measured permanganate-oxidizable carbon (POX-C), basal carbon respiration rate, soil organic matter content and total carbon content. POX-C measures labile carbon, a readily decomposable fraction sensitive to soil management practices (Bongiorno, Bünemann, et al., 2019), providing insight into short-term carbon pools critical for soil health. Basal respiration quantifies the CO_2 released from microbial decomposition, reflecting microbial activity and organic matter turnover rates. Soil organic matter is composed of decomposed plant and animal residues, essential for long-term carbon storage (Chabbi et al., 2017). Total carbon content indicates the soil carbon pool, generally consisting of organic carbon in the sandy soils used in our experiment. Together, these indicators were used to assess the carbon storage function, which results from the balance between organic matter production and its decomposition into CO_2.

POX-C was measured based on the methods described by Culman et al. (2012). Fresh soil was air-dried at ambient room temperature for three consecutive days (Kaiser et al., 2015). Two grams of air-dried soil were weighed into 50 mL Falcon tubes before initiating the oxidation step. Then, 0.2 mol L^{-1} $KMnO_4$ stock solution was prepared before measurement and adjusted the pH to 7.2. The oxidation process was started by adding 18 mL of deionized water and 2 mL of 0.2 mol L^{-1} $KMnO_4$, resulting in a final reaction solution of 20 mL of 0.02 mol L^{-1} $KMnO_4$ and a total of 400 μmol MnO_4^- in each tube. Tubes were capped, horizontally shaken for precisely 2 min on a reciprocal shaker at 120 rev min^{-1}, uncapped and allowed to settle for 10 min in the dark. After settling, the oxidation reaction was terminated by transferring 0.5 mL of supernatant into a fresh 50-mL Falcon tube with 49.5 mL of deionized water, creating a 1:100 dilution. After capping, we inverted the tubes to create a homogenous, well-mixed solution. Next, 800 μL of this diluted solution was transferred to a 96-well plate, and the absorbance was quantified at 550 nm using a spectrophotometer (Bio Tek Synergy H1 Multimode Reader; Agilent Technologies, USA).

We used blanks and a series of standard solutions to determine the intercept and slope of the standard curve. Then, we used the equation below, following Wade et al. (2020) to determine the concentration of POX-C in soil.

$$\text{POX-C}\left(\text{mg kg}^{-1}\text{ soil}\right) = \left[0.02\text{ mol/L} - (a + b \times \text{Abs})\right] \times (9000\text{ mg C/mol}) \times (0.02\text{ L solution/Wt}).$$

In this equation, 0.02 mol L^{-1} represents the initial solution concentration. The variable $a + b \times \text{Abs}$ refers to the concentration of the tested sample. The constant 9000 represents the milligrams of carbon oxidized by 1 mol of MnO_4^- changing from Mn^{7+} to Mn^{4+}. The volume of stock solution reacted is 0.02 L, and Wt corresponds to the weight of the air-dried soil sample in kilograms.

Basal respiration rate was measured using a modified method from Bradford et al. (2008). Four grams of dry-weight equivalent fresh soil were weighed into a centrifuge tube. Before the incubation, we flushed tubes with CO_2-free compressed air. Once all tubes had been flushed, tubes with soil were experimentally incubated at 20° in the dark. Gas samples were taken after 24 h. Gas vials were analysed using a TRACE™ 1600 Gas Chromatograph (Thermo Scientific, USA).

Soil organic matter content was determined by loss on ignition. Fresh soil was first dried at 105°C for 24 h. Then, the soil was ashed in a muffle furnace at 430°C for 24 h and weighed to determine mass loss. We calculated the soil organic matter content (g 100 g^{-1} dry soil) by using the formula: (g 100 g^{-1} dry soil): 100 × (dry soil − ashed soil) × (dry soil)$^{-1}$.

Soil total carbon content was measured in soil samples that were dried at 40°C for 24 h and then ground. The ground soil was weighed and placed in 8 × 5 mm tin capsules and analysed with a Flash Elemental Analyzer (Flash EA1112; Thermo Scientific, United States).

2.4 | Quantification of soil functions, soil multifunctionality and evenness of functionality

To calculate individual soil functions, we used the 'averaging method' described by Byrnes et al. (2014) and Jia et al. (2023) to summarize single individual measurements belonging to one function. Subsequently, we again used the 'averaging' method to summarize the four functions into a multifunctionality index. To do this, soil measurements associated with an individual soil function (Table S1) were first normalized to a range of 0–1 using the maximum method ($f(x) = x_i \times x_{max}^{-1}$) following Maestre et al. (2012), and then averaged to obtain the function index. Values were inverted for measurements where higher raw values indicate lower functional performance. We inverted soil disease suppressiveness, as more infected seedlings in the disease suppressiveness test reflect lower suppressiveness. Similarly, we inverted the basal respiration rate in the carbon storage function calculation, as higher respiration indicates increased carbon loss rather than storage. We weighted all the measurements equally in the calculation (Byrnes et al., 2014; Delgado-Baquerizo, Eldridge, et al., 2017; Jia et al., 2023). All single functions were then weighed equally to calculate mean soil multifunctionality.

We described the evenness of functionality in a similar way to Shannon's Index *H* (Hill, 1973) and Pielou's evenness *J* (Pielou, 1966) based on the equation as follows:

$$H = -\sum_{i=1}^{S} p_i \log(p_i),$$

$$H_{max} = \log_S,$$

$$J = \frac{H}{H_{max}},$$

where S is the number of functions (in our case, always 4), p_i is the relative proportion of the value of each function to the total sum. Hence, for each of the conditioned soils, we compared the same four functions, and if the distributions of p_i were the same, then the conditioned soil had the same evenness of functionality.

2.5 | Statistical analysis

Statistical analysis was performed with R language version 4.3.3 (R Core Team, 2024) through RStudio version RStudio 2023.12.0+369 (Posit Team, 2024). The calculation of single soil functions and soil multifunctionality was conducted using the 'getStdAndMeanFunctions' function in the 'multifunc' package (Byrnes, 2022). Evenness of functionality was assessed using the 'diversity' function in the 'vegan' package (Oksanen et al., 2022), using the normalized values from the single soil functions. We first normalized the evenness data before fitting it into a mixed-effect model.

General linear mixed models were used to evaluate the effect of crop species on individual soil functions, multifunctionality and evenness of functionality ('lmer' function in 'lme4' package; Bates et al., 2015) at the species, within-group and group level. Plant species or crop group were used as a fixed factor, and the replicated blocks were used as a random factor. To validate the appropriateness of the Analysis of Variance (ANOVA) for our model, model diagnosis was performed using the DHARMa package version 0.4.6. For some models Levene's test indicated unequal variances. Data transformation did not improve equality of variances in all cases. Yet, to consider our experimental design into the model structure, we still used ANOVA, but then also conducted a likelihood ratio test for these models to see how consistent results were. Tukey HSD post hoc tests ('glht' function in *multcomp*; Hothorn et al., 2024) were performed for multiple comparisons. Principal component analysis (PCA) was used (prcomp function in *stats* package) to explore which single function explains most of the variation in the multifunctionality index and to see how species separated based on different soil functions. Four individual soil functions and soil multifunctionality were included in the PCA. To test statistically how PCA axes were related to soil functions, we conducted Pearson correlation analyses between soil function and PCA axes. In addition, redundancy analysis (RDA) was performed (rda function in *vegan* package) with Replicate as a co-variate to test whether plant groups significantly structured soil functions. The significance of RDA results was determined using a permutation test with 999 iterations (ANOVA function).

3 | RESULTS

The plant biomass production function depended on the crop functional group that had conditioned the soil ($F_{3,56}=8.075$, $p<0.001$; Figure 2; Figure S1a; Table S2). Plants produced the most total biomass in soils conditioned by the leguminous species group and least in soils conditioned by cereals. Intermediate biomass was produced in soils conditioned by crucifers and the vegcrop group. Interspecific comparisons within groups revealed that among the leguminous species, more biomass was produced in soil conditioned by broad bean than by soybeans and green bean ($F_{2,12}=47.498$, $p<0.001$; Figure S1a; Table S2). At the level of individual species, crop species produced the greatest biomass in soil conditioned by broad bean and the lowest in soil conditioned by wheat ($F_{11,48}=9.986$, $p<0.001$; Figure S1a; Table S2).

The nutrient cycling function, which includes soil mineral N content, potential mineralization rate, total N content and soil P content, differed among crop species groups ($F_{3,52}=4.308$, $p=0.009$; Figure 2). The soil nutrient function was the highest in soils conditioned by crucifers and lowest in soils conditioned by cereals (Table S2; Figure S1b). Within the leguminous group, soil conditioned by broad bean had a higher nutrient cycling function than soils conditioned by soybean and green bean ($F_{2,8}=18.182$, $p=0.001$; Table S2; Figure S1b). Within the cereals, wheat-conditioned soil had a lower nutrient cycling function than oat- and maize-conditioned soil ($F_{2,8}=11.847$, $p=0.004$). Within the vegcrop group, leek-conditioned soil had a higher nutrient cycling function than eggplant- and chilli pepper-conditioned soils ($F_{2,8}=4.674$, $p=0.045$). At the species level, the soil nutrient cycling function was highest in soil conditioned by broad bean and lowest in soils conditioned by wheat ($F_{11,44}=7.854$, $p<0.001$; Figure S1b). The underlying individual parameters showed that soil mineral N content and potential soil mineralization rate were higher in broad bean-conditioned soil than in those conditioned by other species (Figures S2 and S3; Table S5). Broccoli-conditioned soil had the highest total N content, while no significant differences were found in soil available P content (Figure S4; Table S5).

The disease suppressiveness function differed among the groups that had conditioned the soil ($F_{3,56}=3.028$, $p=0.037$; Figure 2; Figure S1c; Table S2). Soil conditioned by cereals was the most effective in disease suppressiveness, and soils conditioned by species in the vegcrop group had the lowest disease suppressiveness. Within the cruciferous group, the pathogen was least suppressed in soil conditioned by cabbage compared with soil conditioned by Chinese cabbage and broccoli. We did not find different responses among species in the legume, cereal and vegcrop groups (Table S2). The pathogen was least suppressed in soil conditioned by cabbage. The disease suppressiveness also varied among the days selected for analysis (Figure S6), and cabbage-conditioned soil was the first in which all seedlings died.

The carbon storage function, comprising soil respiration, POX-C, soil organic matter and total soil carbon content, varied among crop groups that had conditioned the soils ($F_{3,52}=8.144$, $p<0.001$; Figure 2; Figure S1d; Table S2). The carbon storage function was the lowest in soils conditioned by cereals and was highest in soils conditioned by crucifers. Soils conditioned by the legume and vegcrop groups had intermediate carbon storage functions (Figure S1d). Within the vegcrop group, soil conditioned by leek had a lower carbon storage function than soil conditioned by eggplant and chilli pepper. At the species level, soil conditioned by Chinese cabbage and cabbage had a higher carbon storage function than soils conditioned by wheat, green bean and oat. However, there was no difference among soils conditioned by other species. For the measurements underlying the carbon

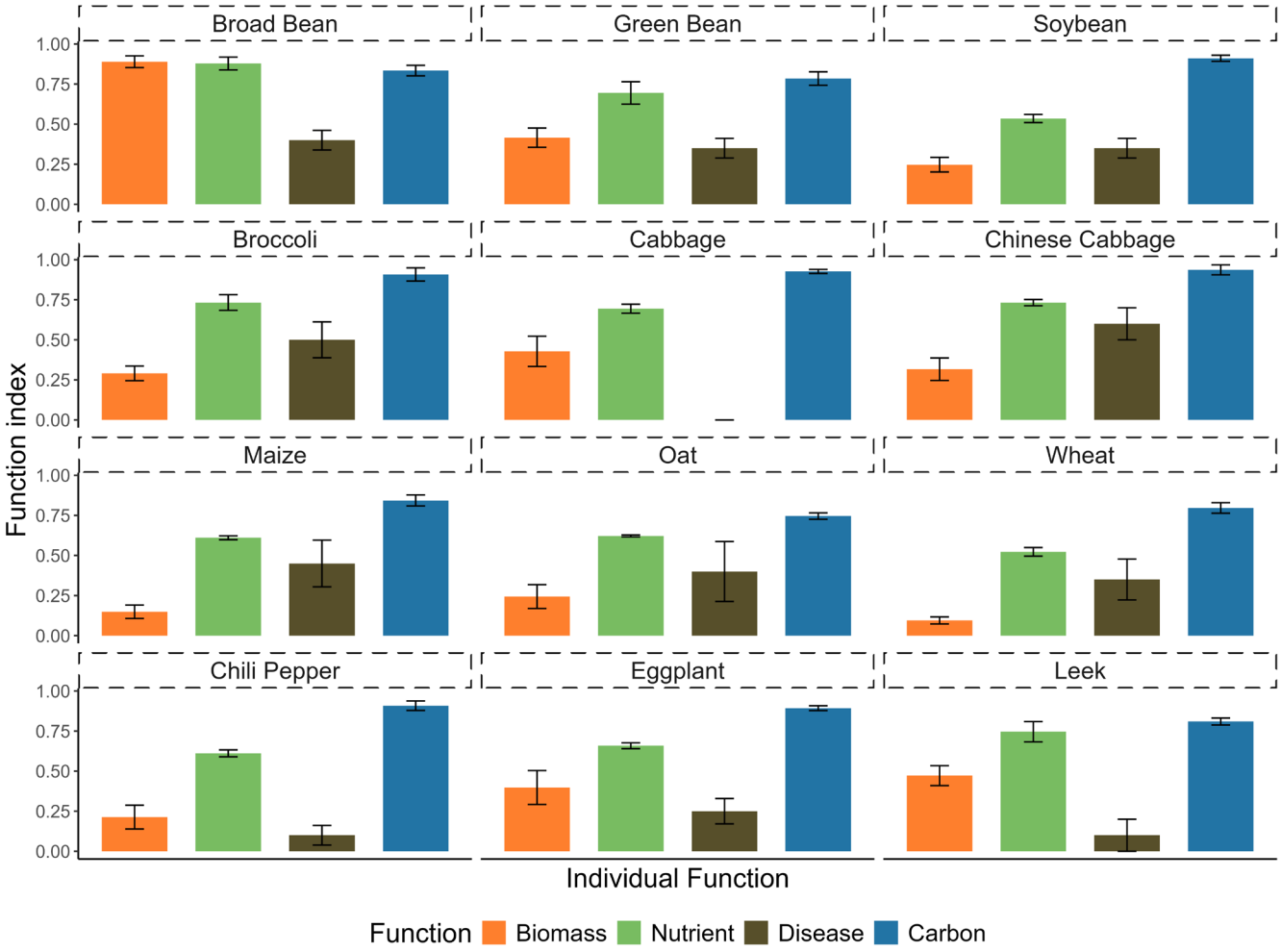

FIGURE 2 Bar diagram representing the effect of conditioning crop species on individual soil functions: Biomass production (Biomass), nutrient cycling (Nutrient), disease suppressiveness (Disease) and carbon storage (Carbon). Each bar represents the mean value of an individual soil function, with error bars representing ± standard error. The Y-axis represents the individual soil function index.

storage function, oat-conditioned soil had the highest, and cabbage-conditioned soil had the lowest soil respiration rate (Figure S8; Table S5). POX-C tended to be marginally significantly higher in soybean-conditioned soils than in other soils (Figure S9; Table S5). Total carbon content was the highest in broccoli-conditioned soil and the lowest in soybean-conditioned soil (Figure S10; Table S5). Soil organic matter content did not differ among conditioned soils.

The multifunctionality index differed among crop groups ($F_{3,56}=5.606$, $p=0.002$; Figure 3a; Table S2). Legumes had the highest and cereals had the lowest multifunctionality. Crucifers and vegcrop tended to have lower multifunctionality. Within the legumes, broad bean-conditioned soil had higher multifunctionality than soils conditioned by green beans and soybeans. Within crucifers, Chinese cabbage- and broccoli-conditioned soils had higher multifunctionality than cabbage-conditioned soils. We did not find different responses among species within the vegcrop and cereal groups. At the level of the individual species, broad bean-conditioned soil had the highest multifunctionality; Chinese cabbage- and broccoli-conditioned soil had an intermediate value, and all other species-conditioned soil had lower multifunctionality.

The evenness of functionality differed among crop groups ($F_{3,52}=5.621$, $p=0.002$; Figure 3b; Table S2). The legume group had the highest evenness of functionality, followed by the crucifer and the cereal group, while the vegcrop group had the lowest evenness. Within the crucifers, species had different evenness of functionality, with the evenness being lower for cabbage than for Chinese cabbage and broccoli. No differences were found among species in the legume, cereal and vegcrop groups. At the species level, cabbage-conditioned and chilli pepper-conditioned soil had lower evenness of functionality compared with soil conditioned by other species.

Overall, multifunctionality and evenness of functionality were positively correlated ($r=0.756$, $p<0.001$; Figure 3c). Also, at the level of each of the four species groups, there was a positive relationship (Figure 3c; Table S3). For legumes, the correlation had a steeper slope, indicating that multifunctionality was more enhanced for a similar change in evenness compared with the other groups (Table S3). The vegcrop group had the highest correlation coefficient, indicating the correlation between multifunctionality and evenness explained 85% of the variation.

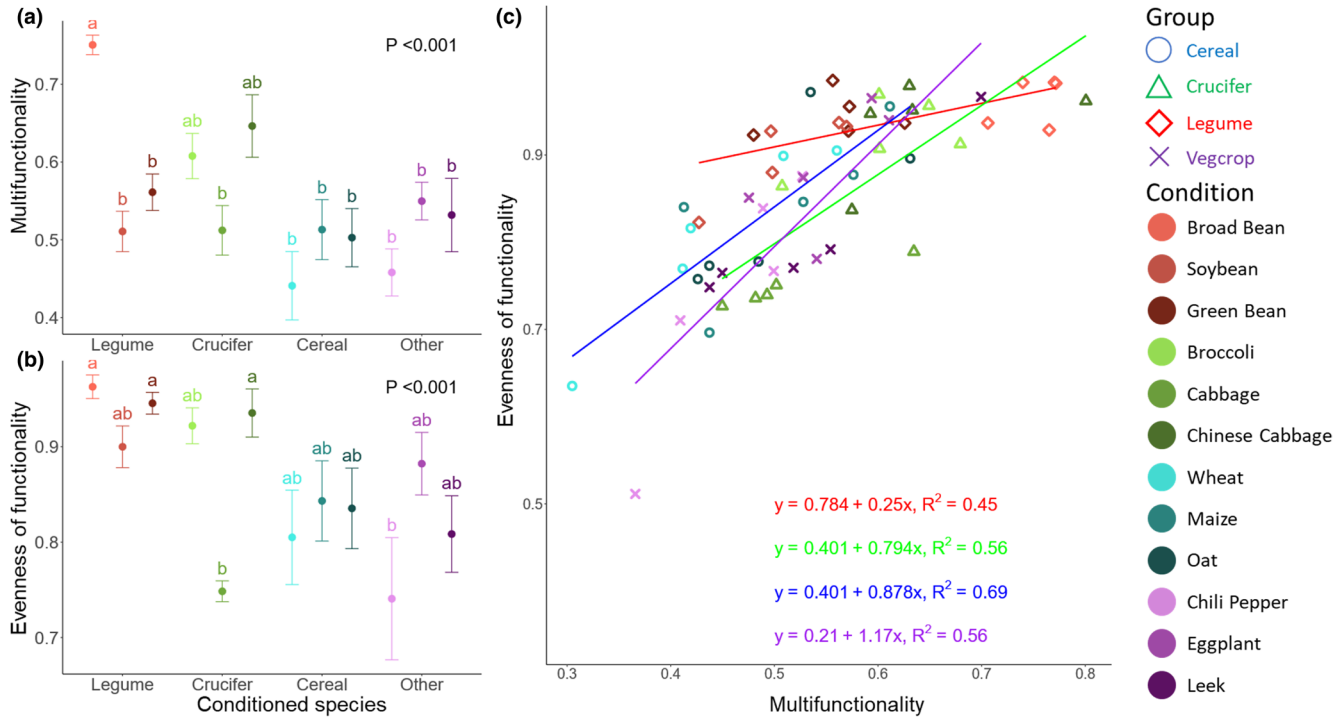

FIGURE 3 Effects of crop species on (a) multifunctionality and (b) evenness. For (a) and (b), dots represent the mean value per species, and error bars are standard errors. Letters indicate significant differences with Tukey's post hoc test at a 95% confidence interval ($p < 0.05$). (c) Scatter plot of soil multifunctionality and the evenness of functionality. The solid line indicates a positive correlation between multifunctionality and the evenness of functionality. Dots represent the value of soil multifunctionality and evenness of functionality along the axis at the level of individual replicates.

In the PCA analysis of individual functions, the first PCA axis explained 49.6% of the variation, while the second PCA axis accounted for 24.6% (Figure 4; Table S4). The analysis showed that biomass production as well as nutrient cycling functions moved into the same direction along the first PCA axis, and increases in these functions were associated with increased multifunctionality. Specifically, broad bean-conditioned soils separated from other species along the first PCA axis, indicating greater multifunctionality, nutrient cycling and biomass production functions associated with this crop species. The disease suppressiveness function mainly separated samples along the second PCA axis, with some individual oat, wheat, Chinese cabbage and broccoli samples being associated with high disease suppressiveness. Finally, the RDA indicated that the plant group significantly structured soil functions ($F_{3,52} = 4.71$, $p = 0.001$), explaining 20.7% of the constrained variance. Almost all replicates for the cereals and crucifers were clustered on the left-hand side of the figure, indicating that none of these species drove high values for biomass and nutrient functions. However, in some cases, such as in oat- and maize-conditioned soils, there were also associations with high disease suppressiveness, while for example, wheat- and cabbage-conditioned soils had low disease suppressiveness. The carbon storage function and the disease suppressiveness function were related and were mainly associated with the second PCA axis but played a smaller role in separating crop species and influencing multifunctionality.

4 | DISCUSSION

In the present work, soil functions, soil multifunctionality and evenness of functionality differed among soils conditioned by the 12 crop species and the four (partly taxonomic) groups of species. Broad bean soils supported the highest biomass production, nutrient cycling function and overall multifunctionality, whereas wheat soils had the lowest. Even though we expected species within crop groups to show similar responses, this was not always the case. For example, among crucifer species, Chinese cabbage and broccoli had the highest disease suppressiveness of all species, while cabbage had the lowest. The PCA showed a partial trade-off between plant biomass production and nutrient cycling functions versus the disease suppressiveness and carbon storage functions, indicating that some plants promoted more disease suppressiveness and carbon storage functions, and some promoted more biomass and nutrient functions. Finally, we found that multifunctionality and evenness of functionality were positively related, although no species performed maximally on all functions. Together, our results show that some crop species, such as broad bean and Chinese cabbage, enhance soil multifunctionality. This effect is driven by the even stimulation of multiple functions rather than the dominance of a single function. Our findings suggest that selecting crop species combinations with complementary effects on functions is a promising approach for sustainable farming to foster more multifunctional soils.

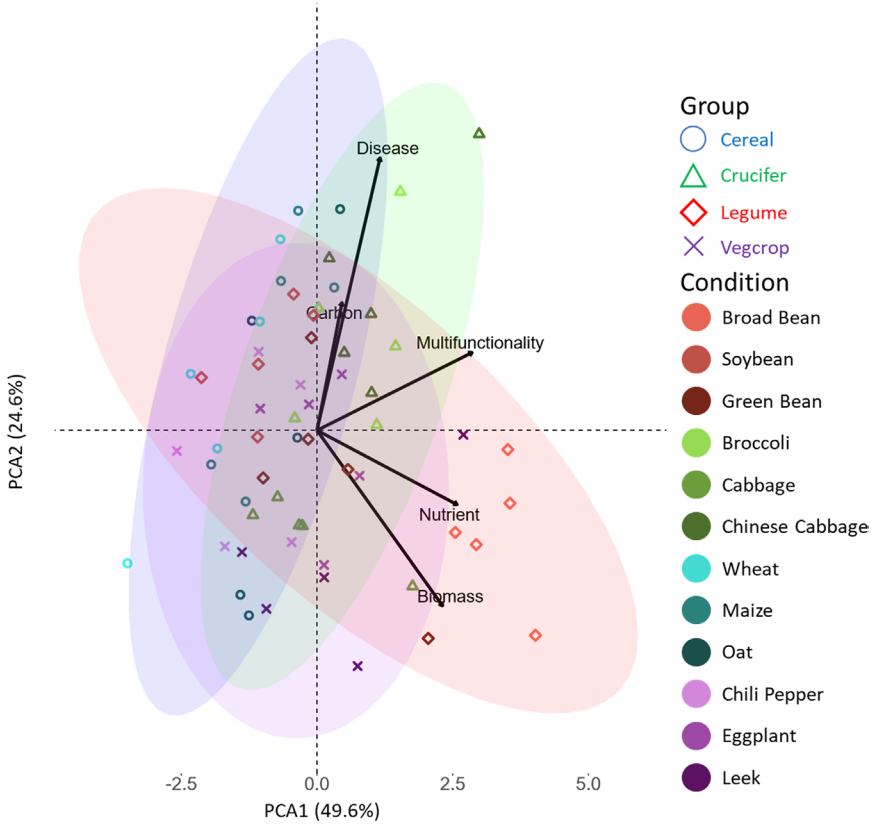

FIGURE 4 Principal component analysis (PCA) of individual soil functions and soil multifunctionality. Arrows represent factor loadings of principal components of each individual soil function and soil multifunctionality. Each colour identifies a crop species, and the shapes represent the four crop groups. The coloured ellipses represent the 95% confidence interval for each group.

4.1 | Effects of crop species within and between groups on soil functions, soil multifunctionality and evenness of functionality

Our results were in line with our first hypothesis that specific crop species differed in their effects on soil functions, soil multifunctionality and evenness of functionality, implying that we can steer soil functioning by choosing crop species specifically. These findings were supported by other studies showing that individual plant species or groups of species can have specific effects on soil functions (Yang et al., 2020). Such effects might be driven by plant species having specific impacts on the biotic and abiotic conditions in the soil via taking up water and minerals, returning organic materials, such as litter and root exudates, and interacting with pathogens and mutualists in their root zone (Paterson, 2003; Wardle, 2006). Some of the effects we found for specific species are well known from earlier work. For example, for broad bean the biomass and nutrient cycling functions were enhanced, which may be because broad bean is a legume. Legumes form a symbiosis with N-fixing bacteria (Kumar et al., 2020; Li et al., 2010) that can fix atmospheric N and thereby enhance soil N availability and plant growth (Burris, 1974).

The nutrient acquisition strategy of wheat and cereals is characterized by rapid growth and quick absorption of soil available nutrients (Huang et al., 2024), which may explain lower nutrient cycling and plant production functions observed for these crops (Peng et al., 2012). The high disease suppressiveness in Chinese cabbage might be driven by glucosinolates, typical for cruciferous species, which are known to be toxic to *R. solani* (Handiseni et al., 2016). This finding can partially depend on the specific plant–pathogen system, here being sugar beet and *R. solani* (Bongiorno, Postma, et al., 2019; Kurm et al., 2023). Nevertheless, it is known that *R. solani* is one of the most common fungal pathogens and hence using this model system can give a representative insight into disease suppressiveness (Schlatter et al., 2017).

Our findings that the carbon storage function was highest for cabbage and not for graminoids and legumes contrast with earlier work showing a higher allocation of carbon to soils for graminoids and legumes (Mathew et al., 2017). It is important to note that our experiment was relatively short, while some carbon parameters, such as soil organic matter content and total carbon content, change slowly over time (Bradford et al., 2016). As a result, we were probably not able to quantify carbon storage. Indeed, we did not find differences in soil organic matter content for any species in our experiments. Instead, our findings are largely driven by changes in labile and dynamic carbon cycling parameters, such as soil respiration. Hence, the lower carbon storage function in broad bean- and oat-conditioned soil may be the result of high respiration in these soils, which indicates high soil carbon consumption. In the future, it will be interesting to perform long-term experiments or tracing studies to better understand the impacts of crop species on carbon storage in soils.

In line with our findings for individual soil functions, specific crop species were also enhancing soil multifunctionality (Yan et al., 2023), particularly broad bean and Chinese cabbage. For broad bean, this was driven by enhanced nutrient cycling and biomass production functions, while for Chinese cabbage, higher carbon storage and disease suppressiveness were observed. We also showed that soils

conditioned by broad bean had a higher evenness of multifunctionality compared with other species, indicating that high multifunctionality was not driven by high performance on a single function. This is an important addition to current multifunctionality calculations, which could give high values even if one function is primarily affected (Byrnes et al., 2014; Maestre et al., 2012; Manning et al., 2018). To some extent our findings on multifunctionality and evenness depend on the measurements used to quantify functions and the function calculations (Dooley et al., 2015; Gamfeldt & Roger, 2017; Garland et al., 2021). For example, we calculated the nutrient cycling function based on measurements related to N mineralization and N and P availability, but we have not included measurements on other (micro)nutrients (Zhang et al., 2021) and enzymes (Delgado-Baquerizo, Trivedi, et al., 2017). Also, decisions related to grouping measurements into individual soil functions (Lucas-Borja & Delgado-Baquerizo, 2019; Luo et al., 2023; Zhu et al., 2023) determine the weight assigned to each variable.

In contrast to our second hypothesis that species within groups would have relatively consistent effects on soil functions due to shared traits among related plant species (Roumet et al., 2006), we observed differences between plant species within some of the crop groups. For example, although legume species are recognized for improving nutrient availability via their symbiosis with rhizobia (Duchene et al., 2017; Li et al., 2012; Paungfoo-Lonhienne et al., 2021), we found that the nutrient cycling function in soybean- and green bean-conditioned soil did not differ from non-legumes and was much lower than in broad bean-conditioned soils. Similarly, disease suppressiveness was higher in Chinese cabbage- and broccoli-conditioned soil than in cabbage-conditioned soil. We know that for some plant families, species show relatively large differences in genetics (Schiessl et al., 2019), traits (Dayoub et al., 2017; Dolatabadian et al., 2020), composition of microbial communities in their root zone (Bever, 2003; Liu, Li, et al., 2021) and impacts on soil abiotic properties (Bever, 1994; Hendriks et al., 2013; Van der Putten et al., 2013). This can potentially explain the variable impacts of species within a crop family or group on soil functions.

Our findings show that not all crops within one family may have similar impacts on soil functions, making it challenging to generalize crop impacts from a higher taxonomic resolution. Consequently, we cannot extrapolate the impact of one crop species on soil functions to other species within the same family, which hinders the development of broadly applicable strategies to design sustainable cropping systems from a multifunctionality perspective. This may be because the family level is too coarse for predicting the specific impacts of crops on soil functions, especially as crop species, or even varieties within crop species, have been bred for specific functions. This variation may make it difficult to develop predictions across crop species. In addition, we selected specific crops that are widely used in crop systems (FAO, 2025), which may have limited the set of crops used in our experiment. Therefore, to improve predictions of how a greater variety of crop species and varieties influence soil functions, future research should focus on screening larger sets of crop species and on integrating measurements on crop traits and the impacts of crops on the soil microbiome and soil properties (Gao et al., 2023; Guo et al., 2022). Additionally, an important next step is to understand how the impact of crops on multifunctionality depends on local environmental conditions in the field.

4.2 | Relationship between multifunctionality and evenness of functionality

Our result indicated that higher evenness of functionality correlates with higher multifunctionality. High evenness of functionality implies that different functions are being supported relatively equally, without any single function dominating at the expense of others. The positive relationship between multifunctionality and evenness was driven by two groups of functions co-responding, as was revealed by the PCA. Crops either stimulated both the biomass and nutrient functions, or enhanced both the disease suppressiveness and carbon storage functions. For biomass and nutrient functions, it may be expected that the positive effects of crops on soil nutrients enhance productivity (Jeffery et al., 2011) and thus multifunctionality. For disease and carbon functions, it is likely that plants that stimulate carbon cycling and storage may provide more resources to the soil food web, which in turn can stimulate soil community diversity and functioning, which may enhance the suppression of soil-borne plant pathogens and diseases (Clocchiatti et al., 2021; Mendes et al., 2011; Rudrappa et al., 2008; Sasse et al., 2018; Zhou et al., 2023). These findings are consistent with the view that there are trade-offs for plants investing in defence versus growth (Karasov et al., 2017). Our results indicated that these trade-offs may remain in the soil as legacies, impacting soil functions. Some of these crop-driven impacts on functions may be relatively strong, as crops have been specifically bred to improve crop yield, disease suppressiveness and nutrient uptake. Further research is needed to investigate whether plant strategies related to growth and defence also create trade-offs in their legacy effects on soil properties and functions. Such knowledge would allow the management of these trade-offs to balance impacts on subsequent crop growth and defence, which is crucial for optimizing soil multifunctionality and, therefore, enhancing the sustainability of agricultural crop production.

5 | CONCLUSIONS

Our research demonstrates that crop species have specific impacts on soil functions and differ in their effects on soil multifunctionality. This suggests that the targeted choice of crop species could be used to steer for soil functions and multifunctionality. However, no single crop species consistently increased all soil functions. Crop species enhanced either nutrient cycling and plant productivity or disease suppressiveness and carbon storage. Therefore, combining crop species with complementary effects on functions in time (rotations) or space (inter/mixed cropping) might be promising to maximize soil multifunctionality. While we tested crop combinations under controlled conditions, these combinations are need to

be tested under field conditions next (Meyer et al., 2018; Tamburini et al., 2020). Such crop combinations could enhance a range of different functions, which may benefit subsequent plant growth (Zhang et al., 2022). Effects of plants on the successors operate via legacy effects of the plants that are kept in the soil as a result of modified abiotic or biotic soil properties (Lapsansky et al., 2016; Li et al., 2023). Specifically, our findings suggest that combinations of broad bean, broccoli and wheat could be promising to enhance disease suppressiveness, nutrient availability and biomass production simultaneously. Unravelling indirect effects of crops on subsequent crops through influencing persistent changes in the soil opens a new avenue for designing intercropping and/or rotation systems that may optimize soil multifunctionality.

AUTHOR CONTRIBUTIONS

Zhaoqi Bin developed the idea with contributions from Wim van der Putten, G. F. (Ciska) Veen, Guangzhou Wang and Junling Zhang. Zhaoqi Bin collected the data and performed the statistical analysis. Zhaoqi Bin wrote the manuscript with revisions by Wim van der Putten, G. F. (Ciska) Veen, Guangzhou Wang and Junling Zhang. The authors read and approved the final manuscript. Our study brings together researchers from China and the Netherlands. From the outset, all authors were actively involved in the research and study design to ensure that the diverse perspectives of both Chinese and Dutch ecologists were incorporated. Additionally, efforts were made to consider relevant work published in Chinese.

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CONFLICT OF INTEREST STATEMENT

The authors declared that they have no conflict of interest with the content of this study. Ciska Veen is an Associate Editor of *Functional Ecology*, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.t76hdr8c7.

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SUPPORTING INFORMATION

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

Figure S1: The effect of crop species on (a) biomass production function, (b) nutrient cycling function, (c) disease suppressiveness function, and (d) carbon cycling function.

Figure S2: Soil mineral nitrogen content of soils conditioned by twelve crop species.

Figure S3: Potential nitrogen mineralization rate of soils conditioned by twelve crop species.

Figure S4: Plant available phosphorus content of soils conditioned by twelve crop species.

Figure S5: Soil total nitrogen content of soils conditioned by twelve crop species.

Figure S6: Disease suppressiveness of soils conditioned by twelve crop species by date.

Figure S7: Disease suppressiveness on Day 16 of soils conditioned by twelve crop species.

Figure S8: Soil basal respiration rate of soils conditioned by twelve crop species.

Figure S9: Permanganate-oxidizable carbon content of soils conditioned by twelve crop species.

Figure S10: Total carbon content of soils conditioned by twelve crop species.

Table S1: Measurement of different indicators per individual soil function.

Table S2: Analysis of Variance Result of different individual soil function, multifunctionality, and evenness of functionality, including degrees of freedom (df) and sum of squares (SS).

Table S3: Pearson's correlation coefficients results between evenness of function and multifunctionality at the group level ($n = 15$) and all species ($n = 60$).

Table S4: Correlation, significant, and contribution of soil function variables on the first two principal components (DIM 1 and DIM 2) in principle component analysis.

Table S5: Analysis of variance result of associated indicators of carbon cycling and nutrient cycling function.

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