RESEARCH ARTICLE

Impacts of plant domestication on soil microbial and nematode communities during litter decomposition

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Abstract

Purpose Plant domestication altered leaf litter quality. Since litter traits relate to soil functions and organisms (i.e., litter decomposition and soil decomposer communities), in this study we explore if domestication-induced changes in litter quality have affected their decomposability, and bacterial, fungal, and nematode communities in the soil.

Methods We collected leaf litter from herbaceous crops and their wild progenitors, and measured litter chemical and physical traits. Then, we performed a litter decomposition assay on a common soil. After three months of litter incubation, we measured mass loss, nematode richness and community composition in ten crops. We also measured soil bacterial and fungal richness and community composition in six crops.

Results Domesticated litters had less carbon (C) and leaf dry matter content (LDMC), which accelerated decomposition in comparison to wild litters. Fungal richness was higher in microcosms incubated with domesticated litters, while the effects of domestication on bacterial richness differed among crops. Domestication did not affect nematode richness. The effects of domestication on bacterial and fungal community compositions differed among crops. Soils with domesticated litters tended to have nematode communities with a higher abundance of bacterial feeding nematodes, in comparison to soils fed with wild litters.

Conclusion Domestication altered decomposition at different levels. Leaf litter decomposability increased with domestication, which might alter resource inputs into the soil. Feeding soils with domesticated litters had idiosyncratic effects on soil microbes, but consistent

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effects on soil nematodes. Overall, domestication altered the linkages between crop residues and soil communities differently for bacteria, fungi, and nematodes.

Introduction

Plant domestication is a type of mutualism in which plants produce a service for humans (i.e. food), and humans manage the domesticated plants' environment and reproduction (Purugganan 2022). Plant evolution in croplands triggered morphological, biochemical and physiological changes from the wild progenitors to the domesticated plants, as the result of two selection forces: natural selection and artificial selection (Doebley et al. 2006; Purugganan and Fuller 2009). Natural selection entails the selection of plant genotypes by conditions that exist in agroecosystems (i.e., climate, nutrient availability, etc.). Artificial selection entails the selection of specific plant traits with desirable characteristics by humans to meet their needs. Plant evolution in agroecosystems has also promoted multiple indirect and unintentional effects on plant traits (Hancock 2012; Milla et al. 2015). For instance, some crops have lost (part of their) chemical defences or have developed softer leaves (Meyer et al. 2012). Domestication probably altered leaf traits, such as carbon (C) and nitrogen (N) contents (Prieto et al. 2017; Robinson et al. 2022; Roucou et al. 2018). Domestication also affected leaf litter traits (García-Palacios et al. 2013). Leaf litter traits influence important soil functions, including litter decomposition and soil communities (Fanin et al. 2014; Freschet et al. 2012). Therefore, domestication might have altered crop litter decomposition and the changes that soil communities undergo during the decomposition process.

Litter decomposition is the process through which soil decomposers and litter-fragmenting soil fauna break down plant residues into smaller pieces and simple molecules (Cotrufo et al. 2010). Litter traits (i.e. chemical composition and physical properties) explain most of the variation in litter decomposition rates (Cornwell et al. 2008), and indicate the quality of litters as a trophic resource for decomposers (Strickland et al. 2009). Leaf litter C, N, and lignin contents usually account for most of the variability in litter decomposability (Cornwell et al. 2008; Freschet et al. 2012). Other nutrients, such as P, Mg or Ca, also explain part of the variance observed during decomposition (García-Palacios et al. 2016a; Pichon et al. 2020). Litter from leaves that are tougher or have low water contents (high leaf-dry matter content; LDMC) tend to decompose more slowly (Kazakou et al. 2009; Pakeman et al. 2011; Pérez Harguindeguy et al. 2015; Rawlik et al. 2022). In general, leaf litter of herbaceous crops have higher quality and thereby decomposes faster than that of their wild progenitors (García-Palacios et al. 2013). This can be explained by shifts in litter chemical properties. Leaf litter of domesticated crops have less C and lignin contents than their wild progenitors, and decomposes faster (García-Palacios et al. 2013; González-Paleo et al. 2022). In a study, cultivated accessions of *Silphium integrifolium* Michx. had thinner leaves with higher N contents than wild accessions (González-Paleo et al. 2022). Changes in litter quality are linked to higher concentrations of nitrate in soils, which may have implications for the management of agroecosystems (García-Palacios et al. 2013). Despite this, studies that consider domestication-induced changes in physical and chemical leaf litter traits and decomposition rates in several crop species are lacking. Moreover, it is unknown if and how these changes in litter quality and decomposition rates also impact soil microbial decomposers and the microfauna that feed on them.

The litter layer shapes the diversity and composition of soil microbial communities (Fanin et al. 2014). Litter traits are an environmental filter for microbial succession (Kraft et al. 2015). For instance, the microbial community underneath forest litter layers are specific to the plant species contributing litter inputs (Prescott and Grayston 2013). Decomposers can change and adapt to specific litter inputs (Strickland et al. 2009). Such adaptation of decomposers feedbacks positively on the decomposition of subsequent litters of similar identity (Veen et al. 2021). Also, bacterial and fungal communities' richness and community structure correlate with litter chemical properties and to each other (Purahong et al. 2016), which suggest that the shifts they undergo during the decomposition process are coordinated. The nematode community might also be shaped by litter traits (García-Palacios et al. 2016b), but their relationship with plant litter is mostly

indirect because many nematodes feed on bacteria and fungi, but do not act as primary decomposers (Yeates 1999; Yeates et al. 1993). However, even if as an indirect effect, soil nematode communities respond differently to litters of different plant species (Wardle et al. 2006). Also, litters with disparate traits support nematode communities with different abundances of bacterial and fungal feeders (García-Palacios et al. 2016b). Relationships between litter traits and soil microbial and nematode communities have also been found in croplands, where maize and wheat litters determine the establishment of different bacterial, fungal, and nematode communities during decomposition (Banerjee et al. 2016; Sauvadet et al. 2016). However, we ignore if domesticated and wild genotypes of crops influence those processes differently. Understanding the capabilities of crop residues to influence the underneath soil communities through decomposition can help to manage nutrient mineralization and disease suppression, and thereby harness plant growth, pest resistance and the stability of plant production (Angulo et al. 2022; Compant et al. 2019; Liu et al. 2022).

In this study, we did not have a directional hypothesis. We compared the decomposability of litters of ten crops and their wild progenitors, and tested if domestication-induced changes in litter traits shape the soil bacterial, fungal, and nematode communities in the soil beneath the litter layer. We addressed the following questions: (1) Did plant domestication change litter traits and litter mass loss, and if so, are those changes consistent across crop species? (2) Do soils underneath domesticated leaf litters develop different bacterial, fungal, and nematode communities than those incubated with leaf litters from their wild progenitors?

Materials and methods

We carried out a leaf litter decomposition assay in a set of pairs of crops and wild progenitors. After incubating the leaf litters for 88 days we measured litter mass loss, nematode richness and number of individuals per taxa (ten crops), and OTU counts of bacteria and fungi (six crops). We tested the influence of plant domestication and species identities by using fixed-effects models of analysis of variance (ANOVA; for decomposability and richness), permutational

multivariate analysis of variance (PERMANOVA; for litter quality and community composition), and analysed which litter traits explained better crop decomposability with a stepwise linear multiple regression. Finally, we visualized the magnitude and direction of domestication effects on soil microbes and nematodes community composition as the distance between the centroids of the samples grouped by species and domestication status in NMDS plots.

Study system and gathering of leaf litters

We selected a set of ten herbaceous crops of six plant families including grasses and forbs (red amaranth, borage, cabbage, millet, artichoke, sunflower, lettuce, tobacco, sorghum, and corn), and gathered seeds of a domesticated and a wild progenitor accession for each crop (Table 1, see also Supporting Information, Table S1, for wild progenitor assignment and seed donors). To obtain leaf litter from each pair of domesticated and wild progenitor, we grew 10–20 individuals of each accession in 2010 at the plant growth facilities of the Universidad Rey Juan Carlos, located in Móstoles, central Spain (40º18′48″ N, 38º52′57″ W, 632 m.a.s.l.; MAT: 15ºC; MAP: 450 mm). After seedlings emerged in the greenhouse, we transplanted plants outdoors into planting beds with a 30 centimetres depth layer of topsoil (soil pH = 7.6, measured in water; total $N = 0.37\%$; organic $C = 5.12\%$). We grew the plants until senescence, which took a slightly different time for each accession. We collected three samples of naturally senesced fresh leaf litter from three different plant individuals per accession. We discarded leaf litter with signs of herbivory or disease; we air-dried the remaining material for one month, and stored it at room temperature until we performed the decomposition assay.

Measurement of leaf litter traits

Prior to plant litter chemical analyses, we grounded the air-dried litter samples in a mill (IKA MF10; IKA-Werke, Staufen, Denmark) to pass a 1-mm screen. We measured C and N in an elemental analyser (varioMAx N/CN; Elementar, Hanau, Germany). We measured leaf litter fibres (cellulose, hemicellulose, and lignin) by the Van Soest method (Van Soest et al. 1991). We measured ash content through pyrolysis at

Table 1 Common and taxonomic names of the domesticated and wild progenitor representatives of each crop included in this study

Domesticated crop	Wild progenitor	Family	Common name
Amaranthus cruentus L.	*Amaranthus hybridus* L.	Amaranthaceae	Red amaranth
Borago officinalis L.	*Borago officinalis* L.	Boraginaceae	Borage
Brassica oleracea L.	*Brassica oleracea* L.	Brassicaceae	Cabbage
Cenchrus americanus (L.) Morrone	*Cenchrus americanus* (L.) Morrone	Poaceae	Millet
Cynara cardunculus L.	*Cynara cardunculus subsp. cardunculus*	Asteraceae	Artichoke
Helianthus annuus L.	*Helianthus annuus* L.	Asteraceae	Sunflower
Lactuca sativa L.	*Lactuca serriola* L.	Asteraceae	Lettuce
Nicotiana tabacum L.	*Nicotiana sylvestris* Speg.	Solanaceae	Tobacco
Sorghum x drummondii (Nees ex Steud.) Millsp. & Chase	*Sorghum bicolor* (L.) Moench	Poaceae	Sorghum
Zea mays L. *subsp. mays*	*Zea mexicana* (Schrad.) Kuntze	Poaceae	Corn

550ºC. To bring the ash into solution we dissolved it in aqua regia. Then, we evaluated P using vanadomolybdic colourimetry (Fiske and Subbarow 1925). We measured K and Ca using complexometric titration. We corrected for moisture, and expressed all litter chemistry variables as % of dry weight. We measured leaf litter dry matter content by dividing the mass of oven dried leaf litter at 60ºC by its water-saturated fresh mass (LDMC, g dry mass * g^{-1} mass at full hydration; Pérez-Harguindeguy et al. 2016). We measured leaf toughness on air dried litter using a purpose-built penetrometer by breaking the leaf litter lamina (N * mm^{-1}; Pérez-Harguindeguy et al. 2016) .

Leaf litter decomposition assay and soil respiration

In September 2015, we bulked together the three litter samples of each domesticated and wild progenitor accession to set up microcosms for each of the ten crops. We built five microcosms for each accession and five control microcosms with no litter, totalling 105 microcosms. To focus on how different litters decompose and influence soil microbial and nematode communities, we incubated all litters on the same soil which we collected at 0–10 cm depth in a nearby permanent Mediterranean grassland (soil pH 7.5, measured in water; organic C 2.04%; total N 0.07%; coordinates 30T 0424133 / 4,469,923 N). We selected this soil to avoid the existence of home-field advantages in the decomposition of our litters. We sieved the soil at 2 mm, homogenised it, and stored it at 4 ºC for two weeks while setting up the microcosms. Although soil sieving might damage some

soil nematodes, they are much smaller than 2 mm in diameter and sieving enabled appropriate homogenisation of the soil.

To set-up the microcosms we weighted 60 g of sieved fresh soil and introduced it into 250 mL plastic Mason jars (9 cm high, 6 cm diameter), with moisture adjusted to 60% water-holding capacity, which is favourable to microbial activity. We cut the litter into 2–3 cm long fragments. Before placing the litter in the microcosms, we placed 0.75 g of litter into Petri dishes and covered these with a soil inoculum for 24 h to promote the colonization of litter by soil microorganisms. This inoculum consisted of sieved fresh soil from the grassland mixed with distilled water (10 kg of soil to 75 L of water proportion; García-Palacios et al. 2013). To simulate a natural soil layer, we placed the soil inoculum-drenched leaf litter from the Petri dishes (0.75 g per microcosm) on top of the soil surface. We closed the microcosms with parafilm, then placed them in five trays randomly (comprising one experimental block); we included one "no-litter" control microcosm per tray to track changes in soil microbial and nematode communities during soil incubation independently of litter. We set the trays in a growth chamber (J.P. Selecta 4,000,699) over 88 days under optimal conditions for the decomposition process (darkness, 20ºC and 95% air humidity). During the incubation period, we randomised the location of trays every two weeks to minimize the effects of potential temperature and moisture gradients within the chamber. We corrected soil moisture every two weeks. We could collect all litter material remaining after the incubation period in each microcosm, since

our microcosms lacked litter-fragmenting fauna. We dried it at 60 °C for 48 h, and then we weighed it to calculate litter mass loss (%). To analyse the soil microbial biomass, we followed a substrate-induced respiration (SIR) method using D-glucose and a MicroResp™ device (Campbell et al. 2003).

Soil microbial and nematode communities

After litter harvest, we collected soil samples to investigate the soil microbial and nematode community responses to the different litters. We analysed soil bacterial and fungal communities in six out of the ten crop-wild progenitor pairs (red amaranth, artichoke, lettuce, sunflower, sorghum and corn). For these analyses, we randomly chose three of the five replicate microcosms per accession of each of the six domesticated crop-wild progenitor pairs, and extracted soil DNA using the DNeasy PowerSoil Kit (QIAGEN GmbH). After extraction, we stored the DNA samples at −20 ℃ and sequenced them at the Illumina MiSeq platform of the Next Generation Genome Sequencing Facility of Wageningen University using the 341 F/805R (bacterial 16 S-rDNA; Herlemann et al. 2011) and FITS7/ITS4 (fungal Internal Transcribed Spacer, ITS, Ihrmark et al. 2012) primer sets.

To obtain an annotated OTU table from the raw MiSeq paired-end reads we performed the following steps. First, we merged the raw reads with a minimum overlap of 25 bp and at least a PHRED score of 25 using the RDP extension to PANDASeq (Masella et al. 2012) named Assembler (Cole et al. 2014). This ensures a base call accuracy of 99.5%. We used Flexbar version 2.5 (Dodt et al. 2012) to remove the primer sequences from the FASTQ files, then we converted the sequences to FASTA format and concatenated them into a single file. We used VSEARCH version 1.0.10 (Rognes et al. 2016) to cluster the sequences into OTUs, using the UPARSE strategy of de-replication, sorting by abundance (with at least two sequences) and clustering using the UCLUST smallmem algorithm (Edgar 2010). Hereafter, we detected chimeric sequences using the UCHIME algorithm (Edgar et al. 2011) implemented in VSEARCH, and we removed them. Finally, we obtained the taxonomic classification for each OTU by using the RDP Classifier version 2.10 (Cole et al. 2014). We implemented all steps in a workflow made with Snakemake (Köster and Rahmann 2012).

We used the rest of the fresh soil (50 g) to extract nematodes in Baermann funnels for 72 h (Baermann 1917). We counted all nematodes under a dissecting microscope and we identified at least 100 individuals to the genus or family level. We measured the water gravimetric soil content by drying soil subsamples at 105ºC for 24 h, and we expressed nematode abundances as number of individuals per 100 g of dry soil. We assigned nematode taxa to trophic groups: bacterivores, fungivores, herbivores, omnivores, and predators (Yeates et al. 1993).

Data analyses

To test for the effects of crop species identity, domestication status, and their interaction on litter mass loss (%) we used a two-way ANOVA model with fixed-effects (*lm* and *anova* of package Base; R Development Core team 2021). To test which crop species were different from each other, we ran post hoc analyses by using the model's adjusted marginal means (*emmeans* and *contrast* of package emmeans; Lenth et al. 2022). We corrected *P*-values for multiple testing using the false discovery rate method (FDR; Benjamini and Hochberg 1995).

To explore how crop species identities and status of domestication influenced litter traits, we used principal components analysis (PCA). Some crops produced little leaf litter, so some trait values were missing. We applied a multiple imputation approach to gain statistical power (Nakagawa and Freckleton 2008). First, we removed two out of 60 replicates because all trait values were missing. We imputed missing values for individual traits (0.79%) by using predictive mean matching (*mice* of package mice, with parameters: m=100, method = "pmm", include=c("sp", "dom_status"), exclude = "id"; Buuren and Groothuis-Oudshoorn 2011), because this method preserves the structure of the data and has high accuracy when there is a low percentage of missing values (Goretzko et al. 2020). Then, we carried out a PCA to visualize how domesticated and wild progenitor accessions cluster according to litter quality variables (*PCA* of package FactoMineR; Lê et al. 2008). To test if crop species identities, domestication status, and their interaction affeted the litter traits that we used in the PCA, we performed a two-way PERMANOVA analysis (*adonis* function in package vegan, setting method = "euclidean"; Oksanen et al. 2020).

To explore whether and which litter quality parameters explained litter mass loss, we ran a multiple linear regression in which litter N, C, lignin, hemicellulose, cellulose, ash content, P, Ca, K, toughness, and LDMC were explanatory variables of litter mass loss rates (%) (*lm* of package Base; R Development Core team 2021). We tested the significance of explanatory variables (i.e., litter traits) using ANOVA (*anova* of Package base; R Development Core team 2021). Moreover, we calculated Pearson correlations of all traits with litter mass loss individually, and tested their significance by performing Pearson correlation tests (*cor.test.* of package Base;R Development Core team 2021). As we did not measure litter traits and mass loss data at the same level of observation (three replicates for trait analyses in the plant growing stage, and five replicates per bulked litter mass loss in the microcosm incubation stage), we calculated for each plant accession trait averages among the replicates. Then, we checked for collinearity between explanatory variables using the variance inflation factor (VIF). We used a linear model in which litter mass loss was the dependent variant, and all litter traits were independent variables. We removed litter ash content because it had a high VIF score (≥ 10) whenever we included litter C in the model (Vittinghoff et al. 2012). To identify the litter traits that accounted for most of the variation in litter mass loss across plant accessions, we selected the best-fitting linear models using Akaike's information criterion (AIC) by running a model selection algorithm (*dredge* of package MuMIn; Bartoń 2022). We selected the model with the lowest AIC as the best model. Then, we used models within a 2 ΔAIC for model averaging and estimated the weighted coefficients, confidence intervals, and relative importance of each litter trait (*model.avg* and *importance* of package MuMIn; Bartoń 2022).

We measured alpha diversity of bacterial and fungal communities as rarefied OTU richness. We calculated rarefied diversity (*rarefy* of package vegan; Oksanen et al. 2020) after rarefaction to the median read count across all samples (Aguirre de Cárcer et al. 2011). The median of read counts was 7539 sequences for bacteria, and 31,610 sequences for fungi. We tested the effects of crop species identity, domestication status, and their interaction on the alpha diversity of soil bacterial and fungal communities (OTU richness; measured in six of the ten crops of the study system), and nematode community (taxa richness; measured in all ten crops of the study system) using two-way ANOVA models (*lm* and *anova* of package Base, (R Development Core team 2021)). We performed post hoc analyses based on the model's adjusted marginal means (*emmeans* and *contrast* of package emmeans; Lenth et al. 2022), and we corrected *P*-values using FDR (Benjamini and Hochberg 1995). We also investigated the effects of crop species identity, domestication status, and their interaction on the beta diversity (i.e., community composition) of soil bacterial, fungal and nematode communities. We calculated beta diversity as the Bray-Curtis dissimilarity among samples in the matrices of square root weighted OTU (bacteria and fungi) or individuals per 100 g of dry soil (nematodes) data. To visualize how crop species identity and status of domestication of litters influenced beta diversity, we performed a non-metric multidimensional scaling (NMDS) by using the Bray-Curtis matrices (*metaMDS* function in package vegan; Oksanen et al. 2020). We tested the effect of crop species identity, domestication status, and their interaction on beta diversity (Bray-Curtis dissimilarity) by performing two-way PERMANOVAs with 10,000 permutations (*adonis* function of package vegan; Oksanen et al. 2020). PERMANOVAs can yield significant differences among groups through differences among centroids, variances or both (Anderson 2001). Thus, when necessary, we ran PERMDISP tests to test if centroids or variance were causing differences among groups in PERMANOVAs (*betadisper* function of package vegan; Oksanen et al. 2020).

To investigate how microbial and nematode richness correlated to community composition, and how the nematode community correlated to soil basal respiration, microbial biomass (SIR), and mass loss, we performed pairwise Mantel tests with 10,000 permutations using Bray-Curtis matrices for community composition data and Euclidean matrices for quantitative data (*mantel.rtest* function of package ade4; Dray and Dufour 2007). We carried out all statistical analyses and visualization in *R 4.1.1* (R Development Core team 2021). Significance level used for all analyses was 0.05. We made all the figures using the *ggplot2* package (Wickham 2016) and Paint.NET 4.3.11.

Results

Plant domestication effects on litter mass loss

Domesticated litters decomposed faster than their wild counterparts (Table 2, Domestication status, $F_{1, 95} = 15.69$, $P = 0.002$). Mass loss rates were 10% higher on average in domesticated litters (ranging from 0.4 to 30%) (Fig. 1). This was consistent across crops, except for *Sorghum* and *Cenchrus*, which decomposed at similar rates regardless of their status of domestication (Table S2, Fig. 1). Moreover, litters from different crop species decomposed at different rates, independently of their domestication status (Table 2, Crop species, $F_{9, 95} = 50.74$, $P < 0.001$). *Brassica*, *Lactuca*, and *Nicotiana* litters decomposed the fastest, and those of *Sorghum* and *Cenchrus* the slowest (Fig. 1).

Plant domestication effects on litter quality traits

Two axes of our ordination analysis explained 61% of the variance we observed in leaf litter traits. The analysis separated the crop species in two groups, grasses and non-grasses (Fig. 2). Grasses had higher leaf toughness, litter cellulose and hemicellulose, and lower litter N, Ca and K contents than non-grasses. Domestication had a consistent effect on most leaf litter traits (Table S3, Domestication status, $F_{9, 95} = 12.90$, $P < 0.001$), resulting in more decomposable leaf litter. In general, litter of domesticated crops had higher hemicellulose, ash content, P, and K, but had lower C, lignin, toughness, and LDMC (Table S4, Fig. S1). However, the magnitude of the effects of domestication on litter traits differed among crop species (Table S3, Crop species * Domestication status interaction, $F_{9, 95}$

= 5.92, $P < 0.001$). The effect of domestication on N, Ca, and cellulose was idiosyncratic among crop species (Table S4, Fig. S1).

Litter quality as a driver of litter mass loss

Litter traits explained up to 84% of the variance observed in litter mass loss. Higher litter C, N, lignin, cellulose, Ca, K, and toughness associated with increased decomposition rate, while higher levels of hemicellulose, P, and LDMC related negatively to litter decomposition rate (Table S5). LDMC alone explained up to 70% of the variance in litter mass loss (Table S6, $\beta = -140.84$). The best-fitting model included LDMC and litter C as predictors, and explained 74% of the variance in litter mass loss (Table S6, $\beta = -143.78$, $\beta = 1.10$). LDMC was the most important predictor for litter decomposability with slower decomposition rate the higher the LDMC (Table S7, $P < 0.001$).
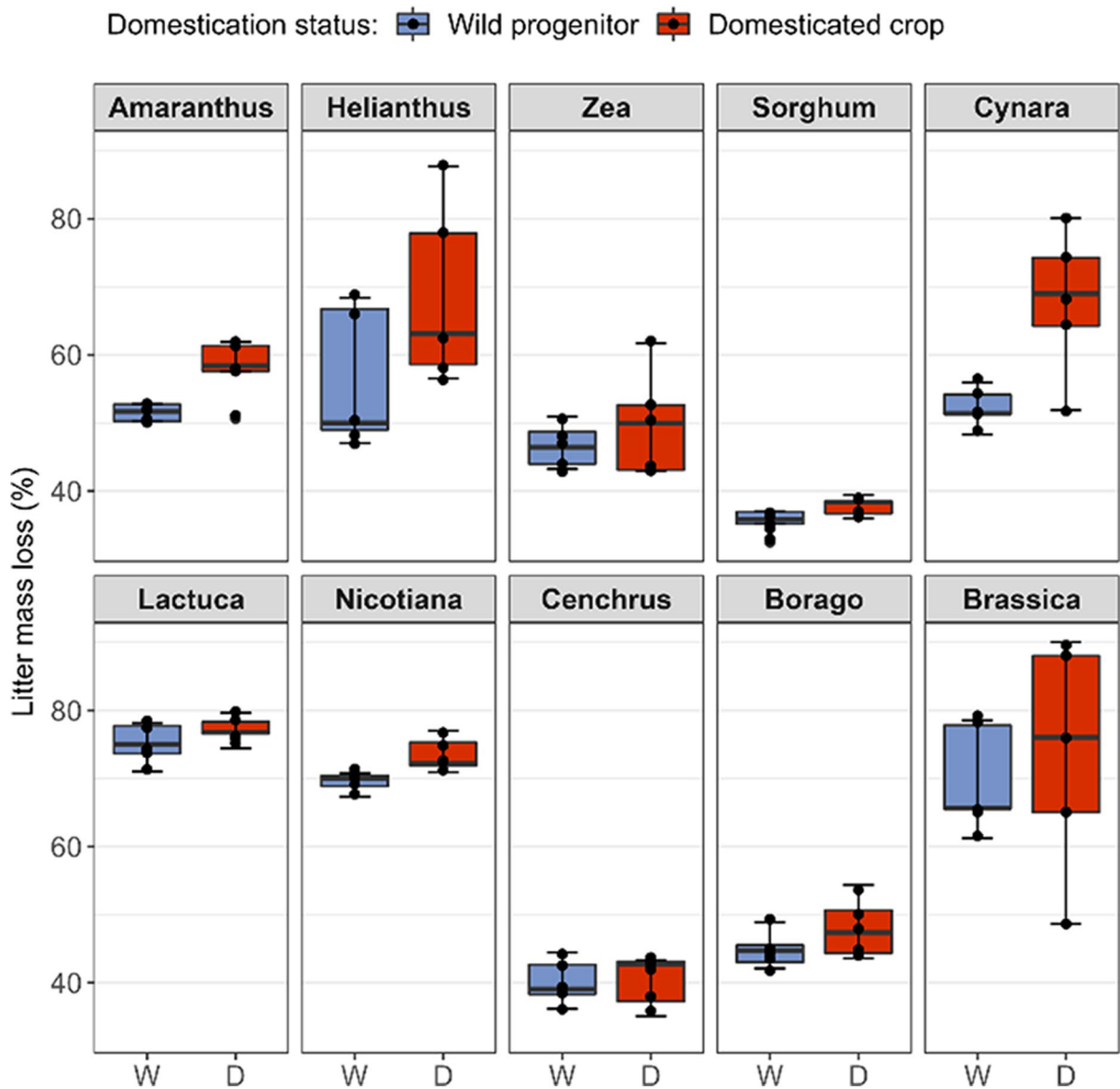
Domestication and species identity effects on the richness of soil microbial and nematode communities

The domestication status of the litters left to decompose on the soil surface of the microcosms affected the soil bacterial OTU richness, but the magnitude and direction of this effect differed among the crop species identities of the litter (Table 3, Crop species * Domestication status interaction, $F_{5, 95} = 7.05$, $P < 0.001$, Fig. 3). Soils incubated with litter of domesticated *Sorghum* had higher OTU richness than those receiving litter of its wild progenitor (Table S8, $P < 0.001$, Fig. 3). In contrast, soils incubated with litter of domesticated *Helianthus* had lower OTU richness than those with litter of its wild progenitor (Table S8, $P < 0.008$, Fig. 3). Soils incubated with litters of *Amaranthus*, *Cynara*, *Lactuca*, and *Zea* exhibited a similar OTU richness regardless of their domestication status (Table S8, Fig. 3). Fungal community OTU richness increased in soils incubated with litters of domesticated accessions (Table 3, Domestication status, $F_{1, 95} = 4.44$, $P = 0.048$, Fig. 3). This effect was consistent across crop species (Table 3, Crop species * Domestication status interaction $F_{5, 95} = 0.59$, $P = 0.707$). In fact, crop species identity of the litters did not change fungi OTU richness (Table 3, Crop species, $F_{5, 95} = 2.42$, $P = 0.072$). Nematode genera richness varied between microcosms incubated with

Table 2 Summary of two-way ANOVA test for main treatment effects and interactions on a matrix containing litter mass loss at the end of the decomposition assay. Significant *P*-values appear in bold

| Independent variables	Df	SS	MS	*F*-value	*P*-value
Crop species identity	9	1.069	0.119	50.74	**< 0.001**
Domestication status	1	0.037	0.037	15.69	**< 0.001**
Crop species identity x Domestication status	9	0.027	0.003	1.28	0.262
Residuals	80	0.187	0.002	N.A.	N.A.

Multiple $R^2 = 0.86$; adjusted $R^2 = 0.82$

Fig. 1 Effects of crop species identity and domestication status on leaf litter mass loss at the end of the microcosm assay (after 88 days of decomposition)

litters of different crops (Table 3, Crop species identity, $F_{9, 95} = 10.30$, $P < 0.001$): soils incubated with litters of *Lactuca* and *Nicotiana* had the lowest, while soils incubated with *Sorghum* litter had the highest nematode richness (Fig. 3). Nematode richness did not differ between microcosm with domesticated or wild litters (Table 3, Domestication status, $F_{1, 95} =$ 0.71, $P = 0.402$; Crop species * Domestication status interaction $F_{9, 95} = 0.85$, $P = 0.570$). In general, mean abundances of each nematode feeding group were similar between microcosms with litters of domesticated and wild accessions (Fig. S2). Bacterivores were the most abundant feeding type of nematodes in all soils.
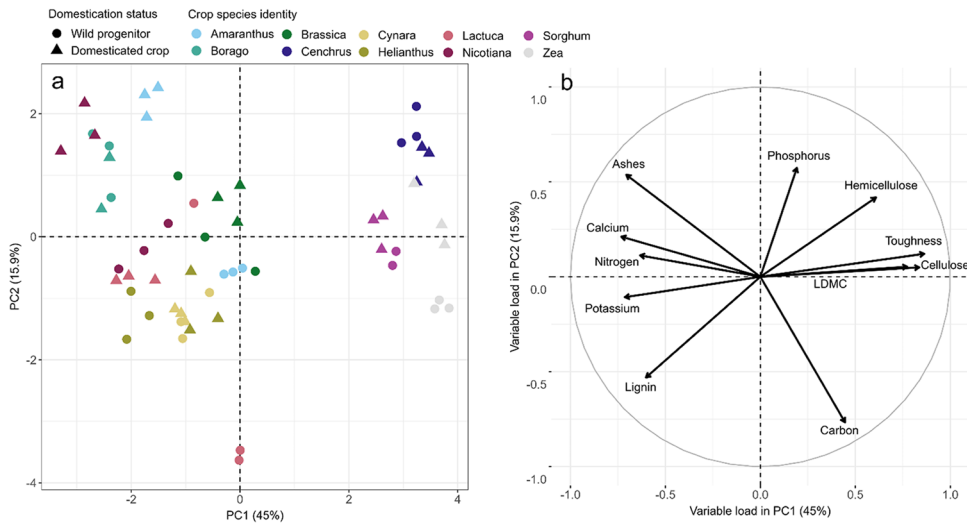
Fig. 2 Principal component analysis (PCA) of leaf litter traits differences between crop species identities and their domestication status. Leaf litter samples are plotted over the two PCA axes with the highest variance explained (**a**). Loads of the leaf litter traits inputted for the PCA ordination plot are plotted (**b**). Domestication-induced changes in all leaf litter traits appear in Table S4 and Fig. S1

Table 3 Summary of two-way ANOVA test for main treatment effects and interactions on a matrix containing richness (α diversity) of soil bacteria, fungi and nematode communities. Significant *P*-values appear in bold

Independent Variables	Bacterial richness		Fungal richness		Nematode richness	
	F-value	*P*-value	*F*-value	*P*-value	*F*-value	*P*-value
Crop species identity	5.65	**0.002**	2.42	0.072	10.30	**< 0.001**
Domestication status	2.08	0.165	4.44	**0.048**	0.71	0.402
Crop species identity * Domestication status	7.05	**< 0.001**	0.59	0.707	0.85	0.570

Plant domestication and species identity effects on the soil microbial and nematode community composition

Soils incubated with litters of the same crop species had similar bacterial and fungal communities (Table 4, Crop species, $F_{5, 95} = 1.76$, $P = 0.003$; $F_{5, 95} = 1.53$, $P = 0.001$, respectively, Fig. 4). Within each crop, the status of domestication of the litters shaped the composition of bacterial and fungal communities in different directions (Table 4, Crop species * Domestication status interaction, $F_{5, 95} = 1.67$, $P = 0.008$; $F_{5, 95} = 1.25$, $P = 0.030$, respectively, Fig. 4). These changes may arise from differences in the abundances of the most abundant groups. For bacteria, these groups were *Acidobacteria, Actinobacteria, Bacteroidetes*, *Proteobacteria, Gemmatimonadetes* and *Verrucomicrobia* (Fig. S3). Regarding fungal communities, the most abundant groups were *Ascomycota, Basidiomycota* and *Zygomycota* (Fig. S4). The strength of domestication-induced shifts in soil bacterial and fungal community compositions was different between crops (Table S10). Soils fed with litters of the same crop species developed similar nematode communities (Table 4, Crop species, $F_{9, 95} = 2.46$, $P < 0.001$, Fig. 4). Soils with litters of *Nicotiana*, *Lactuca*, *Brassica*, *Cenchrus*, *Zea* and *Cynara* associated to higher abundances of generalist
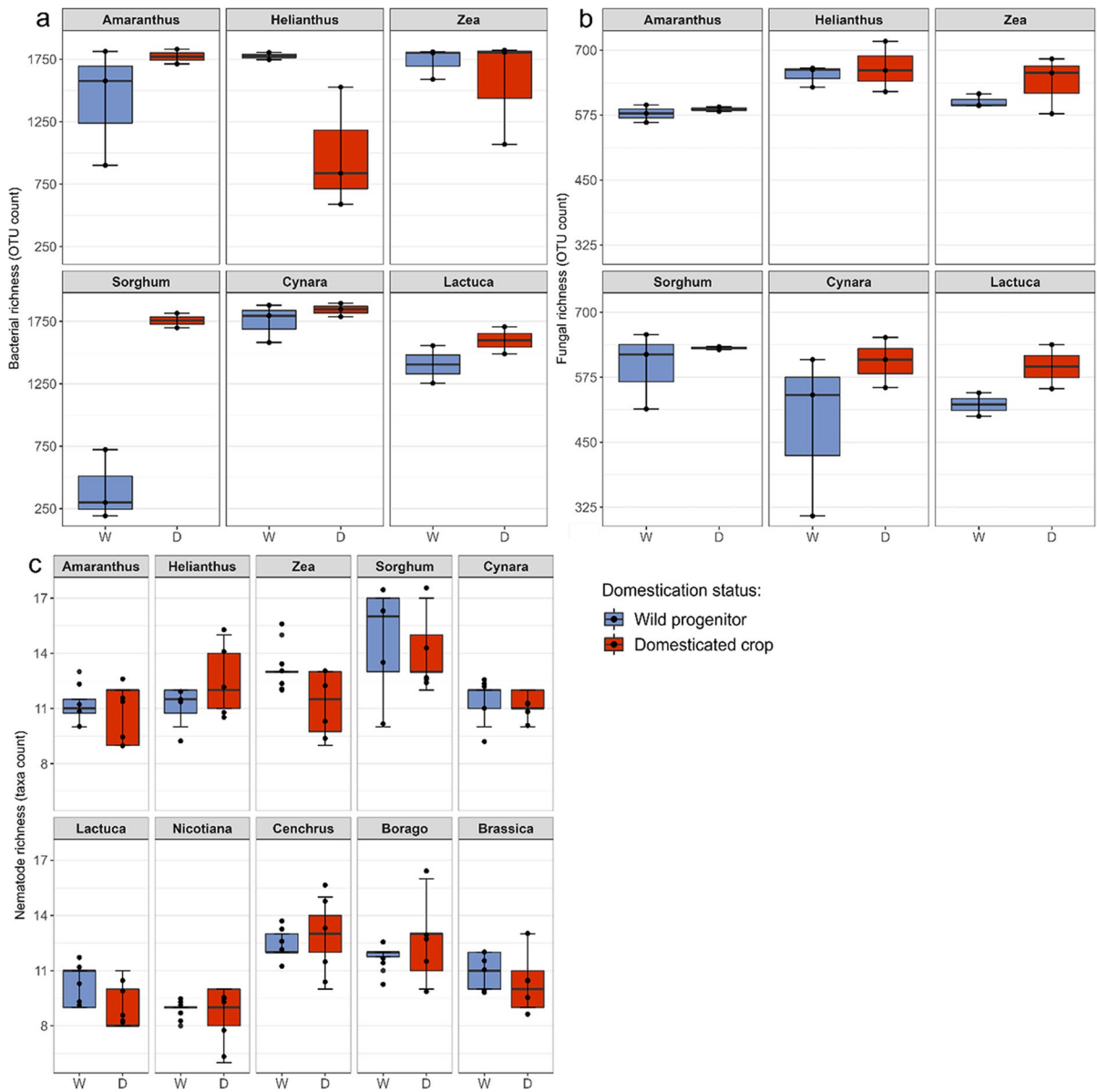
Fig. 3 Effect of crops species identity and domestication status of litters on soil bacterial (**a**), fungal (**b**), and nematode (**c**) richness (α diversity)

bacterivores (*Prismatolaimus* and *Rhabditis*); soils incubated with litters of *Amaranthus*, *Borago*, *Sorghum* and *Helianthus* associated to increased abundances of generalist bacterivores (*Eumonhystera, Teratocephalus* and *Mesorhabditis*), and omnivores/predators (*Clarkus* and *Thornia*); microcosms with *Cynara*, *Sorghum* and *Healianthus* litters also presented higher abundances of plant parasitic nematodes (*Tylenchorhynchus* and *Helicotylenchus*)

(Figs. 4 and 5). Domestication had a consistent effect across crop species (Table 4, Domestication status, $F_{1, 95} = 2.05$, $P = 0.047$), with a similar effect size among crops (Table S10). In general, domestication increased the abundance of bacterial feeders in the community (Figs. 4 and 5).

Bacterial richness correlated positively with bacterial community composition ($r = 0.971$, $P < 0.001$), but fungal richness did not correlate with fungal community

Table 4 Summary of two-way PERMANOVA test for main treatment effects and interactions on a Bray-Curtis dissimilarity matrix containing weighted relative abundances (β diversity) of the taxa present in soil bacteria, fungi and nematode communities. Significant P-values appear in bold

Independent Variables	Bacterial β diversity		Fungal β diversity		Nematode β diversity	
	F-value	P-value	F-value	P-value	F-value	P-value
Crop species identity	1.76	**0.003**	1.53	**0.001**	2.46	**< 0.001**
Domestication status	1.12	0.259	0.98	0.434	2.05	**0.047**
Crop species identity * Domestication status	1.67	**0.008**	1.25	**0.030**	1.06	0.339

composition ($r = 0.203$, $P = 0.140$). Nematode richness correlated positively with nematode community composition ($r = 0.253$, $P < 0.001$). Nematode richness correlated positively to litter mass loss ($r = 0.253$, $P < 0.001$), but did not correlate to any soil respiration

measure or microbial biomass (Table S11). Nematode community composition correlated to litter mass loss ($r = 0.240$, $P < 0.001$) and soil basal respiration (Table S11, $r = 0.067$, $P = 0.042$), but did not correlate to microbial biomass (Table S11, $r = 0.011$, $P = 0.400$).
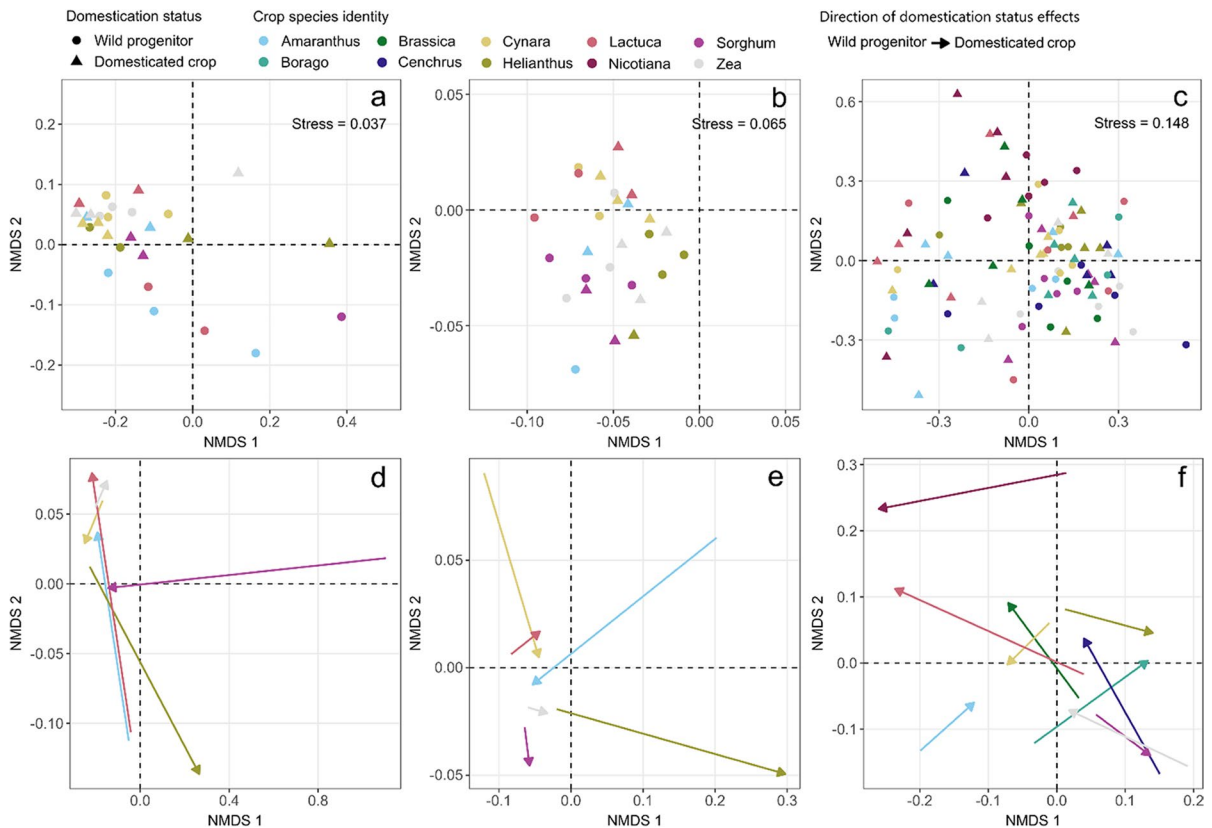
Fig. 4 Non-metric multidimensional scaling (NMDS) analyses of community composition based on the Bray-Curtis dissimilarity matrices of the weighted relative abundances of soil bacterial (**a** = zoom-in version; all points are displayed in Fig. S5), fungal (**b** = zoom-in version; all points are displayed in Fig. S6), and nematodes communities (**c**). The direction and magnitude of domestication-induced changes in community composition of bacteria (**d**), fungi (**e**), and nematodes (**f**) are represented by arrows that cover the distance between centroids of the points belonging to the wild progenitors and the domesticated crops for each of the plant species

Fig. 5 Loadings of the most influential nematode taxa in the NMDS analysis displayed in Fig. 4
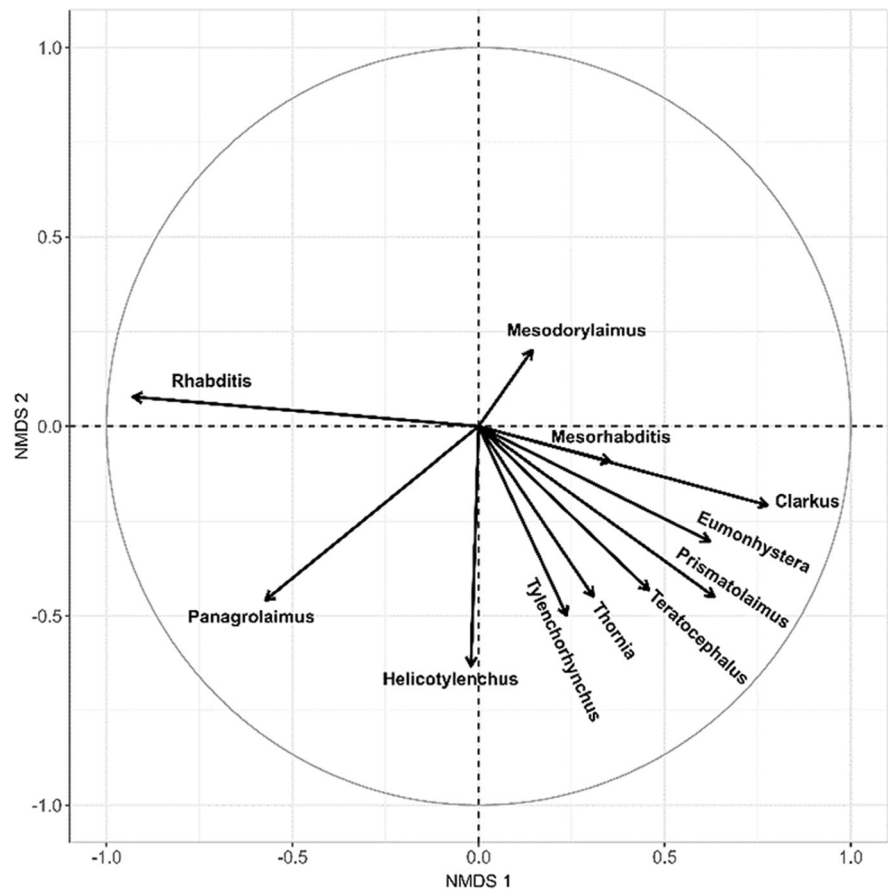
Discussion

Our results showed that leaf litter of domesticated crops decomposes faster than litter of their wild progenitors. This effect was mediated by domestication-induced changes in leaf litters, which were softer, and had less C concentrations and LDMC than their wild counterparts. The faster litter decomposition in the domesticated microcosms impacted the soil bacterial, fungal and nematode communities in different ways. Our results show that domestication-induced changes in crop traits altered the linkages between plant residues and soil organisms in different ways for bacteria, fungi and nematodes.

Domestication impacts on leaf litter decomposability

The litter of domesticated plants decomposed faster than those of their wild progenitors among all crop species. Our results suggest that this is related to an increment in leaf litter quality after domestication,

such as higher P, and lower C, lignin, and LDMC. García-Palacios et al. (2013) and Delgado-Baquerizo et al., (2016) also found that domesticated accessions of herbaceous crops decomposed faster than their wild counterparts, and that these increments correlated with changes in C, N, P, and lignin contents. In another study, leaf litter of domesticated accessions of the perennial herb *Silphium integrifolium* Michx. (Asteraceae) also exhibited higher decomposability when compared to wild accessions, which correlated with lower LDMC in domesticated varieties (González-Paleo et al. 2022). This is similar to previous findings from natural ecosystems, where chemical (i.e., C, N, and lignin contents) and physical (i.e., LDMC) traits explain most of the variation in litter mass loss (Cornwell et al. 2008; Dias et al. 2017; Freschet et al. 2012; García-Palacios et al. 2016a). Therefore, our findings align well with established hypothesis that an increase in litter quality, induced in our study system by plant domestication, speeds up decomposition.

Effects of domestication on soil microbes

Soil fungal community richness increased consistently in soils incubated with domesticated litters, as compared to soils incubated with litters of wild progenitors. This effect was inconsistent (i.e., increasing for some crops and decreasing for others) in bacterial richness. In contrast, previous research reported that bacterial and fungal richness increase or decrease similarly during decomposition (Purahong et al. 2016). A possible explanation for this mismatch would be that our litters lean towards the highly decomposable end of the global spectrum (Zhang et al. 2008), promoting the proliferation of bacteria over fungi. An increment in resource accessibility could downregulate common species of fungi that dominate in the early stages of decomposition, that usually digest not so accessible carbon sources such as cellulose or hemicellulose. This would make room for a wider variety of fungi species, since the resources in our labile litters might have been easily accessible by most fungal species through the use of generalist enzymes like laccase or β-glucosidase (Boer et al. 2005; Eichlerová et al. 2015).

Differences in bacterial and fungal community compositions with domestication were crop species-specific. This finding agrees with previous work, which shows that plant identity (here crop identity) has a strong influence on the composition of leaf litter and soil bacterial and fungal communities (Fanin et al. 2014; Veen et al. 2021). Previous studies have attributed these changes in bacterial and fungal community composition to differences in litter quality (Alfaro et al. 2017; García-Palacios et al. 2016b; Purahong et al. 2016; Rummel et al. 2020). Specifically, bacterial community composition would depend of N, Ca, and cellulose content (Purahong et al. 2016; Rummel et al. 2020), and fungal community composition would depend of N, Ca, and lignin (Alfaro et al. 2017; Purahong et al. 2016). Our results partly support these claims, since we found that domestication had a crop species-specific effect on N, Ca, and cellulose contents (increased for some crops and decreased for others). Therefore, N, Ca, and cellulose might be the drivers of the variations in bacterial and fungal community compositions in our soils because all of them are affected by domestication in a crop species-specific manner. Bacterial richness and community composition were strongly correlated and reacted similarly to domesticated crop litter inputs. However, fungal richness and community composition reacted differently to litter addition of domesticated crops. This is reinforced by the lack of correlation between fungal richness and community composition. Our results contrast with previous studies that suggested that both richness and community composition of bacteria and fungi react similarly to plant litter inputs (Sauvadet et al. 2016). Our findings suggest that domestication caused idiosyncratic shifts in litter quality among crop species, which might have altered the existing dynamics within the microbial communities. This would explain that domestication-induced changes in soil communities are not coordinated between bacteria and fungi in our study system, suggesting that these groups responded differently to changes in litter quality.

Impacts of domestication on soil nematodes

Bacterial feeding nematodes remained the most abundant trophic group among domestication statuses and crop species identities. Nematode community composition mainly changed with the identities of the litters that we added to the soils. Our findings agree with previous studies which reported that bacterivore nematodes are the most abundant trophic group in soils, especially around decomposing plant litter (van den Hoogen et al. 2019; Wasilewska 1991). Even though the nematode community shows specificity to litter types, nematodes do not interact directly with plant residues (Yeates 1999). Rather, nematodes interact with microbes through predation (Jiang et al. 2017). Hence, nematode richness and community composition would be primarily determined by plant litter effects on bacterial and fungal communities (Yeates 1999). Although organic matter decomposition might liberate organic substances with nematicidal activities (i.e., glucosinolate-derived compounds in Brassicas, short-chain fatty acids under anaerobic conditions, or N compounds generated from low C:N organic materials (Oka 2010)), we did not detect clear detrimental effects of decomposition on nematode abundances. For instance, the abundance of nematodes correlates with microbial biomass, whilst both correlate to litter quality and decomposability (Sauvadet et al. 2016). Our data hints that nematode community composition might be related to microbial biomass because we found that plant domestication accelerated decomposition by increasing litter quality. Indeed, nematode

community composition correlated positively with litter mass loss. An accelerated resource input into soils would augment microbial biomass. We expect bacteria to be very abundant in this stage of decomposition. Moreover, nematode community composition correlated weakly with soil basal respiration, but did not correlate with microbial biomass. Bacterivore nematodes feed on bacterial cell aggregates (Rønn et al. 2012), so they probably ingest bacteria independently if they are dead or alive. In accordance to our claim, litter addition of domesticated crops impacted soil nematode community composition by increasing the abundance of bacterial feeders across all soils. Adding litter of domesticated accessions of labile species as *Brassica*, *Lactuca*, and *Nicotiana* increased the abundance of opportunistic bacterivore nematodes (*Rhabditis*, *Panagrolaimus*), which indicate that soil bacterial biomass increases and decreases quickly over time (Ferris and Bongers 2006). However, domesticated accessions of more recalcitrant litters as *Borago*, *Helianthus*, and S*horghum* promoted generalist bacterivores (*Prismatolaimus*, *Eumonhystera*, *Teratocephalus*), which are commonly associated with more stable bacterial populations (Ferris and Bongers 2006), and omnivore-predators, which might increase their populations due to the abundance of nematodes of lower trophic levels (Ferris et al. 2012). Litter from domesticated accessions of *Cynara* and *Sorghum* seemed to be associated with herbivore nematodes. Although no plants grew in the microcosms during our experiment, it is known that herbivore nematodes might survive in the soil for long periods without plant roots (Ribeiro et al. 2020); the reason behind such association to herbivore nematodes remains unclear and deserves further attention. Our findings suggest that nematode community composition in soils fed with the litters of domesticated plants are different than that of soils fed with litters of their wild progenitors. This disruption might mirror the shifts in the bacterial community observed, which are related to domestication-induced changes in litter quality, which would therefore explain why higher abundance of bacterivore nematodes was found across all crop species identities, while the bacterivore taxa groups with higher abundances were crop species-specific.

Remarks on our experimental design and future studies

The novelty of our experiment lies in analysing the effects of domestication on bacterial, fungal and nematode communities in the same soil samples at the same time. Additionally, we investigated this alongside domestication-induced changes in litter quality and decomposability. Since we pooled leaf litter, we produced pseudo-replicates. Therefore, we needed fewer replicates in the experiment but could not analyse trait variability within accessions. As we used leaf litter only, our results might not extrapolate to other types of plant residues (roots and stems). In particular, roots contribute a high share of cropland residues, and dead roots behave differently from leaf litter during decomposition (Hobbie et al. 2010; Sauvadet et al. 2016). A previous study hinted that traits that control leaf litter decomposability in crops might differ from those that control root litter decomposition (Barel et al. 2019). Also, we surveyed soil communities once for the full duration of our experiment. But soil biotas undergo considerable temporal changes throughout the decomposition process (García-Palacios et al. 2016b; Purahong et al. 2016; Veen et al. 2021; Wang et al. 2004; Wardle et al. 2006). For example, *Ascomycota* fungi dominate at the beginning stages of litter decay, while *Basidiomycota* become more abundant later on (Purahong et al. 2016). Future studies should address if and how the effects of domestication on soil biotas, mediated through litter decomposition, vary in the different stages of the process. Temporal variations should also be addressed for other types of plant residues (i.e., stems and roots) because their relationship to microbial and nematode communities remains unknown. We did not find works about the effect of litter leachates on soil nematodes during decomposition. This needs further investigation, since nematodes are important indicators of soil health (Gao et al. 2020). Also, if and how domestication altered litter traits in stem and root residues deserve further exploration since they contribute a high share in litter inputs to agricultural soils.

Conclusion

In this study, we report the impacts of domestication-induced changes in litter traits on soil microbial and nematode communities during the decomposition of plant residues. Domesticated litters generally increased fungal richness while their effects were crop species-specific for bacterial richness (i.e., increasing for some crops and decreasing for others). Bacterial and fungal community composition chiefly depended on the taxonomic identities of the litters added to the soils, and the influence of the status of domestication of the added litters was crop species-specific. This means that the effect of incubating soils with litters of domesticated accessions was quite variable and idiosyncratic among crop species. Incubating soils with litters of domesticated crops increased the abundances of bacterivore nematodes when compared to litters of wild progenitors, but the bacterivore nematode taxa which thrived depended of the plant litter identity. Overall, our results indicate that plant domestication altered the linkages between crop residues and soil organisms in different ways for bacteria, fungi and nematodes.

Data availability All data generated or analysed during this study are included in this published article as a supplementary information file.

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