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Side-effects of plant domestication: ecosystem impacts of changes in litter quality

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Summary

- Domestication took plants from natural environments to agro-ecosystems, where resources are generally plentiful and plant life is better buffered against environmental risks such as drought or pathogens. We hypothesized that predictions derived from the comparison of low vs high resource ecosystems (faster-growing plants promoting faster nutrient cycling in the latter) extrapolate to the process of domestication.
- We conducted the first comprehensive assessment of the consequences of domestication on litter quality and key biogeochemical processes by comparing 24 domesticated crops against their closest wild ancestors. Twelve litter chemistry traits, litter decomposability and indicators of soil carbon (C) and nitrogen (N) cycling were assessed in each domesticated vs wild ancestor pair. These assessments were done in microbial-poor and microbial-rich soils to exemplify intensively and extensively managed agricultural soils, respectively.
- Plant domestication has increased litter quality, encouraging litter decomposability (36% and 44% increase in the microbial-rich and microbial-poor soils, respectively), higher soil NO_3^- availability and lower soil C : N ratios. These effects held true for the majority of the crops surveyed and for soils with different microbial communities.
- Our results support ecological theory predictions derived from the comparison of low- and high-resource ecosystems, suggesting a parallelism between ecosystem-level impacts of natural and artificial selection.

Introduction

Plant domestication and breeding are key historical processes. Current and preceding civilizations would not have flourished without domesticated plants (Diamond, 2002). Domestication relies on a process of artificial selection, changing plant phenotypes for increased yield and promoting a number of traits regarded as favorable by humans (Evans, 1993; Doebley *et al.*, 2006). Knowledge of the genetic basis of this process, or its consequences for yield, palatability and resistance to pests or drought, is reasonably advanced (Denison *et al.*, 2003; Hancock, 2004; Hajjar & Hodgkin, 2006). However, there is little information on the effect that domestication exerts on agro-ecosystem processes relevant to the productivity and sustainability of crops. Here, we make use of predictions from ecological theory to advance knowledge on this area by asking how plant domestication influenced litter quality (i.e. the chemical composition of litter) and ecosystem processes such as litter decomposition or soil nitrogen (N) and carbon (C) dynamics.

In nature, plants from fertile ecosystems generally produce litter of high quality that decomposes readily and promotes fast recycling of nutrients in the soil, whereas the opposite is true for plants from stressful and poorly productive sites (Chapin, 1980; Hobbie, 1992). This occurs because, in nutrient-poor soils, plant fitness is maximized by effectively conserving acquired resources against biotic and abiotic risks. This promotes the evolution of plant organs with high levels of heavy and recalcitrant molecules, for example, lignin, which are not reabsorbed during organ senescence and tend to slow down decomposition and soil nutrient cycling (Quested *et al.*, 2003; Cornwell *et al.*, 2008). Domesticated plants are bred in agricultural environments, which are generally richer in resources such as nutrients, water and light, and are better buffered against environmental risks such as drought, herbivores or pathogens than those where their wild ancestors thrive (Denison *et al.*, 2003; McKey *et al.*, 2012). (We use the term 'wild ancestor' here to refer to the closest wild relative of an existent crop. This term is employed for simplicity, though we are aware that, for many crop species, domestication was a complex evolutionary process where the assignment of a unique ancestral gene pool is only a convenience.) Artificial selection may thus have promoted a similar evolutionary process to that observed in nature. Domesticated crops might have evolved

higher litter qualities than their wild ancestors, promoted by centuries-long selection for fast growth and/or low leaf toughness for consumption under benign habitats. In addition, artificial selection may indirectly have stimulated shifts in plant litter chemistry and toughness. For example, human selection against digestion-inhibiting compounds or C allocation to plant defenses can change leaf chemical composition, as happens with cucumbers (*Cucumis sativus*, Denison *et al.*, 2003), cassava (*Manihot esculenta*, Mondolot *et al.*, 2008), maize (*Zea mays*, Rosenthal & Dirzo, 1997) or beans (*Phaseolus vulgaris,* Lindig-Cisneros *et al.*, 2002).

In summary, literature from diverse lines of inquiry hints that litter quality may have changed substantially along the course of domestication and further breeding. If this is the case, the effects of nutrient inputs through litter decay on the functioning of agro-ecosystems may have diverged from wild ancestors to current agricultural genotypes because of changes in the nutritional quality of litter (Couteaux *et al.*, 1995; Drinkwater *et al.*, 1998; Makkonen *et al.*, 2012). No previous study has tested the ecosystem impacts of plant domestication with a large set of species and under a common experimental design. Here, we explore whether litter–soil feedback patterns described for plants evolved in contrasting natural systems extrapolate to the process of domestication, under the hypothesis that domesticated plants should produce litter of higher quality, promote faster litter decomposition rates and enhance nitrate availability in soils. We analysed the quality of litters obtained from a common garden for a large set of 24 crops, which accounts for 55% of global croplands (http://faostat.fao.org, 2010 data), each represented by domesticated and wild ancestor accessions. The effects of those litters on decomposition and soil nitrogen and carbon dynamics were tested in microbial-poor and microbial-rich soils, intended to exemplify intensively and extensively managed agricultural soils, respectively. If present, the evolution of contrasting litter–soil properties during domestication could bear remarkable consequences for the management of soil fertility in agro-ecosystems through the use of crop residues, and hint at new breeding avenues (Tilman, 1998).

Table 1 Common name and taxonomic status of each accession of the 24 domesticated–wild ancestor pairs selected for the experiment

Domesticated	Wild ancestor	Family	Common name
Amaranthus cruentus	*A. hybridus*	Amaranthaceae	Red amaranth
Avena sativa	*A. sterilis*	Poaceae	Oat
Beta vulgaris var. *cycla*	*Beta vulgaris* ssp. *maritima*	Amaranthaceae	Chard
Borago officinalis	*B. officinalis*	Boraginaceae	Borage
Brassica oleracea var. *acephala*	*B. oleracea*	Brassicaceae	Cabbage
Capsicum anuum	*C. anuum* ssp. *glabriusculum*	Solanaceae	Pepper
Capsicum bacattum var. *pendulum*	*C. bacattum* ssp. *bacattum*	Solanaceae	Chili pepper
Cichorium endivia	*C. intybus*	Asteraceae	Chicory
Cucumis sativus	*C. sativus* ssp. *hardwickii*	Cucurbitaceae	Cucumber
Cynara cardunculus	*C. cardunculus* ssp. *sylvestris*	Asteraceae	Artichoke
Gossypium hirsutum	*G. hirsutum*	Malvaceae	Cotton
Helianthus annuus	*H. annuus*	Asteraceae	Sunflower
Hordeum vulgare	*H. spontaneum*	Poaceae	Barley
Lactuca sativa	*L. serriola*	Asteraceae	Lettuce
Lycopersicon esculentum	*L. pimpinellifolium*	Solanaceae	Tomato
Nicotiana tabacum	*N. sylvestris*	Solanaceae	Tobacco
Pennisetum glaucum	*P. glaucum*	Poaceae	Millet
Secale cereale	*S. ancestrale*	Poaceae	Rye
Sesamum indicum	*S. indicum*	Pedaliaceae	Sesame
Sorghum sudanense	*S. bicolor*	Poaceae	Sorghum
Trifolium repens	*T. repens*	Fabaceae	White clover
Triticum durum	*T. dicoccoides*	Poaceae	Wheat
Vigna unguiculata	*V. unguiculata* ssp. *unguiculata*	Fabaceae	Cowpea
Zea mays ssp. *mays*	*Z. mays* ssp. *mexicana*	Poaceae	Corn

Materials and Methods

Study system and sampling of leaf litters and soils

We studied a set of 24 taxonomically diverse herbaceous crops (Table 1). For each crop we obtained seed lots of two accessions: one representative of a modern, domesticated stage of the species, and another one from its most likely wild ancestor (see the Supporting Information, Table S1, for wild ancestor assignment and seed donors, and Fig. S1, for geographical seed origins of wild accessions). This collection of seeds was grown under a common garden regime in 2010 (16 crops) and in 2011 (8 crops) at the plant growth facilities of the Rey Juan Carlos University, located in Móstoles, central Spain (40°18′48″ N, 38°52′57″ W, 632 m above sea level). Twenty-five seeds per accession were grown to seedlings in the glasshouse for 2–6 wk (depending on species and season). Seedlings were then transplanted outdoors and maintained under ambient light and temperature for 8–24 wk (depending on species and season), but subject to regular dripping irrigation throughout the growing season. In this way, litters were made comparable because all accessions were raised under the same environmental conditions and at the same location. We paid special attention to grow both accessions of each crop synchronously and at the same spots within the experimental garden. Outdoor soil was a mixture of soil and sand (pH = 7.36, N = 0.37%, C = 5.12%). The climate at the common garden site was continental semiarid, with cold winters and a severe summer drought; mean temperature and annual precipitation are 15°C and 450 mm, respectively (Getafe Air Base climatic station 40°18′ N, 3°44′ W, 710 m above sea level, 1971–2000). By the end of the growing season, for each accession we collected three samples of naturally senesced leaf litter from three different individuals to be assayed separately for chemistry composition. All

remaining litter was pooled per accession to obtain a composite sample of litter for decomposability assays. The litter was air-dried for 1 month and then either sent out for chemistry tests, or stored at room temperature until setup of the decomposition assay.

The soils used to test litter effects on decomposability and nutrient cycling were taken from two nearby roadside grasslands (Table S2). The two grasslands differed in time since last major disturbance, representing different successional stages. One site was 0–2 yr old and represents an early-successional stage; the other site was a > 20-yr-old roadside grassland representing a late-successional stage. Roadside grassland soils have special characteristics, such as low organic matter and simple microbial communities (García-Palacios *et al.*, 2011) which, together with their resemblance to agricultural soils (Cramer *et al.*, 2008), make them an appropriate model system for this study. The late-successional grassland showed higher levels of organic matter and microbial functional diversity, but also a greater abundance of bacteria and fungi and a higher fungal : bacterial ratio than the early-successional grassland. As such, we refer to the microcosms with early-successional soil as 'microbial poor' and microcosms with late-successional soil as 'microbial rich'. Thirty soil cores (5 × 10 cm) were removed in each grassland in two dates corresponding with the two different litter decomposability incubations: April and October 2011 (see later). These soil cores were bulked by site, sieved at 2 mm mesh and homogenized in order to get a single pooled sample from either the microbial-rich or the microbial-poor soils. The soil samples were air-dried for 1 d and then sorted in 250 ml Mason jars for a decomposability assay. A subsample of soil was air-dried for 1 month for nutrient cycling analysis.

Litter chemistry analyses

Litter samples were ground in a mill (IKA MF10; IKA-Werke, Staufen, Denmark) to pass a 1-mm screen. The N and C concentrations were measured with an elemental analyser (varioMAx N/CN; Elementar, Hanau, Germany). Leaf fiber (hemicellulose, cellulose and lignin) was assessed by the method of Van Soest *et al.* (1991). Ash analysis was conducted by pyrolysis at 550°C to destroy all organic matter. The ash was dissolved in aqua regia in order to bring into solution. The P and Ca concentrations were evaluated by vanadomolybdic colorimetry and complexometric titrations, respectively. All litter chemical variables were calculated as % dry weight (DW). Several indices of chemistry-based litter quality, relating to proportions of labile and nonlabile compounds in the litter and thus potential predictors of decomposition, were calculated: the lignin : N, lignin : P, N : cellulose, N : P and C : N ratios, and the lignocellulose index (LCI = lignin/lignin + cellulose) (Melillo *et al.*, 1982; Talbot & Treseder, 2012).

Litter decomposability assay

We ran a laboratory decomposition experiment to test for the effects of the addition of litter on soil respiration, a measure of litter decomposability. This experiment consisted of litter + soil (microbial rich) microcosms incubations with two treatments: 24 crop identities and two levels of domestication status (domesticated and wild ancestor). For a subset of 16 pairs of domesticated and wild ancestor, the microbial-poor soil was also used to compare two soils with a contrasting microbial community. We established five microcosms for each treatment combination, giving 240 assemblages in the crop identity × domestication status subset and 320 assemblages in the crop identity × domestication status × soil microbial community subset. We analysed soil cumulative respiration as the amount of CO_2 respired by soil microorganisms decomposing plant litter over the incubation period. The experiment was conducted in two batches (16 crops in April–June 2011 and eight crops in October–December 2011) corresponding to the crop species grown in 2010 and in 2011 at the common garden plantation.

All dry litter samples from each accession were bulked together and homogenized. We introduced 0.75 g of litter into Petri dishes and covered these with a soil microbial inoculum for 24 h to promote colonization of soil microorganisms. To obtain this inoculum, 10 kg of fresh soil from each roadside grassland were mixed with 75 l of water. After that, 60 g of sieved soil were introduced into 250 ml air-tight Mason jars (9 cm high, 6 cm diameter) and moisture was adjusted to 50% water-holding capacity, which is favorable for microbial activity. Microcosms were constructed by carefully placing the soil inoculum-drenched litter on top of the soil surface. Microcosms were placed in five trays and introduced in a growth chamber over 9 wk under optimal conditions for the decomposition process (darkness, 20°C and 95% air humidity). Microcosm location among and within trays was randomized weekly to avoid potential effects of subtle temperature and moisture gradients within the growth chamber. Two 'no-litter' microcosm replicates per soil type were placed in each tray to correct for soil contribution to CO_2 production (Strickland *et al.*, 2009).

Before starting soil respiration measurements, microcosms were left untouched for 3 d to allow microbial colonization of the litter and activation of the decomposition process. Litter decomposability was estimated by monitoring microcosm respiration rates throughout the 9-wk incubation period. The CO_2 respired by soil microorganisms was measured by means of a CO_2 detection solution containing cresol red indicator dye, potassium chloride, sodium bicarbonate and purified agar (García-Palacios *et al.*, 2012). This method is sensitive and precise enough to differentiate soil respiration rates in microcosms with contrasting soil microbial communities and litter qualities, and is able to differentiate the CO_2 production derived from the degradation of small amounts of litter inputs from the CO_2 coming from the basal soil respiration (García-Palacios *et al.*, 2012). The microcosms were left opened during the experiment to prevent CO_2 saturation in the headspace of the jars. At each sampling date, one four-well microplate strip (1 × 8 breakable) filled with aliquots (150 µl) of the detection solution was attached to the side of each jar. The jars were air-tightly closed for 6 h and absorbance was read at 595 nm immediately before and after that period. The well absorbance after 6 h was normalized for any differences

recorded at zero-time before exposure, averaged in each jar and then converted to the headspace CO_2 concentration by a curve calibrated with gas chromatography. The CO_2 concentration (%) was converted to CO_2 production rate (μg CO_2-C g^{-1} soil g^{-1} litter h^{-1}) by using gas constants, incubation temperature, headspace volume in the microcosms, fresh weight (FW) of soil, dry litter weight, incubation time and soil sample %DW (Campbell *et al.*, 2003). Newton integration was applied to the CO_2 production rate to calculate the cumulative respiration at the end of the experiment in each microcosm (mg CO_2-C g^{-1} soil g^{-1} litter). Soil respiration was determined daily during the first week and weekly over the rest of the experiment (Strickland *et al.*, 2009).

Measurement of soil nitrogen and carbon cycling indicators

At the end of the litter incubation period soil from batch 1 (April –June 2011), where pairs of domesticated and wild ancestor were tested in both microbial-rich and microbial-poor soils (8 species pairs and 160 microcosms), was used to measure several indicators of nutrient cycling. Incubated and initial air-dried soil samples were extracted with K_2SO_4 0.5 M in a ratio of 1 : 5. Soil extracts were shaken in an orbital shaker at 200 rpm for 1 h at 20°C, and filtered to pass a 0.45 μm Millipore filter. Nitrogen and carbon variables were measured by colorimetry from these soil extracts. NH_4^+, NO_3^- and total available N were measured following Delgado-Baquerizo *et al.* (2010). Two labile C forms (hexoses and phenols) were measured according to Chantigny *et al.* (2007). The ratio C-phenols : available N and C-hexoses : available N (hereafter C-phe : N and C-hex : N) were calculated as good indicators of labile C : N ratios (Rovira & Vallejo, 2007).

Statistical analyses

For the whole set of 24 crops at the end of the experiment we evaluated the effects of taxonomic crop identity, domestication status (domesticated vs wild ancestor) and batch (incubation in spring 2011 vs in winter 2011) on the cumulative respiration (our measure of litter decomposability) using a three-way nested ANOVA. Domestication and batch were introduced in the models as fixed-effect factors, while crop identity was nested within batch as a random-effect factor. Batch was included in the design to assess the generality of the domestication effects in both laboratory incubations. Note that batch has only two levels, and is thus more appropriately considered as a fixed factor. Cumulative respiration was log-transformed to meet the assumptions of ANOVA. An additional model was run with the subset of 16 crops, the litter of which was tested in two soils with a contrasted microbial community. This model included soil microbial community (microbial poor vs microbial rich) as an additional fixed-effect factor. The residuals of the above models did not depart from a normal distribution. The average% of increase/decrease in litter decomposability was calculated across species in both soils as a measure of effect size.

The influence of domestication status and crop identity on the litter chemistry traits was evaluated with a two-way nested ANOVA and a variance decomposition analysis. For both analyses, domestication status was introduced in the model as a fixed-effect factor, while crop identity was nested within domestication status a random-effect factor. To assess the change in litter quality during crop evolution we calculated the difference between its domesticated and its wild ancestor average values of each of the 12 litter chemistry traits separately for each crop. A principal components analysis (PCA) was made from this matrix of within-crop differences in litter chemistry. Equamax rotation was employed to minimize overdispersion of variable loadings over several axes and reduce the number of extracted factors. Differences between domesticated and wild ancestor in each crop were also computed for cumulative respiration, and its Pearson correlation coefficients with the two main PCA axes were used to assess the relationship between the overall change in litter chemistry traits accompanying domestication and that of litter decomposability. Nested ANOVA, Variance Decomposition analysis, PCA, and Pearson correlations were carried out using SPSS version 14.0 (SPSS Inc., Chicago, IL, USA).

To assess the extent to which litter quality explained variation in decomposability, we used a distance-based linear model (DISTLM, McArdle & Anderson, 2001). This approach is analogous to a traditional regression, but allows the use of data matrices as either dependent or independent variables. In addition, DISTLM does not make distributional assumptions and is compatible with any distance measure. Our two matrices were litter quality (a predictor matrix containing the difference between domesticated and wild ancestor for each of the 12 litter chemistry variables: C, N, lignin, ash, Ca, P, lignin : N, lignin : P, N : cellulose, N : P, C : N and LCI) and decomposability (a response univariate matrix containing the difference between domesticated and wild ancestor for average cumulative respiration). Before DISTLM analyses, we checked for collinearity between explanatory variables using Pearson correlation coefficients (r). Ash, lignin and N : P were removed from the analyses because their r with C, LCI and lignin : P, respectively, was higher than 0.8 (Anderson *et al.*, 2008). We then ran a different model for the microbial rich and poor soils using the Euclidean distance and 9999 permutations of the raw data. The best-fitting parsimonious models were selected using Akaike's information criterion (AIC) and step-wise selection procedures to determine which litter traits influenced decomposability to a greater extent. The model with the lowest AIC value was selected as the best model in each soil. ΔAIC was calculated as the difference between the AIC of each model and that of the best model Differences < 2.0 in Δ AIC between alternative models indicate that they are approximately equivalent in explanatory power (Burnham & Anderson, 2002).

We evaluated the effects of crop identity, domestication status and soil microbial community on soil data (a matrix with NO_3^-, NH_4^+, C-phe : N and C-hex : N) using a three-way permutational ANCOVA-type test (PERMANOVA; Anderson, 2001). This approach was preferred to a traditional MANCOVA because it does not make distributional assumptions (NH_4^+ and C-hex : N data could not be normalized with any transformation) and is compatible with any distance measure. In addition, it allows

inclusion of multivariate covariables. We used domestication status and soil microbial community as fixed factors and crop identity as a random factor. A matrix with the NO_3^-, NH_4^+, C-phe : N and C-hex : N in the 'no-litter' microcosms of each tray was introduced in the analysis as a covariate to take into account the differences in nutrients between soils and correct for soil contributions to the availability of these nutrients before litter addition. Note that considering control (i.e. that is, 'no-litter') microcosms explicitly to correct nutrient cycling indicators of 'litter + soil' microcosms, analogously to the procedure for litter decomposability, would not be correct. The different soil N forms are highly dynamic and turn too rapidly into each other, precluding using control values as stable denominators in response ratios. Data were standardized to the maximum value because of different units in each variable. We used the Euclidean distance and 9999 permutations of the raw data. Distance-based linear models and PERMANOVA were carried out using the PERMANOVA+ module for the PRIMER software (PRIMER-E Ltd, Plymouth Marine Laboratory, UK). To aid in the interpretation of domestication status effects on the soil nutrient cycling indicators, we also performed a PCA. Spearman correlation coefficients were used to study the relationship between the two main PCA axes and the four indicators of nutrient cycling.

Results

Effects of plant domestication on litter quality

Most of the wide variation in litter chemistries (Table S3) was driven by crop identity instead of by domestication status (68% and 17% of total variance, respectively, averaged across all chemistry traits; Table S4). Thus, as our focal aim was to test for the effects of domestication status *per se*, we excluded the overriding influence of among-crops variability in litter chemistry, calculating within-crop differences (domesticated − wild ancestor) for each trait instead of accession-specific scores. Several of these variables indicated that the domesticated crop had higher litter quality for the decomposition process than its corresponding wild ancestor within each crop: higher C, lignin, lignin : N, lignin : P and N : P, but lower ash content, in the wild ancestor (Fig. 1, Table S5). No clear pattern arose for C : N, N, P, Ca, LCI or N : cellulose. Fig. 2 shows how those within-crop differences arranged in the two main components of an ordination diagram and how these differences linked with the within-crop variation in litter decomposability. PC1 was positively related to cell wall traits such as lignin, lignin : N, lignin : P, LCI, C and C : N, and negatively related to ash and P content. The within-crop differences in litter decomposability in both soils were negatively associated with PC1, indicating faster decomposition in the domesticated accession of crops with low lignin : N ratio but high ash or P contents.

Effects of plant domestication on litter decomposability

Overall, litter decomposability from domesticated accessions was 36% higher than that of their wild counterparts (Fig. 3a, $F = 22.45$, $P < 0.001$; see Table S6 for statistical analysis). However, six out of 24 crops showed either similar or even higher decomposability in their wild representative. The range of crop species surveyed here differs widely in the intensity of domestication, from recently to anciently domesticated species. We thus regressed time since domestication against the effect size of domestication on litter decomposability, but found that both

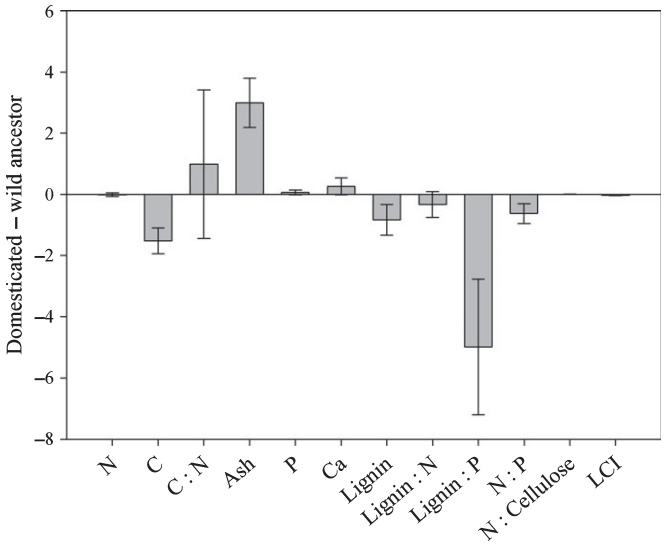

Fig. 1 Within-crop differences (domesticated−wild ancestor) for the average of the 24 crops in the 12 litter chemistry traits measured. Data are means across species ± 1 SE ($n = 24$). LCI, lignocellulose index.

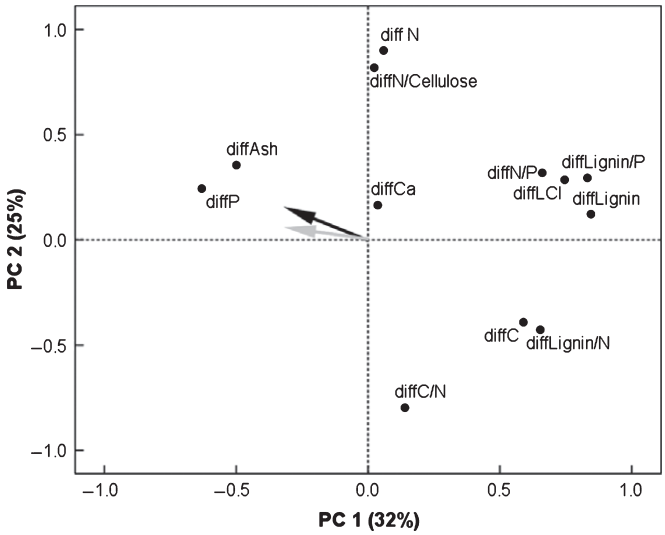

Fig. 2 Principal component analysis of within-crop differences (domesticated−wild ancestor) in litter chemistry traits. Differences within crops, rather than accession-specific means, were used to exclude the overriding effect of crop identities on building the ordination scheme (see the Supporting Information, Table S4), and thus highlight the pure effect of domestication, if any. Black and grey arrows depict the loads of Pearson correlation between within-crop differences in cumulative respiration and the PC1 ($r = -0.31$, $P = 0.141$; and $r = -0.30$, $P = 0.262$; for microbial-rich and microbial-poor soils, respectively) and PC2 ($r = 0.13$, $P = 0.540$; and $r = 0.05$, $P = 0.862$; for microbial-rich and microbial-poor soils, respectively) components. LCI, lignocellulose index.

variables were unrelated (Fig. S2). Domestication significantly increased litter decomposability by an average of 44% when the subset of 16 crops was tested in the microbial-poor soil (Fig. 3b, $F = 31.89$, $P < 0.001$; see Table S6 for statistical analysis). Twelve out of 16 domesticated crops also demonstrated higher average decomposability than their wild ancestors. Interestingly, the effect of domestication on litter decomposability was statistically similar in the microbial-rich and in the microbial-poor soil (Fig. 4, $F = 0.07$, $P = 0.801$ for the interaction term).

Plant domestication effects on litter decomposability are modulated by litter quality

When within-crop differences between domesticated and wild ancestor in all litter chemistry traits were considered together as predictors of differences in decomposability, litter quality explained 53% and 15% of the variance in the microbial-rich and microbial-poor soils, respectively (Table 2). The lignin : N ratio was identified as the best predictor of the within-crop differences in litter decomposability in the microbial-poor soil and represented the 36% of the variation explained by litter quality in the microbial-rich soil. To investigate the direction of this effect, we ran correlations between the differences (domesticated wild ancestor) in lignin : N ratio and the differences in litter decomposability, which showed a negative relation in both soils ($r = -0.44$, $P = 0.031$ and $r = -0.39$, $P = 0.132$ in the microbial rich and poor soils, respectively; Fig. S3). Overall, these results indicate that plant domestication effects on litter decomposability are partly governed by changes in litter quality between domesticated and wild ancestors, and point to the lignin : N ratio being the most important trait determining this relation.

Effects of plant domestication on soil nitrogen and carbon dynamics

Domestication status was a significant predictor of the variation in the overall data matrix containing soil nitrogen and carbon cycling indicators ($F = 4.82$, $P = 0.046$; Table S7). Domesticated

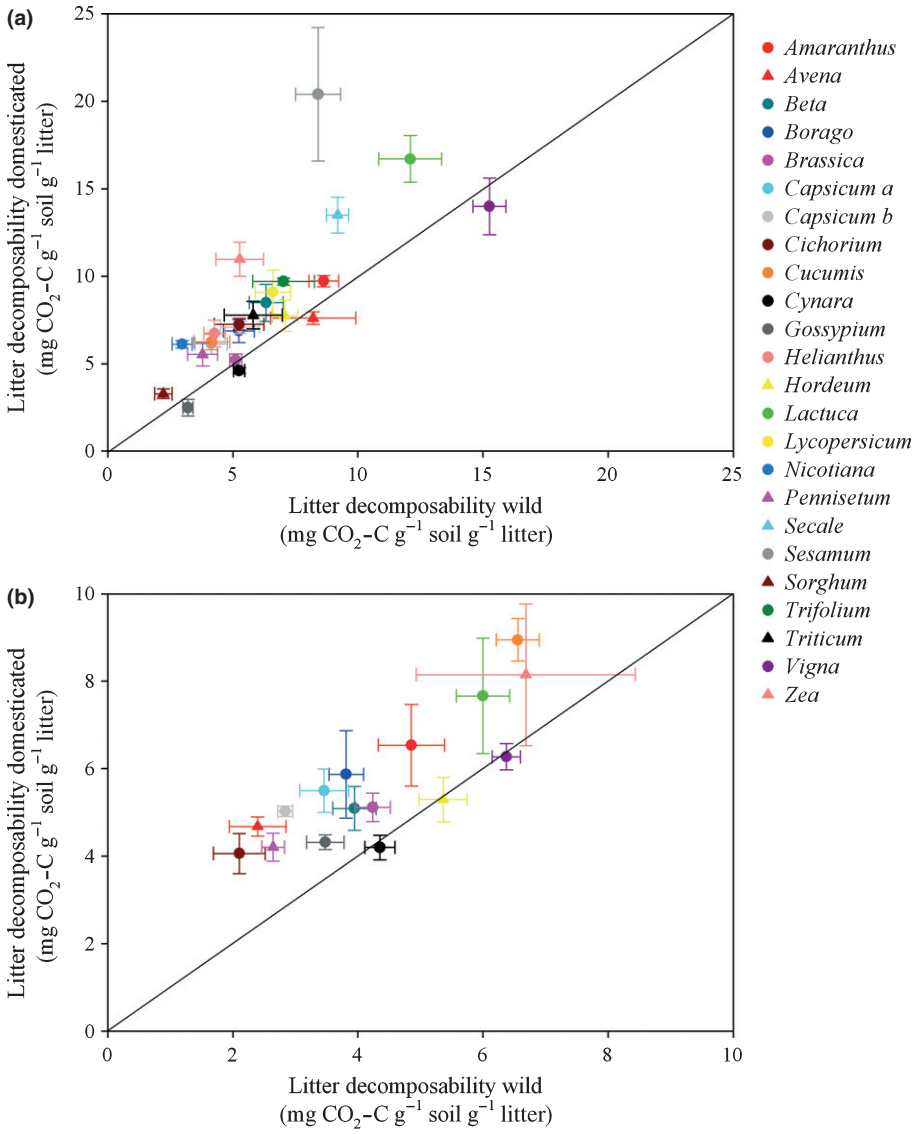

Fig. 3 Bisector plot representing the litter decomposability (measured as cumulative respiration) of domesticated vs wild ancestors microcosms at the end of the experiment. (a) Whole set of 24 crops in which litter decomposability was tested in the microbial-rich soil. (b) Subset of 16 crops in which litter decomposability was tested in the microbial-poor soil. Crops above line 1 : 1 showed higher decomposability in the domesticated than in the wild ancestor microcosms, and vice versa for crops below 1 : 1. *Capsicum a*, *Capsicum annuum*; *Capsicum b*, *Capsicum baccatum*. Circles, eudicot crops; triangles, monocots. Data are means ± 1 SE ($n = 5$). See the Supporting Information, Table S6, for nested ANOVA results.

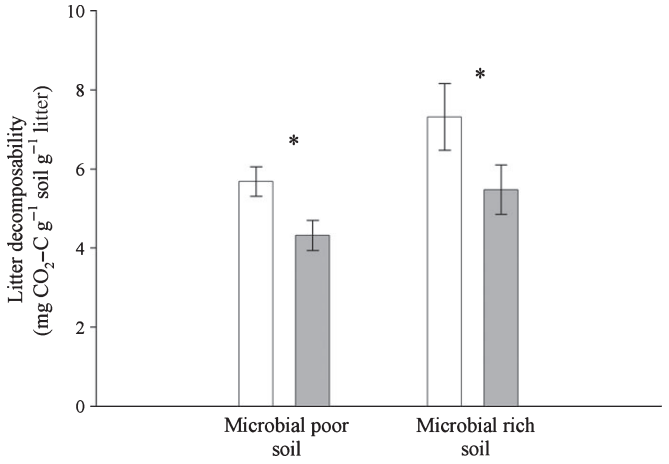

Fig. 4 Litter decomposability of domesticated (open bars) vs wild ancestors (closed bars) microcosms in both microbial-poor and microbial-rich soils at the end of the experiment. Crop identity was collapsed to highlight the generality of the domestication status effect (*, $P < 0.05$) in both microbial-poor and microbial-rich soils. Data are means ± 1 SE ($n = 5$). See the Supporting Information, Table S6, for nested ANOVA results.

microcosms contained higher NO_3^- and lower C-hex : N and C-phe : N than wild ancestors' microcosms after the incubation period (Fig. 5). Regardless of the microbial community evaluated, the effect of domestication status was similar in both the microbial-rich and microbial-poor soils ($F = 0.20$, $P = 0.866$ of the interaction term). Although a significant domestication status × crop identity × soil microbial community interaction was found ($F = 3.10$, $P < 0.001$), most of the crops evaluated in both soils showed higher scores for PC1 in their domesticated than in their wild ancestor accession (Fig. S4). Nevertheless, these differences were more apparent in the microbial rich soil. PC1 was highly and positively related to NO_3^-, and negatively related to C-hex : N and C-phe : N, thus matching with the results shown in Fig. 5.

Discussion

To our knowledge, this study represents the first comprehensive assessment on the after-effects of crop domestication and further breeding on key ecosystem processes. Plant domestication has generally increased litter decomposition rates (36% and 44% increase in the microbial rich and poor soils, respectively), speeding up the entry of nutrients in the soil, increasing NO_3^- availability and decreasing soil labile C : N ratios. This was true for the majority of the crops surveyed here (Figs 3, 5), irrespective of the antiquity of their domestication (Fig. S2), and was partly explained by contrasting litter qualities of domesticated vs wild accessions of each crop. Together, the set of crops of this study included nine out of 19 major crops for food security identified by the United Nations Consultative Group on International Agricultural Research (Hajjar & Hodgkin, 2006), and takes in a diversity of phylogenetic origins, domestication processes, geographies and intensities (e.g. from anciently domesticated Poaceae such as barley (*Hordeum vulgare)*, to incipient Boraginaceae crops such as borage (*Borago officinalis*)). Therefore, our pattern appears general enough to assert that it exists for a fair percentage of domesticated herbaceous species, and may affect most herbaceous croplands where incorporating litter inputs is a management option.

The quality profile of our leaf litters was labile (low lignin and high N content, regardless of domestication) when brought into the context of global variation in litter chemistries (Table S3, Zhang *et al.*, 2008). This resulted in fast decomposition that was readily detectable in our short-term laboratory incubation set up, and in immediate measurable impacts on soil N and C cycling. This scenario is in line with our initial expectations and with ecological theory. Our herbaceous crop species and most of their recognized ancestors lie on the fast-growing, nutrient-acquiring, side of the worldwide spectrum of variation in plant resource use strategies (Craine, 2009). Plant species from that side of the spectrum tend to conserve acquired resources poorly and shed nutrient-rich litter that decomposes fast and quickly returns fertility to the soil system (Aerts & Chapin, 2000). This might have contributed to a beneficial package of predomestication traits that made some wild species more successful candidates for domestication than others (Hancock, 2004; Veneklaas *et al.*, 2012).

Plant domestication effects on litter decomposability were mediated by changes in litter quality, with the lignin : N ratio being the main trait driving this relationship (Fig. 2, Table 2). Litter lignin : N ratios are negatively correlated to litter decay rates across a diversity of ecosystems (Hobbie, 2008; Zhang *et al.*, 2008). The high average N content of our leaf litters suggest that N might not be variable enough in our system to control decay

Table 2 Results of the best-fitting models of within-crop differences in litter decomposability in the microbial-rich and microbial-poor soils

Microbial community	Diff Lignin : N	Diff C : N	Diff LCI	Diff N	R^2	AIC	ΔAIC
Microbial rich (24 crops)					**0.53**	38.51	0.00
					0.46	39.88	1.37
					0.29	44.37	5.86
					0.19	45.28	6.77
Microbial rich (16 crops)					**0.15**	−4.47	0.00

Each column represents a different predictor variable (within-crop differences, domesticated − wild ancestor, in the litter chemistry traits). Statistics of distance-based linear models are shown. The models are ranked according to AIC (Akaike Information Criterion). ΔAIC is the difference between the AIC of each model and that of the best model. Unshaded cells indicate variables that were not included in a particular model. Total variance explained by the best model is shown in bold type. LCI, lignocellulose index.

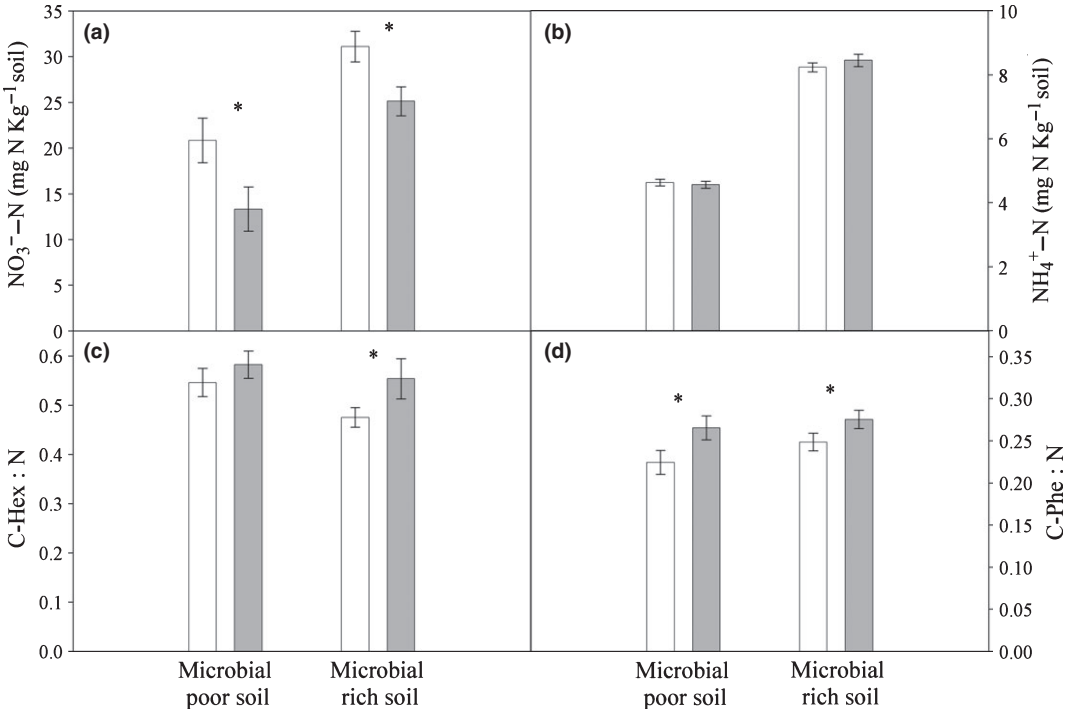

Fig. 5 Soil NO_3^- (a), NH_4^+ (b), C-hex : N (c) and C-phe : N (d) of domesticated (open bars) vs wild ancestor (closed bars) microcosms in both microbial-poor and microbial-rich soils at the end of the experiment. Crop identity was collapsed to highlight the generality of the domestication status effect (*, $P < 0.05$) in both microbial poor and rich soils. Data are means ± 1 SE ($n = 40$). See the Supporting Information, Table S7, for permutational ANCOVA results.

rates by alleviating any N-limitation of litter C degradation (Berg & Staaf, 1980). This is supported by the results of the models in both the microbial-rich and microbial-poor soils (Table 2). Thus, lignin content, and its relation with other cell wall components evaluated with the LCI index, may be the major drivers of decomposition in our study system. Lignin obstructs decomposition because it surrounds cellulose and hemicellulose in plant cell walls (Berg & McClaugherty, 2003), which hinders microbial degradation of these labile litter components (Talbot & Treseder, 2012).

In addition to litter quality, the ability to degrade litter by different communities of decomposers is fundamental to explain variation in decomposition rates (Strickland *et al.*, 2009; Talbot & Treseder, 2012). In this study, the microbial-rich soil decomposed litter faster than the microbial-poor one. However, even though both microbial communities were structurally and functionally contrasted, both decomposed the domesticated litter faster than the wild litter. Thus, the effect of domestication should be common to intensively managed agricultural lands with bacterial-dominated food webs similar to our microbial poor soil or to extensively managed farming systems with fungal-dominated food webs, similar to our microbial rich soil (Bardgett, 2005; De Vries *et al.*, 2012). After decomposition, the next event in the processing of litter is the incorporation of its residues into the soil. Interestingly, we detected higher NO_3^- and lower labile C : N ratios in the domesticated microcosms for both the microbial-rich and microbial-poor soils. These results are in line with the effects that domestication has exerted over litter decomposition. Increased litter quality from domesticated crops thus promotes a significant enhancement of nitrate in the soil and decreases the soil labile C : N ratios, which in turn may promote faster mineralization and nitrate accumulation in agricultural soils (Drinkwater & Snapp, 2007; Robertson & Groffman, 2007).

The consequences of these unintended effects of artificial selection should be useful for the management of agro-ecosystems. The fast decomposition and N release from our domesticated crop litters support the use of plant residues to improve soil fertility in high N-demanding agro-ecosystems. Now, when it is unclear whether high-input agriculture can be economically and ecologically sustained (Hoang & Alauddin, 2010), the use of crop residues is a tenable management option to guarantee the long-term sustainability of agro-ecosystems (Godfray *et al.*, 2010) and minimize the global environmental impacts of high N-fertilization rates (Grandy *et al.*, 2012). In addition, when compared with the typical < 50% N plant use from inorganic fertilizers (Galloway & Cowling, 2002), the more gradual N release from plant residues could stimulate tighter internal N cycling and higher synchrony between soil N availability and plant N demand (Tilman, 1998). However, the implications of our results for the management of agro-ecosystems will be especially significant for those crops where the litter residue left after harvest makes a real contribution to soil fertility (e.g. *Lycopersicon esculentum, B. officinalis, Helianthus annuus*). Even though in some of our crops the residue left after harvesting is not senesced (e.g. *Trifolium repens*) or is only constituted by stems (e.g. *Beta vulgaris var. cycla*), the previous implications for agro-ecosystems may still apply, as interspecific variation in green leaf and leaf litter traits (Aerts, 1996; Quested *et al.*, 2003), as well as in stem and leaf decomposability (Freschet *et al.*, 2012), tend to scale

positively across species. Moreover, similar to our leaf litters here, root residues remain in most agro-systems and root decomposition is most frequently governed by the lignin content of the substrate (Silver & Miya, 2001). Further research is needed to address whether the effects of plant domestication on stems and roots differ from those on leaf litter. Exploring other indirect consequences of domestication and breeding over functioning of agro-ecosystems may help to galvanize efforts aimed to increase plant yield and to promote the long-term sustainability of agro-ecosystems in a context of increasing global human population.

Conclusion

Natural selection has generally favored the evolution of fast-growing plant species in high-resource ecosystems. These species display traits that promote fast litter decomposition and nutrient cycling processes compared with those from resource-poor ecosystems (Cornwell *et al.*, 2008; Craine, 2009; Freschet *et al.*, 2012). Our results show that inadvertent changes in plant traits during domestication have promoted higher litter quality, faster litter decomposition and higher soil NO_3^- availability, and demonstrate for the first time that centuries-long artificial selection has encouraged similar changes in agro-ecosystems. This constitutes a remarkable parallelism between ecosystem-level effects exerted by the evolutionary products of both natural and artificial selection. These experimental results are highly relevant for future plant breeding programs where the effects of domestication over agro-ecosystems processes should be taken into account.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Map showing the location of the seed origin of the 24 wild ancestor accessions.

Fig. S2 Scatter plot of the estimated antiquity of each crop's domestication (time since domestication) of each crop vs the change in decomposability accompanying this process (decomposability of each crop litter minus that of its wild counterpart, $LD_C - LD_W$).

Fig. S3 Pearson correlation between the within-crop differences (domesticated − wild ancestor) in the lignin : N ratio and the differences in litter decomposability (LD) in the microbial rich (a) and microbial poor (b) soils.

Fig. S4 Results of the principal coordinates analysis, showing the effects of domestication status (D, domesticated-circles; W, wild ancestor-triangles), crop identity and soil microbial community (a, microbial rich; b, microbial poor) on the soil nutrient cycling indicators.

Table S1 Origin information of each accession of the 24 domesticated–wild ancestor pairs used and reference sources for wild ancestor assignment

Table S2 Field location and characteristics of the two soils employed for litter incubation assays

Table S3 Mean cumulative respiration (proxy for litter decomposability) and litter chemistry traits of domesticated (D) and wild ancestors (W) microcosms in both the microbial rich (MR) and microbial poor (MP) soils at the end of the experiment

Table S4 Variance decomposition analysis of the several litter chemical traits

Table S5 Within-crop differences (domesticated−wild ancestor) for the average of the 24 crops in the 12 litter chemistry traits measured

Table S6 Summary of three-way (whole set of 24 crops) and four-way (subset of 16 crops) nested ANOVAS for main treatment effects and interactions on the cumulative respiration (proxy for litter decomposability) at the end of the experiment

Table S7 Summary of three-way permutational ANCOVA-type test for main treatment effects and interactions on a matrix containing soil NO_3^-, NH_4^+, C-hex : N and C-phe : N at the end of experiment

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Supporting Information Tables S1–S7, Figs S1–S4

Table S1 Origin information of each accession of the 24 domesticated-wild ancestor pairs used and reference sources for wild ancestor assignment. Domestication status (D: domesticated; W: wild ancestor). Seed donor (IPK: Germplasm bank of the Leibniz Institute of Plant Genetics and Crop Plant Research, Germany; NPGS: National Plant Germplasm System-USDA, U.S.A.; CRF: Centro Nacional de Recursos Fitogenéticos-INIA, Spain; ICARDA: International Center for Agricultural Research in Dry Areas, Syria; * commercial company; CITA: Centro de Investigación y Transferencia Agroalimentaria de Aragón, Spain; CGN: Center for Genetic Resources, The Netherlands; UPV: Seedbank of the Polythecnic University of Valencia, Spain; CIRAD: Centre de Coopération Internationale en Recherche Agronomique pour le Devélopemment, France). Accession identifier refers to the code assigned by each seed donor excepting the commercial companies. N.A. (not available). Accesion country refers to the country where the seeds were collected. Ref: reference source for wild ancestor assignment. N.A.: data not available.

Species	Dom. status	Common name	Seed donor	Accesion Identifier	Country accession	Ref.
Amaranthus cruentus	D	Red amaranth	IPK	AMA169	Nepal	9
Amaranthus hybridus	W	Red amaranth	NPGS	PI632247	USA	9
Avena sativa	D	Oat	CRF	BGE024681	Spain	4
Avena sterilis	W	Oat	ICARDA	IG100379IFMI3096	Turkey	4
Beta vulgaris var. cycla	D	Chard	Clause	N.A.	commercial	4
Beta vulgaris ssp. maritima	W	Chard	IPK	1582	Italy	4
Borago officinalis	D	Borage	CITA	BGE021299	Spain	8
Borago officinalis	W	Borage	CITA	BGE039567	Spain	8
Brassica oleracea var. acephala	D	Cabbage	Rocalba	N.A.	commercial	9
Brassica oleracea	W	Cabbage	CGN	CGN18947	Germany	9
Capsicum anuum	D	Pepper	Mascarell	N.A.	commercial	9
C. anuum ssp. glabriusculum	W	Pepper	NPGS	PI631137	Guatemala	9
Capsicum bacattum var. pendulum	D	Chili pepper	CGN	CGN23297	Peru	9
C. bacattum ssp. bacattum	W	Chili pepper	CGN	CGN23278	Argentina	9

Cichorium endivia	D	Chicory	UPV	BGV009991	commercial	5
Cichorium intybus	W	Chicory	CRF	BGE032596	Spain	5
Cucumis sativus	D	Cucumber	CGN	CGN19820	India	9
C. sativus ssp. hardwickii	W	Cucumber	CGN	CGN24495	India	9
Cynara cardunculus	D	Artichoke	Rocalba	N.A.	commercial	10
C. cardunculus ssp. sylvestris	W	Artichoke	S. Silvestres	N.A.	Spain	10
Gossypium hirsutum	D	Cotton	CRF	BGE006434	USA	9
Gossypium hirsutum	W	Cotton	CIRAD	BG 6050	France	9
Helianthus annuus	D	Sunflower	IPK	HEL 226	USA	9
Helianthus annuus	W	Sunflower	NPGS	PI413093	USA	9
Hordeum vulgare	W	Barley	CRF	BGE025385	Morocco	9
Hordeum spontaneum	D	Barley	CRF	BGE000214	commercial	9
Lactuca sativa	D	Lettuce	Clause	N.A.	commercial	1
Lactuca serriola	W	Lettuce	CRF	BGE034705	Spain	1
Lycopersicon esculentum	D	Tomato	Clause	N.A.	commercial	9
Lycopersicon pimpinellifolium	W	Tomato	NPGS	LA1383	Peru	9
Nicotiana tabacum	W	Tobacco	IPK	Palma3	N.A.	7
Nicotiana sylvestris	D	Tobacco	La Palma	N.A.	commercial	7
Pennisetum glaucum	D	Millet	NPGS	PI586660	B. Faso	6
Pennisetum glaucum	W	Millet	NPGS	PI537068	Niger	6
Secale cereale	W	Rye	NPGS	PI618666	Turkey	9
Secale ancestrale	D	Rye	CRF	BGE010915	commercial	9
Sesamum indicum	D	Sesame	Rocalba	N.A.	commercial	3
Sesamum indicum	W	Sesame	IPK	18	Yemem	3
Sorghum sudanense	W	Sorghum	NPGS	PI524718	Sudan	9
Sorghum bicolor	D	Sorghum	Rocalba	N.A.	commercial	9
Trifolium repens	D	White clover	Intersemillas	N.A.	commercial	2
Trifolium repens	W	White clover	CGN	CGN22513	Kyrgystan	2
Triticum durum	W	Wheat	NPGS	352322	Lebanon	9
Triticum dicoccoides	D	Wheat	CRF	BGE020911	commercial	9
Vigna unguiculata	D	Cowpea	NPGS	PI548784	commercial	11
V. unguiculata ssp. unguiculata	W	Cowpea	NPGS	PI447516	Nigeria	11
Zea mays ssp. mays	D	Corn	NPGS	AMES26252	Brazil	12
Z. mays ssp. mexicana	W	Corn	NPGS	PI566682	Mexico	12

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Table S2 Field location and characteristics of the two soils employed for litter incubation assays. Data are means ± 1 SE (n = 5).

	Microbial poor	Microbial rich
Coordinates (U.T.M.)	30S 0482078 / 4405352 N	30T 0424133 / 4469923 N
Successional stage	Early (3-4 yrs.)	Late (> 20 yrs.)
pH	8.31 ± 0.29	7.15 ± 0.17
Organic C (mg C g soil^{-1})	7.66 ± 0.67	23.02 ± 1.28
NO_3^- - N (mg N Kg soil^{-1})	7.32 ± 0.98	13.80 ± 0.09
NH_4^+ - N (mg N Kg soil^{-1})	10.85 ± 0.35	5.34 ± 0.10
C-Hex:N	0.54 ± 0.10	0.45 ± 0.06
C-Phe:N	0.18 ± 0.03	0.20 ± 0.01
Microbial functional diversity[1]	1.881 ± 0.51	2.627 ± 0.84
Bacteria (DNA copies g^{-1} soil)[2]	$1.36\ 10^8 \pm 8.52\ 10^7$	$3.56\ 10^9 \pm 1.31\ 10^9$
Fungi (DNA copies g^{-1} soil)[2]	$9.24\ 10^6 \pm 3.71\ 10^6$	$9.27\ 10^8 \pm 4.40\ 10^8$
Relative fungal:bacterial ratio	0.07 ± 0.01	0.26 ± 0.02

[1]The functional diversity of the soil microbial communities was quantified using a carbon substrate diversity index or modified Shannon index from the data gathered in García-Palacios *et al.* (2011) with the MicroResp system: $H' = - \Sigma [p\text{i} \ln (p\text{i})]$, where: pi is the ratio of the CO_2 rate for a carbon source to the sum of CO_2 rates for all substrates.
[2]The relative abundance of bacterial 16S and fungal 18s rRNA genes were measured using quantitative PCR (García-Palacios, unpublished data). The bacterial and fungi genes were amplified with the Eub 338-Eub 518 and ITS 1-5.8S primer sets, respectively following Fierer *et al.* (2005).

References Table S2

Fierer N, Jackson JA, Vilgalys R, Jackson RB. 2005. Assessment of soil microbial community structure by use of taxon-specific quantitative PCR assays. *Applied and Environmental Microbiol*ogy **71:** 4117–4120.

García-Palacios P, Bowker MA, Maestre FT, Soliveres S, Valladares F, Papadopoulos J, Escudero A. 2011. Ecosystem development in roadside grasslands: biotic control, plant–soil interactions and dispersal limitations. *Ecological Applications* **21:** 2806–2821.

Table S3 Mean cumulative respiration –proxy for litter decomposability– and litter chemistry traits of domesticated (D) and wild ancestors (W) microcosms in both the microbial rich (MR) and microbial poor (MP) soils at the end of the experiment. *mg CO_2–C g^{-1}soil g^{-1}litter. % of dry weight. – missing data imputed using the Iterative Robust Model-based Imputation method of the VIM R package (http://cran.r-project.org/package=VIM)

Species	Dom. status	Cumulative respiration (MR)*	Cumulative respiration (MP)*	N (%)	C (%)	C:N	Ash (%)	P (%)	Ca (%)	Lignin (%)	Lignin:N	Lignin:P	N:P	N:Cel	LCI
Amaranthus cruentus	D	9.71	7.66	1.7	34.11	20.28	29.16	1.15	5.73	2.85	1.7	2.27	1.53	0.26	0.3
Amaranthus hybridus	W	8.63	6	1.31	39.31	29.98	20.63	0.75	4.3	2.23	1.71	2.96	1.75	0.2	0.25
Avena sativa	D	7.6	6.27	1.47	37.66	25.79	23.66	1.2	1.44	2.45	1.67	2.15	1.29	0.07	0.1
Avena sterilis	W	8.21	6.38	1.26	41.22	32.97	15.65	0.86	1.54	1.29	1.05	1.58	1.49	0.05	0.05
Beta vulgaris var. cycla	D	8.48	5.87	0.66	29.1	43.99	37.08	2.23	1.93	1.39	2.07	0.6	0.3	0.07	0.12
Beta vulgaris ssp. maritima	W	6.33	3.81	0.84	32.32	39.59	33.07	1.25	2.15	2.34	3.01	2.58	0.75	0.08	0.18
Borago officinalis	D	6.87		1.47	31.71	21.94	33.89	0.67	4.41	6.09	4.15	9.88	2.38	0.11	0.31
Borago officinalis	W	5.24		0.79	31.6	40.42	36.65	0.99	4.54	6.51	8.32	6.66	0.8	0.06	0.32
Brassica oleracea var. acephala	D	5.21	5.29	0.77	37.22	49.92	25.07	0.93	6.4	2.46	3.49	3.06	0.84	0.06	0.16
Brassica oleracea	W	5.12	5.36	0.85	37.44	38.18	25.37	0.87	6.07	2.42	2.69	2.63	1.04	0.07	0.16
Capsicum anuum	D	7.07	8.94	1.45	37.02	25.71	29.14	0.28	5.46	2.5	1.73	7.53	5.02	0.15	0.21
C. anuum ssp. glabriusculum	W	6.14	5.11	1.33	40.07	30.29	22.24	0.32	4.45	5.25	3.97	17.52	4.42	0.14	0.36
Capsicum bacattum var. pendulum	D	5.28	6.56	1.84	39.99	22.62	21.55	0.46	4.22	4.79	2.74	12.78	4.34	0.22	0.36
C. bacattum ssp. bacattum	W	4.14	4.24	1.43	40.22	28.19	22.17	0.61	5.88	4.35	3.04	8.52	2.73	0.22	0.4
Cichorium endivia	D	7.25		1.05	39.14	37.6	25.84	0.36	4.37	6.48	6.64	18.31	2.99	0.09	0.33
Cichorium intybus	W	5.25		1.51	42.03	27.92	20.9	0.2	4.58	10.29	6.92	63.41	8.39	0.11	0.43
Cucumis sativus	D	6.24	5.49	0.63	29.08	46.23	39.19	0.83	11.33	2.76	4.39	3.33	0.76	0.05	0.19
C. sativus ssp. hardwickii	W	4.16	3.46	0.7	29.99	42.72	–	–	–	1.57	2.24	–	–	0.07	0.13
Cynara cardunculus	D	4.6	4.2	0.63	38.06	61.6	25.65	0.75	3.82	5.63	8.95	7.52	0.84	0.04	0.27

C. cardunculus ssp. sylvestris	W	5.25	4.35	0.66	38.71	58.58	25.3	0.64	3.57	4.85	7.25	7.78	1.07	0.04	0.24
Gossypium hirsutum	D	2.48	4.06	0.95	40.42	39.57	23.16	2.41	6.01	10.16	10.75	5.03	0.47	0.13	0.59
Gossypium hirsutum	W	3.21	2.11	1.02	38.18	37.51	24.45	3.01	6.37	7.31	7.15	2.45	0.34	0.13	0.48
Helianthus annuus	D	6.72	4.68	0.77	37.28	48.52	23.93	0.33	4.73	5.27	6.94	16.47	2.34	0.06	0.28
Helianthus annuus	W	4.27	2.4	0.8	36.63	46.06	27.68	0.25	5.7	6.8	8.56	26.89	3.24	0.08	0.39
Hordeum vulgare	D	7.73		1.34	40.41	30.35	18.83	0.87	1.13	3.6	2.7	4.17	1.55	0.05	0.12
Hordeum spontaneum	W	7.08		1.3	40.93	31.75	17.72	1.06	1.16	2.95	2.31	2.77	1.23	0.05	0.1
Lactuca sativa	D	16.69	8.15	0.94	37.06	39.58	26.95	0.83	2.48	4.17	4.47	5.02	1.14	0.06	0.21
Lactuca serriola	W	12.1	6.69	1.37	40.04	29.36	21.69	0.32	2.16	7.39	5.28	22.55	4.3	0.09	0.33
Lycopersicon esculentum	D	9.09	6.54	2.2	39.33	21.42	20.65	0.63	6.08	5.36	2.96	8.39	3.33	0.19	0.33
Lycopersicon pimpinellifolium	W	6.6	4.86	2.09	40.84	22.09	18.82	0.49	5.57	15.13	7.63	32.42	4.93	0.23	0.61
Nicotiana tabacum	D	6.12	5.02	1.51	33.1	22.04	32.75	0.57	7.15	1.64	1.07	3.06	2.75	0.11	0.11
Nicotiana sylvestris	W	2.98	2.84	0.99	36.28	37.07	26.86	0.44	6.92	5.31	5.33	12.07	2.29	0.06	0.25
Pennisetum glaucum	D	5.53	4.32	0.36	35.76	101.86	23.85	1.11	1.49	1.8	5.19	1.65	0.33	0.01	0.06
Pennisetum glaucum	W	3.8	3.48	0.55	36.55	69.62	22.37	1.85	2.34	1.28	2.44	0.7	0.29	0.02	0.05
Secale cereale	D	13.5		1.71	44.93	26.27	11.1	0.44	0.91	2.59	1.52	5.69	3.78	0.06	0.08
Secale ancestrale	W	9.19		1.8	45.64	25.53	9.6	0.31	0.96	3.09	1.71	11.25	6.52	0.06	0.09
Sesamum indicum	D	20.4		1.48	44.01	30.2	15.09	0.54	4.66	10.8	7.41	20.16	2.74	0.2	0.59
Sesamum indicum	W	8.41		1.26	45.04	35.76	14.4	0.54	4.92	13.02	10.28	24.72	2.38	0.14	0.58
Sorghum sudanense	D	3.28	4.2	0.58	36.69	64.18	24.93	0.27	2.09	2.25	3.95	8.44	2.13	0.02	0.08
Sorghum bicolor	W	2.23	2.64	0.51	36.82	76.26	23.32	0.24	2.08	2.14	4.5	9.24	2.1	0.02	0.08
Trifolium repens	D	9.7		2.83	45.31	16.02	–	–	–	5.66	2	–	–	0.19	–
Trifolium repens	W	7.03		2.81	46.01	16.39	–	–	–	6.54	2.33	–	–	0.13	–
Triticum durum	D	7.77		0.82	33.76	41.63	30.25	0.6	0.87	2.33	2.84	4.14	1.45	0.04	0.1
Triticum dicoccoides	W	5.82		0.64	40.49	63.17	17.91	0.19	0.75	2.45	3.78	12.18	3.4	0.02	0.07
Vigna unguiculata	D	13.99		1.43	38.48	27.1	24.61	0.93	5.16	6.49	4.57	7.07	1.54	0.11	0.34
V. unguiculata ssp. unguiculata	W	15.26		1.85	36.55	20.18	24.89	1.1	5.6	5.74	3.15	5.23	1.68	0.16	0.33
Zea mays ssp. mays	D	10.97	5.09	0.39	37.99	97.84	20.06	0.93	1.43	1.14	2.95	1.25	0.43	0.02	0.04
Z. mays ssp. mexicana	W	5.28	3.94	0.56	41.3	74.33	16.25	0.51	1.9	1.31	2.53	2.64	1.17	0.02	0.04

Table S4 Variance decomposition analysis of the several litter chemical traits. Variance is expressed as a percentage of total variance. Error represents variance within accessions. Average of the total variance explained by each factor in boldface.

% of total Variance	N	C	C:N	Ash	P	Ca	Lignin	Lignin:N	Lignin:P	N:P	N:Cel	LCI	Average
Crop identity	80.76	77.11	72.29	71.20	74.74	95.98	41.89	59.15	37.04	47.01	75.64	78.39	**67.60**
Domestication status (crop identity)	9.15	15.15	15.85	19.53	16.12	0.85	16.21	26.05	28.26	34.35	13.57	11.04	**17.18**
Error	10.08	7.74	11.85	9.27	9.14	3.18	41.89	14.80	34.69	18.64	10.79	10.57	**15.22**

Table S5 Within-crop differences (domesticated – wild ancestor) for the average of the 24 crops in the 12 litter chemistry traits measured.

Average across species is shown in bold. Capsicum a = *Capsicum annuum*, Capsicum b = *Capsicum baccatum*.

Crop identity	N (%)	C (%)	C:N	Ash (%)	P (%)	Ca (%)	Lignin (%)	Lignin:N	Lignin:P	N:P	N:Cel	LCI
Amaranthus	0.39	-5.19	-9.70	8.53	0.40	1.43	0.62	-0.01	-0.70	-0.23	0.07	0.05
Avena	0.21	-3.56	-7.18	8.01	0.34	-0.10	1.16	0.63	0.57	-0.20	0.02	0.05
Beta	-0.18	-3.21	4.41	4.01	0.99	-0.22	-0.95	-0.93	-1.98	-0.45	-0.01	-0.06
Borago	0.68	0.11	-18.48	-2.76	-0.33	-0.13	-0.42	-4.17	3.22	1.58	0.05	-0.01
Brassica	-0.09	-0.22	11.75	-0.29	0.06	0.34	0.03	0.80	0.43	-0.20	-0.01	0.00
Capsicum a	-0.39	-2.97	3.09	7.59	-0.18	1.24	-2.29	-1.01	-5.25	0.68	-0.07	-0.15
Capsicum b	-0.10	-0.15	2.10	0.07	-0.29	-1.43	0.91	0.92	9.00	1.69	-0.08	-0.04
Cichorium	-0.46	-2.89	9.68	4.94	0.16	-0.21	-3.81	-0.27	-45.10	-5.39	-0.03	-0.10
Cucumis	-0.07	-0.91	3.51	2.02	-0.53	6.05	1.19	2.15	2.17	0.24	-0.02	0.06
Cynara	-0.04	-0.65	3.02	0.35	0.11	0.25	0.79	1.70	-0.26	-0.23	0.00	0.03
Gossypium	-0.07	2.24	2.05	-1.28	-0.60	-0.36	2.85	3.60	2.59	0.13	0.00	0.11
Helianthus	-0.02	0.64	2.46	-3.75	0.09	-0.97	-1.52	-1.63	-10.42	-0.90	-0.02	-0.11
Hordeum	0.04	-0.52	-1.41	1.11	-0.19	-0.03	0.64	0.39	1.40	0.32	0.00	0.02
Lactuca	-0.43	-2.98	10.22	5.27	0.51	0.32	-3.22	-0.81	-17.52	-3.16	-0.03	-0.12
Lycopersicon	0.10	-1.51	-0.68	1.83	0.13	0.51	-9.77	-4.67	-24.03	-1.60	-0.04	-0.29
Nicotiana	0.52	-3.18	-15.03	5.88	0.13	0.23	-3.67	-4.27	-9.01	0.46	0.05	-0.14
Pennisetum	-0.19	-0.79	32.25	1.48	-0.74	-0.85	0.52	2.75	0.94	0.04	-0.01	0.01
Secale	-0.09	-0.70	0.74	1.49	0.13	-0.05	-0.50	-0.20	-5.56	-2.74	0.00	-0.01
Sesamum	0.22	-1.03	-5.56	0.69	0.00	-0.26	-2.22	-2.87	-4.56	0.36	0.07	0.01
Sorghum	0.07	-0.13	-12.09	1.60	0.03	0.01	0.11	-0.55	-0.80	0.04	0.00	0.01
Trifolium	0.02	-0.70	-0.37	9.08	0.53	1.23	-0.88	-0.33	-7.12	-2.68	0.06	0.04
Triticum	0.18	-6.73	-21.54	12.33	0.40	0.12	-0.12	-0.94	-8.04	-1.95	0.02	0.02
Vigna	-0.43	1.93	6.92	-0.28	-0.17	-0.44	0.75	1.41	1.84	-0.13	-0.05	0.00
Zea	-0.17	-3.32	23.51	3.81	0.42	-0.47	-0.17	0.41	-1.39	-0.74	0.00	0.00
Average	**-0.01**	**-1.52**	**0.99**	**2.99**	**0.06**	**0.26**	**-0.83**	**-0.33**	**-4.98**	**-0.63**	**0.00**	**-0.03**

Table S6 Summary of three-way (whole set of 24 crops) and four-way (subset of 16 crops) nested ANOVAS for main treatment effects and interactions on the cumulative respiration – proxy for litter decomposability – at the end of the experiment. Cumulative respiration was log-transformed to meet the assumptions of ANOVA. One-two replicates were lost in five of the crops (*Hordeum*, *Cichorium*, *Capsicum baccatum*, *Sesamum* and *Trifolium*) due to disturbances such as microcosms drying up or falling. Values of *P* below 0.05 are shown in boldface.

Whole set of 24 crops Source of variation	df	MS	*F*	*P*
Domestication	1	0.79	22.45	< **0.001**
Batch	1	2.098	8.30	**0.009**
Crop (Batch)	22	0.263	7.30	< **0.001**
Domestication × Batch	1	0.059	1.68	0.208
Domestication × Crop (Batch)	22	0.036	2.62	< **0.001**
Residual	181			

Subset of 16 crops Source of variation	df	MS	*F*	*P*
Domestication	1	1.272	31.89	< **0.001**
Soil microbial community	1	0.522	17.41	**0.001**
Batch	1	0.84	2.36	0.147
Crop (Batch)	14	0.363	8.07	**0.002**
Domestication × Soil microbial community	1	0.001	0.07	0.801
Domestication × Batch	1	0.071	1.80	0.201
Domestication × Crop (Batch)	14	0.04	1.57	0.203
Soil microbial community × Batch	1	0.537	17.91	< **0.001**
Soil microbial community × Crop (Batch)	14	0.03	1.18	0.380
Domestication × Soil microbial community × Batch	1	0.015	0.59	0.455
Domestication × Soil microbial community × Crop (Batch)	14	0.025	1.95	**0.022**
Residual	243			

Table S7 Summary of three-way permutational ANCOVA-type test for main treatment effects and interactions on a matrix containing soil NO_3^-, NH_4^+, C-Hex:N and C-Phe:N at the end of experiment. NO_3^-, NH_4^+, C-Phe:N and C-Hex:N control represent the 'no-litter' microcosms and were introduced in the analysis as covariates. Values of *P* below 0.05 are shown in boldface.

Source of variation	df	MS	*F*	*P*
NO_3^- control	1	1070.50	2.90	**0.045**
NH_4^+ control	1	338.16	0.92	0.408
C-Hex:N control	1	124.34	0.34	0.793
C-Phe:N control	1	140.90	0.38	0.756
Domestication	1	5147.40	4.82	**0.046**
Soil microbial community	1	49465.00	35.07	**<0.001**
Crop	7	5305.60	14.40	**<0.001**
Domestication × Soil microbial community	1	227.77	0.20	0.866
Domestication × Crop	7	1068.90	2.90	**<0.001**
Soil microbial community × Crop	7	1410.30	3.83	**<0.001**
Domestication × Soil microbial community × Crop	7	1141.70	3.10	**<0.001**
Residual	124			

Fig. S1 Map showing the location of the seed origin of the 24 wild ancestor accessions. Each accession is represented by a red point. Only 22 accessions were mapped since two of the Spanish accessions (*Cichorium intybus* and *Lactuca serriola*) share the same coordinates, and the collection site for *Nicotiana sylvestris* could not be tracked.

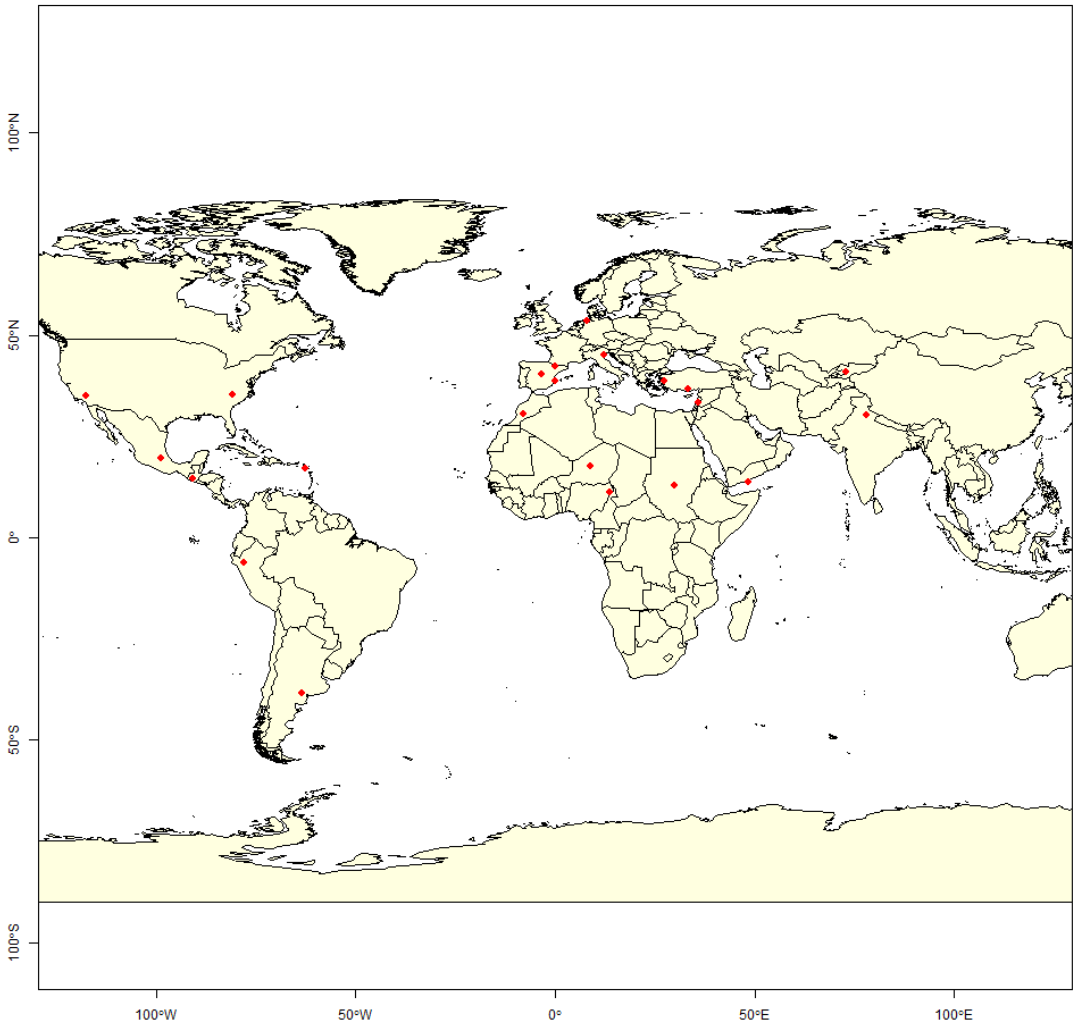

Fig. S2 Scatter plot of the estimated antiquity of each crop´s domestication (time since domestication) of each crop *vs.* the change in decomposability accompanying this

process (decomposability of each crop litter minus that of its wild counterpart, LD_C - LD_W). Subscripts beside each crop are the literature reference (see below) used to retrieve time since domestication data. *Capsicum a* = *Capsicum annuum*, *Capsicum b* = *Capsicum baccatum*. Circles are eudicot crops and triangles monocots. No simple regression model fitted the data.

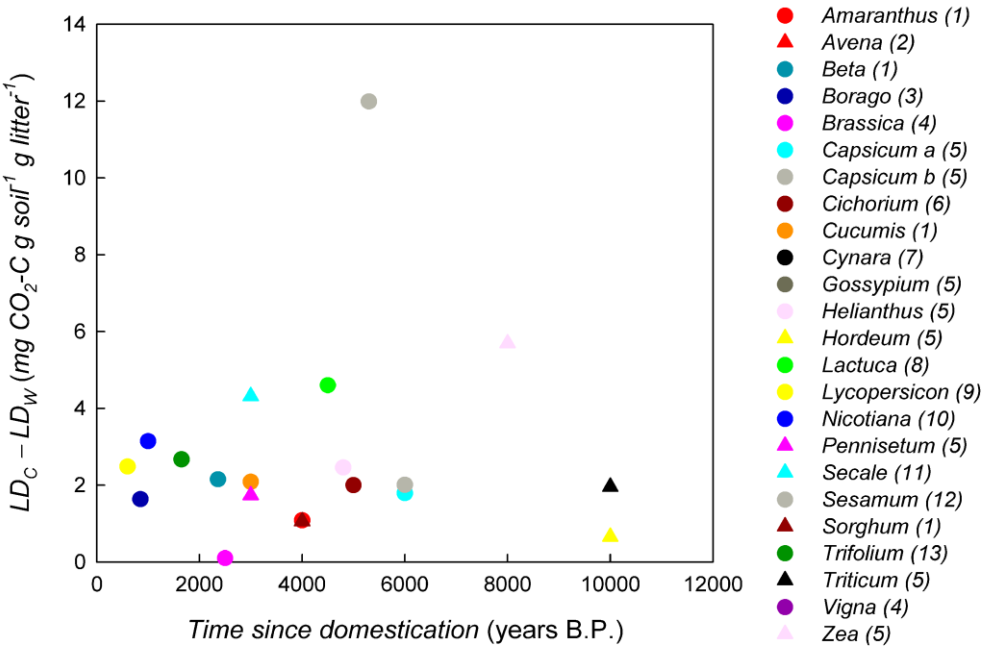

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Fig. S3 Pearson correlation between the within-crop differences (domesticated – wild ancestor) in the lignin:N ratio and the differences in litter decomposability (LD) in the microbial rich (A) and microbial poor (B) soils. *Capsicum a* = *Capsicum annuum*, *Capsicum b* = *Capsicum baccatum*. Circles are eudicot crops and triangles monocots.

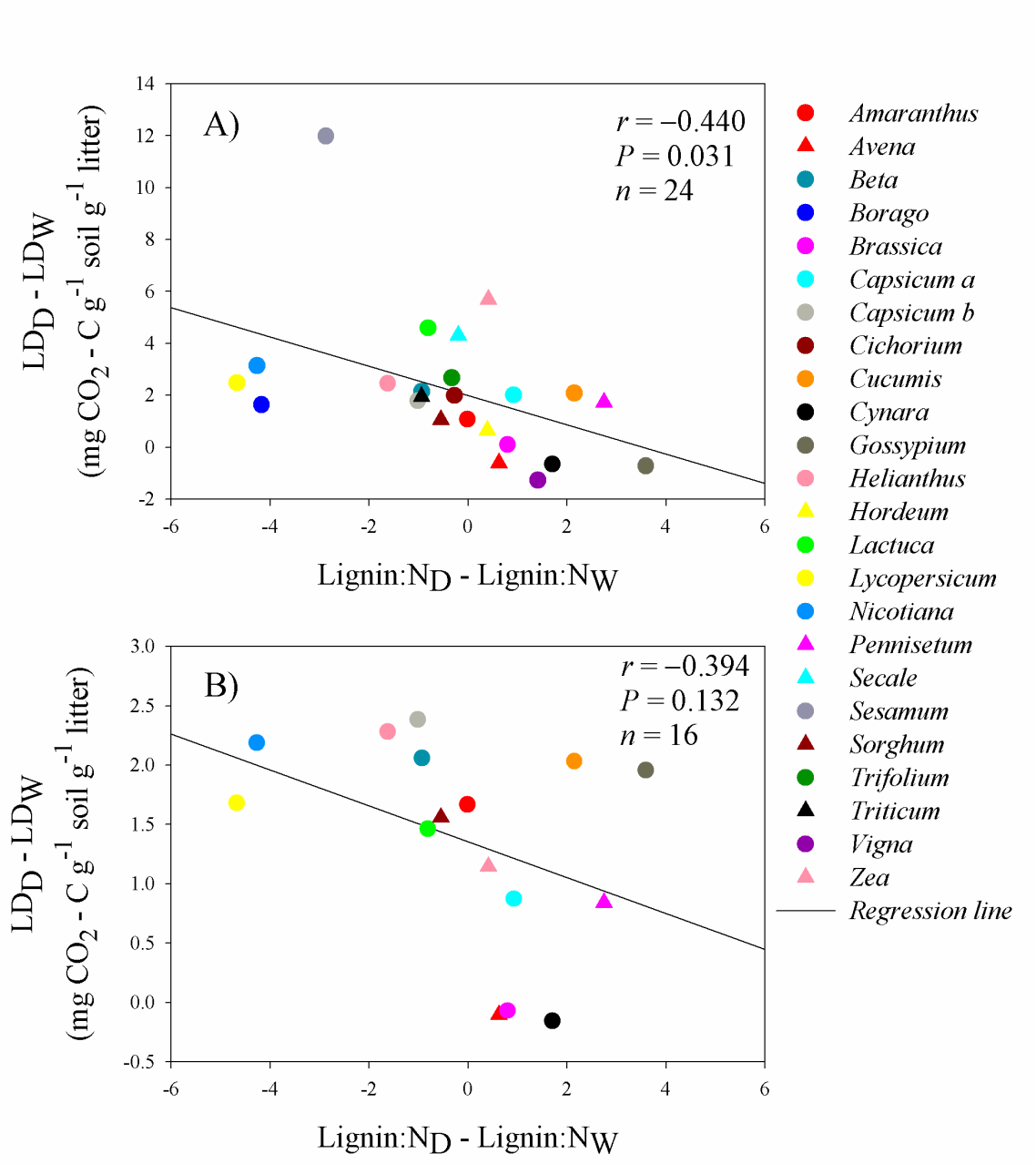
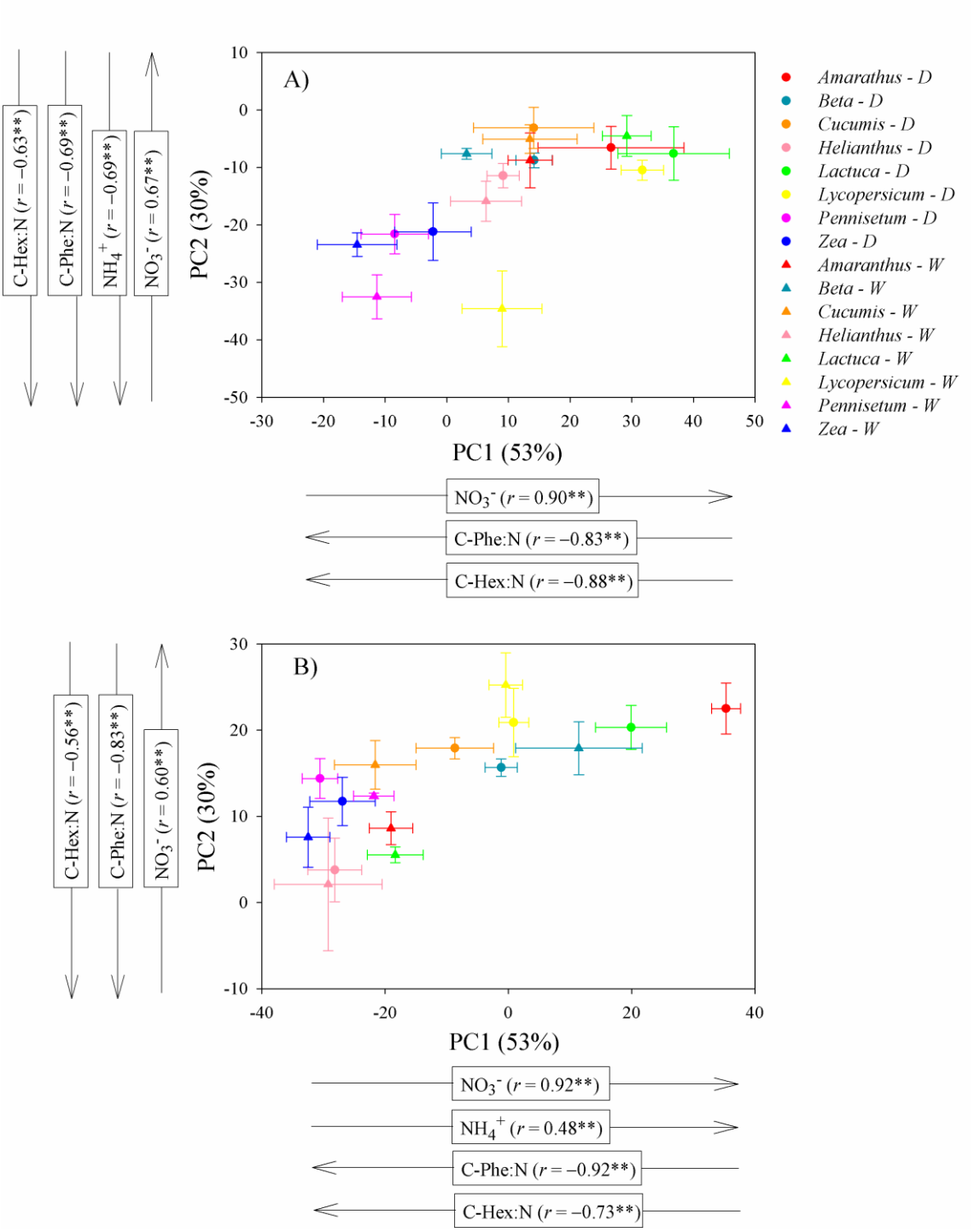


Fig. S4 Results of the principal coordinates analysis, showing the effects of domestication status (D: domesticated-circles and W: wild ancestor-triangles), crop identity and soil microbial community (A: microbial rich and B: microbial poor) on the soil nutrient cycling indicators. Spearman correlations between the original NO_3^-, NH_4^+, C-Hex:N and C-Phe:N and the ordination axes are shown next to them. Values represent means ± SE (n = 5). **P < 0.001.


A)
C-Hex:N (r = –0.63**)
C-Phe:N (r = –0.69**)
NH4+ (r = –0.69**)
NO3- (r = 0.67**)
PC2 (30%)
PC1 (53%)
NO3- (r = 0.90**)
C-Phe:N (r = –0.83**)
C-Hex:N (r = –0.88**)
Amarathus - D
Beta - D
Cucumis - D
Helianthus - D
Lactuca - D
Lycopersicum - D
Pennisetum - D
Zea - D
Amaranthus - W
Beta - W
Cucumis - W
Helianthus - W
Lactuca - W
Lycopersicum - W
Pennisetum - W
Zea - W
B)
C-Hex:N (r = –0.56**)
C-Phe:N (r = –0.83**)
NO3- (r = 0.60**)
PC2 (30%)
PC1 (53%)
NO3- (r = 0.92**)
NH4+ (r = 0.48**)
C-Phe:N (r = –0.92**)
C-Hex:N (r = –0.73**)