Crops and their wild progenitors recruit beneficial and detrimental soil biota in opposing ways

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SUMMARY

- It is widely known that conventional agricultural practices, like tillage or monocropping, promote negative plant soil feedbacks (PSFs). However, the effect of crop domestication on PSF remain less clear. Evolution under cultivation changes crop genotypes, which might alter their interactions with soil organisms, including mutualists and antagonists, and lead to shifts in soil legacies and feedbacks.
- We conducted a two seasons PSF experiment using ten crop species and their wild progenitors. In season one, we grew the wild and domesticated genotypes to train a common soil. In season two, we examined the effects of the soil training on arbuscular mycorrhizal and root-feeding nematodes and plant performance by growing the same genotypes on soils trained in season one.
- Plants showed less mycorrhizal colonization and more nematodes infection in soils trained by domesticated plants. Moreover, domesticated plants were less colonized by mycorrhiza and more by nematodes than their wild progenitor. However, the reaction of plant biomass and PSF indexes to domestication varied among the crops.
- Soil legacies differed between domesticated varieties and their wild progenitors, suggesting an impact of domestication on the recruitment of rhizosphere organisms through an overall negative effect on mycorrhizal mutualism and on plant resistance to herbivores.

KEY WORDS: crop evolution, domestication, mycorrhizal colonization, nematode infection, plant soil feedbacks, root-associated microorganism, wild progenitors.

INTRODUCTION

Plants influence the composition and diversity of soil communities through multiple pathways, including leaf litter inputs and rhizosphere interactions (Klironomos, 2002; Kulmatiski *et al.*, 2008; Van der Heijden *et al.*, 2008; Van der Putten *et al.*, 2013). These plant-mediated changes in belowground organisms can in turn feedback to the plant, altering its performance and productivity. For instance, mycorrhizal fungi typically promote a positive feedback to the plant, while soil pathogens such as root-feeding nematodes may promote negative feedbacks (Van der Heijden *et al.*, 2008). Plant soil feedbacks (PSFs) have attained increasing research attention in the last years, as they are key driving factor of plant species' coexistence and ecosystem functioning in natural ecosystems (Van der Putten *et al.*, 2007), where variation in the strength and direction of PSFs depends on a suite of biotic and abiotic factors (De Long *et al.*, 2019). Conversely, in agricultural systems, farming practices such as high nutrient availability and low plant diversity promote the accumulation of negative feedbacks (Maron *et al.*, 2011; Van der Putten *et al.*, 2013; Zuppinger-Dingley *et al.*, 2014). In this line, negative PSFs have been related with the long-term collapse of intensive crop monocultures (Van der Putten *et al.*, 2013; Mariotte *et al.*, 2018). However, the phenotype of modern crops as compared with their wild progenitors has been conspicuously modified during plant domestication and further breeding (Milla *et al.*, 2014). These domestication-induced changes in crop traits may reduce the crops' ability to recruit beneficial organisms in the rhizosphere (Pérez-Jaramillo *et al.*, 2016). Although the role of farming practices as drivers of PSFs has been extensively studied (refs), the contribution of plant domestication to the accumulation of negative feedbacks in agricultural systems is virtually unknown.

Previous studies have reported differences in the rhizosphere microbial community between domesticated plants and their wild progenitors for a number of crop species, such as wheat, beet, lettuce and bean (Mao *et al.*, 2013; Zachow *et al.*, 2014; Cardinale *et al.*, 2015; Pérez-Jaramillo *et al.*, 2017). These shifts in rhizosphere community composition suggest that crop evolution could alter the outcome of plant soil biota interactions of a wide range of crops. However, whether domestication-mediated differences in rhizosphere microbes have functional consequences in plant-soil feedback is less known. Previous evidence showed that soils trained by domesticated tomatoes promoted more negative PSF than their relatives through shifts in microbial community composition

(Carrillo *et al.*, 2019). Although few case studies have provided useful insights, a broader analysis about the functional consequences of domestication on PSF in crops is missing.

Crop domestication might promote negative PSFs through several mechanisms. First, since crops are selected to improve yield, trade-offs between plant investment in growth vs. defense (Coley *et al.*, 1985; Craine, 2009) has reduced crop resistance to aboveground herbivores in several crops (Chen & Welter, 2007; Turcotte *et al.*, 2015; Whitehead *et al.*, 2016; Simpson *et al.*, 2017). Belowground, under-investment in defense might trigger the proliferation of root-feeding nematodes in the rhizosphere of cultivated plants, which would promote negative feedbacks. Second, crops have evolved under high soil nutrient levels and under human-driven pest control, which might have altered the selective regime of plant defense and root mutualisms. For instance, soil fertilization deter plants from investing in associations with mycorrhizal fungi (Johnson, 1993; Mäder *et al.*, 2000; Nijjer *et al.*, 2010), which reduces the proliferation of these organisms in the soil. In addition, mycorrhizal fungi less mutualistic under fertile conditions (Johnson & Pfleger, 1992; Tawaray, 2003; Johnson, 2010; Remigi *et al.*, 2016), reducing mycorrhizal benefits in domesticated plants under such circumstances (Kiers *et al.*, 2002; Martín-Robles *et al.*, 2018). Finally, plants holding different resource-use strategies promote contrasting PSFs (Baxendale *et al.*, 2014; Kardol *et al.*, 2015; Faucon *et al.*, 2017; De Long *et al.*, 2019), with acquisitive plant species accumulating more negative feedbacks than those in the conservative side of the plant economic spectrum (Lemmermeyer *et al.*, 2015; Laliberté, 2017). Although both modern crops and wild progenitors are resource-acquisitive plants (Milla *et al.*, 2015; Roucou *et al.*, 2018; Martín-Robles *et al.*, 2019), crops show trait values that are even more biased towards this fast-growing strategy (García-Palacios *et al.*, 2013; Milla *et al.*, 2018). Thus, there are several reasons to expect that modern crops promote more negative feedbacks than their wild progenitors.

In this work, we investigated whether crop domestication has modified the strength and direction of PSFs through modifications in the interactions with root-associated mutualists (arbuscular mycorrhizal fungi, AMF) and antagonists (plant parasitic nematodes). To do that, we set up a classic PSF experiment with a taxonomically diverse set of ten herbaceous crops. In a first phase, we grew ten domesticated species and each of their wild progenitors to train a common soil. In a second phase, we examined the effects of the soil training on mycorrhizal and root-feeding nematodes and aboveground

biomass by growing the same plant genotypes on soils previously trained by themselves or by its domesticated or wild progenitor counterpart (Fig. 1). We specifically tested two hypotheses: (i) plants in soils previously trained by the domesticated will have lower mycorrhizal root colonization but higher infection of root-feeding nematodes than their wild progenitor counterpart; and (ii) plant biomass will be reduced in soils previously trained by domesticated plants, and this reduction in plant biomass will be greater in domesticated plants than in wild progenitors.

MATERIALS AND METHODS

Study system and experimental design

We selected ten phylogenetically diverse herbaceous crop species (Table 1) comprising the most relevant families of herbaceous crops for global agriculture (www.fao.org/statistics). The choice of study species was made to include a wide range of variability in the domestication process, such as different target organs of selection (leaves, seeds and fruits) and diverse origins and antiquity of domestication (Table S1, Sauer, 1952; Hancock, 2004). For each crop, we obtained seed lots from two accessions: one belonging to a common domesticated cultivar and another of its recognized wild progenitor. See Table S1 for further information about the criteria for assigning wild progenitors, seed accessions identifiers and seed donors.

We conducted a feedback experiment in the glasshouse consisting of two consecutive phases (*i.e.* Bever 2003; Kulmatiski *et al.*, 2008). In the training phase, we grew plants of the 20 accessions (Table 1) in separate pots filled with the same common soil (Fig. 1). At the end of the training phase we got soil samples of each pot, which are expected to accumulate a genotype-specific suite of soil organisms. The soil organisms' feedback effects on plant biomass of these trainings were tested in a subsequent phase (Fig. 1). In the feedback phase, new plants were grown in sterilized soil inoculated with soil samples of the training phase. We measured the aboveground biomass, and the root colonization by mycorrhizal fungi and root-feeding nematodes in the plants of the feedback phase.

Training phase

The set of wild progenitors and domesticated crops (Table 1) was grown from March to June 2014 in the glasshouse of the Rey Juan Carlos University, located in Móstoles, central Spain (40°18'48"N, 3°52'57"W, 632 m above sea level). Each accession was

replicated three times, resulting in 60 pots (10 crops x 2 domestication status x 3 replicates) set up in a randomized design. We used fresh soil from a nearby roadside grassland characterized by high organic matter content, microbial functional diversity and fungal: bacterial ratio (Table S2, García-Palacios *et al.*, 2013). The soil was collected at 15-30 cm depth, sieved at 2mm to remove coarse root fragments and homogenized before filling the pots for sowing. All seeds were surface-disinfected in 70% ethanol solution for 3 min and pre-germinated on petri dishes on filter paper soaked with sterilized water in dark and cold (4°C) conditions. Pre-germinated seeds were transplanted into pots (6l volume, 20x20x23 cm). Five to 10 seeds were sown per pot, depending on the size of the plants of each species. Pots were watered through automatic water sprinkling to maintain soils near field capacity and rotated every two weeks to control variation in the glasshouse. The mean temperature in the glasshouse varied along the experiment (from 14°C in March to 25°C in June).

We harvested the soils twelve weeks after transplanting, once soils were extensively colonized by roots, which indicates that soil organisms should have interacted extensively with the rooting systems. The soil of each pot was cleaned of visible root fragments, sieved to 2 mm and homogenized. 10 soil samples (200 ml of homogenized soil) were taken per pot. The soil samples were stored for eight months at 4°C until the start of the feedback phase as performed in previous PSFs experiments (refs). In addition, two soil subsamples were collected per pot and frozen at -20°C, to characterize the changes in microbial biomass and organic matter content after the training phase (Methods S1).

Feedback phase

During the feedback phase, the soil samples (= inocula) of the training phase were used to test soil biota feedback effects on aboveground plant biomass. Each accession was grown in sterilized background soil mixed with one of three different soil inocula generated at the training phase: (1) soil inocula trained by the wild progenitor of the crop (hereafter “progenitor soil”), (2) soil inocula trained by the domesticated accession of the crop (hereafter “domesticated soil”) and (3) a sterilized mixture of domesticated and progenitor soil inocula (hereafter “control”) (Fig. 1). This set up was replicated ten times. In total, we used 600 pots (10 crops x 2 domestication statuses x 3 soil trained types x 10 replicates) in the feedback phase.

To prepare the substrate for this phase, we mixed the soil inocula obtained in the training phase with sterilized background soil in a 10 vs 90% proportion, respectively. This approach is commonly used in PSF experiments where the trained soil typically ranges from 1 to 50% of total volume, and the remainder is sterilized soil (Brinkman *et al.*, 2010). The sterilized background soil was prepared by autoclaving a mixture of 75% sand and 25% standard topsoil (topsoil: 93% sand, 5% silt and 1% clay, 0.38% organic matter; pH=8.3). On March 2015, seeds of all accessions were pre-germinated in dark and cold (4°C) conditions. Pre-germinated seeds were individually planted in 2l pots (22x10.5x10.5 cm), placed randomly in the glasshouse. At the beginning of the experiment, all plants were fertilized with 16g of slow release fertilizer (8 g l⁻¹; 16%N, 8%P and 12%K; Basacote Plus 6M, Compo) to prevent nutrient limitation in the sandy substrate. During the growing season, all pots were watered through automatic water sprinkling to maintain soil near field capacity and were randomly rearranged in the glasshouse every two weeks to minimize glasshouse micro-site effects on plant performance. Before flowering, six-seven weeks after sowing, we harvested five to ten randomly-chosen plants per accession and per treatment. We harvested the aboveground biomass of each plant, oven-dried it at 60°C for 72 hours and weighted it (g).

Plant interactions during the feedback phase with root-associated mutualists (AMF) and antagonists (plant parasitic nematodes)

We washed the fresh roots of harvested plants and selected fine root fragments at random (*c.* 80 fresh mg per sample). Root fragments were cleared with 10% KOH at 90°C and transferred to 1% HCl solution to eliminate root pigmentation. After rinsing the root samples in clear water, roots were stained in a staining solution (50% acid lactic, 25% glycerol) with fuchsine 1g l⁻¹ at 90°C and rinsed in a destaining solution identical to the staining solution but without fuchsine (Baker & Gowen, 1996). Clearing, staining and destaining times varied among species to optimise the procedure for the different root types (eg thicker vs thinner or more vs less pigmented roots). Once stained, mycorrhizal colonization and nematode infection rates were measured using the gridline intersect method at x35 magnification (Giovanetti & Mosse, 1980). We quantified AMF colonization (%) and root-feeding nematode infection (%) as the percentage of intercepts of root colonized by hyphae, vesicles and arbuscules, or adults and eggs of nematodes (respectively) from 250 intercepts per sample.

The observed vermiform, migratory root-feeding nematodes were identified as belonging to the genus *Pratylenchus*, which was confirmed by extracting and identifying nematodes from the rhizosphere soil used in the experiment. Although *Pratylenchus* spp. is a polyphagous nematode (Jones & Fosu-Nyarkoref, 2014), host status of all plant species used in this experiment to *Pratylenchus* spp. was checked to discard any effect of plant traits other than those related to domestication. Most of our species were described as susceptible to *Pratylenchus* spp. (Table S1) and several unknown conditions of wild species. Since host status are on occasions based on few nematode species and limited information is available, nematode infection was measured in all wild and domesticated plants. Our results do not show any relation between described host condition and % of nematode infection, and such variable was not considered in the analyses.

Calculation of plant soil feedback index

We calculated a plant soil feedback (PSF) index for each plant to evaluate the effects of soil biota legacies in the training phase on aboveground plant biomass in the feedback phase. PSF index was calculated as $PSF = (M_i - M_{ni}) / M_{ni}$, where M_i is the biomass (log transformed) of species grown in soil that received a biologically active soil inoculum (from domesticated or wild progenitor trained soil) and M_{ni} is the arithmetic mean of biomass (log transformed) of plants that received a sterilized soil inoculum, i.e. control plants (Kardol, 2007; Brinkman *et al.*, 2010). PSF index is positive if biologically active inoculum increases plant biomass, and negative if biomass decreases. This approach provides an estimate of PSFs that it is independent of plant size and that allows comparing the direction and strength of the feedback between species and environments (Brinkman *et al.*, 2010).

Statistical analyses

Prior to data analysis of the feedback phase, we excluded one pot with an extremely high plant biomass value, and 18 control pots that were accidentally contaminated and colonized, even if at low rates, by mycorrhizas or nematodes. These contaminated control plants represented 16% of 110 controls and were randomly distributed across accessions. All subsequent analyses were done with 470 plants and performed with R software v.3.3.0 (R Core Team, 2016).

To assess whether crop domestication and type of soil training have affected the plant ability to interact with beneficial and detrimental root-associated organisms, we used generalized linear mixed-effect models. The differences in mycorrhizal colonization and nematode infection among plants were quantified with binomial error distribution; using the logit link function in the mycorrhizal colonization model and clog-log link function in the case of nematode infection model to deal with numerous zeros (Zuur *et al.* 2009). These models contained mycorrhizal colonization or nematode infection as dependent variables and domestication status (wild progenitor vs domesticated variety), type of soil training (the domestication status that trained the soil in the training phase: “progenitor soil” and “domesticated soil”) and the interaction between them as fixed effects predictors. The model with mycorrhizal colonization as dependent variable included nematode infection as fixed effects and *vice versa*. Both models included crop identity (Table 1) as a random effect over the intercept (random intercept term) and as a random effect over the domestication status parameter (random slope term, analogous to an interaction term in a fixed effects model). In addition, training-pot identity of each soil inoculum in the training phase was included in the random structure of the models. Specifically, training-pot identity was nested in crop identity as a random intercept effect, to account for the variation between training pots within each crop. Generalized linear mixed-effects models were fitted with glmer function of the “lme4” package (Bates *et al.*, 2007).

To assess whether plant biomass and PSF index changed with crop domestication and type of soil training we used mixed effect models. Plant biomass data were log-transformed to meet normality assumptions and homogeneity of variance of the model’s residuals. Both models included domestication status, type of soil training, the interaction between them, mycorrhizal colonization and nematode infection as fixed effects. The random structure was as described previously for mycorrhizal and nematode models. Linear mixed-effect models were fitted with lme function of the “nlme” package (Pinheiro *et al.*, 2015).

In all models, statistical significance of the fixed factors was calculated with type III analysis of variance, obtained with the mixed function of the “afex” package (Singman *et al.* 2015). We estimated the pseudo- R^2 of mixed effects models using the marginal R^2 (R^2_m , variance explained by fixed factors) and conditional R^2 (R^2_c , variance explained

by fixed and random factors) following Johnson (2014), using the `r.squaredGLMM` function of the “MuMIn” package (Barton, 2014). The `r.squaredGLMM` function is not applicable to models with clog-log link function. Therefore, to estimate the marginal R^2_m of the nematodes model we used an equation with the deviance of the model and the null model, but R^2_C was not estimated. Finally, to calculate the significance and least square means of the interaction of domestication and soil training, we conducted post-hoc Tukey pairwise comparisons with the `lsmeans` function of the “lsmeans” package (Lenth, 2016).

RESULTS

Plants modified the soil parameters during the training phase. Overall, the soil training promoted the microbial biomass and reduced the organic matter content (Fig. S1). Although the training effect on soil parameters varied among domestication status and accessions, domesticated plants tended to accumulate more microbial biomass in the soil than wild progenitors (Fig. S2).

Effects of plant domestication and type of soil training on mycorrhizal colonization and nematode infection in the feedback phase

In the feedback phase, domesticated plants were less colonized by arbuscular mycorrhizal fungi (AMF) and showed more root-feeding nematodes than their wild progenitors, irrespective of the type of soil training ($P < 0.0001$, Table 2). In addition, soil training significantly altered mycorrhizal colonization and nematode infection rates ($P < 0.01$ and $P < 0.0001$ respectively, Table 2), and this effect differed between domesticated varieties and wild plants. Wild progenitors were more colonized by AMF when grown in progenitor soils than when grown in domesticated soils, whereas domesticated plants did not show significant differences on mycorrhizal colonization between the types of soil training (domestication status $\times$ type of soil training $P < 0.001$, Table 2, Fig. 2a). The number of nematodes increased in domesticated plants and wild progenitors when grown on domesticated soils; conversely, nematode infection decreased in plants grown in progenitor soils (Fig. 2b). The response pattern to domestication and type of soil training was common to most species in the experiment, although we found substantial variation in overall mycorrhizal colonization and nematode infection rates among the set of species (Fig. 3a-d). Root colonization by AMF ranged between 20-80% depending on crop identity, domestication status and type of soil training (Fig. 3a,b). For instance, maize showed higher mycorrhizal colonization rates (50-80%) than white clover (10-20%; Fig. 3a,b). Similarly, root infection by nematodes was different among crops, domestication statuses and type of soil training, ranging between 0-5% (Fig. 3c,d). For instance, chards were more infected by nematodes than other crops, like leek (Fig. 3c,d). Finally, we did not find significant interactions between mycorrhizal colonization and nematode infection rates (interaction term $P > 0.05$, Table 2).

Effect of plant domestication and type of soil training on plant biomass and plant soil feedback

Aboveground plant biomass in the feedback phase was not affected by domestication status and type of soil training ($P= 0.17$ and $P= 0.8$ respectively, Table 2). Wild progenitors and domesticated plants did not show significant differences in plant biomass (Fig. 2c). Similarly, the plant biomass was not significantly different in domesticated and progenitor soils (Fig. 2c). The biomass of wild progenitors in soils trained by themselves and domesticated plants was not significantly different to sterilized controls (Fig. S3). However, the effect of domestication and type of soil training on plant biomass varied among crops, as informed by the high variance associated with the random term in the plant biomass model (indicated by R^2_m and R^2_c , Table 2). In addition, plant biomass also varied among crops, ranging from 0.5 g, in crops such as leek or white clover, to 5g, in crops such as barley and maize (Fig. 3e,f). Finally, aboveground plant biomass was not affected by either mycorrhizal colonization or nematode infection rates (Table 2, Fig. S4).

Plant soil feedback index, in line with results on plant biomass, was not affected by domestication status and type of soil training ($P= 0.89$ and $P= 0.94$ respectively, Table 2, Fig. 2d). PSF indexes were generally low, ranging from -0.5% to 2% depending on the domestication status, type of soil training and crop identity (Fig. 3g,h). Similarly, the response to type of soil training differed between crops and domestication statuses (Fig. 3g,h). For instance, PSF index increased in response to domesticated soils for crops as amaranth or tomato and decreased in domesticated soils for crops as white clover. Finally, mycorrhizal and nematode infection rates neither influenced the direction or strength of the PSF index scores (Table 2, Fig. S4).

DISCUSSION

Using ten independent domestication events, we investigated the domestication effect on the strength and direction of PSF through modifications in the interactions with root-associated mutualists and antagonists. In support of our first hypothesis, both wild progenitors and domesticated plants showed less AMF and more root-feeding nematodes in soils previously trained by domesticated plants (Fig. 4), indicating that soil biota legacies differed between domestication statuses of the training plants. These results suggest a conspicuous impact of plant domestication on the recruitment of rhizosphere organisms through an overall negative effect on mycorrhizal mutualism and on plant resistance to parasitic root nematodes. We also hypothesized that such shifts in soil biota legacy would trigger negative feedbacks on plant performance. However, plants did not show lower aboveground biomass in domesticated soils, and the response of such biomass to microbial feedbacks was diverse among species.

Domesticated plants of the feedback phase were less colonized by AMF than wild progenitors, suggesting that crop domestication had a negative impact on mycorrhizal symbiosis. A reduction in AMF colonization with domestication has been reported for crops as wheat, breadfruit and sunflower (Hetrick *et al.*, 1993; Xing *et al.*, 2011; Turrini *et al.*, 2016). Plants tend to constrain mycorrhizal colonization under conditions of low dependence on the mycorrhizal symbiosis (Graham *et al.*, 1991). Thereby, the reduction of mycorrhizal colonization might be a consequence of unintended selection for domesticated species less dependent on the mycorrhizal symbiosis (Kiers & Denison, 2014; Pérez-Jaramillo *et al.*, 2016). Likewise, the reduction in mycorrhizal dependence with domestication has been reported for several crops (Baon *et al.*, 1993; Hetrick *et al.*, 1993; Zhu *et al.*, 2001; Tawaraya, 2003; Xing *et al.*, 2011; Turrini *et al.*, 2016), with few exceptions (Lehmann *et al.*, 2012). Less mycorrhizal-dependent plants may be favored in agriculture because fertilization decreases mycorrhizal diversity in soils (Mäder *et al.*, 2000; Oehl *et al.*, 2003; Verbruggen & Kiers, 2010). Moreover, high fertile conditions promote mycorrhizal fungi with less cooperative traits (Kiers & Van der Heijden, 2006; Nijjer *et al.*, 2010; Chagnon *et al.*, 2013), decreasing the benefits of the symbiosis to the plant (Verbruggen & Kiers, 2010; Verbruggen *et al.*, 2015). Also, under fertile conditions plants are less dependent upon the symbiont's contribution to meet nutrient requirements (Johnson, 2010). Mycorrhiza are carbon expensive to the plant (Graham *et al.*, 1991; Johnson, 2010), which under high nutrient availability may invest less in mycorrhiza

symbiosis (Graham & Eissenstat, 1994). Thus, low mycorrhizal abundance and diversity with less mutualistic properties, in combination with less dependence on mycorrhiza for resource acquisition likely reduces the mycorrhizal dependence of domesticated plants. In turn, this can lead to a poor buildup of the AMF inoculum in our soils, reducing AMF root colonization in subsequently grown plants.

Domesticated plants of the feedback phase were also more infected by root feeding nematodes, regardless of the type of soil inoculum received, which suggests that crop domestication has reduced the ability of plants to defend from nematode infection. It is known that evolution under cultivation may decrease the resistance of plants to aboveground herbivores (reviewed in Macfadyen & Bohan, 2010; Whitehead *et al.*, 2016). For instance, domestication decreased resistance to caterpillars in sunflower (Chen & Welter, 2007) and to leafhoppers in maize (Dávila-Flores *et al.*, 2013). However, the consequences of domestication for belowground herbivory have been rarely addressed, especially across multiple crop species. The few studies available to date also suggest that modern cultivars get more infected by root-feeding nematodes than wild progenitors (Rivera *et al.*, 2016), landraces cultivars (Sheedy & Thompson, 2009) or weeds (Roberts *et al.*, 1981; Trudgill & Blok, 2001). The reduction of herbivory resistance with crop domestication might be explained by the resource-availability hypothesis. This hypothesis states that species in resource rich environments invest more in growth than in defense (Coley *et al.*, 1985; Herms & Mattson, 1992; Lemmermeyer *et al.*, 2015). Specifically, domestication may have compromised the defense ability of modern crops in order to increase resources investment in plant growth and yield (Rosenthal & Dirzo, 1997). In this line, previous studies have found trade-offs between resource allocation to mechanical or chemical defense and growth rate in several crop species (Massei & Hartley, 2000; Van der Putten *et al.*, 2006; Kempel *et al.*, 2011; Rodriguez-Saona *et al.*, 2011; Turcotte *et al.*, 2014; Simpson *et al.*, 2017). Thus, breeding for high yield and palatability may have unintended consequences, such as reduced ability to resist root-feeding nematodes, leading to the proliferation of nematodes in the rhizosphere and making soil less suitable for the next crop.

Plants grown in soils trained by domesticated plants were less colonized by mycorrhiza and more infected by nematodes (Fig. 4), indicating that soil microorganism recruited by plants likely differed between domesticates and wild progenitors. Our results, linked with

the fact that mycorrhizal and nematode colonization in the feedback phase differed among domestication statuses, suggest that the rhizosphere of domesticated plants in the training phase promoted less mycorrhizal fungi and more nematodes, which may in turn promote a negative plant-soil feedback upon plant biomass. Previous studies found differences in the training of the rhizosphere microbial communities between domesticated plants and wild progenitors for few crops (Zachow *et al.*, 2014; Bulgarelli *et al.*, 2015; Cardinale *et al.*, 2015; Szoboszlay *et al.*, 2015; Leff *et al.*, 2016; Iannucci *et al.*, 2017; Pérez-Jaramillo *et al.*, 2017). Nevertheless, whether these shifts in rhizosphere microbial communities can affect the outcome of plant soil feedbacks is less studied, with a few exceptions. For instance, Carrillo *et al.* (2019) found that soils trained by domesticated tomatoes promote more negative feedbacks than its wild progenitors, and that was associated with shifts in the microbial biomass. Similarly, Miller & Menalled (2015) found negative feedbacks in plants growing in soils previously trained by crops, in comparison with plants growing in soils trained by wild species. The proliferation of negative feedbacks under domesticated plants might be a consequence of their resource strategy. The development of negative feedbacks is often observed in plants with acquisitive strategies, which are more susceptible to herbivores and pathogens (Baxendale *et al.*, 2014; Cortois *et al.*, 2016; Bardgett, 2017; Laliberté, 2017) and less colonized by AMF (Cortois *et al.* 2016). Recent evidence suggests an evolution of plant's strategies towards acquisitive strategies with crop domestication (Milla *et al.*, 2018; Roucou *et al.*, 2018). Based on acquisitive strategies and associated plant traits, domesticated plants are expected to accumulate more detrimental than beneficial organisms that drive negative feedbacks, whereas the opposite would be expected for their progenitors (Mariotte *et al.*, 2018). However, the marked response in the plant interactions with root-associated mutualists and antagonists found in our study did not feedback to the plant biomass.

In our study soil training did not influence plant growth, even though mycorrhizal colonization and nematode infection varied between soils and domestication statuses. The fact that differential colonization of root mutualists and antagonists did not impact on plant performance could be due to diverse causes. Environmental conditions, such as nutrient availability or competition, play a relevant role in determining the strength and direction of the feedback (Kardol *et al.*, 2013; Bezemer *et al.*, 2018). For instance, fertilization decreased the positive feedbacks of soil biota on eight woody species (Luo *et al.*, 2017). Similarly, mycorrhiza can decrease plant growth under high nutrient

availability, suggesting that the assumption that mycorrhiza provide positive feedbacks does not hold under certain environmental conditions. Thus, the relatively high nutrient levels in our experiment might have suppressed positive mycorrhizal effects on plant growth. Another explanation might relate to the initial density of organisms in the soil in the feedback phase. In our experiment, the soil biota in the feedback phase were provided in a small proportion of the total soil volume, i.e. 10%. Low densities of symbionts and pathogens reduce the strength of feedbacks, particularly in short-term experiments (Brinkman *et al.*, 2010). Moreover, pathogen effects on plant growth are strongly density dependent (Laliberté *et al.*, 2015). Therefore, low density of root-feeding nematodes in the soil at the start of the feedback phase could account for the low infection rates as well as the lack of effects on plant biomass.

CONCLUSION

Plants grown in soils previously trained by domesticated plants showed less mycorrhizal colonization and more nematode infection than when grown in soil from wild progenitors. Moreover, domesticated plants were less colonized by arbuscular mycorrhizal fungi and more infected by root-feeding nematodes than their wild progenitors. Altogether, these results indicate an impact of crop domestication on the recruitment of rhizosphere organisms, probably through an overall reduction association with AMF and plant resistance to herbivores. However, in spite of such legacies, plants grown in soils previously trained by domesticated plants did not show a generalized growth depression in our experiment. This knowledge highlights the importance to undertake plant breeding strategies to optimize the profitable functions of plant-soil interactions for sustainable agriculture.

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AUTHOR CONTRIBUTION

P.G-P, R.M, N.M-R. and G. D. contributed to the design of the study. Field and laboratory work was done by N.M-R., M.R., D.R., R.V., S. S-M. and G. D. Data analyses were performed by N.M-R. N.M-R. led the writing with R.M. and P.G-P. All the authors provided critical reviews of each draft. All authors gave the approval for submission of the final version.

REFERENCES

- Abawi GS, Widmer TL. 2000.** Impact of soil health management practices on soilborne pathogens, nematodes and root diseases of vegetable crops. *Applied Soil Ecology* **15**: 37–47.
- Baker TJ, Gowen SR. 1996.** Staining nematodes and arbuscular mycorrhizae in the same root sample. *Fundamental and Applied Nematology*.
- Baon JB, Smith SE, Alston AM. 1993.** Mycorrhizal responses of barley cultivars differing in P efficiency. *Plant and Soil* **157**: 97–105.
- Bardgett RD. 2017.** Plant trait-based approaches for interrogating belowground function. *Biology and Environment* **117B**: 1–13.
- Barton K. 2013.** MuMIn: Multi-model inference. R package version 1.9. 13. *The Comprehensive R Archive Network (CRAN)*, Vienna, Austria.
- Bates D, Sarkar D, Bates MD, Matrix L. 2007.** The lme4 package. *R package version* 2, 74.
- Baxendale C, Orwin KH, Poly F, Pommier T, Bardgett RD. 2014.** Are plant-soil feedback responses explained by plant traits? *Journal of Physiology* **204**: 408–423.
- Bell T, Tylianakis JM. 2016.** Microbes in the Anthropocene: spillover of agriculturally selected bacteria and their impact on natural ecosystems. *Proceedings of the Royal Society B: Biological Sciences* **283**: 20160896.
- Bever JD. 2003.** Soil community feedback and the coexistence of competitors: Conceptual frameworks and empirical tests. *New Phytologist* **157**: 465–473.
- Bezemer TM, Jing J, Bakx-Schotman JMT, Bijleveld EJ. 2018.** Plant competition alters the temporal dynamics of plant-soil feedbacks. *Journal of Ecology* **106**: 2287–2300.
- Brinkman EP, Van der Putten WH, Bakker E-J, Verhoeven KJF. 2010.** Plant-soil feedback: Experimental approaches, statistical analyses and ecological interpretations. *Journal of Ecology* **98**: 1063–1073.
- Bulgarelli D, Garrido-Oter R, Münch PC, Weiman A, Dröge J, Pan Y, McHardy AC, Schulze-Lefert P. 2015.** Structure and function of the bacterial root microbiota in wild and domesticated barley. *Cell Host and Microbe* **17**: 392–403.
- Cardinale M, Grube M, Erlacher A, Quehenberger J, Berg G. 2015.** Bacterial networks and co-occurrence relationships in the lettuce root microbiota. *Environmental Microbiology* **17**: 239–252.
- Carrillo J, Ingwell LL, Li X, Kaplan I, Systems F, Lafayette W. 2019.** Domesticated tomatoes are more vulnerable to negative plant-soil feedbacks than their wild relatives.

- 526 *Journal of Ecology* **107**(4): 1753–1766.
- 527 **Chagnon PL, Bradley RL, Maherali H, Klironomos JN. 2013.** A trait-based
528 framework to understand life history of mycorrhizal fungi. *Trends in Plant Science* **18**:
529 484–491.
- 530 **Chen YH, Welter SC. 2007.** Crop domestication creates a refuge from parasitism for a
531 native moth. *Journal of Applied Ecology* **44**: 238–245.
- 532 **Coley PD, Bryant JP, Chapin FS. 1985.** Resource Availability and Plant Antiherbivore
533 Defense. *Science* **230**: 895–899.
- 534 **Cortois R, Schröder-Georgi T, Weigelt A, van der Putten WH, De Deyn GB. 2016.**
535 Plant–soil feedbacks: role of plant functional group and plant traits. *Journal of Ecology*
536 **104**: 1608–1617.
- 537 **Craine JM. 2009.** *Resource strategies of wild plants*. Princeton, NJ: Princeton university
538 press.
- 539 **Dávila-Flores AM, De Witt TJ, Bernal JS. 2013.** Facilitated by nature and agriculture:
540 Performance of a specialist herbivore improves with host-plant life history evolution,
541 domestication, and breeding. *Oecologia* **173**: 1425–1437.
- 542 **De Long JR, Fry EL, Veen GF, Kardol P. 2019.** Why are plant–soil feedbacks so
543 unpredictable, and what to do about it? *Functional Ecology* **33**: 118–128.
- 544 **Faucon M-P, Houben D, Lambers H. 2017.** Plant Functional Traits: Soil and Ecosystem
545 Services. *Trends in Plant Science* **22**: 385–394.
- 546 **Fierer N, Ladau J, Clemente JC, Leff JW, Owens SM, Pollard KS, Knight R, Gilbert
547 JA, McCulley RL. 2013.** Reconstructing the microbial diversity and function of pre-
548 agricultural tallgrass prairie soils in the United States. *Science* **342**: 621–4.
- 549 **García-Palacios P, Milla R, Delgado-Baquerizo M, Martín-Robles N, Álvaro-
550 Sánchez M, Wall DH. 2013.** Side-effects of plant domestication: Ecosystem impacts of
551 changes in litter quality. *New Phytologist* **198**: 504–513.
- 552 **Giovanetti, M.; Mosse B. 1980.** An evaluation of techniques for measuring vesicular
553 arbuscular mycorrhizal infection in roots. *New phytologist* **84**: 489–500.
- 554 **Graham JH, Eissenstat DM. 1994.** Host genotype and the formation and function of
555 VA mycorrhizae. *Plant and Soil* **159**: 179–185.
- 556 **Graham JH, Eissenstat DM, Drouillard DL. 1991.** On the Relationship Between a
557 Plant's Mycorrhizal Dependency and Rate of Vesicular-Arbuscular Mycorrhizal
558 Colonization. *Functional Ecology* **5**: 773.
- 559 **Hale IL, Broders K, Iriarte G. 2014.** A Vavilovian approach to discovering crop-

- associated microbes with potential to enhance plant immunity. *Frontiers in Plant Science* **5**: 1–7.
- Hancock JF. 2004.** *Plant evolution and the origin of crop species*. New York, USA: CABI.
- Helgason T, Daniell TJ, Husband R. 1998.** Ploughing up the wood-wide web ? *Nature* **394**: 431.
- Hermes DA, Mattson WJ. 1992.** The Dilemma of Plants: To Grow or Defend. *The Quarterly Review of Biology* **67**: 283–335.
- Hetrick BD, Wilson WT, Cox TS. 1993.** Mycorrhizal dependence of modern wheat cultivars and ancestors: a synthesis. : 512–518.
- Iannucci A, Fragasso M, Beleggia R, Nigro F, Papa R. 2017.** Evolution of the Crop Rhizosphere: Impact of Domestication on Root Exudates in Tetraploid Wheat (*Triticum turgidum* L.). *Frontiers in Plant Science* **8**.
- Johnson NC. 1993.** Can Fertilization of Soil Select Less Mutualistic Mycorrhizae ? *Ecological Applications* **3**: 749–757.
- Johnson NC. 2010.** Tansley review Resource stoichiometry elucidates the structure and function of arbuscular mycorrhizas across scales. *New Phytologist* **185**: 631–647.
- Johnson NC, Pfleger FL. 1992.** Vesicular-arbuscular mycorrhizae and cultural stresses. *Mycorrhizae in sustainable agriculture* **54**: 71–99.
- Johnson PC. 2014.** Extension of Nakagawa & Schielzeth's R^2 GLMM to random slopes models. *Methods in Ecology and Evolution* **5**: 944–946.
- Jones MGK, Fosu-Nyarko J. 2014.** Molecular biology of root lesion nematodes (*Pratylenchus* spp.) and their interaction with host plants. *Annals of applied biology* **164**: 163–181.
- Kardol P. 2007.** *Plant and soil community assembly in secondary succession on ex-arable land. Fundamental and applied approaches*.
- Kardol P, De Deyn GB, Laliberté E, Mariotte P, Hawkes CV. 2013.** Biotic plant-soil feedbacks across temporal scales. *Journal of Ecology* **101**: 309–315.
- Kardol P, Veen GF, Teste FP, Perring MP. 2015.** Peeking into the black box: a trait-based approach to predicting plant – soil feedback. *New Phytologist* **206**: 1–4.
- Kempel A, Schadler M, Chrobock T, Fischer M, van Kleunen M. 2011.** Tradeoffs associated with constitutive and induced plant resistance against herbivory. *Proceedings of the National Academy of Sciences* **108**: 5685–5689.
- Kiers ET, Denison RF. 2014.** Inclusive fitness in agriculture. *Phil. Trans. R. Soc. B* **369**:

20130367.

Kiers ET, Van der Heijden MGA. 2006. Mutualistic Stability in the Arbuscular Mycorrhizal Symbiosis: Exploring Hypotheses of Evolutionary Cooperation. *Ecology* **87**: 1627–1636.

Kiers ET, West SA, Denison RF. 2002. Mediating mutualisms: farm management practices and evolutionary changes in symbiont co-operation. *Journal of Applied Ecology* **39**: 745–754.

Klironomos JN. 2002. Feedback with soil biota contributes to plants rarity and. *Nature* **417**: 67–69.

Kulmatiski A, Beard KH, Stevens JR, Cobbold SM. 2008. Plant-soil feedbacks: A meta-analytical review. *Ecology Letters* **11**: 980–992.

Laliberté E. 2017. Below-ground frontiers in trait-based plant ecology. *New Phytologist* **213**: 1597–1603.

Laliberté E, Lambers H, Burgess TI, Wright SJ. 2015. Phosphorus limitation, soil-borne pathogens and the coexistence of plant species in hyperdiverse forests and shrublands. *New Phytologist* **206**: 507–521.

Leff JW, Lynch RC, Kane NC, Fierer N. 2016. Plant domestication and the assembly of bacterial and fungal communities associated with strains of the common sunflower, *Helianthus annuus*. *New Phytologist* **1**:1-12.

Lehmann A, Barto EK, Powell JR, Rillig MC. 2012. Mycorrhizal responsiveness trends in annual crop plants and their wild relatives—a meta-analysis on studies from 1981 to 2010. *Plant and Soil* **355**: 231–250.

Lemmermeyer S, Lörcher L, van Kleunen M, Dawson W. 2015. Testing the Plant Growth-Defense Hypothesis Belowground: Do Faster-Growing Herbaceous Plant Species Suffer More Negative Effects from Soil Biota than Slower-Growing Ones? *The American Naturalist* **186**: 264–271.

Lenth RV. 2016. Least-squares means: the R package lsmeans. *J Stat Softw* **69**: 1-33.

Luo S, De Deyn GB, Jiang B, Yu S. 2017. Soil biota suppress positive plant diversity effects on productivity at high but not low soil fertility. *Journal of Ecology* **105**: 1766–1774.

Macfadyen S, Bohan DA. 2010. Crop domestication and the disruption of species interactions. *Basic and Applied Ecology* **11**: 116–125.

Mäder P, Edenhofer S, Boller T, Wiemken A, Niggli U. 2000. Arbuscular mycorrhizae in a long-term field trial comparing low-input (organic , biological) and high-input (

- conventional) farming systems in a crop rotation. *Biology and Fertility of Soils* **31**: 150–156.
- Mao L, Liu Y, Shi G, Jiang S, Cheng G, Li X, An L, Feng H. 2013.** Wheat cultivars form distinctive communities of root-associated arbuscular mycorrhiza in a conventional agroecosystem. *Plant and Soil* **374**: 949–961.
- Mariotte P, Mehrabi Z, Bezemer TM, De Deyn GB, Kulmatiski A, Drigo B, Veen GF, van der Heijden MGA, Kardol P. 2018.** Plant-Soil Feedback: Bridging Natural and Agricultural Sciences. *Trends in Ecology and Evolution* **33**(2): 129–142.
- Maron JL, Marler M, Klironomos JN, Cleveland CC. 2011.** Soil fungal pathogens and the relationship between plant diversity and productivity. *Ecology Letters* **14**: 36–41.
- Martín-Robles N, Lehmann A, Seco E, Aroca R, Rillig MC, Milla R. 2018.** Impacts of domestication on the arbuscular mycorrhizal symbiosis of 27 crop species. *New Phytologist* **218**: 322–334.
- Martín-Robles N, Morente-López J, Freschet GT, Poorter H, Roumet C, Milla R. 2019.** Root traits of herbaceous crops: Pre-adaptation to cultivation or evolution under domestication? *Functional ecology* **33**(2): 273–285.
- Massei G, Hartley SE. 2000.** Disarmed by domestication? Induced responses to browsing in wild and cultivated olive. *Oecologia* **122**: 225–231.
- Milla R, Bastida JM, Turcotte MM, Jones G, Violle C, Osborne CP, Chacón-Labela J, Sosinski ÊE, Kattge J, Laughlin DC, *et al.* 2018.** Phylogenetic patterns and phenotypic profiles of the species of plants and mammals farmed for food. *Nature Ecology and Evolution* **2**: 1808–1817.
- Milla R, Morente-Lopez J, Alonso-Rodrigo JM, Martin-Robles N, Stuart Chapin F. 2014.** Shifts and disruptions in resource-use trait syndromes during the evolution of herbaceous crops. *Proceedings of the Royal Society B: Biological Sciences* **281**: 20141429–20141429.
- Milla R, Osborne CP, Turcotte MM, Violle C. 2015.** Plant domestication through an ecological lens. *Trends in Ecology and Evolution* **30**: 463–469.
- Miller ZJ, Menalled FD. 2015.** Impact of species identity and phylogenetic relatedness on biologically-mediated plant-soil feedbacks in a low and a high intensity agroecosystem. *Plant and Soil* **389**: 171–183.
- Moora M, Davison J, Öpik M, Metsis M, Saks Ü, Jairus T, Vasar M, Zobel M. 2014.** Anthropogenic land use shapes the composition and phylogenetic structure of soil arbuscular mycorrhizal fungal communities. *FEMS Microbiology Ecology* **90**: 609–621.

- 662 **Nijjer S, Rogers WE, Siemann E. 2010.** The Impacts of Fertilization on Mycorrhizal
663 Production and Investment in Western Gulf Coast Grasslands. *Am. Midl. Nat* **163**: 124–
664 133.
- 665 **Oehl F, Sieverding E, Ineichen K, Mäder P, Boller T, Wiemken A, Ma P. 2003.**
666 Impact of Land Use Intensity on the Species Diversity of Arbuscular Mycorrhizal Fungi
667 in Agroecosystems of Central Europe. *Applied and Environmental Microbiology* **69**:
668 2816–2824.
- 669 **Pérez-Jaramillo JE, Carrión VJ, Bosse M, Ferrão LFV, De Hollander M, Garcia**
670 **AAF, Ramírez CA, Mendes R, Raaijmakers JM. 2017.** Linking rhizosphere
671 microbiome composition of wild and domesticated *Phaseolus vulgaris* to genotypic and
672 root phenotypic traits. *ISME Journal* **11**: 2244–2257.
- 673 **Pérez-Jaramillo JE, Mendes R, Raaijmakers JM. 2016.** Impact of plant domestication
674 on rhizosphere microbiome assembly and functions. *Plant Molecular Biology* **90**: 635–
675 644.
- 676 **Pieterse CMJ, de Jonge R, Berendsen RL. 2016.** The Soil-Borne Supremacy. *Trends*
677 *in Plant Science* **21**: 171–173.
- 678 **Pinheiro J, Bates D, DebRoy S, Sarkar D. 2015.** nlme: Linear and Nonlinear Mixed
679 Effects Models R package version 3.1–117.
- 680 **Postma-Blaauw MB, De Goede RGM, Bloem J, Faber JH, Brussaard L. 2010.** Soil
681 biota community structure and abundance under agricultural intensification and
682 extensification. *Ecology* **91**: 460–473.
- 683 **R Core Team. 2016.** R: A language and environment for statistical computing. R
684 Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- 685 **Remigi P, Zhu J, Young JPW, Masson-Boivin C. 2016.** Symbiosis within Symbiosis:
686 Evolving Nitrogen-Fixing Legume Symbionts. *Trends in Microbiology* **24**: 63–75.
- 687 **Rivera MJ, Rodriguez-Saona C, Egizi A, Fonseca DM, Jennings DE, Koppenhöfer**
688 **AM. 2016.** Cultivation and domestication of highbush blueberry (*Vaccinium*
689 *corymbosum*) alters abundance, diversity and virulence of entomopathogenic nematodes.
690 *Agriculture, Ecosystems and Environment* **222**: 148–155.
- 691 **Roberts PA, Waines JG, Van Gundy SD. 1981.** Reaction of Wild and Domesticated
692 *Triticum* and *Aegilops* Species To Root-Knot Nematodes (Meloidogyne). *Nematologica*
693 **28**: 182–191.
- 694 **Rodriguez-Saona C, Vorsa N, Singh AP, Johnson-Cicalese J, Szendrei Z, Mescher**
695 **MC, Frost CJ. 2011.** Tracing the history of plant traits under domestication in

- 696 cranberries: Potential consequences on anti-herbivore defences. *Journal of Experimental*
 697 *Botany* **62**: 2633–2644.
- 698 **Rosenthal JP, Dirzo R. 1997.** Effects of life history, domestication and agronomic
 699 selection on plant defence against insects: Evidence from maizes and wild relatives.
 700 *Evolutionary Ecology* **11**: 337–355.
- 701 **Roucou A, Violle C, Fort F, Roumet P, Ecartot M, Vile D. 2018.** Shifts in plant
 702 functional strategies over the course of wheat domestication. *Journal of Applied Ecology*
 703 **55**: 25–37.
- 704 **Sauer CO. 1952.** *Agricultural origins and dispersals*. American Geographical Society,
 705 New York
- 706 **Schmidt JE, Bowles TM, Gaudin ACM. 2016.** Using Ancient Traits to Convert Soil
 707 Health into Crop Yield: Impact of Selection on Maize Root and Rhizosphere Function.
 708 *Frontiers in plant science* **7**: 373.
- 709 **Sheedy JG, Thompson JP. 2009.** Resistance to the root-lesion nematode *Pratylenchus*
 710 *thornei* of Iranian landrace wheat. *Australasian Plant Pathology* **38**: 478–489.
- 711 **Simpson KJ, Wade RN, Rees M, Osborne CP, Hartley SE. 2017.** Still armed after
 712 domestication? Impacts of domestication and agronomic selection on silicon defences in
 713 cereals. *Functional Ecology* **31**: 2108–2117.
- 714 **Stevens CJ, Dise NB, Mountford O, Gowing DJ. 2004.** Impact of Nitrogen Deposition
 715 on the Richness of Grasslands. *Science* **303**: 1876–1879.
- 716 **Szoboszlay M, Lambers J, Chappell J, Kupper J V., Moe LA, McNear DH. 2015.**
 717 Comparison of root system architecture and rhizosphere microbial communities of Balsas
 718 teosinte and domesticated corn cultivars. *Soil Biology and Biochemistry* **80**: 34–44.
- 719 **Tawaraya K. 2003.** Arbuscular mycorrhizal dependency of different plant species and
 720 cultivars. *Soil Science and Plant Nutrition* **49**: 655–668.
- 721 **Thiele-Bruhn S, Bloem J, Vries FT de, Kalbitz K, Wagg C. 2012.** Linking soil
 722 biodiversity and agricultural soil management. *Environmental Sustainability* **4**: 523–528.
- 723 **Treseder KK. 2008.** Nitrogen additions and microbial biomass: A meta-analysis of
 724 ecosystem studies. *Ecology Letters* **11**: 1111–1120.
- 725 **Trudgill DL, Blok VC. 2001.** Apomitic, Poliphagous, Root knot Nematodes:
 726 Exceptionally Successful and Damaging Biotrophic Root Pathogens. *Annual Review of*
 727 *Phytopathology* **39**: 53–77.
- 728 **Turcotte MM, Lochab AK, Turley NE, Johnson MTJ. 2015.** Plant domestication
 729 slows pest evolution. *Ecology Letters* **18**: 907–915.

- Turcotte MM, Turley NE, Johnson MTJ. 2014.** The impact of domestication on resistance to two generalist herbivores across 29 independent domestication events. *New Phytologist* **204**: 671–681.
- Turrini A, Giordani T, Avio L, Natali L, Giovannetti M, Cavallini A. 2016.** Large variation in mycorrhizal colonization among wild accessions, cultivars, and inbreds of sunflower (*Helianthus annuus* L.). *Euphytica* **207**: 331–342.
- Van der Heijden MGA, Bardgett RD, Van Straalen NM. 2008.** The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecology Letters* **11**: 296–310.
- Van der Putten WH, Bardgett RD, Bever JD, Bezemer TM, Casper BB, Fukami T, Kardol P, Klironomos JN, Kulmatiski A, Schweitzer JA, *et al.* 2013.** Plant-soil feedbacks: The past, the present and future challenges. *Journal of Ecology* **101**: 265–276.
- Van der Putten WH, Cook R, Costa S, Davies KG, Fargette M, Freitas H, Hol WHG, Kerry BR, Maher N, Mateille T, *et al.* 2006.** Nematode Interactions in Nature: Models for Sustainable Control of Nematode Pests of Crop Plants? *Advances in Agronomy* **89**: 227–260.
- Van der Putten WH, Kowalchuk GA, Brinkman EP, Doodeman GTA, van der Kaaij RM, Kamp AFD, Menting FBJ, Veenendaal EM. 2007.** Soil Feedback of Exotic Savanna Grass Relates to Pathogen Absence and Mycorrhizal Selectivity. *Ecology* **88**: 978–988.
- Vargas MAT, Mendes IC, Hungria M. 2000.** Response of field-grown bean (*phaseolus vulgaris* l.) to Rhizobium inoculation and nitrogen fertilization in two cerrados soils. *Biology and Fertility of Soils* **32**: 228–233.
- Verbruggen E, Kiers ET. 2010.** Evolutionary ecology of mycorrhizal functional diversity in agricultural systems. *Evolutionary Applications* **3**: 547–560.
- Verbruggen E, Xiang D, Chen B, Xu T, Rillig MC. 2015.** Mycorrhizal fungi associated with high soil N:P ratios are more likely to be lost upon conversion from grasslands to arable agriculture. *Soil Biology and Biochemistry* **86**: 1–4.
- Wardle DA, Bardgett RD, Klironomos JN, Setälä H, van der Putten WH, Wall DH. 2004.** Ecological linkages between aboveground and belowground biota. *Science* **304**: 1629–33.
- Weese DJ, Heath KD, Dentinger BTM, Lau JA. 2015.** Long-term Nitrogen Addition Causes the Evolution of Less Cooperative Mutualists. *Evolution* **69**: 631–642.
- Whitehead SR, Turcotte M, Poveda K. 2016.** Domestication impacts on plant-

- herbivore interactions: a meta-analysis. *Philosophical Transactions of the Royal Society B* **372**(1712): 20160034.
- Wissuwa M, Mazzola M, Picard C. 2009.** Novel approaches in plant breeding for rhizosphere-related traits. *Plant and Soil* **321**: 409–430.
- Xing X, Koch AM, Jones AMP, Ragone D, Murch S, Miranda M, Maxwell AP, Hart MM. 2011.** Mutualism breakdown in breadfruit domestication Subject collections Mutualism breakdown in breadfruit domestication. *Proceedings of the Royal Society B: Biological Sciences* **279**(1731): 1122–1130.
- Yan J, Han XZ, Ji ZJ, Li Y, Wang ET, Xie ZH, Chen WF. 2014.** Abundance and diversity of soybean-nodulating rhizobia in black soil are impacted by land use and crop management. *Applied and environmental microbiology* **80**: 5394–402.
- Zachow C, Müller H, Tilcher R, Berg G. 2014.** Differences between the rhizosphere microbiome of *Beta vulgaris* ssp. *maritima*-ancestor of all beet crops-and modern sugar beets. *Frontiers in Microbiology* **5**: 1–13.
- Zhu YG, Smith SE, Barritt AR, Smith FA. 2001.** Phosphorus (P) efficiencies and mycorrhizal responsiveness of old and modern wheat cultivars. *Plant and Soil* **237**: 249–255.
- Zuppinger-Dingley D, Schmid B, Petermann JS, Yadav V, De Deyn GB, Flynn DFB. 2014.** Selection for niche differentiation in plant communities increases biodiversity effects. *Nature* **515**: 108–111.
- Zuur A, Ieno EN, Walker N, Saveliev AA, Smit GM. 2009.** *Mixed effects models and extensions in ecology with R*. Springer-Verlag New York, USA.

Figure 1. Experimental design to test the effects of plant domestication on plant-soil feedbacks. In the training phase, wild progenitors (up left) and domesticated varieties (down left) of ten crops were grown in separate containers filled with the same common soil. Thereafter, the trained soils were used for growing a new generation of plants in the subsequent feedback phase (right). In this phase, domesticated plants and wild progenitors of each crop were individually grown in soils trained by wild progenitors (yellow solid line and pots), domesticated plants (brown solid line and pots) and in sterilized soil (dashed lines and beige pots).

Figure 2. Responses of domesticated varieties (black lines) and wild progenitors (grey lines) to soil trained by wild progenitors or by domesticated plants. The responses were measured as root colonization by mycorrhizal fungi (a), root-feeding nematodes (b), plant biomass (c) and plant soil feedback (PSF) index (d); $PSF\ index = (\log\ biomass\ in\ active\ soil - \log\ biomass\ in\ sterilized\ soil) / \log\ biomass\ in\ sterilized\ soil$. The symbols, error bars (standard error) and letters show the least squares means (9 replicates per treatment) and 95% confidence interval of wild progenitors (squares, $n = 187$) and domesticated plants (circles, $n = 173$), obtained by mixed models.

Figure 3. Effects of soil training (trained by wild progenitor: “Progenitor soil”, or domesticated plant: “Dom. Soil”) on mycorrhizal colonization (a and b), nematodes infection (c and d), plant biomass (e and f) and plant soil feedback index (PSF, g and h) of wild progenitors (a,c,e and g, $n=158$) and domesticated plants (b,d,f and h, $n=173$). $PSF\ index = (\log\ biomass\ in\ active\ soil - \log\ biomass\ in\ sterilized\ soil) / \log\ biomass\ in\ sterilized\ soil$. The symbols show the mean score of each wild progenitor (squares) and domesticated plants (circles). Colors of the points correspond to crop species.

Figure 4. Conceptual diagram summarizing the main results of this study. During the feedback phase, wild progenitors and domesticated plants were grown in soils trained by their corresponding wild progenitor (a) and its domesticated plant (b) to test the effect of soil legacies in plant performance. Domesticated plants (on the right) accumulated more root feeding nematodes (black dashes) than wild progenitors (on the left), and this pattern was more pronounced in soils trained by domesticated plants (b). In addition, wild progenitors were more colonized by arbuscular mycorrhizal fungi (tangle of blue thick lines) than domesticated plants, and the pattern was stronger in soils trained by wild

820 progenitors (a). Nevertheless, the effect on plant microorganism interactions did not
821 impact on plant performance, which were similar irrespective of the type of soil training.
822 Yet with several plant-soil feedback cycles impacts on plant performance might occur.

Supporting information

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

Figure S1 Soil microbial biomass and soil organic matter change promoted by wild progenitors and domesticated plants during the training phase.

Figure S2 Effect of crops on microbial biomass (a) and soil organic matter change (b) during the training phase.

Figure S3 Effect of soil training on plant biomass.

Figure S4 Scatter plot of root colonization by mycorrhiza (a,b) and nematodes (c, d) in the feedback phase with plant soil feedback index (PSF index).

Table S1 Detailed information of each of the 10 crops used in this experiment, and reference sources for wild progenitor assignment.

Table S2 Field location and characteristics of the soil employed in the training phase.

Methods S1 Measurement of the effects of the training phase on soil microbial biomass and soil organic matter change.

824 Table 1. Common and botanical names of domesticated and wild progenitor taxa of the
 825 crops used in the experiment. See Supporting Information Table S1 for more detailed
 826 information, particularly on bibliographic references used for assigning wild progenitors
 827 for each crop.

828

Botanic family	Crop common name	Wild progenitor	Domesticated taxa
Alliaceae	leek	<i>Allium ampeloprasum</i> L.	<i>Allium porrum</i> L.
Amaranthaceae	amaranth	<i>Amaranthus hybridus</i> L.	<i>Amaranthus cruentus</i> L.
	chard	<i>Beta vulgaris</i> L.	<i>Beta vulgaris</i> L.
Asteraceae	cardoon	<i>Cynara cardunculus</i> L.	<i>Cynara cardunculus</i> L.
Fabaceae	white clover	<i>Trifolium repens</i> L.	<i>Trifolium repens</i> L.
Poaceae	barley	<i>Hordeum spontaneum</i> K.Koch	<i>Hordeum vulgare</i> L.
	maize	<i>Zea mexicana</i> (Schrاد.) Kuntze	<i>Zea mays</i> L.
	sorghum	<i>Sorghum bicolor</i> (L.) Moench	<i>Sorghum drummondii</i> (Nees ex Steud.) Millsp. & Chase
		<i>Capsicum annuum</i> var.	
Solanaceae	pepper	<i>glabriusculum</i> (Dunal) Heiser & Pickersgill	<i>Capsicum annuum</i> L.
	tomato	<i>Solanum pimpinellifolium</i> L.	<i>Solanum esculentum</i> Dunal

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Table 2. Results of mixed-effects models testing the effect of soil training and plant domestication status on plant traits in the feedback phase, where wild progenitors and domesticated plants from 10 crops were grown in soils previously trained by the different wild progenitors and domesticated plant species (training phase). The models tested if root colonization by mycorrhiza and nematodes in the feedback phase were affected by the type of soil training, domestication status (Dom) and the interaction; and if plant biomass and plant soil feedback (PSF) index were affected by the type of soil training, domestication status, their interaction, and AMF colonization and nematode infection rates. The table shows the estimated values and standard errors (SE), *F* and *P* scores of each variable. The significant p-values ($P < 0.05$) are marked in bold. Percentage of variance explained by the fixed effects of the models is indicated by R^2_{marginal} (R^2_{m}), and the variance explained by both the fixed and random effects is indicated by $R^2_{\text{conditional}}$ (R^2_{c}).

	Mycorrhizal colonization (%)			Nematode infection (%)			Plant biomass (g)			PSF index		
	estim value (SE)	$F_{1,360}$	P	estim value (SE)	$F_{1,360}$	P	estim value (SE)	$F_{1,360}$	P	estim value (SE)	$F_{1,360}$	P
Intercept	-1.57 (0.11)	-	-	-5.24 (0.17)	-	-	0.09 (0.195)	-	-	0.01 (0.06)	-	-
Type of soil training	-0.29 (0.11)	6.56	0.01	0.93 (0.11)	51.54	<.0001	-0.01 (0.021)	0.07	0.8	-0.04 (0.06)	0.01	0.94
Domestication status	-0.35 (0.04)	43.22	<.0001	0.48 (0.09)	31.21	<.0001	0.08 (0.06)	2.21	0.17	-0.01 (0.06)	0.02	0.89
Mycorrhizal colonization	-	-	-	-0.5 (0.66)	0.58	0.45	-0.31 (0.22)	1.72	0.19	0.01 (0.29)	0.10	0.76
Nematodes infection	0.08 (2.09)	0.00	0.97	-	-	-	1.19 (1.61)	0.5	0.48	-2.72 (10.00)	0.00	>.99
Dom x Type soil training	0.15 (0.04)	10.73	0.001	0.11 (0.07)	2.46	0.12	0.01 (0.01)	0.3	0.58	-0.01 (0.06)	0.01	0.93
R ² m	0.055			0.08			0.032			0.008		
R ² c	0.232			-			0.903			0.008		

843 The dependent variable Plant biomass was log transformed. Domestication and Type of soil training were factors. Interactions are indicated by x