

The impact of domestication on resistance to two generalist herbivores across 29 independent domestication events

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Summary

- The domestication of crops is among the most important innovations in human history. Here, we test the hypothesis that cultivation and artificial selection for increased productivity of crops reduced plant defenses against herbivores.
- We compared the performance of two economically important generalist herbivores – the leaf-chewing beet armyworm (*Spodoptera exigua*) and the phloem-feeding green peach aphid (*Myzus persicae*) – across 29 crop species and their closely related wild relatives. We also measured putative morphological and chemical defensive traits and correlated them with herbivore performance.
- We show that, on average, domestication significantly reduced resistance to *S. exigua*, but not *M. persicae*, and that most independent domestication events did not cause differences in resistance to either herbivore. In addition, we found that multiple plant traits predicted resistance to *S. exigua* and *M. persicae*, and that domestication frequently altered the strength and direction of correlations between these traits and herbivore performance.
- Our results show that domestication can alter plant defenses, but does not cause strong allocation tradeoffs as predicted by plant defense theory. These results have important implications for understanding the evolutionary ecology of species interactions and for the search for potential resistance traits to be targeted in crop breeding.

Introduction

The advent of agriculture and domestication was among the most important advances that gave rise to modern civilization (Gepts, 2004). Plant domestication is the result of extended cultivation and artificial selection leading to genetically based adaptations for human consumption and growth in agronomic conditions (Evans, 1993; Gepts, 2004). This process began as early as 12 000 yr ago in multiple regions across the globe (Meyer *et al.*, 2012), resulting in the evolution of a series of traits, including increased yield of the harvested organ (e.g. seeds, fruits, roots, etc.), reduced seed dispersal, greater uniformity of germination and flowering date, larger seeds, reduced dormancy and more erect stature (Evans, 1993; Gepts, 2004). A recent analysis comparing 203 crops from 68 families found that many traits often associated with this ‘domestication syndrome’ are exceptions that apply mostly to model crops, especially grasses (Meyer *et al.*, 2012). Although certain frequent evolutionary changes were identified, the results emphasized that a diversity of traits evolve during domestication and these differ among locations, age of domestication and plant growth form. Using a similar approach, we exploit the world’s longest lasting and best-replicated evolution experiment in human history to test the generality of the hypothesis that domestication negatively impacts the resistance of crops against herbivores.

Herbivory is an important driver of plant evolution (Futuyma & Agrawal, 2009) and nutrient cycling (Schmitz, 2008), and causes billions of dollars in economic losses annually (Pimentel, 2009). Domestication is predicted to cause reduced defense against herbivores, when compared with wild ancestral species, for several non-exclusive reasons. First, in some cases, herbivore defenses are directly selected against during domestication because they are harmful or distasteful to humans or livestock (Evans, 1993). For example, wild lupin (*Lupinus albus*) contains high levels of toxic alkaloids, whereas the conspecific domesticated crop sweet lupin (*L. albus*) contains low concentrations of alkaloids and suffers severe herbivory (Wink, 1988). Second, artificial selection may increase the nutritive quality of certain crops (e.g. litter quality; García-Palacios *et al.*, 2013), and this can promote herbivore growth and fitness (Benrey *et al.*, 1998; Behmer, 2009). Finally, predicted resource allocation tradeoffs between growth and defense (Rhoades, 1979; Coley *et al.*, 1985; Herms & Mattson, 1992) may cause selection for increased productivity in crops to result in decreased plant defenses (Kennedy & Barbour, 1992).

A direct comparison of the resistance between crops and wild relatives provides a powerful approach to test the evolutionary effects of domestication on plant defense. Studies that have taken this approach have frequently reported reduced resistance in crops (Wink, 1988; Rosenthal & Dirzo, 1997; Benrey *et al.*,

1998; Mirnezhad *et al.*, 2010; Rodriguez-Saona *et al.*, 2011), but the consistency of this finding is not universal. Some domesticated varieties show no reduction in resistance (Mirnezhad *et al.*, 2010; Rodriguez-Saona *et al.*, 2011), whereas others show no overall effect of domestication (Leiss *et al.*, 2013). A limitation of these studies is that most have only examined one or two independent domestication events. As pointed out by Meyer *et al.* (2012), it is possible that the impacts of domestication are not as consistent as often assumed. Thus, the effects of domestication on plant–herbivore interactions remain unclear. Experiments that examine multiple independent domestication events would provide a powerful test of whether crops generally exhibit lower defenses than their wild relatives. This approach also makes it possible to address whether artificial selection alters the plant defensive function of specific plant traits (Kempel *et al.*, 2011).

We investigated whether domestication leads to the evolution of reduced resistance against herbivores when compared with closely related wild relatives across 29 independent domestication events. In order to compare differences in plant resistance across 58 plant species, we quantified plant defense with standardized bioassays utilizing generalist herbivores. The performance of generalist herbivores provides a comparable measure of investment and effectiveness of defense across a diversity of plant species. We thus tested resistance to two generalist insect herbivores from different feeding guilds: a leaf-chewing caterpillar (*Spodoptera exigua*, Lepidoptera: Noctuidae, the beet armyworm) and a phloem-feeding aphid (*Myzus persicae*, Hemiptera: Aphididae, the green peach aphid). Both are economically important crop pests with a global distribution. In the first two experiments, we asked: are crop species more susceptible to herbivores than their wild relatives? A third experiment tested whether crops have evolved reduced putative defensive morphological and chemical traits. Finally, we correlated herbivore performance and resistance traits to identify the trait mechanisms that underlie herbivore resistance, and whether the effects of these resistance traits on herbivores differ between crop and wild relatives.

Materials and Methods

Selection of plant species

To maximize the generality of our results, we studied 58 plant species that represent 29 independent domestication events across 12 plant families (Fig. 1). We selected herbaceous crops and their closely related wild relatives based on their availability and ease of growth. For most crops, we obtained the living descendants of the putative progenitor species, whereas, for quinoa and canola, we used a closely related congeneric wild species (Supporting information Table S1). We acknowledge that many crop domestication events have complex origins involving hybridization between multiple progenitors (Kole, 2011; Meyer & Purugganan, 2013), and we use the term ‘wild relatives’ to refer to wild species that are direct descendants of one of the progenitor species, as well as closely related wild relatives of modern crops.

We used a single variety for each crop species and one to five accessions per wild relative species (Table S1). We recognize that

there is often genetic variation in resistance among crop varieties and among plant populations (Fritz & Simms, 1992; Mirnezhad *et al.*, 2010). However, we purposefully sacrificed a more in-depth analysis of individual species to focus on whether there are broad general patterns of the effects of domestication on the evolution of resistance. We chose commonly used and available conventional crop varieties that were not genetically modified using transgenic approaches (Table S1). The selection of varieties or accessions occurred without prior knowledge or bias with respect to the levels of resistance. Given that most crop varieties show greatly increased yield compared with their wild relatives, the qualitative prediction of reduced resistance remains regardless of the variety selected. Seeds were obtained from governmental seed banks, private seed companies and colleagues (Table S1).

Selection of herbivores

We quantified the resistance of each plant species to two economically important generalist herbivores from different feeding guilds. We used generalist insects because they constitute important sources of economic damage to crops and can be potent agents of selection on wild plants (Ali & Agrawal, 2012). Generalist insects also provide a standardized means to measure investment and effectiveness of defense across a wide diversity of plant species. We first tested resistance to the beet armyworm (*Spodoptera exigua*), which feeds on > 37 plant families (Normark & Johnson, 2010). This species originated in South-East Asia and is now a globally distributed crop pest, causing significant economic damage (Pearson, 1982). Eggs were obtained from Benzon Research (Carlisle, PA, USA). We then tested resistance to the phloem-feeding and globally distributed green peach aphid (*Myzus persicae*), which can feed on 132 plant families including many crop species (Mackauer & Way, 1976; Normark & Johnson, 2010). This aphid is especially damaging to plants because it can transmit over 100 plant viruses (Van Emden *et al.*, 1969), although our colonies did not cause any visible virus infections on plants. Aphids were collected in 2010 from four separate agricultural tobacco (*Nicotiana tabacum*) fields in North Carolina (USA). We maintained aphids on Chinese cabbage var. Michihli (*Brassica rapa* var. *pekinensis*) in asexual growing conditions using long-day light cycles in the laboratory. Both herbivores grew on most of the plant species tested (see Results).

Experimental growing conditions

We conducted three experiments using identical growing conditions. Given differences in germination and growth among species, we staggered germination dates among crop–wild pairs so that plants were at a similar developmental stage at the start of each experiment. We always planted the species within a pair on similar dates. All plants were grown from seed according to recommended protocols (e.g. www.ars.usda.gov/mw/ames/ncrpis/germ_methods). We transplanted seedlings into 460-ml pots filled with potting soil (BX MYCORRHIZAE™; PRO-MIX®; Premier Tech Horticulture, Quakertown, PA, USA). Plants were grown in a randomized block design within a growth chamber set to 25°C and 55% humidity, with a 16 h : 8 h light : dark cycle. We watered

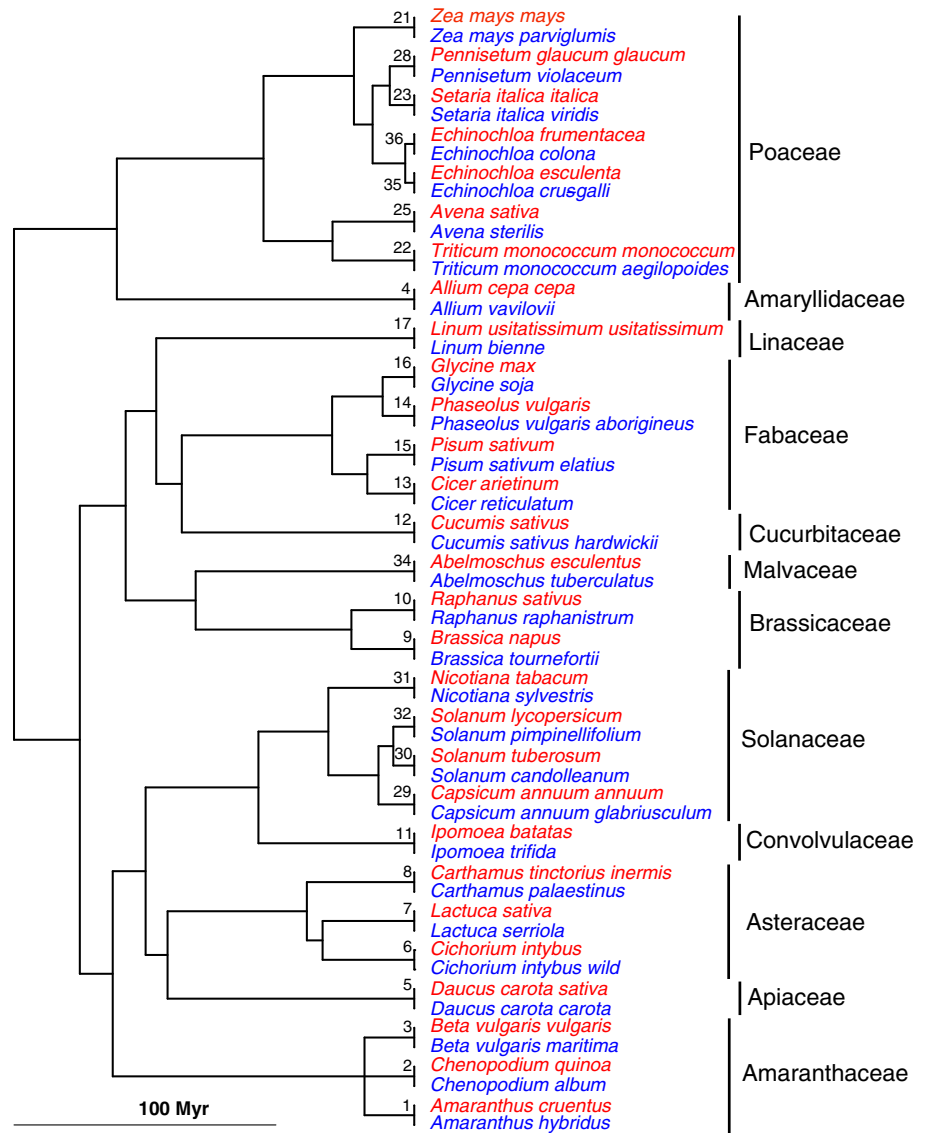


Fig. 1 Phylogeny of the 58 species and 29 independent domestication events across 12 families. Wild relatives are identified in blue and crops are shown in red, with the family names indicated using vertical lines to the right of the species names. Each event is identified with a crop–wild pair number that corresponds to subsequent figures. The phylogeny was created using Phylomatic (Webb & Donoghue, 2005) and time calibrated using multiple fossil dates (Supporting Information Methods S3). We provide a 100 million yr (Myr) scale below the phylogeny.

plants as needed and fertilized with a solution of all-purpose soluble fertilizer every week (0.36 g l⁻¹ of water, Miracle-Gro[®], 24-8-16 with micronutrients; Scotts Canada Ltd, Mississauga, ON, Canada). Seedlings were grown until the two to four true leaf stage, and were then covered with a transparent polyester mesh bag (Heritage Voile, #23170; Fabricland, Mississauga, ON, Canada) supported by a wire frame. Within the mesh bags, the photosynthetically active radiation intensity was 107 μmol m⁻² s⁻¹. At this point, we applied the various treatments described below.

Expt A: caterpillar performance In late May to early June 2012, 11 replicate seedlings per species were grown and bagged on 25 June 2012. Six replicate plants each received three neonate (1-d-old) *S. exigua* caterpillars. The remaining five replicates were caterpillar-free controls. After 10 d of feeding, we counted the surviving caterpillars, placed them in individual test tubes overnight to permit defecation and measured their wet weight. We calculated the average weight of a surviving caterpillar per replicate plant. Plants were harvested 12 d after insect removal, and all

aboveground biomass was oven dried for 1 wk and weighed. We quantified plant tolerance to caterpillar damage as the mean plant dry weight of the caterpillar treatment minus that of the control treatment, divided by the control treatment.

Expt B: aphid performance New plants were prepared in August 2012. Seven replicate plants per species received 16 third instar aphids and the remaining four replicates were aphid-free controls. After 17 d, or approximately three aphid generations, we cut all plants at their bases and brushed or knocked off all aphids onto a sheet. Aphids were counted by the authors M.M.T. or N.E.T. Aboveground plant biomass was harvested, dried, weighed and used to calculate tolerance as already described.

Expt C: plant traits The final experiment quantified the constitutive resistance traits that herbivores would experience when they initially established on plants. Six replicate plants of each species were germinated in March and April 2012 and bagged as described above. After 16 additional days of growth, plants were

harvested. From each plant, we measured leaf toughness (g), trichome density (trichomes mm^{-2}), specific leaf area 'SLA' ($\text{mm}^2 \text{mg}^{-1}$ dry) and leaf dry matter content 'LDMC' (mg dry g^{-1} wet) (see Supporting Information Methods S1 for details). Phloem was extracted from aboveground tissues using 5 mM Na_2EDTA (Wilkinson & Douglas, 2003). Species was treated as the unit of replication in subsequent analyses of plant traits, and extracts from each replicate plant were combined and filtered. Phloem sugar concentration was measured by converting sucrose to glucose using invertase. We then quantified glucose concentration using an oxidation assay (Methods S1; Wilkinson & Douglas, 2003). The remaining aboveground plant tissue was used to measure percentage carbon and percentage nitrogen on an elemental combustion analyzer (Methods S1). We also measured total phenolic concentration and phenolic oxidative activity using an acetone extraction followed by a Folin–Ciocalteu colorimetric assay, following the methods of Salminen & Karonen (2011; Methods S1). Finally, we also calculated the relative growth rate 'RGR' of each plant species using the plants from Expt B. We used log mean dry weights of the controls minus log seed weight divided by the number of days from germination to harvest.

Statistical analyses

Domestication and herbivore performance We tested the impact of domestication on herbivore resistance using linear mixed-effects models. We first quantified the differences in caterpillar survival using a generalized linear mixed-effects (GLMM) model with a binomial error distribution and a 'logit' link function. The response variable was the number of surviving and the number of dead caterpillars on each replicate plant. The fixed effect was domestication status. We included crop–wild pairs as a random effect to account for variation caused by the phylogenetic non-independence of crops and their wild relatives. We also included species identity nested within pair as a random effect to avoid pseudoreplication of replicate plants within species. Finally, we included the interaction between pair and domestication as a random effect. We tested the significance of each term with likelihood ratio tests by comparing the fit of nested models using maximum likelihood 'ML' (Bates, 2010).

We repeated these analyses for the $\log_e(+1)$ -transformed weight of surviving caterpillars and also with the $\log_e(+1)$ -transformed number of aphids using linear mixed-effects models (LME). Transformations improved the normality of residuals. The weights of dead or missing caterpillars were not included in the analyses unless all caterpillars on a given species of plant died, in which case we assigned their weight as zero. For aphids, we included a fixed effect for the identity of the counter (M.M.T. or N.E.T.). All analyses were conducted in R 3.0.2 and the mixed models utilized the 'lme4' package (Bates, 2010; R Core Team, 2013). A summary of our R script is available in Supporting Information (Methods S2). In addition to these experiment-wide analyses, we also conducted separate analyses on each crop–wild pair individually. For caterpillar survival, we used GLMM models with a binomial error distribution, whereas, for caterpillar growth and the number of aphids, we used two-sample t -tests.

We tested whether the age of domestication, defined as the earliest record of the domesticated form, the age of cultivation, defined as the earliest date of exploitation of the wild ancestor, or the focal tissue under selection (e.g. root, leaves) had an impact on the change in herbivore performance between crop and wild relatives (Table S1). We tested two classifications of tissues: one with the following groups: seed, root, leaf and fruit; and a simplified grouping with vegetative versus reproductive tissue. We calculated the proportional effect size of domestication on herbivore performance for each crop–wild pair by subtracting the crop's mean value from that of the wild relative, and dividing by the mean value for both. We then fitted an LME model with this effect size as the response variable; the estimated date of cultivation or domestication was treated as a fixed effect and plant family as a random effect. This was repeated for each herbivore performance measure, and a similar analysis was conducted for the type of tissue under selection.

Plant traits under domestication We examined whether domestication consistently changed a series of morphological and chemical traits thought to be associated with resistance and tolerance to herbivores. Each trait was analyzed separately using LME models conducted on the log-transformed species mean values ($n = 58$). The LME models included terms for domestication as a fixed effect, pair as a random effect and the interaction between domestication and pair as a random effect. Simpler analyses using paired t -tests yielded similar results.

The effect of plant traits on herbivore performance Our final objective was to understand the mechanistic underpinnings of resistance to the generalist herbivores, and to test whether domestication impacts the function of plant traits in resistance. We therefore tested the impact of nine plant traits on the three measures of herbivore performance using multiple regressions, and evaluated whether these traits interacted with domestication history. We excluded phenolic oxidation and C:N ratio because these were highly correlated with total phenolics (Pearson's $r = 0.93$, $P < 2 \times 10^{-16}$) and percentage nitrogen ($r = -0.94$, $P < 2 \times 10^{-16}$), respectively. Analyses were conducted using plant species means, where all plant traits were $\log_e(+1)$ transformed to improve normality, followed by standardization by the standard deviation of each trait, which facilitated comparison of the effects of each trait on herbivore performance (Schielzeth, 2010). The full regression model included domestication status, the nine plant traits (see Table 2, traits 'B' to 'J') and the domestication by trait interactions (Methods S2). Given limitations in sample size, trait-by-trait interactions were excluded. These multivariate analyses cannot cope with missing data (Bartoń, 2013), and so the mean leaf toughness of all species was used for *Daucus carota carota* and *Linum bienne*, whose leaves were too small for measurements.

We first compared the fit of four different modeling approaches on the full model for each herbivore performance trait using restricted maximum likelihood (REML). We compared an LME model that included crop–wild pair and pair nested within plant family as random factors with three different

phylogenetic generalized least-squares (PGLS) models (Grafen, 1989). These PGLS models use phylogenetic relationships to account for non-independence of species data points. One PGLS model used a star phylogeny, representing an assumption that there is no phylogenetic structure. The other two used a dated phylogeny created with the Phylomatic online tool (Fig. 1; Webb & Donoghue, 2005), fitted with either a model of neutral 'Brownian motion' trait evolution or an 'Ornstein–Uhlenbeck' model of stabilizing selection (Grafen, 1989; Hansen, 1997). Details of phylogenetic inference and analysis are given in Methods S3. Comparisons of the four modeling approaches, using Akaike information criterion (AIC) scores, revealed that LME models always fitted better than PGLS analyses (Table S2), and so we focus here on the multiple regression analysis using the LME approach.

Herbivore response variables were transformed in the same manner as before, and we used a GLMM analysis for caterpillar survival and LME analyses for caterpillar growth and the number

of aphids. For each herbivore response variable, we compared 20 195 possible models using the 'dredge' function in the MuMIn package (Bartoń, 2013). The fit of the models was estimated using ML and we identified the best fitting model for each herbivore response variable as the model with the lowest AIC value, plus all models with $\Delta AIC < 2$ when compared with this best fitting model. We tested the importance of each trait by extracting a trait's model coefficient averaged across the best fitting models, weighted by each model's AIC weight.

Results

Herbivore performance

Domestication increased caterpillar survival by 13.5% ($P = 0.03$, GLMM, Table 1, Fig. 2a). Individual t -tests showed significantly higher survival on crop species relative to wild relatives for beets, lettuce, Einkorn wheat, pepper and potato (all $P < 0.05$, Fig. 2a),

Table 1 Linear mixed-effect models testing whether domestication alters herbivore performance

| Herbivore performance | Wild relatives | Crops | Percentage change | P values | | | | |
|--------------------------|-------------------|-------------------|-------------------|--------------|--------------|-------------------|-------------------|-------------------|
| | | | | Dom | Counter | Species | Pair | Pair \times Dom |
| Caterpillar survival (%) | 0.74 (0.67, 0.80) | 0.84 (0.80, 0.88) | 13.5 | 0.027 | | < 0.001 | < 0.001 | 0.78 |
| Caterpillar growth (mg) | 21.7 (17.5, 26.8) | 26.7 (21.8, 32.7) | 23.0 | 0.330 | | < 0.001 | 0.011 | 0.99 |
| Number of aphids | 36.2 (22.2, 58.4) | 50.6 (28.6, 89.1) | 39.8 | 0.203 | 0.002 | < 0.001 | < 0.001 | 0.16 |

Performance was measured as the fraction of surviving caterpillars (*Spodoptera exigua*) on each plant, caterpillar growth and the number of aphids (*Myzus persicae*). We report the back-transformed fixed-effect estimate means with \pm 1SE values in parentheses, followed by the percentage change caused by domestication. The percentage change represents the impact of domestication on the trait value (crop – wild)/wild \times 100%. For each model term, we present P values from likelihood ratio tests. 'Dom' represents domestication status and 'Counter' is the individual that counted each aphid sample. Plant species was nested within pair, which represents each crop–wild pairing. Terms that significantly impact herbivore performance are shown in bold.

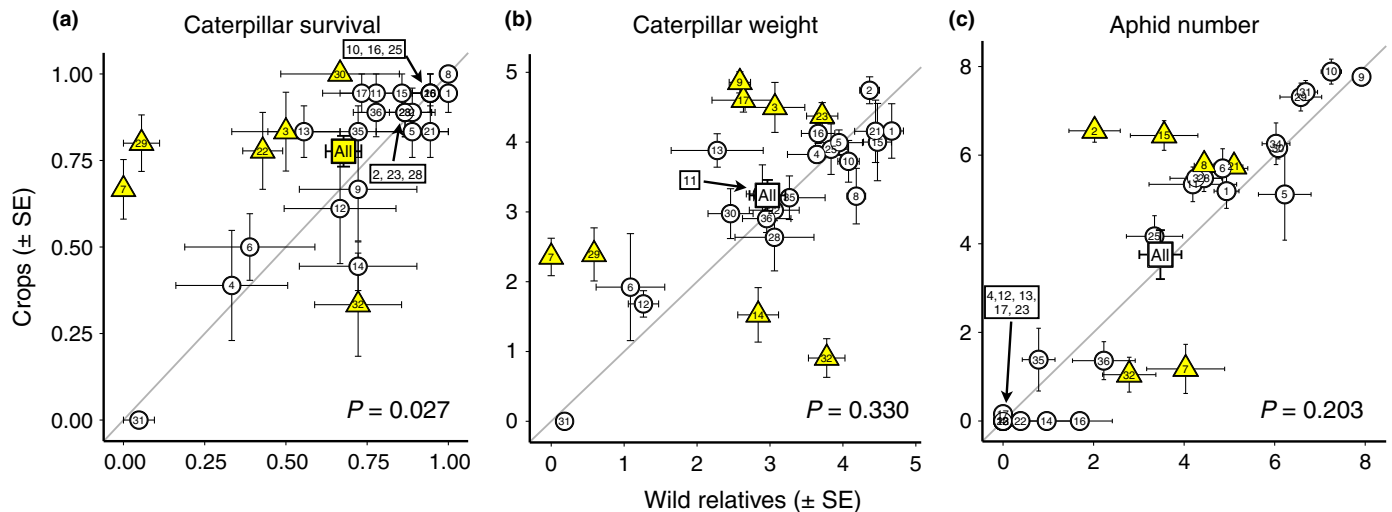


Fig. 2 Crops and wild relatives exhibit inconsistent differences in resistance to generalist herbivores (*Spodoptera exigua* and *Myzus persicae*). Here, we plot the performance of herbivores on crop species (vertical axis) versus wild relatives (horizontal axis) for each crop–wild pair (see Fig. 1 for identity of pair). Herbivore performance was measured as (a) percentage caterpillar survival, (b) $\log_e(+1)$ -transformed caterpillar growth and (c) $\log_e(+1)$ -transformed aphid number. The overall impact of domestication on herbivore performance across all crop–wild pairs is represented by the large square, with the P value given in the lower right corner. The gray line represents the 1 : 1 expectation where herbivores perform equally well on crop and wild relatives. Specific pairs that differ significantly from the 1 : 1 expectation (according to t -tests) are represented by yellow triangles, whereas non-significant pairs are shown as white circles.

Table 2 Multiple regression results averaged across best-fitting models explaining herbivore performance

| Plant traits | Std. β coeff. | SE | <i>P</i> | Std. β coeff. | SE | <i>P</i> | Std. β coeff. | SE | <i>P</i> |
|----------------------------------|----------------------|-------------|-------------------|---------------------|-------------|-------------------|---------------------|-------------|-------------------|
| | Caterpillar survival | | | Caterpillar growth | | | Aphid abundance | | |
| Intercept | 5.35 | 1.09 | < 0.001 | 3.51 | 0.26 | < 0.001 | 3.74 | 0.71 | < 0.001 |
| Domestication | -2.76 | 0.95 | 0.004 | -0.46 | 0.23 | 0.046 | 0.24 | 0.23 | 0.296 |
| Phloem sugar | -0.79 | 0.87 | 0.368 | 0.04 | 0.14 | 0.757 | -0.21 | 0.23 | 0.350 |
| Percentage carbon | 1.26 | 0.94 | 0.182 | -0.02 | 0.18 | 0.906 | 0.75 | 0.37 | 0.040 |
| Percentage nitrogen | 1.37 | 0.77 | 0.076 | 0.55 | 0.16 | 0.000 | -0.07 | 0.45 | 0.878 |
| RGR | -0.76 | 0.80 | 0.339 | -0.05 | 0.13 | 0.709 | 0.14 | 0.28 | 0.606 |
| Total phenolics | 1.93 | 1.05 | 0.066 | -0.25 | 0.19 | 0.189 | 0.62 | 0.38 | 0.100 |
| LDMC | 0.73 | 0.53 | 0.172 | 0.27 | 0.16 | 0.103 | -1.08 | 0.47 | 0.021 |
| SLA | 0.89 | 1.31 | 0.497 | 0.07 | 0.17 | 0.686 | -1.08 | 0.57 | 0.057 |
| Toughness | -0.61 | 0.48 | 0.205 | -0.04 | 0.17 | 0.835 | -0.33 | 0.33 | 0.309 |
| Trichomes | -0.58 | 0.90 | 0.518 | -0.63 | 0.22 | 0.004 | -1.06 | 0.36 | 0.004 |
| Dom \times phloem sugar | 2.07 | 0.89 | 0.020 | | | | 0.44 | 0.27 | 0.112 |
| Dom \times percentage carbon | -1.75 | 1.10 | 0.111 | | | | -0.48 | 0.26 | 0.070 |
| Dom \times percentage nitrogen | -1.15 | 0.84 | 0.171 | -0.17 | 0.23 | 0.476 | | | |
| Dom \times RGR | 1.56 | 0.69 | 0.023 | | | | 0.33 | 0.23 | 0.155 |
| Dom \times total phenolics | -2.53 | 0.96 | 0.008 | -0.13 | 0.26 | 0.613 | -0.24 | 0.25 | 0.339 |
| Dom \times SLA | -2.62 | 1.33 | 0.048 | | | | 0.74 | 0.36 | 0.039 |
| Dom \times trichomes | 1.86 | 0.88 | 0.035 | 0.45 | 0.23 | 0.052 | 0.38 | 0.24 | 0.122 |
| Dom \times LDMC | | | | -0.07 | 0.25 | 0.782 | 0.75 | 0.29 | 0.009 |

We present the standardized β coefficients, and their standard errors, of model terms retained by the best-fitting models, $\Delta\text{AIC} < 2$ (Table S4), averaged according to their Akaike information criterion (AIC) weights. The standardized β coefficients represent the relative effect of each trait on the response variable in standard deviation units. For the domestication term, negative values represent higher herbivore performance (i.e. reduced resistance) on the crop species. The Dom \times toughness term was not present in any of the best models. Trait abbreviations: LDMC, leaf dry matter content; RGR, relative growth rate; SLA, specific leaf area. Traits significantly related to herbivore performance are shown in bold.

and significantly lower survival on tomatoes. Caterpillar growth was, on average, 23% higher on crops than on wild relatives, but this effect was not significant ($P=0.33$, Table 1), unless we accounted for variation in plant traits ($P=0.046$, Table 2). A greater number of individual domestication events significantly increased caterpillar growth (i.e. lettuce, pepper, canola, flax, Foxtail millet and beets) than significantly reduced it (i.e. tomato and common beans; Fig. 2b). Given the significant impact of which author counted the aphids ($P=0.002$, Table 1), all aphid analyses included this factor. Despite the fact that aphids grew 40% faster on crops overall, this effect was not significant ($P=0.20$, Table 1). A re-analysis that excluded four crop-wild pairs without any aphid survivors gave the same result ($P=0.23$). Certain domestication events significantly increased susceptibility to aphids (i.e. quinoa, safflower, peas and corn), whereas two crops (i.e. lettuce and tomato) exhibited significantly greater resistance than their wild relatives (Fig. 2c). Most independent domestication events did not significantly impact any measure of herbivore performance (Fig. 2). The effect of crop-wild pair had a large significant effect on all measures of herbivore performance, indicating phylogenetic non-independence in resistance within pairs (Table 1). The interaction between domestication and pair was not significant for any measure of herbivore performance (Table 1).

Caterpillar survival and growth were highly correlated (Pearson's $r=0.79$, $P<0.001$), but neither of these measures of performance was correlated with aphid number ($r=0.05$, $P=0.72$; $r=-0.02$, $P=0.90$; respectively). Domestication did not have a significant impact on host breadth of either the caterpillar

or the aphid. Caterpillars survived on all but a single crop and a single wild relative, from different pairs (Fig. 2a). The aphids survived on 24 of 29 wild relatives and only 22 of 29 crops, but this difference was not significant ($P=0.747$, χ^2 test for independence; Fig. 2c). Finally, the tissue under selection (all $P>0.77$), the date of first cultivation (all $P>0.14$) and the date of domestication (all $P>0.11$) were not related to changes in resistance to caterpillars or aphids between crops and wild relatives.

Effects of domestication on plant traits

Domestication had few consistent effects on the morphological and chemical plant traits examined. Analyses revealed that domestication increased RGR, with crops adding, on average, 3.5% more dry biomass per day than their wild relatives (Supporting Information Fig. S1, $P=0.03$, Tables S2 and S3). Strong trends of reduced trichome density and LDMC were observed in crops, but were non-significant ($P=0.17$ and $P=0.09$, respectively; Fig. S1; Table S3). Moreover, tolerance to aphid and caterpillar damage did not differ among crops and wild relatives (Fig. S1; Table S3). No chemical traits differed significantly between crops and their wild relatives (Fig. S1; Table S3).

Resistance traits and domestication history

Multiple plant traits predicted resistance against herbivores, and domestication frequently altered the strength and direction of correlations between plant traits and herbivore performance. Independent of domestication, no trait predicted variation in

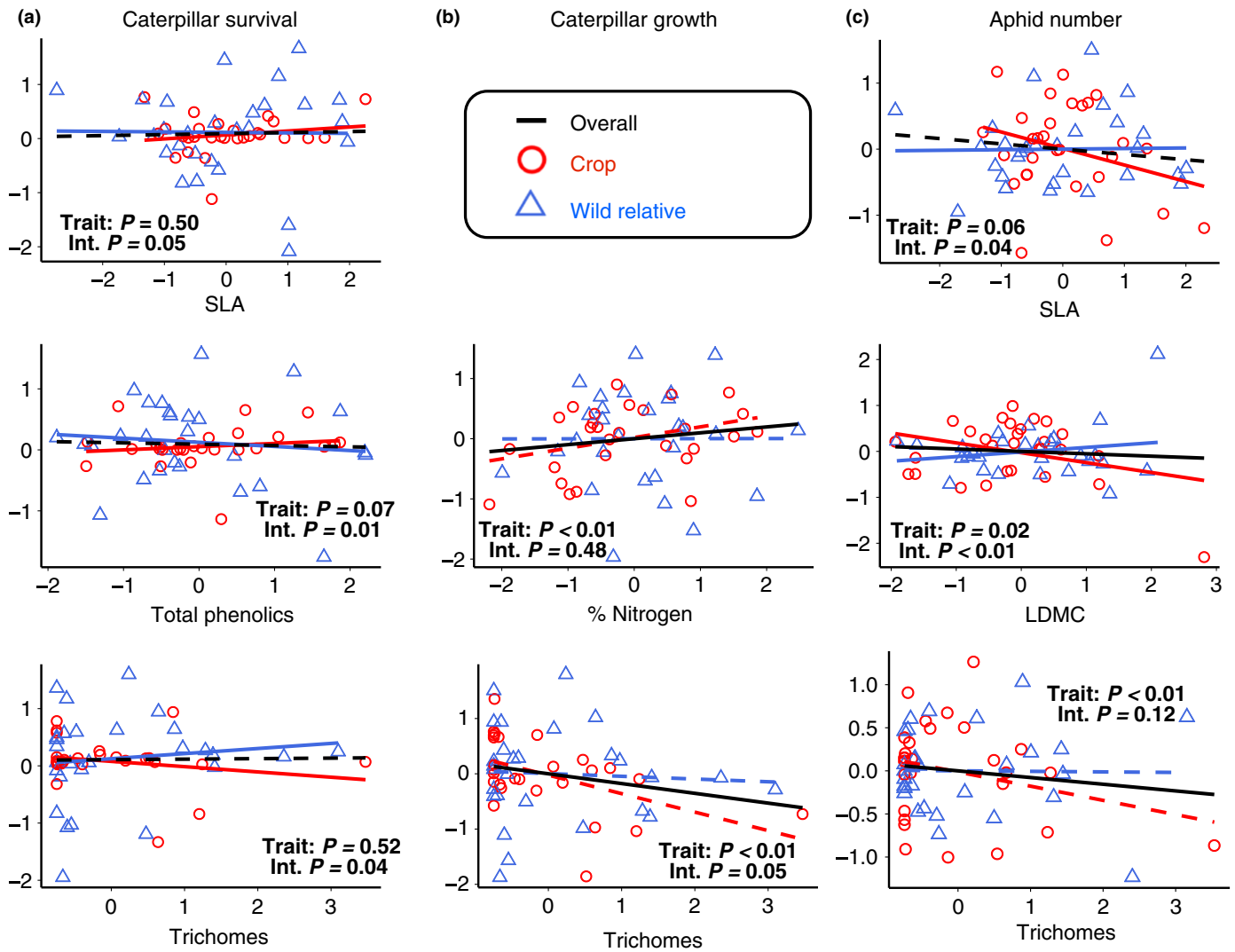


Fig. 3 Plant traits correlated with herbivore performance. A representative sample of plant traits that were significantly correlated with herbivore performance, including traits whose impact differs among crops and wild relatives. Vertical axes present residuals of models that include all terms that were present in the best-fitting models (Table 2), except those on their respective horizontal axes. All plant traits were $\log_e(+1)$ transformed and standardized. Herbivore performance was measured as (a) percentage caterpillar survival (*Spodoptera exigua*), (b) $\log_e(+1)$ -transformed caterpillar growth, and (c) $\log_e(+1)$ -transformed aphid number (*Myzus persicae*). Correlations across all species ‘overall’ are illustrated in black, whereas domestication by trait interactions are illustrated with red (crops) and blue (wild relatives) lines. Main effects or interactions that are significant are presented with solid lines, whereas non-significant effects are dashed (Table 2). Trait abbreviations: LDMC, leaf dry matter content; SLA, specific leaf area.

caterpillar survival, whereas caterpillar growth was positively related to percentage nitrogen ($\beta = 0.55$, $P < 0.001$, LME, Table 2; Fig. 3b) and negatively correlated with trichome density ($\beta = -0.63$, $P = 0.004$). Aphid population growth was similarly negatively correlated with trichomes ($\beta = -1.06$, $P = 0.004$) and LDMC ($\beta = -1.08$, $P = 0.021$, LME, Table 2; Fig. 3c), and positively associated with percentage carbon ($\beta = 0.75$, $P = 0.040$). However, domestication and variation in plant traits frequently interacted to affect herbivore performance, especially caterpillar survival. Phloem sugar concentration, RGR, total phenolics, SLA and trichome density interacted with domestication to affect caterpillar survival (all $|\beta| > 1.55$, all $P < 0.05$, Table 2; Fig. 3a). Some of these interactions involved qualitative changes in the effects of traits. For example, trichome density was

positively related to caterpillar survival in wild relatives, but negatively related to survival on crops ($\beta = 1.86$, Table 2; Fig. 3a). Domestication also strongly interacted with SLA and LDMC to affect aphid abundance (Table 2; Fig. 3c). In the case of caterpillar growth, trichomes interacted with domestication, but this effect was only weakly significant ($\beta = 0.45$, $P = 0.052$, Table 2; Fig. 3b). Interestingly, this analysis accounting for trait variation also showed a significant positive effect of domestication on caterpillar growth ($P = 0.046$), unlike the focused analysis in Table 1. This suggests that a loss of resistance is detectable for caterpillar growth only when accounting for variation in plant traits.

Although we tested many traits and trait-by-domestication interactions, we identified a significantly larger frequency of

significant results than expected by chance ($P < 0.001$, binomial expansion test using a critical P value of 0.05, across all herbivore performance traits excluding intercepts).

Discussion

Plant domestication is predicted to cause the evolution of decreased resistance to herbivores (Herms & Mattson, 1992; Kennedy & Barbour, 1992). Using 29 independent domestication events, we found that domestication reduced resistance to one generalist leaf-chewing herbivore, whereas it had no overall effect on the population growth of a generalist aphid. We measured a range of morphological and chemical traits and found that crops only differed from their wild relatives in having slightly higher RGR. Across both herbivores, domestication altered the plant traits that were most strongly associated with herbivore performance, suggesting that artificial selection alters how plants defend themselves against herbivores. These results have important implications for our understanding of plant defense evolution and the identification of potential resistance traits to be targeted in crop breeding.

The elusive tradeoff between growth and defense

Plant defense theory predicts that evolution of increased yield will come at the expense of reduced resistance to enemies because of allocation tradeoffs between growth and defense (Coley *et al.*, 1985; Herms & Mattson, 1992; Kennedy & Barbour, 1992; Evans, 1993). Previous research generally supports this prediction (Wink, 1988; Rosenthal & Dirzo, 1997; Benrey *et al.*, 1998; Mirnezhad *et al.*, 2010), but not in all cases (Mirnezhad *et al.*, 2010; Leiss *et al.*, 2013).

We found that resistance to caterpillars was lower on crops than on wild relatives (Tables 1 and 2), but this effect was inconsistent across crop–wild species pairs (Fig. 2). Moreover, there was no consistent difference in resistance to aphids between crops and their wild relatives (Table 1). Thus, our results do not provide strong support for the predicted tradeoff between growth and defense. This conclusion is further supported by the fact that plant RGR was not significantly correlated with any measure of herbivore performance (Table 2), even though RGR was higher in crops. Our study also calls into question whether domestication itself leads to a consistent loss of defense against enemies. Indeed, we found that domestication can lead to such predicted changes, but these changes may depend on the insect's feeding guild and are dependent on the specific domestication event (Fig. 2). Overall, our findings parallel the conclusions of Meyer *et al.* (2012), who found weaker support for the generality of the impact of domestication on plant traits than is often assumed.

Allocation tradeoffs may be less important than often assumed because evolutionary changes in the rate of resource acquisition, or resource availability, can circumvent such tradeoffs (Coley *et al.*, 1985; Herms & Mattson, 1992; Reznick *et al.*, 2000; Agrawal, 2011). Another challenge is that resources are not simply allocated between productivity and defense. The inclusion of additional resource sinks (e.g. storage organs, mutualistic

interactions, competitive ability, resistance to abiotic stress, etc.) complicates predictions (Mole, 1994). Future research could test the impact of resource availability and domestication with carefully designed experiments that compare rates of resource acquisition, resource use efficiency, herbivore resistance and productivity conducted in both wild and nutrient-supplemented conditions.

The costs and benefits of plant defenses can also be mediated by ecological interactions (Strauss *et al.*, 2002; Stamp, 2003). For example, investment in plant defense can lead to opportunity costs, such as the loss of competitive ability (Coley *et al.*, 1985; Kempel *et al.*, 2011; but see Lind *et al.*, 2013). Greater plant defense can also lead to ecological costs (Simms, 1992; Strauss, 1997), such as reduced indirect defenses from predators and parasites (Chen & Welter, 2007) or reduced attraction of pollinators (Adler *et al.*, 2012). Koricheva's (2002) meta-analysis provides support for the idea that selection on defense is often mediated by opportunity and ecological costs. She found that negative correlations between fitness and defense were apparent in the field, but not under controlled environmental conditions. An important limitation of our study is that we conducted our experiments on young plants in growth chambers. Ontogeny is known to impact plant defense (Boege & Marquis, 2005), and our results could be contingent on the fact that the experiment was conducted when plants were in the seedling–sapling stage. In addition, our experiment did not control for the plant's parental environment, and thus maternal and epigenetic effects could have an impact on resistance to herbivores. To understand the generality of our results, it will be important for future experiments to examine plants in the field over their entire lifespan (ideally over multiple generations), where the presence of competing plants, additional herbivores, pollinators and predators may allow for the expression of the costs already discussed.

Effects of domestication on resistance traits

Domestication is widely thought to lead to predictable changes in multiple plant traits, including increased growth and reduced chemical resistance (Wink, 1988; Herms & Mattson, 1992). We measured numerous plant traits previously associated with herbivory, but only RGR increased significantly with domestication, whereas trichome density and LDMC showed non-significant reductions in crops (Fig. S1). Although we did not comprehensively measure plant chemistry, especially family-specific secondary metabolites (e.g. glucosinolates in the Brassicaceae), we did measure a major class of secondary metabolites (e.g. total phenolics). Overall, these results suggest that domestication does not cause predictable reductions in resistance traits against herbivores. Nevertheless, multiple traits were correlated with herbivore performance (Table 2; Fig. 3), and the traits influencing aphid performance differed from those affecting caterpillar performance. This result is further supported by the lack of a correlation between caterpillar performance and aphid growth. Thus, the impacts of domestication on the evolution of resistance to multiple enemies can be independent (Wise & Rausher, 2013).

Although domestication did not cause consistent changes in specific resistance traits, it did alter how plant traits were correlated with herbivore performance. Domestication changed the direction and magnitude of correlations between plant traits and the performance of both caterpillars and aphids. Kempel *et al.* (2011) also found that domestication of ornamental garden plant species altered tradeoffs between constitutive defense, induced defense, growth and competitive ability compared with wild species. These results suggest that, although domestication may not cause predictable changes in individual traits, it may consistently alter how plants defend themselves. Further examination of the interactions between domestication and resistance traits could provide insight into the impacts of artificial selection on plant defense.

We hypothesize that agronomic selection can have an impact on the defensive role of resistance traits in two non-exclusive ways. First, agronomic selection against certain non-favored traits (e.g. family-specific secondary chemicals) could directly increase the importance of other resistance traits in crops. Under this scenario, we would expect certain plant traits to be strongly correlated with herbivore performance only in the crop and not in the wild relative, or vice versa. This process might explain some of our results concerning caterpillar survival, as exemplified by trichome density (Fig. 3a). A second process could be indirect, where agronomic selection for increased productivity causes the correlated evolution of resistance traits. Indeed, selection on agronomic traits is well known to cause genome-wide patterns of correlated evolution because of genetic linkage and increased linkage disequilibrium as a result of population bottlenecks associated with domestication (Wright *et al.*, 2005; Meyer & Purugganan, 2013). This hypothesis might predict that specific traits have a significant impact for all plant species, but that the strength or direction of effect under agronomic selection is changed, relative to wild plants, because of correlated changes in other linked traits. These processes could explain aphid performance, as plant traits show significant main effects (across all species), as well as strong interactions with domestication history (Fig. 3c). Resistance to herbivores is often viewed as being controlled by a suite of interdependent quantitative traits (Kursar & Coley, 2003; Agrawal, 2007), and thus artificial selection on agronomic traits might frequently alter resistance in complex ways.

Conclusion

Our comparative approach revealed that domestication reduced resistance to one of the two generalist herbivores studied, but many specific domestication events did not cause differences in resistance to either herbivore. The diversity of outcomes observed emphasizes the importance of studying multiple domestication events. Further comparative studies are needed to understand how domestication alters the defensive function of specific plant traits and the genetic mechanisms underlying these effects. Our results lead to several tentative conclusions about the effects of domestication on plant defenses against herbivores. First, the impact of domestication on defense is not as consistent as often assumed. Second, allocation to defenses in crops and their wild

relatives is not limited by allocation tradeoffs. Third, the polygenic nature and complex genetic architecture of many agronomic traits is likely to cause diverse and somewhat unpredictable impacts of domestication on defense, which itself is controlled by many quantitative traits and their underlying genes. Fourth, complex trait and genetic interactions imply that resistance traits found in wild relatives might not confer the same benefits when introgressed into crops. This implies that extensive testing is required when attempting to breed resistance into crop varieties using wild relatives. Although numerous questions remain, large-scale comparative studies provide crucial insight into an evolutionary process driven by artificial selection that is of immense importance to human society.

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Supporting Information

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

Fig. S1 The impact of domestication on putative morphological and chemical plant traits.

Table S1 List of crop species and their closely related wild relatives including tissues under selection, dates of cultivation and domestication, seed sources, accession or varieties used, and references

Table S2 A comparison of the fit of four analytical approaches to test how plant traits impact herbivore performance

Table S3 Results of linear mixed-effects models (LME) analyses testing whether domestication consistently drives changes in morphological and chemical plant traits

Table S4 Best-fitting multivariate models, $\Delta\text{AIC} < 2$, explaining the variation in three herbivore performance traits

Methods S1 Methodological details of plant trait characterization.

Methods S2 Summary of focal R script for statistical analyses.

Methods S3 Phylogenetic inference and explicit analyses of resistance traits.

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