

LETTER

Plant domestication slows pest evolution

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Abstract

Agricultural practices such as breeding resistant varieties and pesticide use can cause rapid evolution of pest species, but it remains unknown how plant domestication itself impacts pest contemporary evolution. Using experimental evolution on a comparative phylogenetic scale, we compared the evolutionary dynamics of a globally important economic pest – the green peach aphid (*Myzus persicae*) – growing on 34 plant taxa, represented by 17 crop species and their wild relatives. Domestication slowed aphid evolution by 13.5%, maintained 10.4% greater aphid genotypic diversity and 5.6% higher genotypic richness. The direction of evolution (i.e. which genotypes increased in frequency) differed among independent domestication events but was correlated with specific plant traits. Individual-based simulation models suggested that domestication affects aphid evolution directly by reducing the strength of selection and indirectly by increasing aphid density and thus weakening genetic drift. Our results suggest that phenotypic changes during domestication can alter pest evolutionary dynamics.

Keywords

Agroecology, artificial selection, clonal sorting, contemporary evolution, crop ancestors, herbivory, individual-based model, pest resistance, plant breeding, plant–herbivore interactions.

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INTRODUCTION

Over the past 12 000 years, humans have domesticated hundreds of plant and animal species from wild populations. Domestication results from conscious and unconscious selection for traits beneficial to humans, as well as natural selection for growth under cultivation (Gepts 2004; Fuller *et al.* 2014). Domestication of crops and livestock has increased food supply, altered the patterns of human habitation and transformed much of the arable surface of the planet into farmland. Yet, agricultural production is under threat by many pests that cause severe economic losses (Oerke 2006). It is therefore crucial to understand how the process of domestication alters the ecology of plant–pest interactions (Turcotte *et al.* 2014). Moreover, anthropogenic activities such as agriculture can strongly influence the contemporary evolution of pests (Gould 1998; Palumbi 2001). Here, we test the hypothesis that crop domestication itself can cause pest populations to exhibit divergent evolutionary dynamics on crops compared to their wild relatives.

Crop domestication is generally associated with decreased resistance to pest insects (Macfadyen & Bohan 2010; Chen *et al.* 2015; but see Turcotte *et al.* 2014). Reduced resistance is attributed to selection against plant defences such as toxins (Wink 1988), increased host nutritional quality for consumers (Benrey *et al.* 1998), resource allocation trade-offs between growth and defence (Rosenthal & Dirzo 1997), and disruptions of tri-trophic interactions with enemies of herbivores (Chen & Welter 2007). Other studies, however, show weaker or inconsistent support for the loss of resistance in crops (Leiss

et al. 2013). One limitation of previous studies is that they often examine only a single independent domestication event (e.g. comparing maize to teosinte), and recent studies emphasise the importance of comparisons across multiple independent domestication events (Meyer *et al.* 2012; García-Palacios *et al.* 2013). We recently conducted a large comparative phylogenetic test of the hypothesis that domestication decreases resistance against pest insects. We compared the performance of two generalist herbivores from different feeding guilds (*Spodoptera exigua* and *Myzus persicae*) across 29 independent domestication events (Turcotte *et al.* 2014). Our results showed that domestication reduces plant defences in some specific crops, but in most cases it does not, which suggests weaker allocation tradeoffs than are often assumed in plant defence theory. Although our understanding of how domestication impacts ecological species interactions is improving (Chen *et al.* 2015), our knowledge of how domestication impacts the evolution of interacting species remains poor.

Agricultural pests (e.g. insect herbivores, microbial pathogens, weeds, etc.) are classic models of rapid evolution. Large-scale monocultures, containing little genetic diversity, generate strong selective pressures on pests to adapt and exploit these resources (Gould 1998; Palumbi 2001; Macfadyen & Bohan 2010). Pest species can rapidly evolve to exploit new host plants (Feder *et al.* 1994), or specialise on varieties of existing hosts including those that have been bred to be more resistant to pests (Gould 1979; Barrett 1983; Georgiou & Saito 1983; Hawthorne & Via 2001). For example, Hessian flies repeatedly evolve counter-resistance to exploit newly introduced resistant

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wheat cultivars (Rausher 2001). Finally, resistance to new pesticides (Georgiou & Saito 1983; Gould 1988; Palumbi 2001; Van Emden & Harrington 2007) and transgenic crops (Gould 1998; Tabashnik *et al.* 2004; Gassmann *et al.* 2014) often evolves within less than a decade. Although agricultural practices frequently promote pest evolution, we know little about how evolutionary changes during domestication itself drives pest contemporary evolution.

Here, we utilise experimental evolution in a comparative phylogenetic context to answer the question: Does crop domestication alter contemporary evolutionary dynamics of a pest insect? Our experiment focused on the evolution of the super-generalist phloem-feeding green peach aphid (*M. persicae* Sulzer (1776), Hemiptera: Aphididae), which is a globally important pest (Van Emden & Harrington 2007). We allowed aphid populations to evolve on replicate plants from 34 plant taxa, represented by 17 pairs of independently domesticated crop species and their close wild relatives (Fig. 1). Domestication could alter pest evolutionary dynamics in a number of important ways. First, traits associated with domesticated crops might alter selection to favour different pest genotypes and phenotypes. Second, domestication often reduces plant defences (Wink 1988; although see Turcotte *et al.* 2014), which might cause relaxed selection on pest populations feeding on crops compared to those feeding on wild relatives. Finally, the relative importance of drift and selection could change if crops support different pest densities (Wright 1931). We also used individual-based simulations to explore causative evolutionary mechanisms of our results. Overall, this study represents the first large-scale comparative examination of how domestication affects pest evolution.

MATERIAL AND METHODS

Our previous study tested whether domestication reduces resistance to generalist herbivores (Turcotte *et al.* 2014). We challenged 58 plant species, representing 29 herbaceous crops and 29 closely related wild relatives of each crop species, to damage by two generalist herbivores (*M. persicae* and *S. exigua*). Here, we examine the evolutionary changes that occurred in the surviving aphid populations, represented by 17 independent domestication events, and the plant traits that predict the observed evolutionary dynamics.

Study organisms

Herbaceous crop species were selected based on availability of closely related wild relatives. The term 'wild relatives' refers to extant descendants of the putative progenitor species or closely related wild species (Fig. 1). Estimated dates of domestication and the tissues targeted during cultivation are found in Table S1. We selected commonly used crop varieties that were not transgenically modified, without prior knowledge of their level of resistance to aphids. Wild relatives were a mixture of up to five accessions depending on seed availability. Most, 13 out of the 17 species pairs, used in this study had the same number of crop accessions as they did wild populations (Table S2). We acknowledge that crop varieties and wild populations can differ in resistance

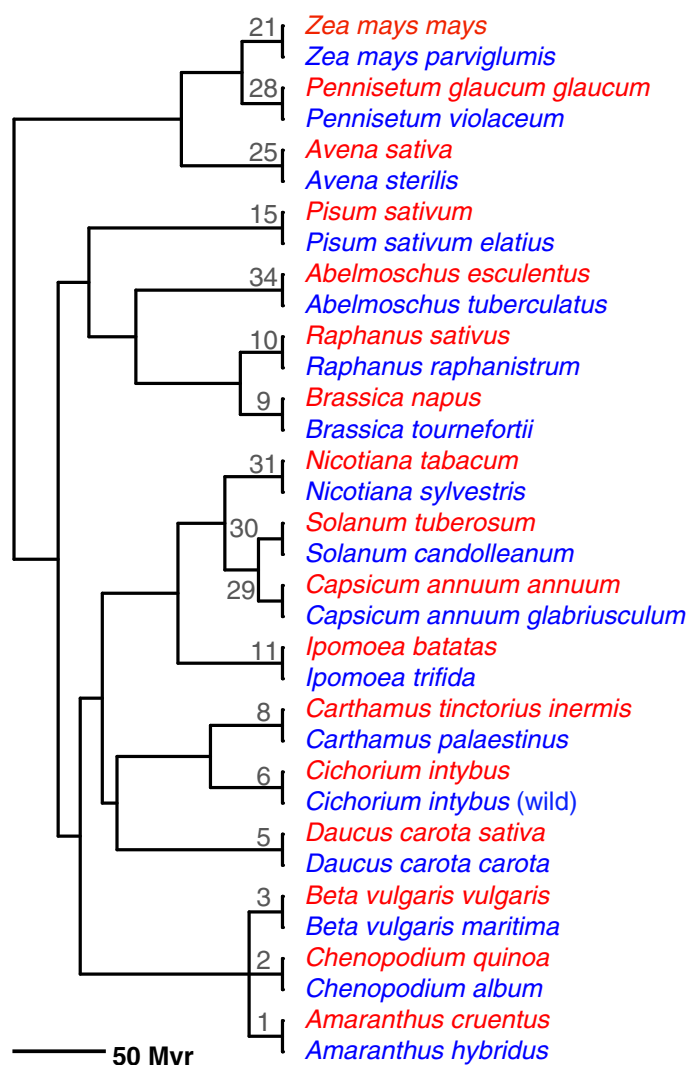


Figure 1 Phylogeny illustrating the evolutionary relationships between the 34 plant taxa used in the experiment. Each crop species (in red) is paired with a closely related wild relative (in blue) representing 17 independent domestication events. Each crop-wild species pair is identified with a pair number (in grey). The phylogeny was pruned from a large phylogeny reported in (Turcotte *et al.* 2014), which was created using Phylomatic (Webb & Donoghue 2005).

and similar variation might exist for their selective impacts on herbivores. However, we did not test for differences among varieties or accessions within species because our aim was to maximise the number of independent domestication events. Details of collections and seed sources are provided in Turcotte *et al.* (2014).

We utilised the green peach aphid to investigate how plant domestication impacts pest evolutionary dynamics. *Myzus persicae* is an important economic pest of many crops because of its global distribution, its ability to feed on 132 plant families (Normark & Johnson 2010), it rapidly evolves pesticide resistance, and spreads plant viruses (Van Emden & Harrington 2007). Due to cyclical parthenogenic reproduction, under long-day conditions, these aphids reproduce clonally within < 7 days (Mackauer & Way 1976). During this period,

M. persicae populations can rapidly evolve through changes in the relative frequency of clones (Turcotte *et al.* 2011b, 2013). Here, we used four aphid clonal lineages that were collected in 2010 from four agricultural tobacco (*Nicotiana tabacum*) fields in North Carolina, USA. The aphid clones were selected based on the criteria that they differed in growth rate on Chinese cabbage (*Brassica rapa* var. *pekinensis*) and exhibited unique genotypes using microsatellite markers (Turley & Johnson 2015). The number of aphid clones used in our experiments reflects the number of aphid genotypes that often occur on wild and cultivated plants in natural settings (Vorburger *et al.* 2003a; Vorburger 2006; M.M. Turcotte *unpublished results*). Prior to the experiment, clonal colonies were maintained on Chinese cabbage under long-day (16 h) light cycles.

Experimental design and data collection

We provide a concise description of our experimental design here and full details are found in Turcotte *et al.* (2014). All plants were grown from seed in an environmental growth chamber set to 25 °C and 55% humidity, with a 16 : 8 h light : dark cycle. Each plant was individually caged in mesh, watered regularly and fertilised with a liquid solution weekly. We grew all 58 plants species in two separate experiments; we staggered germination to have all seedlings at the 2–4 true leaf stage when treatments were applied in a randomised block design.

In August 2012, seven replicate plants per species were inoculated with 16 third instar *M. persicae*, represented by four aphids per clone. Aphids were removed from the plants and counted after 17 days (~2–3 generations). This short duration was used because evolution is typically fastest in the first generations of a selection event and plants would have incurred high mortality if the experiment ran longer. We collected 10–21 aphids (mean = 15.9, SE = 0.06) for genotyping. Populations with fewer than 10 surviving aphids were removed and species with less than three replicate populations were discarded. In the end, 17 crop-wild species pairs (34 taxa) had sufficient quantities of aphids for inclusion (Fig. 1). In total, 3333 aphids were individually genotyped from 210 populations using three microsatellite loci. Methods were modified from Turcotte *et al.* (2011a) and details are provided in Appendix S1.

We measured morphological and chemical plant traits that might impact *M. persicae*'s growth and evolution by growing six replicates of each species in March–April 2012. Plants were caged for 17 days and received no aphids. We measured leaf toughness, trichome density, specific leaf area (SLA), leaf dry matter content (LDMC), total phenolic concentration, phenolic oxidative activity, per cent carbon and nitrogen, phloem glucose concentration and relative growth rate (details in Turcotte *et al.* 2014).

Statistical analyses

We quantified the rate of evolution by calculating the Euclidean distance from the initial frequency of aphid clones on day 0 to their final frequency after 2–3 generations (day 17):

$$\text{Rate of evolution} = [(f_{1f} - f_{1i})^2 + (f_{2f} - f_{2i})^2 + (f_{3f} - f_{3i})^2 + (f_{4f} - f_{4i})^2]^{0.5}$$

where, ' $f_{\#}$ ' is the frequency of that specific clone and the subscripts 'i' and 'f' refer to the initial and final clone frequencies, respectively. In all cases $f_{\#i}$ equalled 0.25. Using these final clone frequencies we also quantified genotypic diversity using Simpson's Reciprocal Index (1/D):

$$\text{Genotypic Diversity} = 1 / \sum (f_{1f}^2 + f_{2f}^2 + f_{3f}^2 + f_{4f}^2)$$

This measure of diversity incorporates information about the number of genotypes and their evenness. High 1/D values indicate high richness and evenness. The initial frequency of clones has maximum diversity (1/D = 4), which can only decline in our experiments. In addition we quantified genotypic richness as the number of surviving clonal lineages. All three evolutionary metrics were calculated for each aphid population growing on a single plant. Finally, we quantified the outcome of evolution, or its direction, by analysing the final frequencies of aphid genotypes with an unconstrained correspondence analysis using the 'cca' function in the 'vegan' package (Okasanen *et al.* 2013) of R (R Core Team 2014). We extracted the three orthogonal correspondence analysis axis scores for each replicate population.

We first tested whether rapid evolution occurred in aphid populations. We did so using Hotelling's multivariate T^2 test by comparing the final frequency of aphid clones to their initial frequencies. To avoid collinearity we dropped the frequency of Clone 10. We tested the impact of plant domestication across all domestication events as well as the importance of unique crop-wild relative species pairs on the ecological and evolutionary dynamics of aphids. Individual populations were the unit of replication, thus each dependent variable was calculated for each aphid population separately. Evolutionary metrics (e.g. the rate of evolution) were each analysed using separate univariate linear models fit using domestication status (categorical), crop-wild relative pair (categorical) and their interaction as explanatory factors. For aphid density, we also included the author (M.M.T. or N.E.T.) that counted that replicate as an explanatory factor. We tested the significance of each factor using Type-III ANOVA's, and if the interaction was non-significant we removed it and used a Type-II ANOVA. ANOVAs were fit using the 'ANOVA' function in the 'car' package (Fox & Weisberg 2011). We complimented these analyses by testing each crop-wild relative pair individually using two-sample *t*-tests. For the direction of evolution we also tested all CA axes together using a MANOVA analysis.

Separate analyses tested whether specific plant traits influenced aphid evolution. All trait analyses used species as the unit of replication and trait data were standardised before analyses. Evolutionary metrics for each species were calculated as the average of the values of their replicate populations. We also included aphid population size (log +1) as a measure of plant resistance against *M. persicae*. We fit univariate linear mixed-effect models with domestication status and plant traits as fixed factors and crop-wild relative pair as a random factor. Models that included all plant traits and

their interactions with domestication status did not converge because of too few degrees of freedom. We eliminated four plant traits (SLA, per cent carbon, total phenolics and leaf toughness) that did not show strong correlations with any of the evolutionary metrics (Pearson's correlation tests, all $P > 0.10$) and reran the model with the six remaining plant traits (RGR, trichome density, LDMC, phloem glucose concentration, leaf per cent nitrogen and aphid resistance) and their interaction with domestication as fixed effects. We tested the 10 evolutionary response variables separately using this model. We did not adjust for multiple tests because such *post hoc* 'corrections' are often too conservative (Perneger 1998) and we focused on the most important subset of response variables. For each model we then tested the importance of the six plant traits using likelihood ratio tests that compared nested models. All tests respected marginality and were fit using 'lme' in the 'nlme' package (Pinheiro *et al.* 2014). Results from phylogenetically explicit analyses are not presented as they provided a poor fit to the data because of the near-zero branch lengths separating crops and wild relatives with large phenotypic divergence.

Individual-based simulations

We developed individual-based simulation models to better understand how drift and selection might explain our experimental results. This was motivated by the observation that aphids reached different densities when growing on crops vs. wild relatives. These models had exponential population growth and no size or age structure. Daily individual rates of survival and reproduction were parameterised with data collected from the experiment, averaged across all plant species and replicates (see Appendix S1). The analyses sampled simulations in a manner that reflected our experimental methods, with 16 aphids sampled from each of seven simulated populations.

We compared the evolutionary dynamics between simulations that included only genetic drift to simulations that incorporated both drift and selection. We manipulated natural selection by assigning each aphid clone either equal (drift only) or unequal fitness (drift and selection). Fitness differences were based on observed final frequency of clones in the experiment. Genetic drift occurred in our simulations due to the stochastic nature of the model and its relative strength was manipulated by altering population size. We conducted simulations at different final densities, including those matching the average densities observed on crops and wild relatives, as well as a wider range to explore general patterns.

RESULTS

Evolutionary dynamics of aphid populations

Aphid populations rapidly evolved in 2–3 generations (17 days) on multiple plant species. All aphid clones started at a frequency of 0.25 on day 0, and final frequencies of clones varied between 0 and 1 within individual populations. According to Hotelling's multivariate T^2 -tests, aphid popula-

tions showed significant changes in clonal frequencies on 11 (5 crops, 6 wild relatives) of the 34 plant taxa ($P < 0.05$; Table S1). This frequency of statistical significance is greater than expected by chance (binomial probability test, $P < 0.0001$, using a critical P value of 0.05). If we average the final clonal frequencies across all plants we find that it differed significantly from the initial frequency (Fig. S1, $T^2 = 16.0$, d.f. = 31, $P < 0.001$) and there was an overall selective advantage for clone 1 (Fig. S1). This same pattern occurred if we analysed either the wild relatives ($T^2 = 6.9$, d.f. = 14, $P = 0.004$) or crop species separately ($T^2 = 9.0$, d.f. = 14, $P = 0.001$). Given this evidence for rapid evolution across multiple species, we then tested the role of domestication.

Domestication slowed aphid evolution and reduced the loss of genotypic diversity and richness across the 17 crop-wild species pairs. The rate of evolution, quantified as the Euclidean distance in multivariate genotypic space, was on average 13.5% lower on crops than on their wild relatives (Fig. 2a; $F_{1,192} = 6.86$, $P = 0.01$; Table S4). This pattern is also evident in Fig. 3 where the final genotypic composition of aphid populations tended to be further from the initial composition on wild relatives than crops. Populations began at maximum genotypic diversity and richness and these values declined during the experiment. Domestication reduced the rate of this decline, with aphid populations grown on crops retaining 10.4% higher diversity (Fig. 2b; $F_{1,192} = 8.68$, $P = 0.004$; Table S4), and 5.6% greater richness (Fig. 2c; $F_{1,192} = 4.54$, $P = 0.034$). Although the identity of crop-wild species pairs was always statistically significant, there were no significant interactions between domestication and pair for any evolutionary response variable (Fig. 2, Table S4), indicating that the effects of domestication were statistically consistent across pairs.

Domestication did not consistently select for specific aphid clones. Unconstrained correspondence analysis constructed three orthogonal axes that explained 36.3, 33.4 and 30.3% of the variation in the outcome of evolution (final genotype frequencies; Table S5). Domestication did not have a significant effect on any of the axis scores (Table S6). Instead, domestication favoured different aphid clones on different crop species (Fig. 3, Fig. S2). By contrast, crop-wild species pair had a strong effect on each axis score, and domestication and species pair did not interact (Table S6). Similar results were found with MANOVA on all CA scores, where species pair was highly significant (Pillai = 0.60, $F_{48,528} = 2.76$, $P < 0.0001$) and domestication (Pillai = 0.02, $F_{3,174} = 1.25$, $P = 0.292$) and the domestication-by-pair interaction (Pillai = 0.30, $F_{48,528} = 1.22$, $P = 0.156$) were non-significant. Analyses of the frequencies of individual clones showed that three out of four clones were only influenced by pair identity (Table S6, Fig. S2). Conversely, the frequency of clone 7 was influenced only by a significant pair-domestication interaction (Table S6), suggesting that domestication did alter changes in the frequency of this clone on specific species pairs (Fig. S2).

Interestingly, wild and domesticated tobacco selected for a unique composition of aphid clones compared to other species (Fig. 3a). The clustering of wild and domesticated tobacco in the ordination shows that this result is explained by unique

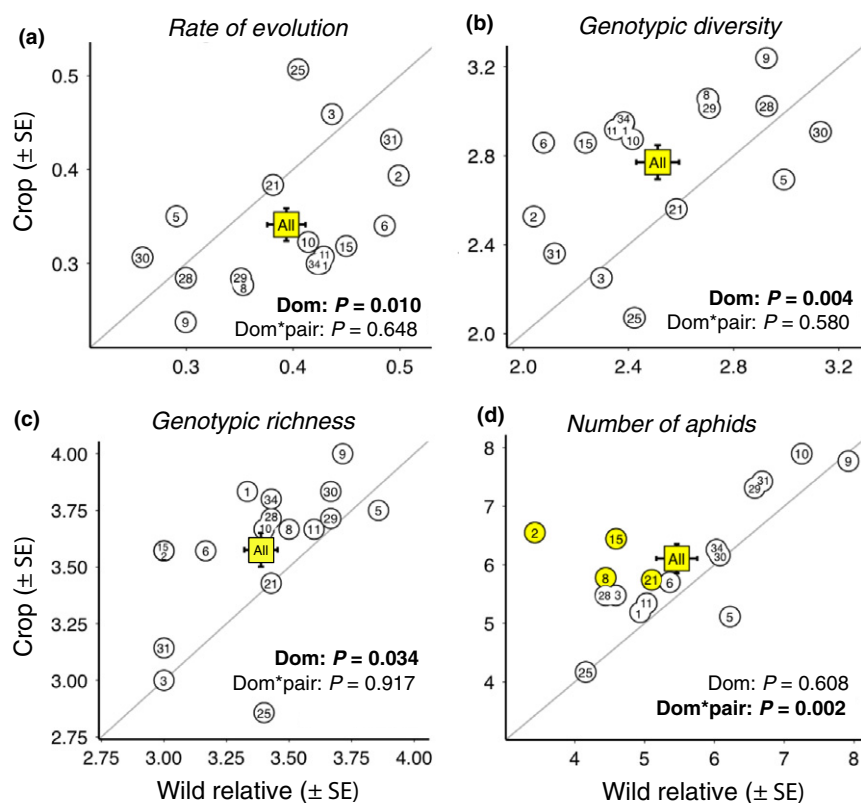


Figure 2 The evolutionary and ecological impacts of plant domestication on *Myzus persicae*. Figures represent the mean values of (a) the rate of evolution (Euclidean distance of final genotype frequencies), (b) the genotypic diversity (measured as Simpson's Reciprocal Index), (c) genotypic richness and (d) the final density of aphids after $\log_e(+1)$ transformation. Each circle represents a crop-wild relative pair and their identities are found in Figure 1. The large square represents the overall mean (\pm SE) impact of domestication across all pairs and its significance value is found in the lower right corner. Symbols filled with yellow differ significantly (according to *t*-tests) from the 1 : 1 expectation, which is represented by the grey line.

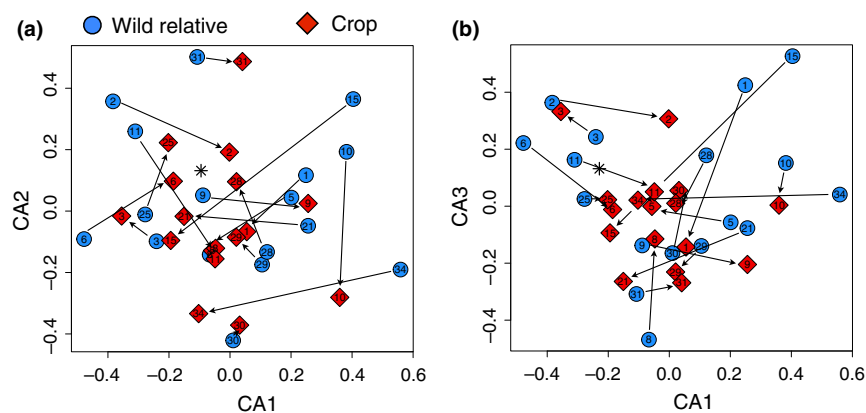


Figure 3 Multivariate analyses reveal that domestication does not consistently favour the same aphid genotypes. Points are mean unconstrained correspondence analysis scores that represent the average multivariate genotypic composition of the aphid populations on day 17 on crop species (red diamonds) and on wild relatives (blue circles). Axis loadings are found in Table S5. The '*' represents the initial frequency of clones on day 0. The direction of the arrows indicates how the genotypic composition of aphids is changing for each independent domestication event relative to their wild relative. Longer arrows suggest more extensive (or rapid) evolutionary divergence. Because arrows diverge in different directions among the crop-wild pairs, it shows that domestication in general does not favour a specific aphid clone consistently across all domestication events. Pair numbers correspond to those in Fig. 1.

characteristic of tobacco plants, as opposed to an effect of domestication. Additional analyses including all species also reveal that the tissue under selection and the date of domestication had little impact on aphid evolution (Table S7).

Plant traits correlated with evolutionary dynamics

Numerous chemical and morphological plant traits (Table S2) were significantly correlated with aphid evolutionary dynamics

and the impact of certain traits changed depending on domestication history (i.e. a domestication-by-trait interaction). The rate of aphid evolution increased with plant relative growth rate 'RGR' and decreased with aphid population size (LME, d.f. = 15, $P < 0.05$, Table S8). Conversely, genotypic diversity decreased with RGR and increased with population size. Both evolutionary response variables were influenced by the interaction between domestication and trichome density and aphid population size. Genotypic richness was influenced by the interaction between domestication and LDMC as well as the interaction between domestication and trichome density. Lastly, the final frequencies of aphid clones, analysed as univariate or multivariate metrics, correlated with different plant traits (Table S8). The effect of these traits on the direction of evolution often depended on the domestication history of the plant. All plant traits included in the analyses significantly influenced at least one measure of aphid evolution. These results suggest that variation in plant traits imposed selection on aphids and that domestication frequently altered the direction and/or strength of this selection.

Mechanisms of evolution

Both natural selection and genetic drift contributed to our results. The importance of natural selection was evident

because: replicate populations often evolved in the same direction (Table S3) and variation in plant traits were correlated with the genotypic composition of aphid populations (Table S8). However, drift could also be an important evolutionary mechanism driving the differences we observed because of variation in aphid population size. Population size is negatively correlated with the strength of drift (Wright 1931) and we found that aphids reached 91% higher final density on crops than on wild relatives (Fig. 2d, Table S4). Our previous study (Turcotte *et al.* 2014) found no difference in aphid performance due to domestication. This discrepancy occurs because here we use only those species pairs that exhibited adequate survival of aphids for genetic analyses in both the crop and wild species within each pair. As expected, final aphid density was negatively correlated with the rate of evolution (Fig. S3), and it was a significant predictor of multiple evolutionary response variables (Table S8).

Individual-based simulations suggested that both genetic drift and selection caused the observed differences in the rate of evolution, genotypic diversity and richness. First, using a wide breadth of final population sizes we confirmed that the rate of evolution and the loss of genotypic diversity and richness increased in smaller populations (Fig. 4a–c). These results remain true in simulations that included only drift or those that included drift and selection. The impact of drift on

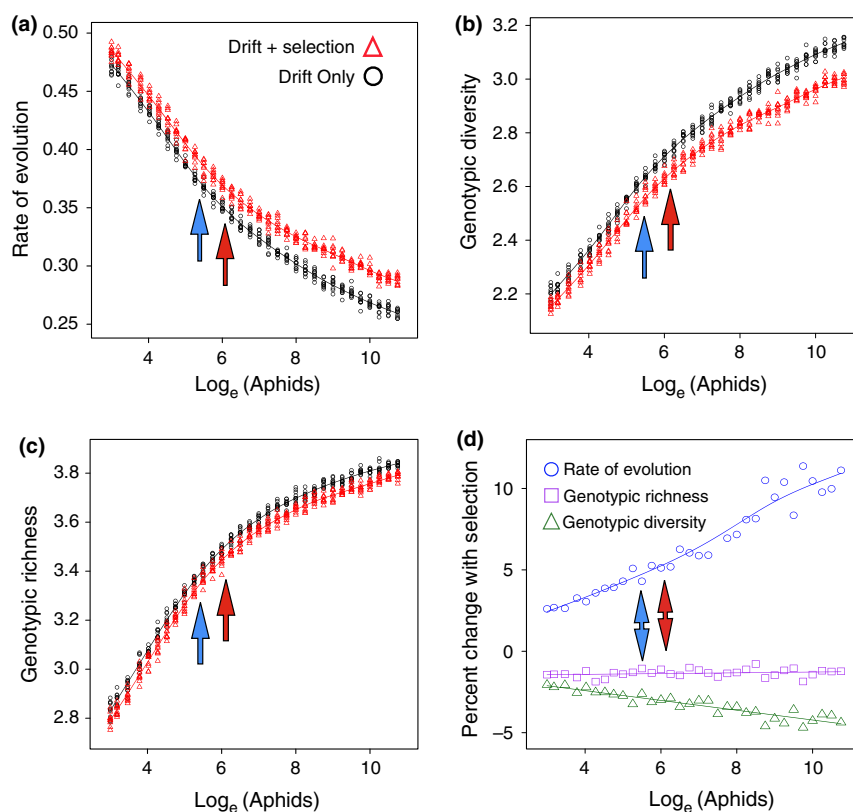


Figure 4 Simulation results exploring how population size and the presence of selection impact aphid evolutionary dynamics. Results of 10 replicated simulations at each given final population size for (a) the rate of evolution, (b) genotypic diversity and (c) genotypic richness. In these figures, black circles represent simulations where aphid clones had equal fitness (only drift), whereas the red triangles were simulations with fitness differences among clones (drift + selection). Panel (d) represents the per cent change in the three evolutionary metrics when selection is acting, calculated as $(\text{Drift + Selection} - \text{Drift Only}) / \text{Drift Only} \times 100\%$. To help visualisation we added cubic smoothing splines to each treatment and blue arrows to indicate the final mean observed density of aphids growing on wild relatives in the experiment and red arrows crops.

these evolutionary metrics declined with larger population sizes. Simulations also showed that in the presence of selection, populations evolved faster and lost more diversity and richness at all population sizes (Fig. 4d). Moreover, the impact of selection on the rate of evolution and genotypic diversity increased, whereas that of drift decreased, at higher densities (Fig. 4d).

To reveal the mechanisms driving our results, we compared aphid populations growing at densities equivalent to those observed across the experiment (wild relatives $N_f = 234$ and crops $N_f = 448$, Table S4). Under pure drift, the increase in population size from wild relatives to crops reduced the rate of evolution by 6.12% (Table 1). Next, we isolated the impact of selection on the rate of evolution by comparing simulations with pure drift vs. simulations with drift and selection. We parameterised these models using the observed density and frequency of aphids growing on all crops or growing on all wild relatives (Table S4; Fig. S1). On average, across both sets of parameters, if selection is not operating then the rate of evolution is slowed by 4.85% (Table 1). When both selection and drift operate simultaneously the rate of evolution was 7.2% slower for the parameters that matched those of aphids growing on crops than on wild relatives, which is the closest value to the observed difference of 13.5% (Table 1). Similar results were observed for genotypic diversity and richness. These results imply that both increased drift and stronger selection on wild species together caused increased evolutionary rates and reduced genotypic diversity and richness of aphid populations (Table 1).

DISCUSSION

Our experimental results provide evidence that crop domestication can impact contemporary evolution of an economically important generalist pest insect. Aphid populations diverged in genetic composition in just 17 days (2–3 generations), revealing three important results. First, domestication reduced the rate of aphid evolution by 13.5%, and maintained greater

aphid genotypic diversity and richness. Second, independent domestication events selected for different clones. Finally, simulations suggested that natural selection and genetic drift played similar roles in driving the observed differences in the rate of evolution between crops and wild relatives. These results have important implications for understanding how certain pests evolve within agroecosystems.

Evolutionary dynamics of pests in agroecosystems

Agricultural practices can favour rapid evolution in pest species. First, crops are often planted as large monocultures. Second, many crops are consistently planted year after year leading to temporal stability in the host characteristics to which pests adapt. Third, agricultural practices frequently reduce the diversity and density of natural enemies (reviewed in Chen *et al.* 2015). These three conditions can lead to strong persistent selection and large population sizes of pests that increase the rate of pest adaptation to their crop hosts (Gould 1998; Peck *et al.* 1999; Macfadyen & Bohan 2010; Gassmann *et al.* 2014). Furthermore, the widespread use of pesticides and the development of pest-resistant varieties can generate selective pressures that promote rapid pest evolution (Georghiou & Saito 1983; Gould 1998; Palumbi 2001; Macfadyen & Bohan 2010; Gassmann *et al.* 2014). Our study highlights another mechanism by which agriculture impacts pest evolution – changes in the quality of host plants due to domestication itself.

Mechanisms by which domestication impacts pest evolution

The traits associated with domesticated crops can alter the direction and strength of selection experienced by plant pests. For example, barnyard grass (*Echinochloa crus-galli*) is an economically devastating weed that has evolved morphological characteristics mimicking cultivated rice (Barrett 1983). Similarly, traits associated with domesticated crops could alter the strength or direction of selection and the evolution of pest herbivores. Our results are partially consistent with this idea. Adaptive evolution of aphids is supported in our experiment by the many plant traits that predicted changes in the frequency of aphid clones (Table S8). Furthermore, the traits that predicted aphid evolution frequently differed between crops and wild relatives. When we compare the traits that are important for aphid evolution (Table S8) to those that affect aphid performance (Turcotte *et al.* 2014), we find that only LDMC is important for both metrics. This suggests that most plant traits conferring resistance to our aphids impacted the four clones equally and thus did not contribute to natural selection among the clones. However, the impact of genetic drift was also apparent in our study (Fig. S3; Table S8). Our individual-based analyses further suggest that selection and genetic drift had roughly equal effects on slowing the evolutionary rate of aphid populations on crops. Thus, domestication altered the evolution of *M. persicae* through both adaptive (i.e. the strength and direction of selection) and non-adaptive mechanisms. Our interpretation is that domestication has consistently increased the quality of plants as hosts for aphids, and thereby relaxed selection on aphid populations while causing greater aphid density. This greater aphid density

Table 1 Simulation results comparing the impact of an increase in population size and the absence of selection on aphid evolutionary dynamics

	Observed (%)	Simulated		
		Increase in N_f : Drift only (%)	Increase in N_f : Drift + Selection (%)	Removal of selection (%)
Rate of evolution	–13.5	–6.12	–7.22	–4.85
Genotypic diversity	+10.4	3.88	4.94	3.15
Genotypic richness	+5.6	3.17	3.46	1.5

The results shown represent the per cent difference in evolutionary dynamics for aphids growing on crops and wild relatives. The simulations show how an increase in final aphid density (N_f) equivalent to that observed (Wild relative = 234 and Crop = 448) impacts the evolutionary metrics under pure drift or drift + selection. The last column represents the average effect of removing selection that was calculated by comparing simulations with and without selection at both densities.

on crops compared to wild relatives has ultimately modified the balance between selection and drift.

Evolution of different types of pests on crops

The feeding guild of herbivores could influence how domestication impacts pest evolution. Although our study utilised a single highly polyphagous phloem-feeding herbivore, our recent research on a polyphagous leaf chewing caterpillar (*S. exigua*) suggests that other feeding guilds may exhibit similar evolutionary responses (Turcotte *et al.* 2014). *Spodoptera exigua* exhibited higher survival on a diverse assemblage of crops than wild relatives, and as with aphids, domestication altered which traits predicted resistance. This could lead to differential selection on this caterpillar by crops vs. wild relatives and increased genetic drift on wild relatives. Whether these patterns translate into altered evolutionary dynamics in *S. exigua* and other generalist herbivores from various feeding guilds requires further study.

The extent of specialisation by pests could also impact patterns of evolution (Cornell & Hawkins 2003). A comparison of the final frequencies of aphid clones (Fig. S1 and S2) across all plant species suggest that clone 1 is either a better competitor than other clones, or it represents what Lynch (1984) called a GPG (general purpose genotype) – a genotype with broad ecological tolerances and high fitness across environments. Clone 1's ability to increase in frequency on all but 2 of 34 species (Fig. S2), might help explain the dominant presence of certain aphid genotypes in nature (Vorburger *et al.* 2003b). By definition, specialist pest species do not have GPG and their evolutionary dynamics might differ greatly. Some specialists can detoxify defensive compounds (Karban & Agrawal 2002), utilise secondary metabolites as oviposition and feeding cues (Renwick 2002), or sequester them as defences against natural enemies (Kazana *et al.* 2007) leading to similar or better performance on defended than on undefended plants. Based on these observations, one might predict that specialist insects will exhibit similar or reduced selection on crops and exhibit a different pattern than the generalist aphid we studied. Experiments comparing the evolutionary dynamics of specialist pests are needed to test these important problems.

Implications and conclusions

Our comparative experimental evolution approach revealed that crop domestication can affect the evolutionary dynamics of an aphid pest in a predictable fashion. Therefore, to understand how pest species evolve under agricultural conditions, it is important to account for ecological changes related to cultivation, application of pesticides, breeding of resistance, as well as changes in plant traits themselves that occur during domestication. Although our study focused on the asexual phase of aphid reproduction, such short-term evolutionary dynamics can lead to the elimination of low fitness genotypes from populations. Recent field and greenhouse experiments also show that rapid evolutionary change, even in the absence of pesticides, can greatly alter population dynamics (Turcotte *et al.* 2011b, 2013). Thus, understanding the evolutionary dynamics of pest species is of great importance because it could help identify the best approaches one should use to

control herbivore densities and prevent the evolution of resistance (Georghiou & Saito 1983; Gould 1998; Rausher 2001; Tabashnik *et al.* 2004; Hufbauer & Roderick 2005).

Finally, the use of comparative experimental research is a promising approach to further our understanding of the consequences of domestication (Meyer *et al.* 2012; García-Palacios *et al.* 2013; Turcotte *et al.* 2014). Our main results would not have been apparent had we only studied one or a few domestication events and suggests that our conclusions are robust to the inclusion of different crop varieties or wild accessions. Future studies should utilise comparative approaches to explore the evolutionary dynamics of different types of enemies such as specialists or plant pathogens. In addition we will need to unravel the impact of domestication on more complex and natural communities including herbivore enemies (Gould *et al.* 1991; Chen & Welter 2007; Chen *et al.* 2015), as well as quantify the relative importance of how domestication itself vs. agricultural practices impact pest evolution.

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AUTHORSHIP

All authors helped design the research. MMT, AKL and NET conducted the experiments and collected the data. AKL conducted the genotyping. MMT acquired seeds, performed statistical analyses, created the simulations and wrote the manuscript. All authors contributed to revisions of the manuscript and analyses.

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