

Crop Domestication and Its Impact on Naturally Selected Trophic Interactions

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Annu. Rev. Entomol. 2015. 60:35–58

First published online as a Review in Advance on October 8, 2014

The *Annual Review of Entomology* is online at ento.annualreviews.org

This article's doi:
10.1146/annurev-ento-010814-020601

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Keywords

agroecosystem, plant resistance, natural versus agricultural, artificial selection, insect herbivores, natural enemies

Abstract

Crop domestication is the process of artificially selecting plants to increase their suitability to human requirements: taste, yield, storage, and cultivation practices. There is increasing evidence that crop domestication can profoundly alter interactions among plants, herbivores, and their natural enemies. Overall, little is known about how these interactions are affected by domestication in the geographical ranges where these crops originate, where they are sympatric with the ancestral plant and share the associated arthropod community. In general, domestication consistently has reduced chemical resistance against herbivorous insects, improving herbivore and natural enemy performance on crop plants. More studies are needed to understand how changes in morphology and resistance-related traits arising from domestication may interact with environmental variation to affect species interactions across multiple scales in agroecosystems and natural ecosystems.

Domestication:

process of artificial selection by which populations are adapted to the conditions of cultivation and human taste

Crop: any cultivated plant that is harvested for human use

Cultivation: activities that are associated with the rearing of crops in agriculture, such as tillage, fertilization, and pest control activities

Tritrophic interactions:

interactions among plants, herbivores, and their natural enemies

Wild ancestor: wild species that was selected upon to create a domesticated crop

Species interactions:

positive and negative associations between species

Natural ecosystem:

natural unit comprising interacting endemic organisms and an environment that is free of human management

Agroecosystem:

organisms and environment in an agricultural area, which are collectively considered an ecosystem

INTRODUCTION

The domestication of agricultural crops has been considered a key historical innovation that enabled the development of large, complex civilizations (55). Crop plants have been deliberately selected by humans for desirable traits and to be adapted to the conditions of cultivation (52, 133). There is accumulating evidence that crop domestication has profoundly altered tritrophic interactions between plants, insects, and their natural enemies. In general, domesticated crop plants tend to possess more exaggerated physical traits (52, 131, 133), simpler morphologies (32, 46, 52, 124), altered nutritional content, and reduced plant defenses (56, 81, 93, 136) compared with their wild ancestors. Although the major orders of phytophagous insects arose ~300 Mya (130), the oldest archaeological remains of domesticated crops are only ~13,000 years old (73). Therefore, phytophagous insects and their natural enemies evolved with wild crop ancestors for hundreds of millions of years prior to all domestication events. Given that the traits of domesticated crops have arisen from artificial selection rather than natural selection, domesticated crop phenotypes are likely to be ecologically novel with respect to species within higher trophic levels. A key question, then, is to understand how domestication has shaped plant traits and how, in turn, these plant traits may influence species interactions in agriculture.

No previous review of crop food webs has explicitly controlled for the biogeographical origins of the crops, herbivores, and natural enemies to determine how endemic insects adapted to wild progenitors respond to phenotypic traits that have been altered by domestication. Although variation in plant traits has been widely reviewed before (83, 110, 114), only a subset of studies have examined how species interactions differ between natural ecosystems and agroecosystems. Moreover, most studies on tritrophic interactions focus on crop taxa that are not native to the study region or that involve arthropods that do not share significant evolutionary history with the study plant (51, 113, 122, 143). These studies contribute to understanding insect ecology, but the lack of shared phylogenetic history between wild and cultivated plants limits their relevance for understanding how crop domestication has influenced the ecology and evolution of species interactions. To isolate the specific effects of domestication, we focus on agricultural systems that occur near or within the geographic regions where the crop species originated or on studies that explicitly account for insect-plant coevolutionary history. Most of the major domesticated crops originated from a limited set of geographic regions (149) that are known as Vavilov's centers of origin (52). Within these centers of origin, wild crop ancestors are sympatric with domesticated crops and share arthropod assemblages (67), which have likely been associated with wild ancestors for millions of years prior to crop domestication.

Domestication and cultivation are distinct human activities that strongly influence plant phenotypic variation, and a large proportion of the phenotypic variation observed in domesticated crops can be explained by genetics (86). Many domesticated crops possess a suite of selected characteristics, which have collectively been called the domestication syndrome (52, 64). This syndrome includes the following major traits: reduction or loss of means of dispersal, brittle rachis, reduced grain shattering, reduction or loss of dormancy, more compact growth habit, early maturation, increased size and biomass of plant structures (gigantism), photoperiod insensitivity, and reduction or loss of toxic compounds (52). The traits that characterize the domestication syndrome have been considered to be more applicable to annual crops than to perennial, tree, or shrub crops (99).

Recent reviews on plant domestication (45, 99, 112) have linked the emergence of domesticated forms to the specific molecular mechanisms involved in the artificial selection of cultivated crops. However, these and previous reviews have not specifically examined how selection on traits typical of the domestication syndrome may influence tritrophic interactions. The present review explores the consequences of crop domestication on the ecology and evolution of the interactions

between plants, herbivorous insects, and their natural enemies. We discuss the changes in phenotypic characteristics of the domestication syndrome and highlight the importance of controlling for phylogenetic relationships and geography by isolating the direct effect of crop domestication on species interactions. We review studies examining how plant and insect interactions may differ in agroecosystems and in the natural ecosystems of their wild ancestors. We examine changes in morphological, chemical resistance, and infochemical traits in relation to domestication and how these changes may influence behavioral and physiological patterns of herbivore–natural enemy interactions. Finally, we discuss emerging patterns and opportunities for further research uncovered by this review.

Geography Underlies Interactions Between Insects and Domesticated Plants

The archaeological record and genetic data point to distinct geographic regions where most crops were initially domesticated (94, 99, 105), whereas wild ancestors frequently occur over broad geographic ranges (133). Among the 203 crops reviewed by Meyer et al. (99), 88% were first domesticated within the native range of their wild progenitors. Therefore, insect species associated with the wild progenitor likely share the longest evolutionary history with the crop. In general, the endemic insect biodiversity associated with wild ancestors has been largely undescribed, a void evident within databases on lepidopteran host associations (92). Because of their historical association with the plant genera from which crops were domesticated, differential responses of endemic insects to wild progenitors and domesticated crops can provide insight on how crop domestication has altered species interactions. We used specific criteria to select studies for our review: (a) studies that explicitly compared species interactions on a crop and its wild progenitor, (b) field studies that were conducted within the natural range of the wild ancestor to sample endemic insect species, and (c) laboratory studies in which insects and plants originated from the native range of the wild progenitor. A study that did not fit these criteria was included only if the key findings were not influenced by biogeography or species identity.

Domestication as an Evolutionary Process

Crop domestication has long been viewed as an evolutionary process in that the development of new and improved cultivars is based on selection (55). In contrast to natural evolution, domestication is due to humans as selective agents; but, just like natural selection, domestication fully depends on genetic variation, mutations, inheritance, and demography (42, 112, 123). The evolutionary history of crop plants can be quite complex because they can be derived from single or multiple domestication events, subject to multiple selective agents (see sidebar Crop Domestication as a Dynamic Process Driven by Human Practices). Domestication may vary in the strength of selection, amount of human-assisted migration, and level of hybridization during the formation of the crop (97). Whereas crops such as *Brassica oleracea* Italica group (broccoli), *Daucus carota* subsp. *sativus* (carrot), and *Oryza sativa* (rice) are derived from a single wild species, other crops, such as *Fragaria* × *ananassa* (strawberry), *Triticum aestivum* (wheat), and *Lactuca sativa* (lettuce), are derived from hybridization between two or more distinct species (48, 147). Because of the global importance of crops for food security, the majority of the published plant genome sequences are of crop plants. The availability of these genomes has enabled a greater resolution of the domestication history, specific geographic origin (94, 147), and particular genomic changes underlying crop phenotypes (65, 112).

The emerging consensus is that domestication causes a distinct imprint on crop genomes (45, 112). Although introgression from secondary hybridization events can raise genetic diversity

Center of origin: geographical area where a group of organisms was first domesticated and where they are native

Domestication syndrome: suite of traits that commonly differ between wild and domesticated plants

Morphological traits: characteristics that refer to the structural form and that can be measured or quantified

Plant chemical resistance: reduction or prevention of herbivory by compounds produced by plants

CROP DOMESTICATION AS A DYNAMIC PROCESS DRIVEN BY HUMAN PRACTICES

Crop domestication is a dynamic and continuous process that strongly reflects human tastes and styles of crop production. By definition, the centers of domestication are genetically diverse because they include modern cultivars, local varieties or landraces, and hybrids that are the result of past and present human selection. Within the centers of crop origin, wild plants, landraces, cultivars, and weedy types can coexist in the same region (14). The great diversity of local landraces is often maintained by different traditional agricultural practices carried out by different ethnic groups within a heterogeneous environment (3, 15). Moreover, the use and management of wild and weedy species within traditional agricultural practices may involve artificial selection, resulting in the initial or incipient phases of plant domestication (23). It is not uncommon for indigenous farmers to combine the use of crop plants with the management of wild and weedy types or to use traditional agricultural systems in which several crops are grown together. In Mesoamerica, for example, some ethnic groups use 5,000 to 7,000 plant species, many of which have been described to be in an incipient state of domestication (24). Within these centers, varying management intensities in different localities may cause the same species to display wide variation in morphological and chemical traits such as the loss of chemical resistance (12). However as Thrall et al. (142) state, spatiotemporal patterns, plant population sizes, plant isolation and dispersal, and genetic variation likely differ, for both the plants and associated species, between native ecosystems and agroecosystems.

throughout the genome (147), domestication typically causes losses in genetic diversity throughout the genome through genetic drift and bottlenecks (65, 99). For traits under artificial selection, traits associated with the domestication syndrome appear to be determined by only a few genomic regions (65, 112). Artificial selection on desirable traits can result in a distinct loss of genetic variation within targeted regions, resulting in a molecular signature of positive selection, or a selective sweep (112). Because many of the quantitative trait loci under selection during domestication are physically clustered, multiple traits associated with the domestication syndrome can be rapidly fixed within a population (44, 63, 140). This is the case of maize, where relatively few clustered genes are responsible for significant differences between teosinte and maize (44).

Domestication can influence species interactions either by changes in expression of single genes associated with resistance or through selection on quantitative traits. The genetics underlying domestication syndrome traits can be due to regulatory changes and/or protein changes in particular genes, structural variation, transposable elements, or genome duplication (45, 112). Although some domestication traits have been shown to be due to recessive alleles, other traits act in a dominant manner (18). For instance, the gene *Terpene Synthase 23* catalyzes the production of (*E*)- β -caryophyllene from farnesyl diphosphate. (*E*)- β -caryophyllene is a component of maize volatile emissions, which have been shown to be important for recruiting entomopathogenic nematodes and parasitic wasps. *Terpene Synthase 23* is transcribed at a very low level in North American varieties, suggesting a regulatory region has been inadvertently altered by artificial selection (84). In contrast, the progenitor of domesticated maize, teosinte, and European maize varieties express this gene and emit volatiles in response to herbivory (84). On the other hand, selection on quantitative traits associated with the domestication syndrome may result in inadvertent trade-offs in growth. For instance, in the sunflower (*Helianthus annuus*), the phytomelanin layer, a hard, blackened layer within the seed coat that protects the seed from herbivory (78), maps to the same region as apical branching (140). Therefore, selection for reduced branching appears to be associated with reduced physical defenses against herbivory.

Quantitative trait locus: a DNA region that is associated with characteristics that display continuous variation

Domestication genes are the genes that underlie the major shifts in plant traits during domestication. Because they are generally maladaptive in the wild, domestication genes are projected to be at low frequencies within wild populations (139). In contrast, genes associated with resistance to herbivores can be expected to be more prevalent in populations of wild ancestors because they are more likely to be under selection, but they may be more varied in their occurrence (104, 137). Indeed, genetic variation exists within the wild ancestor–crop gene pool for plant traits associated with herbivore resistance (21, 47, 137). Large-scale screenings have shown that populations of wild ancestors vary considerably in resistance to insect herbivores, and the percentage of resistant accessions may vary from 1% to 45% within populations (21, 35, 50, 121). We did not find comparative screening efforts for the effects of plant resistance on natural enemies.

There is increasing interest in understanding how evolutionary processes at the level of individual species can affect the ecology of entire communities (79). Although the genes that underlie domestication are being characterized with increasing frequency (45, 65, 112), less is known about how domestication favors the presence and expression of genes that are important in species interactions. Crop domestication systems are ideal systems for understanding how selection on plant genomes can influence community-wide effects. Ultimately, this knowledge can guide breeding efforts and determine the feasibility of reintroducing ecologically important genes back into commercial agricultural germplasm.

Currently, the genetic diversity found within wild-weedy-domesticated complexes is highly valued for plant conservation and breeding programs (156). However, the arthropod diversity associated with wild ancestors, landraces, and weedy species, and the genetic diversity within species, has not yet been widely considered for breeding purposes. Nevertheless, wild-weedy-domesticated complexes in domestication centers can play a key role in maintaining biodiversity and genetic diversity of herbivores and their natural enemies. Conservation of insect genetic diversity may be especially important if insect populations are structured by their association with wild or cultivated plants. Recent studies reveal current and ancient events that have shaped the evolution of multitrophic assemblages (4, 88), such as human-mediated dispersal, founder effects, genetic drift, human selection, and local environmental selective pressures. These factors may act alone or together to cause different evolutionary dynamics for insect populations attacking domesticated and wild plants. For example, human-mediated migration has been identified as a key factor influencing the population genetic structure of corn leafhoppers (*Dalbulus maidis*) (98) and bean beetles (*Acanthoscelides obtectus*, *Zabrotes subfasciatus*, and *Z. sylvestris*) associated with wild and domesticated plants (4, 61).

Landrace: local variety of a plant species that has developed over time under a traditional farming system

Weedy type: plants often descended from hybridization between wild and cultivated plants

TRITROPHIC FIELD PATTERNS IN AGROECOSYSTEMS AND NATURAL ECOSYSTEMS DOMINATED BY WILD ANCESTORS

Although insect herbivores have been widely observed to be more abundant in agroecosystems than in natural ecosystems (51, 113, 125, 144), most studies have focused largely on how plant diversity or landscape diversity contributes to insect abundance (5, 91, 113, 119, 128, 144), rather than on how domestication specifically contributes to patterns of species interaction. To understand how plant domestication can shape patterns of species interactions, researchers must conduct field studies within the geographic region of crop origin and consider the shared evolutionary history between endemic herbivores and the plant species. Agroecosystems and natural ecosystems differ in several factors besides the presence of the crop or wild plant: Plant density, annual tillage, phenology, fertilization, and irrigation are factors that can directly shape patterns of insect community structure and function (**Figure 1**; 33, 36, 95, 152). The nature and magnitude of

insect interactions with wild and domesticated plants may differ at multiple spatial scales between agroecosystems and natural ecosystems (**Figure 1**). In addition, plant phenotypes observed in the field are influenced by genetic and environmental variation. Domesticated and wild plants have been selected to respond differently to nutrient availability (54), which further deepens differences in plant phenotypic variation across natural ecosystems and agroecosystems (152). Comparing the effects of traits at the levels of the individual, population, and habitat on herbivore and natural enemy behavior and efficacy can help resolve the relative contributions of domestication history (genetic) and cultivation patterns (environment) to species interactions (**Figure 1**). Finally, crop domestication has selected for plants that respond positively to cultivation (86); crops and wild ancestors may display trade-offs in growth and defense against herbivores based on the habitat in which they were selected (152).

Within agroecosystems, domesticated crops tend to be more frequently attacked and suffer higher levels of herbivory than wild ancestors (32, 38, 123). When crops and wild ancestors are grown next to each other within agroecosystems, insect biodiversity may be similar (32). When grown together in a nutrient-poor natural ecosystem, domesticated crops and wild ancestors may appear more phenotypically similar and therefore experience similar attack rates (38). Because most common garden studies are conducted in agroecosystems and not natural ecosystems, the relative importance of genotype versus environment has not been resolved, and the possibility of trade-offs in growth and herbivory in relation to nutrient availability has not been fully explored.

Comparisons at the field level have shown that the insect community is less diverse, with dominance concentrated in fewer species in agroecosystems than in natural ecosystems dominated by wild progenitors (25, 33, 36, 100). Losses in species richness can reach 50%, demonstrating that food webs tend to be far simpler in agroecosystems than in related natural ecosystems (33). For example, grasslands dominated by *Oryza rufipogon* supported seven times more taxonomically unique species than fields of cultivated rice, *O. sativa* (33). Also, many herbivorous species are common in wild populations of *H. annuus* but rare in cultivated *H. annuus* agroecosystems (100). Therefore, large-scale differences in biodiversity, community structure, and function exist between agroecosystems and natural ecosystems. A greater focus on these interactions may explain how herbivorous species are controlled in natural ecosystems. It is important to note that domestication may also enable plants to grow under particular cultivation practices. For instance, selection for rapid annual plant growth of rice (*O. sativa*) has enabled frequent tillage of cultivated fields, reducing the abundance and diversity of the detrital food web, which is an alternative food source for invertebrate predators (33).

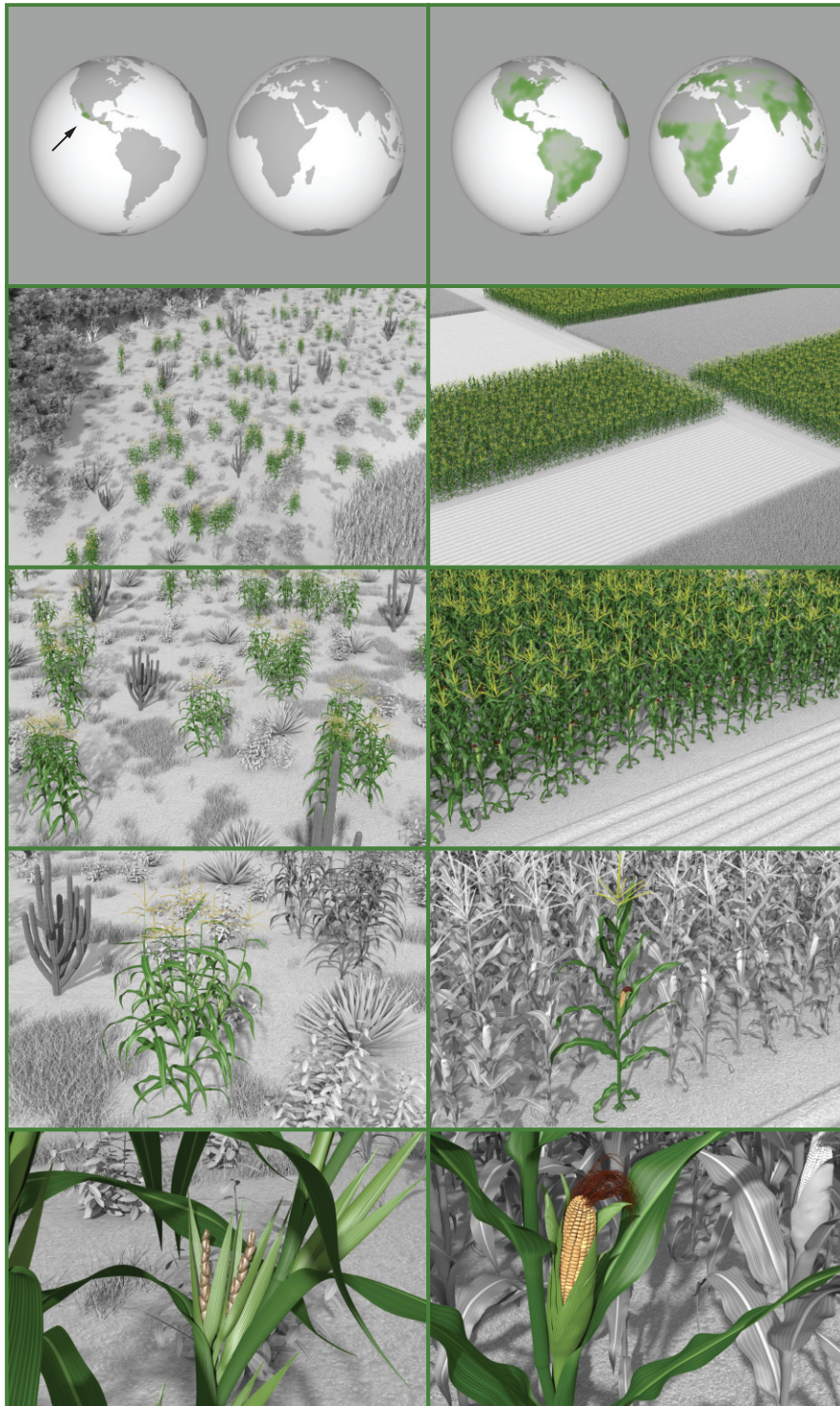
In agroecosystems such as sunflowers and cranberries, most insect herbivores do not attain outbreak densities, suggesting that they are regulated by natural enemies (26, 29, 96, 117). However, a subset of insect herbivores are able to exploit domesticated crops and become pests, attaining densities that can be 30 to 800 times greater than in natural ecosystems (33, 36, 69, 101, 103). There are many possibilities as to why insect herbivores differ in their ability to exploit host plants in agroecosystems. On the one hand, losses in biodiversity may occur in the transition

Figure 1

Wild ancestors and domesticated crops incorporate different levels of phenotypic variation at the plant level and at higher spatial scales owing to habitat heterogeneity and agricultural management. For instance, teosinte plants (*left*), the wild progenitor of maize and maize plants (*right*), are phenotypically different at the level of plant traits and at the individual plant level. Plants respond to differences in abiotic conditions that are found in agroecosystems and natural ecosystems, which contributes to differences in species interactions at increasing spatial scales (from *top* to *bottom*: region, landscape, habitat or field, individual plant, plant trait).

Wild ancestor: teosinte

Crop: maize



Region

Climate
Elevation
Time since crop introduction
Biogeographical history

Landscape

Frequency of disturbance
Habitat diversity

Habitat or field

Plant species diversity
Plant species density
Soil community and nutrients
Plant genetic diversity
Frequency of disturbance
Tillage
Apparency

Individual plant

Plant architecture
Branching
Plant phenology
Chemical defense
Infochemical induction
Nutrient composition

Plant trait

Gigantism
Trichomes
Tissue toughness
Morphology
Shattering

from natural ecosystems to agroecosystems if insects are habitat specialists and unable to adapt to cultivated conditions (33), if herbivores vary in their response to the plant changes associated with domestication (32, 155), or if a small number of insect species are able to exclusively feed on the domesticated crop for their entire development (69, 77). On the other hand, domestication may weaken plant defenses, allowing generalist herbivores to be more successful in agroecosystems (56). Furthermore, even within a species, some insect herbivore genotypes appear to vary in their potential to become insect pests in agroecosystems (76, 98, 151).

The effects of cultivation on the diversity and impact of natural enemies vary by system and herbivore species. Parasitoids associated with different herbivores may be more diverse and have a greater impact in natural sunflower ecosystems than in agroecosystems (30, 36, 141), may be similar in diversity and impact (27, 111), or may have greater impact in agroecosystems (27). Predators were more abundant in natural ecosystems of wild rice than in irrigated rice agroecosystems, suggesting that the structural complexity and greater habitat persistence in wild rice enable a much more complex and diverse predator trophic level (33). Parasitoids in agroecosystems and natural ecosystems may be genetically differentiated in their behavior, suggesting that different habitats can exert selective effects on foraging behavior (148). Overall, how cultivation of domesticated crops influences natural enemy diversity and activity is still largely unresolved.

EFFECTS OF CROP DOMESTICATION ON TRITROPHIC INTERACTIONS

Major Patterns

Tritrophic interactions can be extraordinarily complex, and plant traits can influence herbivore species and their natural enemies in different ways (see sidebar Plant Resistance to Insect Herbivores Involves Multiple Traits). Insect herbivores with different feeding strategies might differ in how they are affected by changes in plant chemistry, morphology, or phenology, which determines their ability to exploit domesticated plants. For example, stem-boring species may be more affected by changes in plant architecture and organ enlargement, whereas leaf-feeding and sap-feeding herbivores may be more affected by changes in nutrient quality (32). Plant resistance levels can increase in response to herbivory; so-called herbivore-induced defenses are well documented (1, 82). Domestication may reduce the expression of induced defenses (137) or have no effect (6, 120).

Domestication has been hypothesized to directly alter the ability of plants to defend themselves against herbivore attack. Because plant metabolites are required for both growth and

PLANT RESISTANCE TO INSECT HERBIVORES INVOLVES MULTIPLE TRAITS

In natural ecosystems, plants have evolved a range of traits, such as chemical and morphological adaptations that reduce or prevent herbivory. These resistance strategies are often divided into traits that directly interfere with herbivore behavior or physiology and traits that indirectly influence the activity of the herbivores' natural enemies. Constitutive defenses are defenses that are continually expressed, whereas induced defenses are defenses that are increased following herbivory. In general, gross morphological traits such as the extent of branching and overall size are more strongly associated with variation in herbivory across plant and insect species (22). Resistance traits—chemical and morphological, direct and indirect—are often dynamic and change in response to variation in abiotic and biotic factors (129), as well as with plant ontogeny (7).

resistance (72), increased selection for yield may result in a trade-off in resistance (123). In several systems, trade-offs have been found between growth and resistance along a domestication gradient, supporting the assertion that selection for higher yields has reduced the ability of crop plants to limit herbivory (8, 43, 123, 153). However, the existence of trade-offs between yield and resistance has been examined in only two annual crops: lima bean (*Phaseolus lunatus*; 6) and maize (*Zea mays*; 43, 123). Although Turcotte et al. (145) found evidence that domestication reduced resistance to a generalist herbivore across 29 crop species, they did not find evidence of strong trade-offs between plant productivity and resistance. It is possible that trade-offs would be observed if specialist herbivores adapted to the wild progenitor were used instead of generalist herbivores. Plants may allocate proportionally greater defenses for protection against specialist herbivores.

In spite of an extensive review of the literature, we found relatively few studies that directly examined the effect of domestication on species interactions that fit our review criteria. We used different combinations of the search terms “wild” or “wild ancestor” or “wild progenitor”; “cultivated” or “domesticated” or “agricultural”; “natural ecosystems” or “wild ecosystems”; and “cultivated ecosystems” or “agricultural ecosystems” or “agroecosystems” within Web of Science and CAB Abstracts. We also searched the two databases for plant resistance screening studies. Combining these with studies of crop domestication and molecular evolution of crops under domestication, we developed a library of 1,532 studies. We then examined where each study was conducted and whether the area of study corresponded with the geographic distribution of the wild progenitor (133). We found that the effects of domestication on species interactions have been examined in only 12 crops (**Table 1**). In general, domesticated plants are more likely to be attacked by herbivores and support higher herbivore densities under cultivated conditions (32, 38, 137, 138, 154). Insect herbivores prefer to oviposit on domesticated crops rather than their wild progenitors (all studies testing this relationship, $N = 17$). Herbivores perform better, developing faster and achieving higher body weights on domesticated crops than on their wild ancestors (all studies, $N = 17$). Consistent with these performance results, in all of the studies that examined plant chemistry (11 out of 25), crop domestication led to a decrease in secondary metabolites associated with resistance, which corroborates the observations by Meyer et al. (99), who found a decline in levels of secondary metabolites across 203 separate crops.

Although crop domestication has clearly favored herbivore growth and abundance, the effects on the performance and abundance of natural enemies are less clear (**Table 1**). In the studies cited in **Table 1**, parasitoids were more likely to survive and have better performance on herbivores feeding on domesticated crops. However, many studies have been conducted exclusively under laboratory conditions, so it is unclear how increased parasitoid performance on domesticated crops may influence pest control, especially because other factors may influence natural enemy impact in the field (**Figure 1**). For example, parasitoid performance in the laboratory is not necessarily correlated with parasitoid performance in the field (155). Domestication can also negatively affect natural foraging behavior, host location, and access to insect herbivores (37–39).

The studies cited in **Table 1** focus on insect herbivores that are known agricultural pests. This emphasis on pest taxa may bias the assessment of domestication because insect herbivores that become pests may have intrinsically better performance on domesticated crops, enabling them to be more successful as pests in agricultural systems. It can be expected that herbivore guilds vary in their responses to crop domestication and cultivation, which may explain the observed absence or scarcity of some insect herbivores in agroecosystems (32, 33, 100). Without an examination of how nonpest herbivores respond to domestication, the asymmetry in the selection of insect taxa limits the development of a realistic perspective as to how crop domestication has influenced species interactions.

Table 1 Trait alteration in cultivated compared with domesticated plants and its effect on herbivores and their natural enemies^a

Crop (genus)	Crop selection trait of interest	Herbivore	Impact on herbivores (cultivar versus wild)	Natural enemies	Impact on natural enemies (cultivar versus wild)	Reference(s)
Bean (<i>Phaseolus</i>)	↑ Seed size (Morph/Chem) ↓ Lectin protein arcelin	<i>Zabrotes subfasciatus</i> (S), <i>Acanthoscelides obtectus</i>	↑ Survival ↑ Performance ↑ Oviposition	NA	NA	21
	↑ Seed size (Morph/Chem)	<i>Zabrotes subfasciatus</i> (S)	NA	<i>Stenocorse bruchivora</i> (S), <i>Dinarmus basalis</i> (G)	Host selectivity S > G ↑ Parasitism success G ↓ S depends on parasitoid origin	19, 20
	↑ Seed size (Morph/Chem)	<i>Zabrotes subfasciatus</i> (S)	↑ Development ↑ Body mass ↓ Beetles per seed Ø Oviposition	<i>Stenocorse bruchivora</i> (S)	↑ Body mass	9
Broad bean (<i>Vicia</i>)	↓ Trichome density ↑ Nonprotein amino acids (Morph/Chem)	<i>Acyrtosiphon pisum</i> (O), <i>Megoura viciae</i> (S), <i>Aphis fabae</i> (G)	↑ Nymphal performance	NA	NA	74
Cabbage (<i>Brassica</i>)	Quantitative and qualitative variation in PVOs ↓ Isothiocyanates (Chem)	<i>Pieris rapae</i> (S)	NA	<i>Cotesia rubecula</i> (S)	↓ Attraction	57
	↓ Foliar constitutive glucosinolates (Chem)	<i>Pieris rapae</i> (S), <i>Plutella xylostella</i> (S), <i>Mamestra brassicae</i> (G)	↑ Egg-to-adult performance (S+G) ↑ Survival (G)	S and G parasitoids of the herbivores	Performance parasitoids = performance herbivores	56, 60, 71
	↓ Foliar constitutive and inducible glucosinolates (Chem)	<i>Pieris rapae</i> (S)	↑ Larval body mass ↑ Parasitoid encapsulation	<i>Cotesia glomerata</i> (S)	↓ Egg survival	17
	↓ Inducibility of foliar glucosinolates (Chem)	<i>Mamestra brassicae</i> (G)	Correlation between inducibility and herbivore performance and survival	<i>Microplitis mediator</i> (G)	Correlation between inducibility and parasitoid performance, but survival is less affected	70

Carrot (<i>Daucus</i>)	<ul style="list-style-type: none"> ↓ Terpenoids and phenylpropanoids Ø Leaf hairs ↓ Chlorogenic acid (Chem/Morph) 	<i>Frankliniella occidentalis</i> (G)	<ul style="list-style-type: none"> ↑ Thrips susceptibility in biofortified carrots Ø Thrips resistance in nonbiofortified and wild carrot 	NA	NA	90
Cranberry (<i>Vaccinium</i>)	<ul style="list-style-type: none"> ↓ Induced sesquiterpene emissions ↓ Constitutive defense (Chem) 	<i>Lynantria dispar</i> (G)	<ul style="list-style-type: none"> ↑ Development 	NA	NA	120
Maize (<i>Zea</i>)	<ul style="list-style-type: none"> Loss of emission of (<i>E</i>)-β-caryophyllene ↓ Transcription of terpene synthase (Chem) 	<i>Spodoptera littoralis</i> (G), <i>Diabrotica virgifera virgifera</i> (S)	NA	<i>Cotesia marginiventris</i> (G)	<ul style="list-style-type: none"> ↓ Attraction in experienced wasps ↓ Attraction in entomopathogenic nematodes 	62, 84
	<ul style="list-style-type: none"> ↓ Gene expression of three inducible defense genes (Chem) 	<i>Spodoptera frugiperda</i> (G)	<ul style="list-style-type: none"> ↑ Development ↑ Survival ↑ Pupal size 	NA	NA	137
	<ul style="list-style-type: none"> ↓ Leaf toughness ↑ Trichome density ↓ Tillers (Chem/Morph/Arch) 	<i>Dalbulus maidis</i> (S)	<ul style="list-style-type: none"> ↑ Oviposition ↑ Nymphal performance 	NA	NA	8, 43
	<ul style="list-style-type: none"> ↓ Tillers 	<i>Spodoptera frugiperda</i> (G)	<ul style="list-style-type: none"> ↑ Frequency larval infestation in the field ↑ Larval performance 	NA	NA	138
Pigeon pea (<i>Cajanus</i>)	<ul style="list-style-type: none"> Change in chemical composition (Chem) 	<i>Helicoverpa armigera</i> (G)	<ul style="list-style-type: none"> ↑ Larval preference for domesticated accessions 	NA	NA	136
Rice (<i>Oryza</i>)	<ul style="list-style-type: none"> ↓ Tillering ↓ Seed retention (Arch, Growth) 	Herbivore assemblage, stem-boring moths	<ul style="list-style-type: none"> ↑ Larval abundance Ø Arthropod diversity and total abundance ↑ Abundance of individual species 	NA	<ul style="list-style-type: none"> ↓ Abundance of <i>Pardosa</i> spiders 	32

(Continued)

Table 1 (Continued)

Crop (genus)	Crop selection trait of interest	Herbivore	Impact on herbivores (cultivar versus wild)	Natural enemies	Impact on natural enemies (cultivar versus wild)	Reference(s)
Safflower (<i>Carthamus</i>)	NA	<i>Acanthiophilus helianthi</i> (S?)	↑ Larvae per infested head ↑ Eggs laid ↓ Larval mortality	NA	NA	126
Sunflower (<i>Helianthus</i>)	↑ Flower head ↓ Seed coat toughness (Chem/Morph)	<i>Homocidus electellum</i> (S)	↑ Moth oviposition ↑ Larval densities per head ↑ Larval development ↑ Higher survival	<i>Dolichogenidea homocidomae</i>	↓ Parasitism efficacy, or no parasitism, unable to access hosts	36–39
	↓ Tissue toughness of petiole ↑ % water in tissues ↓ Resin exudate (Chem/Morph)	<i>Dectes texanus</i>	↑ Oviposition ↑ Feeding damage prior to oviposition	NA	Parasitism on wild sunflower only	100, 102
Wheat (<i>Triticum</i>)	Looser glumes allow free-threshing (Morph)	<i>Sitodiplosis mosellana</i>	↑ Larval abundance per glume	NA	NA	154

Abbreviations: Arch, architectural; Chem, chemical; G, generalist; Morph, morphological; NA, not assessed; O, oligophagous; PVOCs, plant volatile organic compounds; S, specialist.

^aDirection of effects: ↑, increased or faster (development); ↓, decreased or slower; †, variable; Ø, no effect.

Morphological Traits

Domesticated crops have long been observed to strongly differ from their wild progenitors in morphological traits. Darwin (42) extensively described the phenotypic variation of domesticated crops and their wild progenitors as evidence of selection. We review traits that contribute to the domestication syndrome within annual crops (52).

Enlargement of plant structures. The enlargement of specific plant structures is the most widely emphasized of all of the changes that arise from domestication (45, 131, 133). Striking examples of gigantism can be found by comparing crops such as tomato (*Lycopersicum esculentum*), maize (*Z. mays*), beans (*Phaseolus vulgaris*), artichokes (*Cynara cardunculus* var. *scolymus*), sunflower (*H. annuus*), and squash (*Cucurbita pepo*) with their wild ancestors. The plant vigor hypothesis proposed by Price (115) predicts that insect herbivores will tend to oviposit on plant organs that grow faster and larger (40). We found some support for this idea. For instance, in domesticated sunflower, increased flower size from domestication is positively correlated with landing and egg-laying effort of female sunflower moths, *Homoeosoma electellum* (37), but increased seed size is negatively associated with parasitoid accessibility to *H. electellum* larvae (38). As a result, selection for gigantism may interfere with natural control and explain the observation (36, 39, 141) that *H. electellum* is parasitized less frequently in sunflower agroecosystems than in natural sunflower ecosystems. However, parasitoids have a slightly greater effect on the banded sunflower moth, *Cochylis hospes* (27), which has a life history similar to that of *H. electellum* (26). Therefore, the life history of natural enemies and herbivores may influence whether selection for gigantism could result in enemy-free space for herbivores.

Alteration of glumes and spines. The grains of most wild cereals are enclosed by glumes, lemmas, and paleas, which protect them from damage by seed feeders, in particular birds (52). Glumes are membranous bracts that form the husk of cereal grains. Across five lineages of wheat within the genus *Triticum*, domestication has selected for larger seed size and greater free-threshing, meaning that the seeds easily separate from the glume (154). This trait strongly affects susceptibility to herbivore attack. For instance, female wheat midges, *Sitodiplosis mosellana*, lay their eggs on the glumes, and the larvae crawl in between the glume and seed to feed on the seed (87). By selecting for a looser glume attachment to the seed, wheat domestication has increased plant susceptibility to the wheat midge.

Decreased branching and tillering. Crop domestication has frequently selected for a simplification of plant architecture, with reduced branching and tillering, as these changes in morphology result in higher yields (52, 68). Domestication of cereal species can reduce the number of tillers by 40–80% (35, 124). The greater tillering ability of wild ancestors appears to be an important strategy to tolerate herbivory, giving plants more opportunities and nodal points to compensate for the damage to the apical meristem (35, 124). Therefore, reduced branching and tillering associated with domestication can dramatically reduce crop tolerance to herbivory (124, 153). In addition, decreases in tillering can lead to simpler habitats. For example, wild rice produces more tillers that are less erect than those of domesticated rice, resulting in greater habitat diversity and higher densities of lycosid spiders, a keystone predator (32).

Greater phenological uniformity. In addition to being bred for a reduction in total number of branches or tillers, domesticated cereals have been bred for greater phenological uniformity. When flowering occurs uniformly, all tillers may be susceptible at the same time to boring insects (34), and

a single female can cause proportionally greater damage to domesticated plants than to the more heterogeneously flowering wild relatives (35). If many eggs are laid during a narrow phenological window within an agroecosystem that is genetically uniform, the majority of herbivores may fall within a narrow age distribution, which may destabilize parasitoid-host dynamics (108).

Other morphological traits. Domestication has decreased tissue toughness, reduced trichome density, and increased tissue palatability in most crop plants; all of these changes facilitate herbivore access to plant structures and may allow insect herbivores to develop faster (8, 100, 102). For example, a decline in leaf toughness in maize associated with domestication is associated with higher ovipositional preference by the specialist corn leafhopper, *Dalbulus maidis*. Also, the longhorned borer *Dectes texanus* can chew more easily on the leaf petiole of domesticated sunflowers than on the leaf petiole of wild sunflowers, enabling it to oviposit more frequently and more easily into leaf holes on the former (102). In addition, wild sunflowers exude more resinous substance than do domesticated sunflowers, which helps to protect wild plants from *D. texanus* (102).

Plant Resistance Metabolites

Among various plant traits, secondary metabolites play an important role in insect-plant interactions (11, 53). Secondary metabolites are characteristic of specific plant species or families; they may stimulate oviposition and feeding by specialist insect herbivores (126), whereas they may deter or physiologically hamper more polyphagous herbivores (2, 129). Levels of plant secondary metabolites are often dynamic and vary with abiotic and biotic factors (129), as well as with plant ontogeny (7, 116). Studies that compare chemical resistance traits in wild and cultivated systems are increasing in number, and their outcomes are very consistent: Domesticated plants provide a better food resource for herbivores than their more toxic wild progenitors (**Table 1**). Several of these studies have strengthened this evidence by including plant species or varieties that can be traced along a domestication gradient (9, 43, 74, 120) and have reported a positive correlation between domestication status and herbivore performance.

Performance of herbivores and their natural enemies mediated by secondary metabolites.

Food plant quality for insect herbivores is to a large extent determined by sufficiently high levels of primary metabolites and low levels of chemicals that impair herbivore growth and development (132). One of the most important consequences of plant domestication on species interactions is the loss or reduction of plant metabolites that are toxic for herbivores (see recent reviews 31, 99). However, there are exceptions. Although the wild carrot (*D. carota*) had higher levels of chlorogenic acid, it was not more resistant than domesticated varieties of carrot to Western flower thrips (*Frankliniella occidentalis*) (90). Also, levels of direct and indirect chemical resistance traits in the leaves of wild and domesticated lima bean accessions (*P. lunatus*) did not depend on domestication status (6).

As part of the domestication syndrome, changes in secondary metabolite content may be correlated with other physical and chemical traits, such as nutrient content, size, or biomass. For example, performance of bruchid beetles (*A. obtectus*, *Z. subfasciatus*) has repeatedly been shown to be better on several varieties of domesticated beans of the genus *Phaseolus* than on wild beans (9, 20, 155). Compared with wild beans, domesticated beans contain lower concentrations of phenolics and cyanogenic glycosides, but they are also larger, softer, and more nutritious (134).

In response to herbivory, concentrations of specific defense secondary metabolites often increase (1, 82), and these increases may be greater in magnitude in wild ancestors. For instance, upon herbivore damage, foliar glucosinolate concentrations increase more dramatically in wild

than in domesticated cabbage (*Brassica oleracea*) accessions (56, 60, 70, 71). In contrast, induction of plant resistance using the phytohormone jasmonic acid was similar in cranberry varieties that differ in their degree of domestication (120) and in wild and domesticated lima bean accessions (6). These studies suggest that the strength of plant-induced defenses has not necessarily been altered by domestication.

Natural enemies of insect herbivores obtain their nutrition from plants indirectly via their prey, and variation in prey quality can be affected by plant secondary chemistry. As a result, natural enemies can be affected by variation in plant secondary chemistry, either through direct exposure to chemicals ingested by the herbivore or indirectly by reduced herbivore growth (58, 110). Plant chemical resistance traits often affect herbivores and their natural enemies in a similar way (58, 146). Most of the evidence for these effects comes from studies that compare different host plant species (49, 135), different cultivars (66), and different genotypes (127). However, relatively few studies have investigated the effect of domestication on the growth and development of both the herbivores and their natural enemies (9, 19, 20, 56, 60, 71, 75, 89).

Parasitoids of herbivores can be both positively and negatively affected by plant domestication. Studies with wild and domesticated brassicaceous plant species and bean (*Phaseolus*) species have found that parasitoids perform better on domesticated crops than on wild relatives (9, 10, 16, 20, 56, 60, 71). For Brassicaceae, levels of inducible glucosinolates correlate with the performance of crucifer specialists and their parasitoids, whereas the performance of a generalist herbivore (*Mamestra brassicae*) correlated with concentrations of constitutively expressed glucosinolates (60). However, an increase in the nutritional quality of some domesticated crucifers can also negatively affect parasitoids. The immune response of *Pieris rapae* larvae to prevent successful parasitism is generally better on domesticated than on wild plants (10, 17). Larvae encapsulate a higher proportion of eggs of the parasitoid *Cotesia glomerata* when reared on more nutritious domesticated cabbage than when reared on wild crucifers (10), whereas this response is compromised when larvae feed on previously damaged (induced) plants that produce smaller, weaker larvae (17).

Behavior of herbivores and natural enemies mediated by infochemicals. Secondary metabolites also play an important role in host location behavior of both the herbivores and their natural enemies (150). Infochemical-mediated foraging is better studied for natural enemies of the insect herbivores than for the herbivores themselves. Despite the numerous studies on attractiveness of herbivore-induced plant volatiles to parasitoids and predators of insect herbivores, very little is known about the qualitative and quantitative aspects of volatile blends that determine parasitoid and predator attraction (41, 57). Consequently, changes in total emission rates of volatile secondary metabolites in domesticated versus wild plants may have limited value in predicting the effect on volatile-mediated foraging on an herbivore and its natural enemies. Yet, for now, these quantitative comparisons are all that are available, and they indicate that plant domestication has led to lowered volatile emissions (Table 1).

Comparisons of herbivore-induced volatile emissions on wild and domesticated plants show that domestication does not lead to a consistent pattern across crops. In maize, the range of quantitative variation in volatile emissions was substantial but similar among maize varieties and teosinte, whereas the composition of the blend appears to be preserved (62). In contrast, American maize varieties did not emit the terpene (*E*)- β -caryophyllene, which mediated the attraction of a parasitic wasp and an entomopathogenic nematode in laboratory studies conducted in Europe (84). Also, in wild and domesticated cabbage (*B. oleracea*), the quality and quantity of the herbivore-induced volatile blend differ, and wild cabbage is more attractive to *Cotesia rubecula*, a specialist endoparasitoid of *P. rapae* caterpillars, despite the parasitoid's long history with the cultivar (57). Interestingly, isothiocyanates, which are secondary metabolites characteristic of the Brassicaceae

and result from a breakdown of glucosinolates, are produced only by the wild populations, reflecting the reduced levels of these compounds in domesticated cabbage (85). Isothiocyanates play a role both in host location of parasitoids of crucifer-feeding insects (13) and in food plant location of herbivores (107, 118). Yet little is known about how host plant selection has led to reduced levels of glucosinolates in domesticated cabbage. Interestingly, in contrast to specialist herbivores (e.g., *P. rapae*, *Papilio brassicae*, *Plutella xylostella*, *Brevicoryne brassicae*), generalist herbivores, such as *M. brassicae* and *Myzus persicae*, are serious pests on domesticated cabbage but are scarce on naturally growing wild *B. oleracea* populations in the United Kingdom (106, 109). This difference suggests that changes in plant defense traits and/or cultural practices for domesticated cabbage affect the interaction with generalists more than the interaction with specialists.

Although there seems to be a general pattern of reduced attraction of natural enemies to infochemicals emitted by domesticated crops compared with wild ancestors, there are exceptions. For example, *Diadegma semiclausum*, a specialist endoparasitoid of *P. xylostella* caterpillars, did not differentiate behaviorally between domesticated and wild black mustard (*Brassica nigra*) (59), whereas the more generalist *C. glomerata*, an endoparasitoid of pierid caterpillars, was less attracted to the wild brassica plants (9, 59). The opposite pattern was found for parasitoids of bean beetles (*A. obtectus*, *Z. subfasciatus*). The specialist parasitoid *Stenocorse bruchivora* parasitized more hosts on domesticated beans on which they performed best, whereas the generalist parasitoid *Dinarmus basalis* did not show any preference for wild or domesticated seeds (19).

CONCLUSIONS

We reviewed studies that examined the consequences of crop domestication for plant-insect interactions, with an emphasis on centers of origin, where crop plants coexist with their wild relatives and with the associated endemic herbivores and natural enemies. Although the number of studies is limited and it is difficult to identify general patterns, this research field is growing rapidly. The reviewed studies indicate that particular domestication syndromes can result in habitat-specific interactions that may positively affect certain types of insects and not others, depending on the habitat in which they are observed. In addition, the cultural and social environment in which these interactions occur further influences the outcome of crop domestication and may determine arthropod community structure in a particular region. More studies are needed in the geographic region of origin to understand the role of crop domestication in shaping insect behavioral responses, patterns of natural enemy attack, predator-prey dynamics, and pest regulation in the field.

What is clear is that, as information in this field accumulates, progress in understanding the effects of domestication on species interactions not only provides more basic knowledge on how artificially selected plant traits can affect insect herbivores and their natural enemies, and possibly entire communities (*sensu* 80), but also may help to develop better strategies for managing insect pests. This can be particularly useful in managing pests and diseases through crop diversification and biological control with natural enemies. We end this review with several open questions that we hope will stimulate future research and motivate scientists from different disciplines, including plant genomics, entomology, crop breeding, and evolutionary biology, to work together and bring a much-needed multidisciplinary approach to this exciting research field.

SUMMARY POINTS

1. Biological systems that comprise domesticated plants and their wild relatives provide ideal models to test and compare the short-term effects of artificial selection and the long-term evolutionary outcomes of natural selection.

2. Domestication has frequently resulted in reduced plant resistance against herbivorous insects, which has enhanced the performance of both herbivores and their natural enemies.
3. Studies in the centers of origin of crop plants that compare tritrophic interactions on domesticated crops and wild ancestors are scarce and biased toward a few well-studied annual crop species.
4. Both environmental (agricultural practices) and genetic (domestication syndromes) factors contribute to the susceptibility of cultivars to insect herbivores, and it is the interplay between these factors that is expected to affect the structure and function of insect herbivore communities in agroecosystems.
5. No consistent patterns could be discerned with respect to changes in infochemicals emitted by domesticated and wild plants and their effects on the behavior of insect natural enemies.
6. Morphological changes arising from domestication can disrupt herbivore-natural enemy interactions, but the extent of the disruption may depend on the life history strategies of insect herbivores and their natural enemies.
7. Limited access to geographic centers of crop origin has been a major barrier to understanding the field consequences for many laboratory observations.

FUTURE ISSUES

1. Have insect herbivores and their natural enemies adapted to domesticated crops?
2. What are the relative impacts of domestication syndromes, evolutionary processes, and agricultural practices and their interaction on arthropod diversity, community structure, and potential for pest control?
3. Does the observed reduction in plant defenses in domesticated plants apply to all tissues, or is it specific to plant parts that are used for human and livestock consumption?
4. How does the introduction of genes from wild crop relatives into domesticated crops influence the possible trade-off between yield and defense in crop plants?
5. How do insect life history, degree of specialization (generalists versus specialists), genetic variation, and behavioral plasticity influence the ability of herbivores and natural enemies to exploit domesticated plants?
6. Are trophic interactions among species in agricultural systems and naturally evolved natural systems comparable?
7. To what extent do insect responses to local landraces and particular agricultural practices characterize their response to the crop species in general?
8. To what extent are the relationships between plants, herbivores, and their natural enemies on wild and cultivated systems influenced by spatial scale (i.e., individual plant traits versus habitat or ecosystem)?

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We are grateful for the discussions with Julio Bernal, Jeffrey Harvey, Andre Kessler, Raul Medina, J.P. Michaud, Andrew Michel, Cesar Rodriguez-Saona, Gwen Shlichta, Sean Steffan, Chase Stratton, and Ted Turlings during the inception and writing of this manuscript. The illustration was prepared by Thomas Degen. We also thank the Swiss National Science Foundation (Project No. 31003A_127364) and the Vermont Agricultural Experiment Station for financial support.

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