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Crop domestication, global human-mediated migration, and the unresolved role of geography in pest control

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Abstract

Ecological pest management seeks to improve pest control through the manipulation of ecological processes that promote natural enemies and suppress pests. These approaches can involve cultural practices such as reduced tillage, increased use of non-crop plants that provide food and shelter for natural enemies, and intercropping to enhance the abundance and diversity of natural enemies. A major assumption of ecological pest management is that these activities can be equally effective for all insect herbivores. Here, I propose that these strategies may only be effective for a subset of pests and geographic regions because most insect pests have complex evolutionary histories that make them difficult to manage. I discuss how crop domestication and human-mediated migration are major evolutionary events that shape the geography of interactions between plants, herbivores, and natural enemies. Insect herbivores can evolve to be pests through three major modes: 1) herbivores associated with the crop wild ancestor may shift onto the domesticated crop, 2) herbivores may host-shift from native host plants onto an introduced crop, or 3) human-mediated migration can introduce insect pests into new cropping regions. The resulting geographic structure can influence the success of pest management by altering ecological factors such as: species distributions, patterns of biodiversity, community structure, and natural enemy attack rates. I discuss how the different modes of insect pest evolution structure a set of relevant questions and approaches for ecological pest management. By acknowledging how agricultural history and geography shape the ecology and evolution of insect pests, we may collectively develop a better capacity to identify where and how ecological pest management approaches can be most broadly effective.

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Introduction

Ecological pest management seeks to improve pest control through the manipulation of ecological processes that promote natural enemies and suppress pests (National Research Council, 1996). Ecological pest management can be viewed as a subset of Integrated Pest Management, but with a greater emphasis on preventative pest control strategies such as: increased soil organic matter, reduced soil tillage, conservation of non-crop habitat, vegetation management to enhance natural enemies and deter pests, increased crop diversity, and the use of biological control agents (Landis et al., 2000; Zehnder et al., 2007). Management approaches that focus on retaining and promoting the biological diversity of natural enemies (predators and parasitoids) within agroecosystems are also called conservation biological control (van Driesche et al., 2008), which emphasizes enhancing densities of natural enemies already present in the environment.

A core premise of ecological pest management is that increasing biodiversity in agroecosystems to mimic natural ecosystems will reduce insect outbreaks (Root, 1973; Risch, 1987; Landis et al., 2000), ideas that have resonated with the sustainable agriculture community (Soule and Piper, 1991; Jackson et al., 2002). For example, increasing plant diversity leads to greater food (insect prey and nectar) and shelter for natural enemies (Landis et al., 2000; Zehnder et al., 2007; Fiedler et al., 2008). Also, increasing intraspecific crop diversity and breeding for resistant crop varieties can slow the rate of growth of insect pest populations (Price et al., 2011; Tooker and Frank, 2012). While ecological pest management has enjoyed many successes, there has been

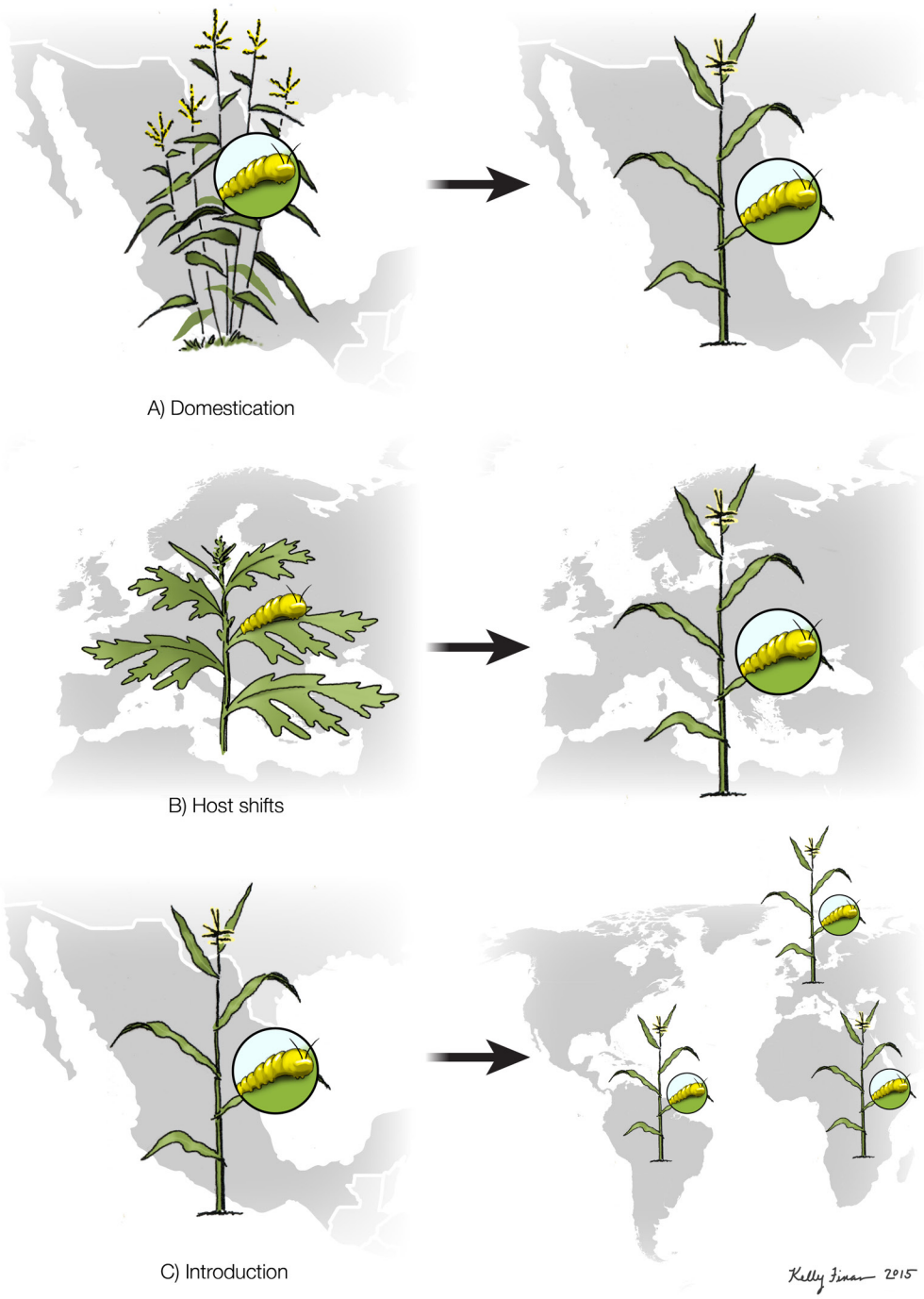

Figure 1

Insect herbivores can evolve to become pests under the following conditions.

A) Insect herbivores may be associated with the wild ancestor and shift to feed on the crop following domestication. Example: the stemboring caterpillar *Diatraea grandiosella* (Lepidoptera: Crambidae), previously associated with teosinte, *Zea mays ssp. parviglumis,* likely shifted onto maize *Zea mays ssp. mays* during domestication (Rosenthal and Dirzo, 1997; de Lange et al., 2014). B) Insects may host shift from their original host plant onto an introduced crop plant. Example: the European corn borer, *Ostrinia nubilalis* (Lepidoptera: Crambidae) shifted from feeding on mugwort (*Artemisia vulgaris* L.) and hop (*Humulus lupulus* L.) onto maize following its introduction into Europe in the 1500s (Bourguet et al., 2014). C) Insect herbivores associated with the crop plant can be introduced to other cropping regions around the world. Example: the cotton bollworm, *Helicoverpa armigera* and the corn earworm, *H. zea* (Lepidoptera: Noctuidae), both attack maize. *H. armigera* likely colonized the Americas ~1.5–2 million years ago, and gave rise to the closely related *H. zea,* and the two species can successfully mate together (Behere et al., 2007). Both *H. armigera* and *H. zea* are maize pests in South America, after the recent introduction of the former; they are maize pests throughout the world, with *Helicoverpa zea* distributed throughout the Americas and *H. armigera* throughout Europe, Africa, Asia, Australia, and Oceania (http://www.cabi.org/isc/datasheet/26757, http://www.cabi.org/isc/datasheet/26776).

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little discussion on whether the same approaches can be applied broadly to different pests and geographic locations. In this paper, I contend that the evolutionary histories of insect pests are centrally important in influencing the success of ecological pest management.

Humans have strongly shaped the evolutionary histories of insect agricultural pests (Fig. 1), resulting in three major modes of evolution for agricultural pests. First, insect herbivores previously adapted to the crop wild ancestor can shift onto the domesticated crop (Fig 1a; Chen et al., 2015a). Second, insect herbivores can host shift from their native host plants onto introduced crops (Fig 1b; Bush, 1969; Shiral and Morimoto, 1999; Calcagno et al., 2007). Third, human-aided migration supports the invasion of insect herbivores to new geographic regions (Fig. 1c; Grapputo et al., 2005; Guillemaud et al., 2015). These three pathways are not mutually exclusive, as insects can evolve to be pests through a combination of these processes. Since geographical distributions of wild relatives can be globally fragmented, complex scenarios are possible for

how pests evolve (Nardi et al., 2010). Therefore, native and invasive insect pests have different but equally complex ecological and evolutionary histories that contribute to the difficulty in managing these pests (Rebe et al., 2004; Alvarez et al., 2005; Alyokhin et al., 2008; Medina et al., 2012; Rinkevich et al., 2012; Chu et al., 2013; Leiss et al., 2013; Piiroinen et al., 2013).

Human-mediated introductions shape geographical patterns of biodiversity, influencing the balance between coevolved and novel species within food webs. Patterns of biodiversity are strongly determined by geography; for example, plant endemicity is the most important predictor of the diversity and complexity of arthropod food webs (Burghardt and Tallamy, 2013). When plants are transported to new regions during human-mediated migration, the majority of coevolved herbivores and natural enemies are left behind in the region of origin (van den Bosch, 1971). Most studies on ecological pest management and insect-plant interactions have been conducted in the United States, Europe, Australia, and New Zealand (Gurr et al., 2012), developed countries where agriculture consists primarily of introduced crops that support novel food webs with species assemblages derived from host-shifts and introductions. In contrast, relatively little is known on how domestication and cultivation should influence ecological pest management within a crop's region of origin. The majority of domesticated crops originate from what is considered the developing world, regions such as Central America, South America, Central Africa, Middle East, South Asia to Southeast Asia, and East Asia (Vavilov, 1926, 1951; Meyer et al., 2012), where sympatric wild ancestors and crops host endemic food webs (Chen et al., 2015a). But comparatively less funding for research in these regions means that novel food webs in developed countries have been more extensively studied than endemic food webs in the centers of origin of major crops.

The objective of this commentary is to develop a broader vision for ecological pest management that accounts for how geography and agricultural history can influence the structure and function of food webs. I discuss how the major modes of pest evolution shape patterns of insect-plant interaction and natural enemy activity. Using specific examples, I illustrate how pest evolution scenarios can complicate ecological pest management. In closing, I present a framework on how the modes of pest evolution should shape the relevant questions and approaches for future research needed to better resolve the role of geography in ecological pest management.

Crop domestication

Crop domestication has been considered one of the key developments that enabled the rise of major civilizations (Diamond, 2002; Gepts, 2004; Fuller et al., 2014). As early as 13,000 years ago (Hillman et al., 2001), different groups of people gradually domesticated crop plants to become the major food crops eaten widely today (Khoury et al., 2014). Although wild ancestors tend to be much more widely distributed than domesticated crops (Smartt and Simmonds, 1995), many crops originate from distinct geographic regions, which have been called Vavilov centers (Vavilov, 1926, 1951; Evans, 1993; Meyer et al., 2012). Phytophagous insects and plants have interacted for hundreds of millions of years, prior to the emergence of domesticated crops (Chen et al., 2015a). Therefore, agricultural crops are a recent ecological phenomenon for insect assemblages adapted to utilize wild ancestors.

Crop domestication can have complex effects on tritrophic interactions and pest control (Chen et al., 2015a). Insect herbivores typically perform better on agricultural plants than on wild ancestors, due to reductions in secondary compounds during crop domestication (Harvey et al., 2007; Rodriguez-Saona et al., 2011; Dávila-Flores et al., 2013; Szczepaniec et al., 2013; Turcotte et al., 2014). Crop domestication may facilitate herbivore populations in other ways as well. Herbivores can be less attacked (Chen and Welter, 2005) and gain greater protection from their natural enemies on domesticated crops compared to their wild ancestors (Chen & Welter, 2003, 2007). Specialized natural enemies can be less attracted to domesticated crops than wild ancestors (Gols et al., 2011). Although herbivore guilds appear to differ in their responsiveness to selection on some plant traits more than others, herbivores frequently respond positively to selection on traits targeted by domestication (Chen et al., 2015b).

The sunflower moth, *Homoeosoma electellum* (Lepidoptera: Pyralidae), the major pest of sunflowers in North America exemplifies how crop domestication can disrupt tritrophic interactions. The moth is far more abundant and less parasitized (< 5%) in agricultural sunflower fields than in neighboring wild sunflower fields (Chen and Welter, 2002). In common garden studies, agricultural sunflowers host higher sunflower larval densities than wild sunflowers (Chen and Welter, 2005). Behavioral studies confirm that female moths are more attracted to land on agricultural flowers and lay more eggs on them (Chen and Welter, 2003). However, the major parasitoid of *H. electellum*, *Dolichogenidea homoeosomae* (Hymenoptera: Braconidae) forages much more poorly on agricultural flowers and is less successful in attacking larvae on them (Chen and Welter, 2003). Moth larvae develop faster on agricultural sunflowers compared to wild sunflowers (Chen and Welter, 2005, 2007). By developing faster, larvae on agricultural sunflowers are able to grow more quickly and burrow deeper in the developing seeds, where they are effectively protected from parasitism (Chen and Welter, 2007). In summary, crop domestication appears to have created enemy-free space for *H. electellum*, which may explain why the moth is the most important pest of sunflowers in North America (Charlet et al., 1997).

Crop domestication can also alter secondary chemistry, altering tritrophic interactions. Domestication of the cabbage, *Brassica oleraceae* L., for instance, has reduced the concentration of glucosinolates, secondary compounds that are highly toxic to generalist herbivores. By reducing levels of glucosinolates, cabbage domestication has benefitted a generalist moth, *Mamestra brassicae* (Lepidoptera: Noctuidae), more than a specialist moth, *Pieris rapae* (Lepidoptera: Pieridae) (Gols et al., 2008). Crop domestication has also allowed parasitoids to perform better on *M. brassicae.* Endoparasitoids of *M. brassicae* depend upon the performance of the host larvae, so endoparasitoids attacking *M. brassicae* benefit more from domestication than specialist parasitoids that attack *P. rapae*. Crop domestication can also affect the release of herbivore-induced volatile compounds, which are plant signals that parasitoids use to locate their caterpillar hosts. For example, Gols et al. (2011) found that the parasitoid *Cotesia rubecula* (Hymenoptera: Braconidae) was more attracted to wild cabbage than cultivated cabbage, due to the presence of isothiocyanates in wild cabbage. If parasitoids are less attracted to crop plants, there may be lower overall parasitoid recruitment to agricultural fields.

It is important to recognize, however, that crop domestication may not always disrupt tritrophic interactions. Many herbivores may be less common on domesticated crops than on their wild ancestors (Chen et al., 2013, 2015a), specialist herbivores can perform more poorly on domesticated crops (Chacon-Fuentes et al., 2015), and parasitoids may be unaffected or even more inclined to attack larger herbivores on crop plants (Benrey et al., 1998; Campan and Benrey, 2004). Although herbivores are generally expected to benefit from domestication, predicting the community-wide effects of crop domestication on pest control remains challenging due to variation in behavior of individual herbivore and parasitoid species (Chen et al., 2015b).

More research is needed to understand how native ecosystems that support wild ancestors differ from agroecosystems in a crop's region of origin. In addition to the direct effects of domestication on species interactions, cultivation of domesticated crops can also alter patterns of biodiversity, community dominance, presence of natural enemies, and impact of natural enemies (Teetes and Randolph, 1969; Chen and Welter, 2002, 2005; Chen and Bernal, 2011; Chen et al., 2013). Studies that aim to disentangle the relative effects of domestication and cultivation on biodiversity would provide insight on how the origins of agriculture may lead to the deregulation of native pests. If domestication disrupts species interactions, then there is potential for breeding efforts to reintroduce traits that may have been lost from the crop gene pool during domestication. If cultivation more strongly causes losses in diversity and community function, then conservation biological control approaches could be more effective in attracting and retaining natural enemies within agroecosystems.

Human-mediated migration of crops triggers host shifts

Following the early history of crop domestication in centers of origin, different groups of people introduced crops into new geographic regions as they migrated around the world (Abbo et al., 2006; Roullier et al., 2013). During the 1500s, the global exchange of crop plants particularly intensified, a period dubbed the Columbian Exchange (Crosby, 1972). The level of global trade during the Columbian Exchange was unprecedented, and was a major force in shaping the current global distribution of crops (Mann, 2012). Despite geographically disparate origins for domestication events (Smartt and Simmonds, 1995), human-mediated migration of food crops has led to a homogenization of the major food crops around the world (Khoury et al., 2014).

When crops are introduced into new regions, a portion of the native herbivore assemblage may shift onto the introduced crop. Approximately 60% of agricultural insect pests in the US are estimated to have host-shifted onto introduced crops (Pimentel, 1991). Indeed, host shifts by native insects onto introduced plants are the most widely reported cases of rapid evolution within the Anthropocene (Carroll, 2007). Novel food webs associated with introduced crops show some general patterns. First, host shifts appear to be highly localized. For example, only 15% of the insect herbivores associated with cacao are found in more than a single cacao production area (Strong, 1974). Second, the likelihood of host shifts is dependent upon the degree of genetic relatedness between the introduced crop and native host plant. Introduced plants that are phylogenetically distant from the local flora are less colonized by native insect herbivores than more closely related ones (Hill and Kotanen, 2009). Across 900 lepidopteran food webs, Pearse and Altermatt (2013) found that host shifts onto introduced plants by native herbivores is phylogenetically constrained. Third, the length of time since introduction influences herbivore diversity. The number of herbivore species associated with crop plants increases asymptotically based upon the length of time since crop introduction and the amount of area under cultivation (Strong, 1974; Strong et al., 1977; Banerjee, 1981). Finally, an increase in human trade tends to increase the likelihood of herbivore recruitment onto introduced crops (Ezcurra et al., 1978; Hulme, 2009). As a result, patterns of biodiversity in agriculture result from a complex interplay between natural history, agricultural history, and patterns of global migration and trade.

Conservation biological control has assumed that herbivore populations feeding on native plants are genetically similar to host-shifted populations on introduced crops, but recent evidence challenges this idea. Native herbivore populations that shift onto agricultural crops can become genetically differentiated from populations that remain on the original host plant (Vialatte et al., 2005; Michel et al., 2010; Lavandero et al., 2011;

Midamegbe et al., 2011; Barman et al., 2012; Bourguet et al., 2014). Because host shifts create new ecological opportunities for herbivores, population can diverge via ecological speciation in sympatry (Bush, 1969; Berlocher and Feder, 2002). Native and host-shifted populations that are genetically structured may differ phenotypically in traits such as defense against natural enemies, host use, and seasonal adaptations.

Host shifts by native herbivores can lead to a loss in pest control., For example, the introduction of apples by Europeans to the Northeastern US in the 1800s caused the native apple maggot, *Rhagoletis pomonella* Walsh (Diptera: Tephridae) to shift from feeding on hawthorn, *Craetagus* spp., onto apple (Bush, 1969). Apple and hawthorn flies show clear evidence for differences in reproductive isolation, host odor preferences, and genetic differentiation throughout the US (Feder and Filchak, 1999; Filchak et al., 2000; Michel et al., 2010). Apple flies emerge an average three weeks earlier than hawthorn flies (Feder and Filchak, 1999). By shifting onto apple, *R. pomonella* reduced its exposure to natural enemies. *Rhagoletis pomonella* is less attacked by parasitoids on apple than on its native hawthorn tree (13% vs. 46%; Feder, 1995). Host shifts by insect herbivores also appear to create new ecological niches for parasitoids to exploit as well. For instance, association with *R. pomonella* on apple appears to have caused all three of its major parasitoids to show signs of incipient speciation (Forbes et al., 2009; Hood et al., 2015).

The introduction of maize into Europe in the 1500s caused the European corn borer, in the genus *Ostrinia*, to host shift from mugwort, *Artemisia vulgaris*, onto maize (Martel et al., 2003). Moth populations on maize are reproductively isolated from populations that feed on mugwort (Calcagno et al., 2007; Bourguet et al., 2014). The two host races also appear to be genetically isolated. Mugwort moths emerge a mean 10 days earlier than moths associated with maize (Thomas et al., 2003). Furthermore, the two subpopulations respond to different isomeric blends of pheromone, which cases them to be reproductively isolated (Thomas et al., 2003). By shifting onto maize, *O. nubilis* was able to escape many of its natural enemies and reduce its mortality due to parasitism (Thomas et al., 2003; Pelissie et al., 2010).

Host shifts by herbivores onto novel crops appears to disrupt natural enemies. In order to improve ecological pest management, more effort is needed to determining how pest have evolved to utilize novel host plants, and whether these novel adaptations may in turn limit conservation biological control. Insect herbivores appear to adapt to novel hosts and cropping systems more easily than do their natural enemies (Hare, 1990; Gratton and Welter, 1999; Toepfer and Kuhlmann, 2004; Pelissie et al., 2010). By feeding on introduced crops, insect herbivores may adapt to novel physical, chemical, semiochemical, and phenological plant traits. These changes may hamper natural enemy activity. Although some natural enemies were found to follow herbivores onto introduced crops with varying degrees of success (Forbes et al., 2009; Pelissie et al., 2010; Hood et al., 2015), other natural enemies are not able to utilize novel host plants or cropping systems (Charlet and Brewer, 1999; Chen and Welter, 2002; Chen et al., 2013) More research is needed to determine whether natural enemies can behaviorally adapt to novel plant traits, and if there are evolutionary barriers to successful pest control.

Human-mediated migration of invasive pests

As agricultural crops were introduced into new geographic regions, insect herbivores capable of exploiting the crops frequently accompanied them, giving rise to globally invasive pests (Elton, 1958; Ezcurra et al., 1978; Mann, 2012). Many herbivores that develop a close association with a crop have the potential to become globally invasive pests. Introduced insect herbivores can evolve to be pests through the following means: adaptation to the crop following domestication and cultivation (Medina et al., 2012; Chen et al., 2013, 2015a), host shifts from congeneric plant species (Berlocher, 1984; Nardi et al., 2010; Izzo et al., 2014), or host shifts from more distantly-related host plant taxa (Bush, 1969; Shiral and Morimoto, 1999; Forister et al., 2007; Pelissie et al., 2010). Insect herbivores evolve to become invasive pests along a generalized trajectory: host association with the crop plant, evolution of invasive traits, and post-colonization evolution within the invaded region. In contrast to the two previous modes of pest evolution where evolution happens in a particular geographic region, invasive species occupy broad distributions, and subpopulations can evolve different adaptations in any number of geographic locations.

After adapting to crop plants, insect pests can evolve adaptations suitable for human-altered environments, allowing these populations to serve as the source for new invaders to colonize other geographic regions (Hufbauer et al., 2012). Adaptation to human-altered environments may involve greater tolerance of physiological stress, increased population growth rates, and higher levels of disturbance (Hufbauer et al., 2012). Particularly invasive populations may also arise in a secondary location, and then serve as a source for widely successful invaders, a phenomenon called the 'bridgehead effect' (Lombaert et al., 2010). For example, the invasion of the western corn rootworm, *Diabrotica virgifera virgifera* (Coleoptera: Chrysomelidae) into Europe conforms to the bridgehead scenario. The beetle is native to Mexico (de Lange et al., 2014), but the invasive populations that colonized Europe evolved in the US (Miller et al., 2005; Ciosi et al., 2008). Therefore, human-mediated migration of insect pests can involve complex invasion pathways that can shape the genetic diversity of insect pests.

Invasions create new opportunities for insect herbivores to rapidly adapt to novel introduced environments (Sakai et al., 2001; Lee, 2002). Human-mediated migration may somehow promote the evolution of introduced pest species, especially if species are selected to adapt to local environmental and agricultural conditions (Thrall et al., 2011; Hufbauer et al., 2012). While some pests appear to show significant post-colonization evolution, others do not appear to have evolved significantly. The limited evidence is mixed. For instance, the green peach aphid, *Myzus persicae* (Hemiptera: Aphididae) has not appeared to evolve in a significant way following its global invasion (Bacigalupe et al., 2013). On the other hand, the Colorado potato beetle, *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) is thought to originate from the highlands of Mexico (Tower, 1906; Casagrande, 1987; Jacques, 1988). The beetle has evolved greater cold tolerance and overwintering strategies allowing it to expand northwards into temperate regions (Izzo et al., 2013; Lehmann et al., 2014). In addition, the beetle has expanded its host range from wild *Solanum* hosts to include several crop plants such as potato, eggplant, and tomato (Jacques, 1988; Lu et al., 2001; Izzo et al., 2014). Finally, the beetle has repeatedly been able to evolve resistance to all of the major insecticides (Alyokhin et al., 2008). As a result, the beetle is the most important global pest of potatoes and is distributed throughout the Northern Hemisphere (Weber, 2003). The ability of the beetle to rapidly evolve adaptations to novel climates may have allowed it to escape its major natural enemies. Among the many natural enemies attacking the beetle in Mexico (Cappaert et al., 1991), none of them can adequately control the beetle because they cannot persist in colder temperate climates (Lashomb, 1987; Hilbeck and Kennedy, 1996; O'Neil et al., 2005).

Cosmopolitan insect pests present the ultimate challenge for ecological pest management. For example, the Mediterrean fruit fly, *Ceratitis capitate* Wiedemann (Diptera: Tephritidae) is considered one of the most feared and destructive insect pests (Aluja and Mangan, 2008). The fly has a host range of over 300 plants (Liquido et al., 1991), and has invaded numerous countries in all of the major continents (Malacrida et al., 2007). Genetic studies support the scenario that the medfly originated from Eastern Africa and spread to the Mediterranean area (Bonizzoni et al., 2004). The global invasion of medfly has led to geographic populations that vary in biologically and ecologically important phenotypic traits. Geographic medfly populations appear to differ in adult life history traits (Diamantidis et al., 2009), reproductive courtship signaling (Diamantidis et al., 2008), and response to selection (Diamantidis et al., 2011a). Despite originating from the same location, geographic populations of medfly exhibit different population growth rates, suggesting that populations vary in their invasion potential (Diamantidis et al., 2011b). It is important to note that none of the numerous classical biological control projects targeting *C. capitata* have been successful (Ovruski et al., 2004; Garcia and Ricalde, 2012; Vargas et al., 2012). As a result, area-wide management of the fly through mass releases of sterile insects has been much more effective (Scolari et al., 2014). A lingering question is whether ecological pest management is possible at all for globally invasive pests. The fly has established in such a wide range of environmental conditions that developing successful classical biological control projects throughout the introduced range seems difficult if not impossible to achieve.

Human-mediated migration has facilitated the ability of insect pests to exploit new territories and evade their natural enemies. The assumption of classical biological control is that natural enemies found in the region of origin are the most effective at controlling introduced insect herbivores and plants (van den Bosch, 1971). However, invasive species can evolve greater invasiveness in intermediary locations, where their native natural enemies are not present. Under these circumstances, it is unclear where the most effective natural enemies should be found.

Geography and pest control

A major unresolved question is whether community metrics such as higher biodiversity and abundance or losses of key natural enemy species are important for pest control. The relationship between increased biodiversity and pest control is mixed. Increases in natural enemy diversity can have positive, negative or no effect on pest control (Straub et al., 2008). One possible reason for this mixed relationship may be a sampling effect: the increase of biodiversity leads to a higher probability that a highly effective predator species will be present (Straub and Snyder, 2006). If this finding is indicative of general patterns in the field, then the geographic distribution of key natural enemy species may be more important than natural enemy diversity and abundance in pest control success.

I propose that the mode of insect pest evolution structures a pest's ecological interactions and the most promising approaches towards control of that pest (Table 1). By incorporating a broader geographic perspective, research studies could start to resolve the relative roles of domestication, cultivation, and human-aided translocations in shaping the patterns of biodiversity and pest control. Table 1 describes a framework of open questions for developing ecological pest management approaches. The questions and approaches vary greatly in terms of risk, research investment, and likelihood of success.

Table 1. Modes of insect pest evolution in agriculture, ecological observations, and possible impacts on pest control. Each mode of insect pest evolution structures a set of relevant questions and possible approaches towards ecological pest management

Pest evolution	Ecological Observations	Impact on pest control	Relevant questions	Approaches towards pest control in agroecosystems
Domestication	Crop domestication can favor herbivores but not natural enemies (Chen et al., 2015a).	Insect herbivores may be more difficult to control on crop plants than on their wild relatives.	Is there more existing genetic variation in plant resistance to coevolved herbivores that may also promote natural enemy activity?	Genes for host plant resistance may be found in wild ancestor or relative populations for herbivores.
			How has cultivation shaped insect-plant interactions and natural enemy activity?	Conservation biological control approaches can mitigate the negative effects of cultivation.
			Have natural enemies adapted to domesticated crops?	Identification of plant traits that promote natural enemy activity can be utilized within breeding programs to improve their efficiency on domesticated crops.
			Which non-crop plants do endemic natural enemies naturally utilize in natural ecosystems?	Determine how native plants that are used by natural enemies can be incorporated using habitat management schemes.
Host shifts	Host shifts of insect herbivores occur more readily between closely related plant taxa than distantly related taxa (Hill and Kotanen, 2009, 2010).	Natural enemies may not readily be able to follow insect herbivores onto novel host plants.	Should there be genetic variation in host plant resistance to novel herbivores that arrive via host shifts?	Breeding for host plant resistance may not be as effective for novel insect herbivores.
			Have natural enemies been able to follow herbivores in cropping systems?	Identify the key traits that conserve natural enemies in order improve the design for conservation biological control approaches.
			Have natural enemies learned or adapted to locate their herbivorous prey on a new host plant?	Examining whether natural enemies can be selected to improve their efficiency on the novel host plants.
			Which non-crop plants do endemic natural enemies naturally utilize in natural ecosystems?	Determine how native plants that are used by natural enemies can be incorporated using habitat management schemes.
Human-aided transport	Some invasive insect herbivores appear to readily adapt to novel environmental conditions (Izzo et al., 2013; Lehmann et al., 2014; Izzo et al., 2014).	Natural enemies may not be able to adapt as readily to novel environmental conditions.	Should there be genetic variation in host plant resistance to novel pests?	Depending upon the agricultural history of the pests, breeding for host plant resistance may not be as effective for novel insect herbivores.
			How effective are native natural enemies in targeting novel hosts?	Determine whether native natural enemies can be selected to target novel hosts.
			Do invasions promote insect pest evolution?	Determine whether insect pest evolution can be controlled.
			What barriers exist for classically-introduced natural enemies to adapt to novel environments and ecological niches?	Identification of the key barriers for natural enemy adaptation. Can natural enemies be selected to adapt to novel environmental conditions and ecological niches?
			Which non-crop plants within the introduced region can provide additional food and shelter for natural enemies?	Identifying plants that can provide food, host alternative non-pest herbivores, or shelter can improve natural enemy activity in agroecosystems.

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For native herbivores that have evolved to become pests via domestication, more examination is to needed to disentangle how domestication and cultivation influence species interactions (Table 1). Researchers are urged to develop experimental designs that account both for domestication (genetic) and cultivation (environment) factors. If cultivation practices have disrupted natural enemy activity, then utilizing conservation biological control approaches will be a more promising approach towards pest control. On the other hand, if natural enemy activity is disrupted by domestication, then more investigation is needed to determine whether plant traits that promote natural enemy activity can be bred into the crop germplasm. Breeding for high levels of plant resistance may be more effective against generalist herbivores than specialist herbivores, because chewing specialist herbivores may already possess the biochemical pathways to detoxify specialized toxins (Gols et al., 2008; Shlichta et al., 2014). For sap-sucking and galling herbivores, continued efforts to breed for defense could be very important but the sustainability of resistance could be short-lived, because plants and herbivores appear to be engaged in reciprocal defense and virulence responses (Smith and Chuang, 2014; Habachi-Houimli et al., 2015; Zhao et al., 2015). Finally, for natural enemies that have adapted to domestication crops, it would be useful to understand how to increase their effectiveness. Could natural enemies themselves be selected upon?

For herbivores that become pests via host shifts, the most important issue is to understand why natural enemies cannot follow herbivores onto crop plants (Table 1). Is it due to plant effects or cultivation? As discussed above, pests derived from host shifts occupy novel ecological niches. Should there be plant resistance to insect herbivores that do not share a significantly coevolutionary history? The lack of shared history with the target herbivores would suggest that plant resistance would be unlikely to be highly specialized. If native natural enemies are unable to forage on novel crops, it is unclear as to how plant breeding could be effective for enhancing natural enemy activity. Can natural enemy foraging behavior be selected for greater effectiveness? If natural enemies are mainly inhibited by the hostile conditions of agricultural cultivation, then conservation biological control approaches through habitat management will be more likely to be successful.

Human-mediated introductions of invasive insects present a different set of challenges for ecological pest management. Given that invasive pests are selected to adapt to a wide range of geographic regions, climates, cropping systems, and environments, which geographic populations of natural enemies are the most likely to be successful? Attempts to manage invasive pests typically involve introductions of a small number of parasitoid species through classical biological control rather than conservation biological control (Hawkins et al., 1999; van Driesche et al., 2008). An important question is to determine whether native natural enemies or natural enemies introduced from the region of pest origin may be more effective against invasive insect pests (Michaud and Grant, 2005). Cases such as the Brown citrus aphid show how native natural enemies can control introduced herbivores without the aid of a classically-introduced natural enemy (Michaud, 2002). Therefore, it is important not to discount the potential of conservation biological control approaches for controlling invasive pests. If candidate natural enemies are not effective, which natural enemies may be the most amenable to selection? Also, can native natural enemies be selected to attack novel hosts, or can classically-introduced natural enemies adapt as easily to novel environmental conditions? Classically-introduced natural enemies do not appear to adapt to novel climates and ecological niches as well as herbivores (Lashomb, 1987; Hilbeck and Kennedy, 1998; O'Neil et al., 2005), but it is possible that natural enemies may not have to evolve as significantly in order to be successful (Roderick and Navajas, 2003).

Conclusions

Agricultural research seeks to extend the broad geographic distribution of crops, by breeding and supporting crops to tolerate an increasingly wider array of environmental and biological challenges. Due to these efforts over thousands of years, the same crop plants are found around the world, often hosting dramatically different herbivore and natural enemy assemblages. Humans have shaped patterns of biodiversity, selection histories, and the geographical distribution of traits within herbivore and natural enemy populations. By focusing on a critical subset of questions based upon different modes of pest evolution, I urge researchers to work towards developing a critical framework on where and how ecological pest management approaches can best be applied. Ultimately, examining how humans have influenced the evolutionary ecology of insect-plant interactions is important for understanding how we can collectively achieve truly sustainable pest management in different geographic regions around the world.

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- Contributed to conception and design: YHC
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Competing interests

The author declares that no competing interest exists.

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