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The eco-evolutionary impacts of domestication and agricultural practices on wild species

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Agriculture is a dominant evolutionary force that drives the evolution of both domesticated and wild species. However, the various mechanisms of agriculture-induced evolution and their socio-ecological consequences are not often synthetically discussed. Here, we explore how agricultural practices and evolutionary changes in domesticated species cause evolution in wild species. We do so by examining three processes by which agriculture drives evolution. First, differences in the traits of domesticated species, compared with their wild ancestors, alter the selective environment and create opportunities for wild species to specialize. Second, selection caused by agricultural practices, including both those meant to maximize productivity and those meant to control pest species, can lead to pest adaptation. Third, agriculture can cause non-selective changes in patterns of gene flow in wild species. We review evidence for these processes and then discuss their ecological and sociological impacts. We finish by identifying important knowledge gaps and future directions related to the eco-evolutionary impacts of agriculture including their extent, how to prevent the detrimental evolution of wild species, and finally, how to use evolution to minimize the ecological impacts of agriculture.

This article is part of the themed issue 'Human influences on evolution, and the ecological and societal consequences'.

1. Introduction

Agricultural development has been one of humanity's most important endeavours. Yet, agriculture causes significant ecological and evolutionary impacts on wild species and ecosystem processes. Understanding these impacts is crucial for the proper development and implementation of sustainable agricultural practices. The impacts of agriculture on wild species ultimately stem from two interdependent forces: direct impacts of agricultural practices (tillage, land use change, pesticides, etc.) and indirect impacts arising from evolutionary changes that occur in domesticated species. Agricultural practices, including classical breeding and genetic engineering, as well as natural selection during cultivation and rearing, have driven rapid evolutionary changes in domesticated plants and animals [1,2]. Evolutionary changes in domesticated species not only increase yields but can also alter the impacts of agriculture by enabling further intensification (e.g. higher densities due to the evolution of erect crop structure), allowing expansion into previously unfavourable habitats (e.g. breeding stress tolerant varieties), and altering resources needed for production (e.g. breeding high yielding varieties with weak pest resistance) [3]. Thus, when examining the evolutionary impacts of agriculture on wild species, we must consider the joint impact of agricultural practices and evolution of domesticated species.

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Here, we explore reciprocal feedback between agriculture-induced ecological and evolutionary changes by addressing two important questions: (i) How do agricultural practices and evolution of domesticated species drive evolutionary changes in wild species? and (ii) What are the ecological and societal consequences of these evolutionary changes? To address these questions, we first briefly review the ecological impacts of agriculture. We then categorize three non-exclusive processes by which wild species evolve in response to agriculture—adaptation to domesticated species, adaptation to agricultural practices and changes in gene flow—and discuss their broader eco-evolutionary and sociological impacts. Finally, we highlight knowledge gaps and future directions.

2. Ecological impacts of agriculture

Innovations in agriculture over the past decades have led to remarkable increases in food production that have helped sustain our growing human population [4]. At the same time, it is hard to overstate agriculture's ecological impact. Now encompassing approximately 40% of Earth's land surface, agriculture has replaced the majority of Earth's grasslands, savannahs and vast swathes of forest [4]. Agriculture is also responsible for 30–35% of global carbon emissions, 70% of global freshwater withdrawals and a 500% increase in global fertilizer use over the past 50 years [4].

Unsurprisingly, the impacts of agriculture on biodiversity and ecosystem services have been severe. Declines of 20–50% in vertebrate, invertebrate and plant species richness follow conversion of natural habitats to cropland and pasture [5]. Moreover, pesticides and agriculture-induced habitat loss are collapsing pollinator populations [6], as well as beneficial insects that control damaging crop pests [7,8]. However, by diversifying their farms with adjacent habitat patches, multiple crop species, hedgerows and grass strips, growers can sustain biodiversity [9,10], enhance soil quality, nutrient cycling, water-holding capacity, pollination, pest control and in some cases increase yields [11]. Yet adoption of diversification practices has been slow, and, as agriculture continues to expand [4] and intensify globally, the evolutionary trajectories of wild species are being fundamentally altered.

3. Evolutionary impacts of agriculture and their socio-ecological consequences

There are numerous well-documented examples of how agricultural practices and domestication can drive evolution in wild species. Here, we consider wild species as any species that is not the direct target of cultivation. Some of these wild species interbreed with the domesticated species, others interact ecologically, and yet others interact indirectly (e.g. predators of agricultural pests). Species that interact with domesticates include a diversity of wild antagonists (e.g. consumers, parasites or disease agents) and competitors. Wild species can be closely related wild relatives or unrelated taxa that have a shared evolutionary history with the wild ancestors of domesticated species and have evolved in parallel to the domesticated species. Other interactions arise through opportunistic host-shifting [12,13]. Thus, novel communities of antagonists may exist in agricultural habitats.

In this review, we categorize existing evidence that agriculture drives evolution in wild species through three evolutionary mechanisms (figure 1). First, because domesticated species differ greatly in their phenotypes compared with wild ancestors, selection can favour wild species to specialize on traits of these over-abundant organisms. Second, at least three types of agricultural practices create strong selective pressures that drive the evolution of wild species. These practices include agricultural intensification and the control of antagonistic species either through cultural practices, such as crop rotation, or through the use of pesticides and genetically engineered (GE) species. Third, agriculture also causes evolutionary changes in wild species through non-selective mechanisms such as gene flow. This can occur either directly, i.e. genetic exchange can occur between domesticated species and wild relatives, or indirectly, i.e. agricultural practices, such as the transportation of livestock, can alter the genetic structure of non-related species.

(a) Adaptation to the traits of domesticated species

Because domesticated species differ greatly in their phenotypes compared with their wild ancestors [14], organisms that interact with domesticates experience enormous selective pressures to adapt to these novel phenotypes. For example, *Colias* butterflies have shifted hosts from wild legumes to domesticated alfalfa, leading to genetically distinct 'pest' and 'non-pest' populations, each of which performs better on its own host [15]. As host races continue to diverge, they may eventually form incipient species, as has been documented in *Rhagoletis* flies after they shifted from wild hawthorn to domesticated apples [16,17]. Clear adaptations to host traits, such as the immune response, are also commonly observed in diseases that infect both wild and domesticated animal hosts (e.g. [18]). Experimental evolution studies have further confirmed that phenotypic differences between domesticates and their wild counterparts can have important implications for the evolution of interacting species [19,20]. For example, seed beetles evolving on domesticated cowpea evolve smaller body sizes, shorter development times, and reduced larval competitiveness than those evolving on a wild relative (mungbean) [19].

In response to pest damage, agricultural producers have bred domesticated varieties for higher resistance, or tolerance, to numerous antagonists. This approach is common in crops [3] and is gaining in interest in livestock [21]. Yet, wild antagonistic species have repeatedly, and often very quickly, evolved counter adaptations to these new resistant varieties [22]. The best-known example of this is the repeated development of cereal cultivars resistant to fungal pathogens in the mid-twentieth century. Pathogens very quickly, and repeatedly, evolved mechanisms to overcome these new resistant varieties within only a few years [22–24].

(b) Adaptation to agricultural practices

Farm level decisions and management strategies can alter ecosystems in profound ways [2,22], leading to altered selective pressures on wild organisms. Existing evidence has documented wild species evolution in response to at least three types of agricultural practices: agricultural intensification, cultural practices that suppress pests and pesticide application.

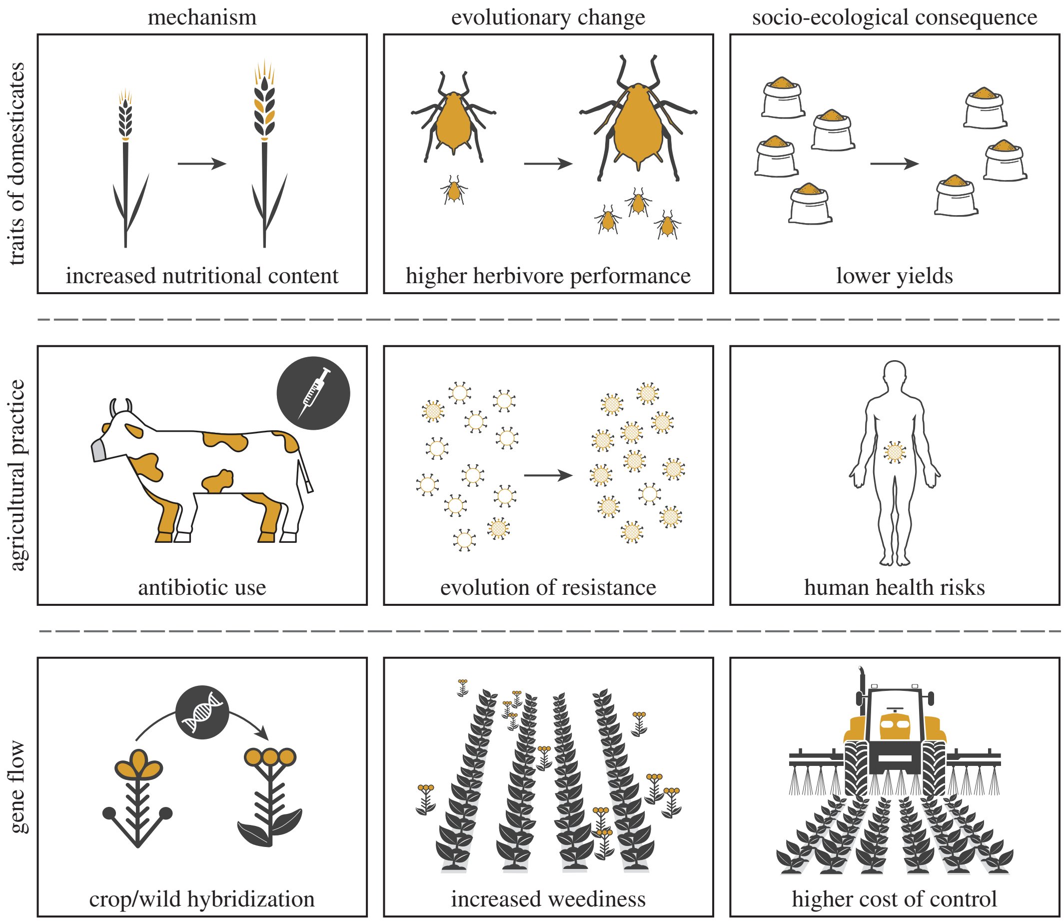

Figure 1. Each row represents an example of one of the three mechanisms by which agriculture can drive the evolution of wild species and a socio-ecological impact of that evolutionary change. (Online version in colour.)

(i) Adaptation to agricultural intensification

One of the most important drivers of rapid evolution in wild species is the homogenization of agricultural habitats and the high density of domesticated species in order to maximize production [13,22]. As mentioned above, wild species often evolve in response to host traits. This process is accelerated when farms or farming regions specialize on a single breed or cultivar, a common practice, and thereby amplify local selection on pests [23,25]. In addition, agro-ecosystems are less environmentally variable—due to practices such as irrigation, fertilization and tillage—which can lead to more consistent selective pressures [13]. Comparative and modelling studies have linked this homogeneity with more rapid pest evolution [23,24,26,27]. As a result, there have been numerous calls to increase diversity within agricultural systems [28,29].

(ii) Adaptation to cultural practices

Cultural practices, which are management practices that suppress pests, weeds or diseases without chemical substances, have been used for millennia and have generated strong selection on wild organisms [26]. For instance, weed species have evolved to morphologically mimic crops and, in this way, evade eradication by practices such as hand-weeding or seed sorting and cleaning [30]. A classic example is barnyard grass (*Echinochloa crus-galli* var. *oryzicola*), a native of East Asian rice fields that more closely resembles rice than its own close relatives in a number of traits, including seed and seedling morphology, phenology and ability to establish in flooded soils [30].

Management strategies that should minimize pest evolution can also be undermined. For instance, annual rotations between corn and soya beans have historically been used in the United States to control corn pests. However, these practices have selected for 'rotation resistance' in both the northern (*Diabrotica barberi*) and the western (*Diabrotica virgifera*) corn rootworms. Interestingly, the adaptation mechanisms have been different for these two species. The northern corn rootworm survives the soya bean rotation with an extended diapause of 2 or more years [31]. However, adults of the western corn rootworm have developed an ovipositional preference for soya beans over corn, allowing larvae to emerge each spring in cornfields (reviewed in [32]). Although the genetic changes remain unconfirmed for both species, clear differences in the behaviour, movement patterns and oviposition preferences of 'wild' and 'rotation resistant' types of western corn rootworms suggest a genetic basis for the oviposition preference on soya bean [33].

(iii) Adaptation in response to pesticides

Perhaps, the most well-documented example of rapid evolution in agricultural systems is the evolution of pesticide resistance in numerous species of herbivores, weeds, parasites and pathogens [1,34–37]. A number of factors dictate the rate and frequency of pesticide evolution. The scale of agriculture and application rate of pesticides is key, as well as the enormous population sizes of the pest species, which increases the likelihood that resistant genotypes already exist [23]. In addition, certain pesticides have very targeted mechanisms of action that could be undermined by a single dominant allele [38]. Moreover, resistance in microbial pests can sometimes be transferred across species by way of horizontal gene or plasmid transfer [39,40].

A dramatic example of insecticide resistance is the Colorado potato beetle (*Leptinotarsa decemlineata*), a highly problematic potato pest that has evolved resistance to at least 55 active ingredients designed for its control [37]. Numerous other examples of evolutionary resistance have occurred in the past two decades due to the extensive adoption of transgenic Bt corn and cotton. There are now populations of at least five species of insect pests in which more than 50% of individuals are reportedly resistant to Bt toxins [41].

The widespread use of herbicides has also resulted in the rapid evolution of herbicide resistance. It is estimated that 530 weed species have evolved resistance to herbicides in the United States alone [37]. In particular, with the heavy use of glyphosate in millions of acres of transgenic crops, to date at least 35 species of weeds have evolved resistance to glyphosate through a number of different mechanisms [37,42].

Parallel evolutionary processes occur as a result of treatment of livestock and farmed fish. For example, at least 10 species of gastrointestinal nematodes associated with cattle have evolved resistance to antihelmintic drugs [35] and numerous ectoparasitic arthropods affecting cattle, sheep, poultry and farm-raised salmon have evolved resistance to insecticides and acaricides [43]. In addition, the widespread use of antimicrobials in both livestock and crop production has led to the evolution of resistance in numerous disease agents [39,40].

(c) Evolution through changes in gene flow

(i) Direct gene flow to wild species

Gene flow is commonly observed between domesticated species and their wild relatives [44,45], and even a small amount of migration between populations, such as a single immigrant per generation, effectively works as a genetic homogenization factor [46]. In the context of gene flow between domesticated and wild organisms, however, it is not obvious whether a small amount of genetic exchange is enough to impact wild populations because artificial selection may cause domesticated organisms to have more deleterious genes than their wild counterparts.

Theoretical predictions suggest that both demographic and genetic consequences of reproductive interactions between domesticated and wild organisms depend strongly on the fitness of domesticated organisms in the wild [47]. This is important for two reasons. First, a low survival rate of domesticated organisms in the wild reduces the opportunity for them to reproduce with their wild counterparts. Second, because the immigrants from the domesticated group can be highly abundant, introgression of 'deleterious domestication genes' into the wild might still occur. In this case, the wild population might suffer from a negative effect of the reproductive interaction, and the effect may last for generations after introgression [48].

To date, however, only a few examples of negative effects from the introgression of 'deleterious domestication genes' in wild populations have been reported. Reproductive success of hatchery-born fish (*Oncorhynchus mykiss*) in the wild is one example. Araki *et al*. [49] reported that hatchery-born parents experienced more than a 50% fitness decline (reduced number of successful offspring in the wild) after a single generation of captive rearing. More importantly, the 'deleterious domestication genes' seemed to have been transmitted to the following generations, which reduced productivity of the wild population years later [50].

Introgression from domesticated to wild species has also been reported in several plant species, sometimes leading to the creation of new weeds with important ecological impacts [44,51]. For instance, California wild radish is a hybrid between cultivated radish (*Raphanus sativus*) and wild jointed charlock (*R. raphanistrum*) that has invaded and damaged natural communities in the western United States [51]. In addition, recent examples suggest that GE crops can spread transgenic genes into wild populations. For example, gene flow from oilseed rape (*Brassica napus*) has transferred herbicide-tolerance transgenes into the wild weed *B. rapa* and other closely related species [52,53].

(ii) Changes in genetic structure of wild species

Agriculture can also impact gene flow in wild species that are not related to domesticated species [22]. High host density and low genetic and species variation can lead to higher pathogen densities that can promote genetic exchange [13]. In addition, parasite specialization on livestock can cause a homogenization of genetic structure across large geographical areas that raise the same domesticated species [54]. In addition, the transportation of livestock, feed or equipment can promote gene flow between pest populations among different agricultural areas or between natural and agricultural communities leading to hybridization [13,22,25,55]. On the other hand, long distance transportation can also create genetic bottlenecks in wild species. For example, until recently, the worldwide distribution of the pathogen that caused the Irish potato famine was a single clone spread by agriculture [56].

(d) Socio-ecological impacts of evolution in wild species

Evolution of wild species in response to agriculture can impact humanity in numerous important ways [57]. Achieving agricultural sustainability will require that we understand and mitigate these socio-ecological impacts, which include deterioration of ecosystem services, economic losses and impacts on human health (figure 1).

(i) Impacts on ecosystem services

Evolution of wild species in response to agriculture can both directly and indirectly impact the provision of multiple ecosystem services. Most obviously, it has been long recognized that rapid evolution in pests, pathogens and weeds can cause stark declines in crop production. For example, pesticide resistance among tobacco budworm in Texas and northern Mexico in 1970 caused the eventual abandonment of 285 000 ha of cotton [58]. Globally, crop losses from pests, pathogens and weeds amount to 25–40% of the production of our most important food crops [59]. Increased damages thus have real potential to not only decrease grower profits, but also significantly impact global food supply and human nutrition.

To compensate for evolutionary resistance among crop pests, growers are often forced to apply more pesticides [58], which may in turn have indirect consequences for many ecosystem services. For example, pesticides strongly affect pollination, water quality, biodiversity and human health [6,60,61]. Increased pesticide applications may also inadvertently cause declines in natural pest control and crop yields if natural enemies of crop pests are susceptible. A classic example is when the brown planthopper began devastating rice yields in Indonesia in the 1980s as insecticide use increased and its natural enemies declined [58]. When President Soeharto banned 57 of 64 rice pesticides and integrated pest management spread, both natural enemies and rice yields significantly rebounded. This example highlights how diversified farming strategies [11] can leverage natural enemy activity to control pests and thereby mitigate the need for excessive pesticide applications. Remarkably, conserving natural enemies may not only reduce pests directly, but also slow pesticide resistance evolution in pests [29], further reducing the need for excessive spraying.

(ii) Economic impacts

As wild species evolve in response to agriculture, they can create significant economic costs associated with both the control of pests and the reduction of benefits provided by beneficial wild species. The evolutionary specialization of pests to the traits of domesticated species or to agricultural conditions can lead to higher pest densities as well as an expansion of host species targets, both of which will cause direct economic harm [32,34]. In addition, the rapid adaptation of pests creates a continued need for investment in costly new control methods [23]. Breeding new resistance varieties is time consuming, costly and might trade off with yield. Rapid pest evolution, be it through selection or the horizontal transfer of resistance genes, can also reduce the economic incentives for the development of new pesticides [28,62]. This economic risk is magnified when cross-resistance evolves, i.e. resistance to one pesticide provides full or partial resistance to another [38]. When such control methods fail, farmers must resort to the use of more expensive or environmentally damaging approaches such as the manual removal of weeds [51,53], the application of multiple pesticides [59], the use of GE crops that express multiple resistance genes [41] or the use of broad-spectrum pesticides [39].

Economic losses can also occur through a loss in the value of wild species themselves. For instance, reduced fitness of wild fish populations due to gene flow could have a potential impact on the persistence or recovery of wild fish populations and thus their economic value [47,48].

(iii) Medical impacts

Finally, the impacts of evolution in wild species in response to agriculture extend to human health in at least three important ways. First, the evolution of pesticide resistance can spread to human pathogens. Certain livestock pathogens have evolved resistance to antimicrobials and now infect human populations or have transferred antibiotic resistance to human pathogens through horizontal gene transfer [39,40]. Second, the intricate association between farmers and livestock, as well as the actual consumption of animals, creates opportunities for pests that have adapted to domesticated animals to host switch to humans. For instance, the history of influenza is tightly linked to the evolution of pathogens in swine with numerous examples of host switching and rapid evolutionary changes [63]. Third, when farmers compensate for pesticide resistance by increasing dosage or spray frequencies, increased pesticide exposure among farmworkers and their families may result in compromised well-being. In the Salinas Valley of California, pesticide exposure has been linked to poorer working memory, IQ, verbal comprehension and perceptual reasoning scores in farmworker children [60].

4. Knowledge gaps and future directions

Our review has summarized a wealth of knowledge concerning the evolution of wild species and its socio-ecological impacts. It has also revealed several important research gaps and future directions, six of which we highlight below.

(a) How common are evolutionary changes in wild species?

Research continues to reveal examples where agriculture drives phenotypic changes in wild species. However, in most cases, we do not know if these are caused by genetic or plastic changes. For example, bee populations seem to respond to agricultural intensification by developing smaller body sizes [64,65], but whether this difference is genetic or plastic remains unknown. The answer is crucial for both predicting the eco-evolutionary impacts of agriculture and mitigating their consequences (e.g. on ecosystem functions such as pollination).

Our review shows that research on agriculture's evolutionary impacts has disproportionately focused on direct antagonists and competitors of domesticated species. Given the ubiquity of evolution in these species, we also expect evolution in higher trophic levels (e.g. insect parasitoids) and mutualists (e.g. pollinators). Although strong evidence is still missing, we suspect this is due mostly to a lack of research.

Finally, our review highlights that most studies of evolution in agricultural systems have focused on changes in physiology or morphology. We suspect that evolution is also common in other traits such as behaviour. One promising example is that the locomotory behaviour and activity of *Cotesia glomerata* parasitoids attacking caterpillars differ among parasitoids collected on different domesticated versus wild plant species, even after one generation in a common garden [66].

(b) How do evolutionary changes influence the composition and structure of ecological communities?

Although our review focused on well-studied cases of evolutionary change in wild species, it is unknown whether these evolutionary changes have cascading effects on community composition and species interactions [57,67]. There are multiple examples showing that increasing agricultural extent and/or intensity can cause the homogenization and filtering of bird and arthropod communities [9,10,68]. Is it possible that some of these changes in composition are partly driven by evolutionary changes in one or more species in response to agriculture? At a completely different scale, microbial community responses to agriculture lead to similar questions about how much change can be attributed to rapid evolution. Recent studies show that the abundance, composition and function of the microbiota in the rhizosphere depend not only on soil properties, but also on plant species and genotype [69,70]. In addition to the effects on community composition, agriculture-induced evolution may also affect community structure by altering the outcome of species interactions between wild species [40]. For instance, in the case of the corn rootworm evolving 'rotation resistance' [32,33], one might predict that the loss of ovipositional fidelity of the western corn rootworm to corn would also affect interactions between corn rootworms and wild plants, potentially leading to an increase in damage to alternative wild hosts such as foxtail and barnyard grass [32,71]. Understanding the community impacts of rapid evolution would revolutionize our understanding of the main drivers currently changing species composition and trait variation in agro-ecosystems across the globe.

(c) What is the relative importance of trait evolution in domesticated species versus agricultural practices in driving ecological impacts and evolution in wild species?

Our review distinguishes between two interwoven forces that drive the evolutionary impacts of agriculture on wild species: selection imposed by the traits of domesticates and selection imposed by agricultural practices. Yet, in practice, these two mechanisms can be difficult to distinguish. For example, ecologists are interested in testing how crop domestication impacts plant–herbivore interactions [72,73], but simply comparing what occurs in agricultural fields versus wild communities confounds the effects of environment and species domestication histories. Comparisons of plant–herbivore interactions among crops and wild relatives in common garden conditions can help isolate the effects of trait evolution in domesticates. Studies suggest that these trait changes can alter crop resistance to herbivores as well as modify current pest evolutionary dynamics [20,73,74]. The next challenge will be to experimentally quantify the impacts of agricultural practices themselves, by manipulating cultivation conditions, and to compare their effect versus those of evolution during domestication [20,72].

(d) How do we mitigate the impact of gene flow to wild populations?

Little research has focused on developing strategies for mitigating gene flow between domesticated and wild populations. Theoretically, the impact of gene flow between domesticated and wild populations would be mitigated if: (i) the effectiveness of the reproductive interaction could be reduced, and/or (ii) genetic differences between domesticated and wild populations were minimized. To reduce the effectiveness of reproduction, domestic and wild species should be spatially or temporally separated during periods of reproduction. In reality, however, establishing reproductive barriers is difficult for both livestock and crops, unless they are physically separated before they mature [45].

Reducing genetic differences between domesticated and wild populations may also be possible to help conserve wild, threatened species. For example, using local fish stocks for hatcheries could reduce genome-wide differences between domesticated fish and their wild counterparts. Moreover, rearing fish in semi-natural environments might reduce evolution of 'deleterious domestication genes'. In general, however, there is a major knowledge gap on how to mitigate the impacts of gene flow without losing the contributions from economically important, domesticated species.

(e) What are the best approaches to slow evolution in agricultural pests?

Managing pest evolution is critical for maintaining current and future agricultural production [1,38,62]. Four main strategies exist, but their relative efficacies remain unclear. The first strategy is to diversify selection, either spatially or temporally [26,28]. This can be accomplished by rotating pesticides with different modes of action or crop species and varieties with different defence mechanisms [1,23]. Another approach is to use multiple selective pressures concurrently, by pyramiding resistance genes within a cultivar, applying multiple pesticides or by increasing species diversity [24]. Finally, growers can increase the ecological or landscape complexity of the agricultural system to promote the presence of competitors and enemies of pests [8,24], which, as noted above, can in turn slow rates of resistance evolution among pests [28,29]. These changes increase the importance of physiological or genetic trade-offs by favouring different combinations of traits, which should slow the rate of pest evolution [23,28].

A second approach, that is gaining interest, is for breeders to select for pest tolerance instead of pest resistance. Tolerant breeds maintain their fitness, or yield, without harming the attacking pests. It is thought that tolerant hosts do not impose selection on their pests and thus break the 'coevolutionary cycle' limiting pest counter adaptation [75,76].

The third strategy is to manipulate the pest's mating structure using refugia, wherein a large pest population grows on a fraction of the host population that is not protected. This large population will not evolve resistance and will mate with the smaller pest population that is evolving resistance in the protected host population. This prevents resistance evolution. The ideal size, position and composition of refugia remain an active area of investigation [27].

Finally, the fourth strategy is to limit dispersal. One of the most important determinants of the rate of pest evolution is their population size, which impacts levels of genetic variation and the rate of new mutations. By limiting dispersal of pests and their vectors, one can reduce the effective population size of pests and slow evolution [23]. This can be accomplished using sanitation protocols during transportation, limiting the movement of seeds or livestock or increasing distance among farms that focus on the same domesticated species.

Empirically confirming which of these strategies is best is challenging because controlled field experiments at appropriate spatial and temporal scales are difficult [38]. Although the use of experimental evolution is gaining interest [29,38], most of our current insight comes from simulation modelling and retrospective analyses [22]. Three general lessons are emerging from these studies. First, the widespread application of a single approach is likely to fail. Second, using complementary strategies, that require very different adaptive mechanisms to overcome, is most likely to delay pest evolution [29,38,39]. Third, the successful application of these strategies requires that they remain economically feasible in the short-term and are robust to imperfect compliance rates [24,41].

(f) How can we use breeding to mitigate the ecological impacts of agriculture?

As the ecological impacts of agriculture become more apparent, breeders have begun exploring how they might be mitigated through artificial selection and genetic engineering. Breeding for pest resistance has a long tradition [3,24] and can reduce ecological impacts by reducing the need for pesticides and other control methods [29]. Recently, breeders have begun to target ecological impacts of the domesticated species themselves. For instance, ruminants produce large quantities of methane, which is linked to global warming. Reductions in methane production could be achieved by indirectly selecting for traits that improve livestock production efficiency, e.g. by selecting for higher feed conversion efficiency or improved fertility, both of which reduce methane produced per unit of product produced. Additionally, breeders could directly select for reduced methane production itself [77,78].

Similarly, crop breeders are attempting to reduce fertilizer requirements and greenhouse gas emissions used during production and distribution. Numerous targets are being investigated including the efficiency of photosynthesis and loss due to photorespiration, the minimization of yield loss to abiotic and biotic stresses, and nutrient use efficiency [79]. In both animal and plant breeding, concurrent selection for a greater diversity of favoured traits is becoming more feasible with the use of genomic selection.

5. Conclusion

Agricultural practices and the evolution of domesticated species have large ecological impacts. Our review highlights that these processes also have complex evolutionary impacts on multiple wild species. Although examples of evolutionary changes in the antagonists of domesticated species abound, it remains unclear how far the evolutionary impacts of agriculture ripple through broader ecological communities. The potential impacts are numerous given the reciprocal natural of ecological and evolutionary dynamics on short time scales [20,57,67]. Continuing to explore these impacts provides an excellent opportunity to test important basic questions in the life sciences [2,20,73]. Furthermore, the evolution of wild species has enormous impacts on the sustainability of agriculture, the economics of food production and human health. Understanding the downstream evolutionary impacts of agriculture is thus crucial in pest management and long-term sustainability. Mitigating these impacts, while considering current economic viability, remains a major challenge for farmers, evolutionary-ecologists, economists and even politicians.

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