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## Towards evolutionary agroecology\*\*

### *Hacia la agroecología evolutiva*

**Abstract** | Agroecology derives much of its strength from interactions between disciplines that produce a holistic perspective on agricultural systems and issues. Although ongoing integration of social dynamics into agroecology has strengthened the field, evolution and genetics have not been embraced to the same degree, despite the fact that they have been discussed in some common agroecology texts. I argue that the field of agroecology could extend its reach and depth by embracing the evolutionary study of agroecosystems. Areas of evolutionary inquiry with relevance to agriculture focus on long or short term processes, encompass a range of scales, incorporate molecular or quantitative genetic analyses, and explore ecological processes to differing degrees. Many research areas that use an evolutionary lens and focus on agricultural systems could enhance agroecology. Some examples include (i) identifying crop adaptations that can be utilized for sustainable agroecosystems; (ii) improving function and adaptive capacity of agroecosystems by promoting genetic diversity within crops; and (iii) improving weed control through explorations of gene flow or hybridization amongst crops and their wild relatives. Future bridging of the agroecology–evolution divide could enhance the nascent field of evolutionary agroecology.

**Keywords** | agroecology, evolution, genetic diversity, selection, gene flow, adaptation, transgenic

**Resumen** | La agroecología debe mucha de su fortaleza de las interacciones entre disciplinas, las cuales producen una perspectiva holística de los sistemas agrícolas. Aunque la integración actualmente en marcha del estudio de la dinámica social como parte de la

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agroecología ha fortalecido el campo, la evolución y la genética no han sido incorporadas en el mismo grado, a pesar de haber sido discutidas en algunos textos clásicos de agroecología. En este artículo, argumento que abrazando el estudio evolutivo de los agroecosistemas el campo de la agroecología podría extender y profundizar su alcance. Las áreas de investigación evolutiva de relevancia para la agricultura se centran en procesos de corto y largo plazo, abarcando un amplio rango de escalas, incorporando análisis de genética cuantitativa y molecular, así como la exploración de procesos ecológicos a diferentes escalas. Muchas de las áreas que utilizan una perspectiva evolutiva y se enfocan en la agricultura podrían mejorar la agroecología, algunos ejemplos son: (i) identificar en los cultivos adaptaciones que podrían ser útiles en agroecosistemas sustentables; (ii) mejorar las funciones y capacidades adaptativas de los agroecosistemas mediante la promoción de la diversidad genética dentro de los cultivos y (iii) mejorar el control de malezas a través de la exploración del flujo génico e hibridación entre los cultivos y sus parientes silvestres. En el futuro, superar la separación agroecología–evolución podría dar relieve al naciente campo de la agroecología evolutiva.

**Palabras clave** | agroecología, evolución, diversidad genética, selección, flujo génico, adaptación, transgénicos.

## Introduction

AGROECOLOGY'S STRENGTH is in its interdisciplinary nature. Since its inception, agroecology has embraced that multiple disciplines should engage with each other to holistically design and analyze agricultural systems. Rather than putting plant pathology, weed science, and soil management, for instance, into separate fields with little opportunity for mutual influence, agroecology has integrated those different disciplines (e.g., Carroll *et al.* 1990). Importantly, agroecology also has a strong history of seeing the social dynamics of agriculture as essential to understanding the biology. This reciprocal relationship between humans and the environment is core to agroecology's pursuits. Thus, agroecology is not only a production system, but also a movement that encourages the questioning of industrial agriculture and that helps shape the values of citizens who approach agriculture ecologically (Wezel *et al.* 2009; Méndez *et al.* 2013).

The space that agroecology provides for study is inherently broad—from basic ecology to social sciences and activism (Wezel *et al.* 2009; Méndez *et al.* 2013). Yet it is easy to name typical areas of study within agroecology where basic studies are then applied to improve production and sustainability of the system. For instance, within the biological realm, knowledge of plant physiological responses to aspects of the abiotic environment (light, temperature, nutrients, etc.) can be applied to optimize crop growth; the understanding of soil type and quality can be applied to soil health and plant nutrition; exploration of plant

competition and facilitation can improve weed control and intercropping; a better understanding of the ecology and population biology of pests can be applied to control them; consideration of the flows of matter and energy within and between systems can be used to ascertain system sustainability; and understanding of the role of biodiversity and biological interactions in system can be used to improve ecosystem function. On the social side, understanding social processes in rural and urban settings can help illuminate social determinants of characteristics of our food and farming systems. Exploration of the politics and role of agribusiness in shaping food and farming systems can identify points of leverage for making change.

Many of these areas of research, especially those in the biological realm, mirror important areas in the discipline of ecology. What differs is that they are applied to agricultural systems and not natural ones. Additionally, biological work in agroecology explicitly incorporates the human element, whereas not all ecological studies do (though now they do more and more: Alberti *et al.* 2003). Nevertheless, what tends to be uncommon within agroecology is an evolutionary perspective. Perhaps, agroecology will need to grow to encompass evolution as happened to ecology (e.g., Bradshaw 1984; Antonovics 1992; Purugganan and Gibson 2003).

Yet evolutionary biology has been partner to ecology for a while. In fact, in academia, many departments dominated by ecologists are called some version of “Ecology and Evolutionary Biology,” giving equal weight to ecological and evolutionary lines of research. In the past half a century, a field that bridges the two, namely evolutionary ecology, has also emerged (the journal so-named had its first issue in 1987). In ecology and evolutionary biology departments, genetics has become an important tool for investigating ecological and evolutionary processes. Yet despite the importance of plant breeding in agriculture and all the molecular and quantitative genetic work that has been performed on our crops, genetics is less well-integrated into the holistic view of agroecology, where methods tend to emphasize whole plant responses, soil microbial communities, and fluxes and flows of nutrients, among others. This lack of engagement with genetics exists even though many agroecology textbooks have a chapter on genetic resources or genetics (e.g., Carroll *et al.* 1990; Gliessman 2006) that may mention concepts such as adaptation and genetic variation, especially as applied to crops. Despite the inclusion of these evolutionary and genetic concepts in seminal works, little of the literature on genetics or genetic resources claim agroecology as its true home. Perhaps this may be due, in part, to a lack of interest in evolutionary work by the agroecological community due to the perception that evolutionary change requires very long periods of time that misalign with the annual management timeline of agriculture.

Others have noted this lack of evolutionary emphasis in agroecology and multiple authors have highlighted the value that an evolutionary perspective can bring to agriculture. For instance, Denison *et al.* (2003) has argued that the only way for plant breeding to continue to enhance yield is to focus on problems that natural selection has not already optimized. By taking this view, problems such as increasing individual yield or photosynthetic efficiency may seem unworthy of breeders' time, while those such as increasing group fitness or resistance to evolving pests are ripe for investment. Similarly, Weiner *et al.* (2010) argue that breeding for increased total yield at the expense of individual plant performance can be combined with knowledge of ecological responses to crop planting density to improve crop management systems—an approach they call evolutionary agroecology. As mentioned above, the agroecological canon contains chapters on genetic resources (Gliessman 2006) and ecological genetics (Carroll *et al.* 1990), though these perspectives rarely infuse agroecology.

Therefore, I argue that although agroecology's very strength is its interdisciplinary nature, nevertheless it can be seen as insufficiently so because evolutionary and genetic perspectives receive little attention. In this paper, I aim to delve a bit deeper into what encompasses evolutionary research, elaborate on the evolutionary work that has been carried out in agriculture, and highlight some fruitful areas of research that could broaden agroecology's reach and import if embraced by the community. In doing so, we can introduce evolutionary agroecology into the agroecological pantheon.

## Areas of research in evolution

It can be helpful to clarify what areas of research are encompassed within evolutionary biology as relevant to agricultural systems. These nodes of study can focus on long or short term processes, encompass a range of scales, be oriented towards molecular or quantitative genetic analyses, and explore ecological processes to differing degrees. Macroevolutionary topics of research within evolution tend to incorporate long term perspectives. Such work might explore the creation, extinction, and diversity of species and their relationships to one another. For instance, some seek to understand the relationships of species within and among plant families (especially those that include important crop species), as well as variation within families for important traits (Meyer *et al.* 2012). This long term perspective sometimes integrates an understanding of factors, such as biogeography, that affect the generation of biodiversity.

Others studies tend to have a short term, microevolutionary perspective that can span from millennia (which is short on an evolutionary scale) to rapid evolution that occurs over even shorter periods of time. In fact, agriculture has

become an important system in which to study the effects of rapid evolution because intense management can drive evolutionary processes (e.g., Gould 1991). In these microevolutionary studies, major forces of evolution are of explicit interest, namely selection (and subsequent adaptation), gene flow, drift, and mutation (Silvertown and Lovett Doust 1993). Many researchers employ modeling techniques of various sorts to understand the interplay between different evolutionary processes (e.g., Yeaman and Whitlock 2011).

Researchers may try to find evidence (phenotypic and/or molecular) of the effects of these evolutionary processes in the resulting patterns of quantitative or molecular genetic variation, including in crop species (Mercer *et al.* 2008; Samberg *et al.* 2013; Meyer *et al.* 2016). These patterns can provide clues into evolutionary forces that have shaped the species. Molecular aspects of this work have been enhanced by on-going developments in genotyping (e.g., genotyping-by-sequencing), and evolutionary researchers now also attempt to identify genes involved in various traits, especially those involved in important adaptations (e.g., Fournier *et al.* 2011; Lasky *et al.* 2015). Often they ask questions about the identity and number of genes involved, what their effects are on traits and fitness, how interdependent they may be, and how they evolve.

While selection is often heavily affected by the abiotic and biotic conditions surrounding a population, there are areas of evolutionary research that are more or less explicit about links to the ecological context. For instance, in evolutionary ecology, that ecological context is paramount. Evolutionary forces such as selection are studied as they operate in the context of interactions of species with their environment and with each other (Antonovics 1992). For instance, many have studied the rapid evolution that can follow gene flow in hybrid zones and try to explore its dependence on the ecological context (Wu and Campbell 2006). Additionally, there would then also be an emphasis on the mechanisms of adaptation that organisms employ to tolerate biotic and abiotic factors they face (Angert 2006). However, other areas of study that fall into the intersection of evolution and ecology may not be typical of evolutionary ecology. For instance, some researchers explore the importance of the genetic variation found within and among species as a mechanism of tolerance to environmental variation or even as a booster of ecosystem function (Kettenring *et al.* 2014).

This is not to say that agricultural researchers have not taken an evolutionary perspective on their work. In fact, some veins of agricultural research are ripe with evolutionary thought—especially those that have had to confront the issues that evolution can cause in managed systems. The study of the development and spread of pesticide resistance has a strong evolutionary history (e.g., Tabashnik 1994). Researchers have documented a multitude of cases of pesticide resistance and their mechanisms (Gould 1991), investigated the forms and

strengths of selection pressures being exerted (Metcalf *et al.* 2000), clarified correlated selection responses on other traits, modeled selection responses based on varied ecological contexts (Mallet and Porter 1992), and much more. Within plant pathology, especially, this evolutionary perspective has extended to documenting the diversity within pathogen populations with the evolutionary potential this confers (McDonald and Linde 2002), considering how to manage pathogens with the use of disease-resistant varieties, and studying the evolutionary dynamics of pathogens that are developing new resistance mechanisms (Stahl and Bishop 2000). However, the agroecology community has generally not embraced these themes. From where does this division between those using genetics to explore evolutionary concepts and the ecologically-oriented agroecological community arise? Perhaps agroecologists see the intense selection pressures of pest control in conventional agricultural systems that drive evolution as not applying to more sustainable systems? It is hard to know whether that is true, due to the paucity of studies in this area. Yet I would argue that there could be exciting synergies created by integration of the evolutionary and ecological perspectives to improve our understanding of agricultural systems, their potential, and their dynamics.

### **How an evolutionary perspective can broaden agroecology's impacts**

There are a number of areas of evolutionary study that engage with agriculture. However, further engagement would broaden agroecology's impact and reach. I will focus here on elaborating three areas of research that have been primary in my laboratory, though many others could be discussed. Here I explain the premise of each and how evolutionary and genetic perspectives help us investigate essential agroecological issues. First, use of an evolutionary perspective can illuminate the adaptations that crops possess, which can be utilized in production or breeding for sustainable systems. Second, viewing genetic diversity within crops and weeds through an evolutionary lens may improve agroecosystem function, such as primary productivity, as well as adaptive capacity. Third, explorations of gene flow or hybridization between neighboring crop fields, between crops and neighboring related weed species, and between populations of weeds can illuminate, and help to eliminate, weed issues.

#### ***Adaptations for sustainability***

Agroecology takes as one of its goals, the sustainable design of cropping systems. From a biological perspective, consideration of soil, pest, crop, and water management are all of primary part of that, as well as landscape connectivity and fluxes and flows in the system. An important part of this is also the choice

of genetic materials. Choice of genetic materials can be done at the level of an individual farmer saving seed from the year before, getting seed from his or her neighbor, or purchasing improved varieties. Choice of genetic materials can also occur at the level of breeding programs identifying traits that are important to agroecosystem sustainability, as well as sources for those traits. For instance, given the increasing variability in precipitation with climate change, identification of sources of drought–and flooding–tolerance for farmers to utilize, or to use in breeding programs, would be beneficial. But could an evolutionary perspective improve this endeavor?

The evolutionary forces that operate on crops result in patterns of genetic variation, some of which is adaptive, or specifically beneficial to plant performance. The relatively recent evolutionary processes affecting crops include natural and intentional selection by the environment and humans, respectively, which have left their marks on crop diversity and crop traits (Mercer and Perales 2010). For instance, human selection has resulted in the domestication of many crops, and the fixation of domestication traits (Meyer and Purugganan 2013) that facilitated human use and cultivation has provided great use–value to human societies (Jardón–Barbolla 2015; Jardón–Barbolla, in this issue). The environment, on the other hand, has selected for traits that improve productivity under conditions experienced by crops in a given geographic area or agroecozone (Mercer *et al.* 2008; Anderson *et al.* 2016). Crops whose seeds are saved yearly, typically landraces or traditional varieties, as well as wild relatives of crops, have evolved over time in response to these geographically variable biotic and abiotic factors (e.g., moisture availability), often resulting in local adaptation (Zeven 1998). Mechanisms for adaptation can be due to phenology or timing of development (e.g., flowering time), morphology (e.g., leaf size), physiology (e.g., stomatal density), or other traits.

To best choose seed lots or varieties of crops that will fit well into a sustainable agroecosystem, the farmer should consider the traits s/he wants the crop to have. Particular climatic adaptations, such as drought tolerance, may be essential for boosting the resilience of the agroecosystem to the vagaries of weather. For farmers seeking out such traits in available varieties or for those who would like to breed crops to enhance those same traits, identification of relevant crop varieties or breeding material is essential.

There are a few types of evolutionary studies that might be useful where relevant adaptations need to be identified in existing seed lots or in potential breeding materials. In the first type of study, a researcher assesses the adaptation of diverse genetic materials to relevant conditions. To do so, s/he will grow diverse genetic materials under one or a range of common conditions to distinguish varieties that do well in particular areas or under particular sets of condi-

tions (e.g., Mercer *et al.* 2008; Orozco–Ramírez *et al.* 2014). However, relating the performance measured to other measured trait values allows researchers to identify the traits conferring that adaptation (e.g., Etterson and Shaw 2001). These kinds of studies can be especially helpful to better understand the underlying bases of climatic adaptation and to identify varieties that farmers might want to use. For participatory or evolutionary breeding programs, this kind of information can be helpful to evaluate different varieties, to choose varieties for crosses, and to judge advanced materials (e.g., Bellon *et al.* 2003).

There is a second form of study that can identify crop materials with relevant adaptations or find sources of genetic variants that may be beneficial to use in breeding programs by using molecular genetic approaches. By genotyping crop materials at many or thousands of loci throughout the genome, researchers can then look for relationships between genetic variation and relevant phenotypes. For instance, to uncover loci that may control drought tolerance, researchers could phenotype genetic materials for their drought responses and then relate those phenotypes to genotypes (e.g., Lasky *et al.* 2015). The identified loci are then good candidates (or are linked to good candidates) for influencing the traits of interest. Relating genotype to phenotype can be done on a range of accessions using genome-wide association studies (GWAS) (Tiffin and Ross-Ibarra 2014; Meyer *et al.* 2016) or using populations generated from controlled crosses for quantitative trait locus (QTL) analysis (Alimi *et al.* 2013a; Almeida *et al.* 2014). These kinds of analyses can also be done using, as phenotypes, the environmental variables describing the locations where crop materials were sourced, such as those describing temperatures and precipitation (Lasky *et al.* 2015; Anderson *et al.* 2016). By doing so, researchers can clarify the materials that possess genotypes likely to produce phenotypes of interest. Both types of research can contribute to an understanding of which crops are important within agroecosystems, how humans and the environment have molded them, and what might be useful materials to deploy in sustainable cropping systems. Combining the two may be our best bet.

### *Genetic diversity—ecosystem function*

We rely on many ecosystem functions in agriculture. Many components of the agroecosystem play important roles that improve the outcomes and properties of the system. While primary production is of obvious interest, other functions such as pest resistance and nutrient cycling are also essential. Within agroecology there has been an interest in understanding how cultural practices and diversification of crop species can improve ecosystem functions (Altieri 1999). For instance, many have explored how adding additional crop species into a system can increase its resilience in the face of disturbances (Lin 2011; Jacobi

*et al.* 2015; Liebman and Schulte 2015). Since agroecosystems in industrialized countries are often species poor, opportunities for improvement abound in that context.

Yet crops utilized in industrialized settings (organic or sustainable farms included) also tend to harbor low genetic diversity compared to their wild progenitors—a form of diversity in plants that can also increase ecosystem function (Kettenring *et al.* 2014). Varieties of crops that farmers use have often been improved or bred intensively. That breeding process itself, as well as the process of domestication that preceded it, reduces genetic variation in a number of ways (Yamasaki *et al.* 2005). Domestication reduces genetic diversity (or the number of genetic variants or alleles) at loci associated with domestication traits, such as lack of seed shattering (Meyer and Purugganan 2013). Thus, so-called domestication genes will often lack diversity in landraces or modern varieties as compared to wild relatives of crops (Hufford *et al.* 2012). Modern plant breeding also reduces the diversity of alleles at loci associated with improvement traits (Lam *et al.* 2010), such as those associated with yield or quality. Thus, improvement genes will be less diverse in modern varieties than in landraces and be less diverse in landraces than in wild relatives (Yamasaki *et al.* 2005). Transgenic varieties are an extreme of this since a new locus is “created” with the insertion of a transgene and only one allele exists (the transgene), although there is also the null allele (or lack of the transgene). Hybrid varieties, or varieties that are created by crossing two inbred lines, each lacking diversity, also harbor less genetic variation than the open-pollinated varieties that preceded them. Even neutral genes, which are not selected upon, will likely lose some diversity during domestication due to genetic bottlenecks imposed along the way. This comparative lack of diversity throughout the genome of modern, hybrid (and sometimes transgenic) varieties is unfortunate due to the benefits that genetic diversity can bring to ecosystems (Kettenring *et al.* 2014). Nevertheless, open-pollinated varieties are still used by some in industrialized countries (especially those who plan to save seed) and are common in the developing world, especially in centers of crop origin where open-pollinated landraces are used. In such contexts, farmers may be able to harness two benefits of genetic diversity within crops: improved ecosystem function through ecological means and greater adaptability and resilience through evolutionary processes in the face of climatic fluctuations.

Unfortunately, we know little about how genetic diversity within varieties affects agroecosystem function within monocultures. However, by marrying ecological and evolutionary perspectives (Kettenring *et al.* 2014), we are coming to understand that, in natural ecosystems, genetic diversity can augment function in species-poor natural ecosystems in a number of ways. Genetic diversity can

increase annual productivity (Crutsinger *et al.* 2006), reproductive success (Williams 2001), and arthropod diversity (Bangert *et al.* 2005), while also augmenting resistance and resilience to disturbance (Hughes *et al.* 2004; Elhers *et al.* 2008). Genetic diversity affects ecosystem function via additive effects, such as sampling effects, and non-additive effects, such as complementarity (Kettenring *et al.* 2014). For instance, after experiencing climatic extremes, plots with higher levels of eelgrass genotypes had greater performance and abundance of fauna due to complementarity between genotypes (some did better in mixture than in monoculture) (Reusch *et al.* 2005). We would do well to investigate these issues in agroecosystems.

In addition to exploiting the effect of genetic diversity on ecosystem function, genetic diversity can also enable adaptive evolution in the face of changing conditions. For landraces or open-pollinated varieties where seed is saved from year to year by farmers, selection of various sorts operates on crop populations. The ways that selection can affect a response in a plant population is a central question in evolutionary biology (Lynch and Walsh 1998). Response to selection ( $R$ ) is directly related to the amount of genetic variation that the population has in the traits being selected upon ( $h^2$ ) and the strength of selection ( $s$ ) ( $R = h^2s$ : the breeders' equation). Thus, for crop populations to adapt in the face of climate change, they require variation in traits that increase their performance under the new conditions, e.g., reduced precipitation (Mercer and Perales 2010). For example, in landraces of pearl millet grown in the Sahel, a recent, long-term drought has caused rapid evolution of earlier flowering time (Vigouroux *et al.* 2011). Gene flow may also be key to facilitating adaptation to new conditions since it can introduce novel alleles that are beneficial under new conditions (Davis and Shaw 2001; Mercer and Perales 2010), which can be accomplished through hybridization or seed sharing among crop populations (Bellon *et al.* 2011). Ultimately, taking an evolutionary perspective here can help us understand how to increase agroecosystem resilience as conditions shift.

Many studies in these areas could help agroecology embrace the importance of genetic diversity within crops. Research comparing ecosystem functionality or adaptive potential when more or less genetically diverse crop populations are used could further clarify how adaptive evolution and genetic diversity–ecosystem function effects might operate in agroecosystems. Unfortunately, simply comparing open-pollinated (OP) to hybrid varieties often confounds genetic diversity with degree of breeding, thereby reducing the apparent benefits of diversity (Campbell *et al.* 2014). Since we would expect a range in the amounts and pattern of genetic variation typical of different crops based on their mating systems (i.e., sexual vs asexual, outcrossing vs self-pollinating) and the structure of any farmer seed-sharing networks, studies could investigate what this

means for the size of ecological and evolutionary responses possible. Different agroecosystem functions may respond differently to genetic diversity, and different traits would be experiencing different selection pressures, so studies could explore the range of related responses. If these kinds of studies clarify benefits of diversity, it would be prudent to broaden the genetic base of crops to augment the resilience of individual crop populations, agroecosystems, and even agricultural landscapes (via metapopulation dynamics: van Heerwaarden *et al.* 2010). Participatory plant breeding may be well-suited to play this role.

### *(Trans–)gene flow*

With the advent of transgenic crops in the mid–1990s, the fact that crops have the ability to hybridize or cross with their wild relatives became abundantly clear. The new technologies raised concerns in the agricultural and ecological communities due to the potential adverse effects that novel genes may have when out of place (Snow and Palma 1997). This issue galvanized the scientific and activist communities alike and spawned a range of scientific studies that had a distinctly evolutionary perspective (reviewed in Ellstrand 2004; Mercer *et al.* 2006; Campbell *et al.* 2007). It also highlighted the need to understand gene flow between crop fields (from transgenic to non–transgenic crops) or among weeds (from those that received a transgene from a crop to those that did not) (Beckie *et al.* 2003; Ellstrand 2004).

The issue of gene flow generally, and transgene flow as a specific case, fits within evolutionary biology because gene flow is one of the fundamental evolutionary processes shaping the genetics of populations. Gene flow can homogenize populations that hybridize with one another, but it is also able to introduce novel genetic variants on which selection can act (Lenormand 2002). Transgenes constitute a form of novel genetic variant (as opposed to a naturally occurring mutation) and the planting of transgenic crops introduces to the landscape a large source of crop alleles, as well as the novel transgene. In the case of gene flow between transgenic crops and neighboring wild relatives, their hybridization often results in crop–wild hybrids in the wild population (Burke *et al.* 2002). Thus, once gene flow has occurred, the questions around how the genes affect the wild population become largely about selection: will the lineage initiated by this crop–wild hybrid be maintained in the population, increase in frequency, or be lost? Will selection, or just simply drift, be implicated? How will the particular ecological context in which the wild population and its hybrids live affect this outcome (Mercer *et al.* 2014), especially given ecological differences between agricultural and wild environments? The frequency of gene flow can also influence the outcomes (Ellstrand 2004). Here it becomes clear that agroecology, which is intimately interested in the movement of nutrients and pesticides off–

farm, could encompass work that seeks to understand the movement and effect of novel genes or crop variants of other genes in wild, weedy, and crop contexts.

A number of methods are utilized to illuminate the gene flow and selection occurring in crop–wild hybrid zones. While the possibility for gene flow can be estimated using controlled hand–pollination, natural rates of gene flow can be documented at different spatial scales (e.g., Arias *et al.* 1994; Watrud *et al.* 2004) using some indicator (molecular, phenotypic) to identify hybridization events. Hybrids generated through gene flow can then be tested for their ability to survive and reproduce to evaluate their fitness (e.g., Cummings *et al.* 2002; Mercer *et al.* 2006). When hybrid fitness is then compared to that of their wild counterparts, we can begin to understand the selective dynamics affecting plants possessing crop alleles, including hybrids of different advanced generations. Fitness at different parts of the life cycle, such as the seed and seedling stages, can also clarify how selection may change at different times (Weiss *et al.* 2013; Kost *et al.* 2014; Pace *et al.* 2015). In addition, selective dynamics can change under different ecological conditions, affecting the likelihood of introgression of crop alleles. For instance, since competition and herbicide application had been shown to affect the fitness of hybrids relative to wilds (Mercer *et al.* 2007), studies manipulating different aspects of competition have elaborated on those dynamics (Mercer *et al.* 2014). Thus, bringing an evolutionary perspective to bear on the question of gene flow in transgenic crops has helped us address an important agroecological question concerning the effects of a management tool (transgenic crops) on neighboring cultivated, wild, and weedy neighbors via gene flow and selection.

## Conclusions

Agroecology has not intentionally excluded evolutionary thinking, but it has not necessarily embraced it. Both the agroecological and evolutionary communities alike must recognize the people working at the intersection of the two. Better integration of an evolutionary perspective into agroecology and greater representation of agriculture within evolution is certain to inspire novel avenues for research, allowing for exciting synergies. For instance, evolution of pest populations in the face of climate change is a major issue facing agriculture. Agroecology can only gain if these evolutionary dimensions of agroecosystem change are included when working to enhance the resilience of agroecosystems. Hopefully a new generation of agroecologists will be inspired to work at this juncture, cultivating the field we may come to call evolutionary agroecology. ■

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