

EDITORIAL

Evolutionary change in agriculture: the past, present and future

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In this special issue of *Evolutionary Applications*, we draw together a series of diverse studies that provide a sample of some of the ways in which evolution driven by both conscious and unconscious selection by humans has shaped the development of modern agriculture. Agriculture has been a crucible of evolutionary change ever since its inception thousands of years ago, and this change permeates agricultural endeavours at all levels of biological organisation, ranging from the individual gene through to whole communities. Agro-ecosystems thus provide one of the most cogent examples of situations where anthropogenic effects are major determinants of biotic interactions within and among species and communities, suggesting a central role for the application of evolutionary principles. This is particularly the case, given global concerns regarding food production and food security, and increasingly, the expectation that agricultural productivity gains must be achieved with greater efficiencies, and reduced environmental impact.

In the development of human society, the shift to a relatively settled way of life from a nomadic hunter-gatherer life-style was enormously profound, and made possible only by the development and adoption of early agricultural practices. In turn, this change in human life-style had major impacts on the environment of agriculture and hence the traits and characteristics of plants and animals that were favoured both consciously and unconsciously by humans. Very often traits suited to species growing *without* human protection/husbandry were not suitable for agriculture and were rapidly lost (e.g. seed shattering), while others were specifically favoured by the more protected environment agriculture provided, and increased in frequency (e.g. seed retention).

As agriculture developed, the environment of the field and paddock became increasingly differentiated from that of the natural environments in which plants and animals originally evolved. For plants, nutrient availability generally rose, plant density and genetic uniformity increased, and the balance in competition shifted from inter-specific considerations to intra-specific ones (particularly with the general reduction in species diversity). Tilling and crop

rotation were further agronomic practices that were introduced partly for fertility reasons but also for control of natural enemies, as rotation causes shifts in whole fungal pathogen communities. It is interesting to note that another generation of changes to tilling practices – minimum tillage – is to some extent now altering ecological and evolutionary interactions at the plant–soil interface towards a different set of fungal control issues. Similarly for animals, domestication created a more predictable environment with increased resource availability during harsh times and protection from predators, but increased threats from contagious diseases, all subtly influencing the evolutionary make-up of our livestock.

Over the last few thousand years, domestication, selection and hybridisation, both unconscious and conscious, has also led to significant changes in the appearance of plants and animals and their nutritional value. Examples are seen in virtually all plant and animal species that are farmed. In horticulture, this diversity is often highly prized in the form of different varieties that are preserved for subtle variations in flavour, texture or simply appearance (e.g. in potato, tomato, apple). In a similar way, extensive selection in farmyard fowls (chickens, ducks, geese and turkeys), and in pigs, sheep and cattle have given rise to very many distinctive breeds that differ in milk production, flesh texture and flavour, and obvious appearance, as well as in less obvious traits, such as patterns of social behaviour. Extensive agriculture has also seen similar major changes that have resulted in significant increases in yield and productivity. In plants, perhaps one of the most dramatic changes to have occurred within a species is found in the emergence of modern high-yielding hybrid maize from its close relative teosinte, and the subsequent application of a number of induced mutations and the introduction of an F1 hybrid system. Similarly dramatic changes have occurred in meat and fibre production and quality in selected beef and sheep varieties respectively.

In essence, throughout the history of agriculture, changes in agronomic and animal husbandry practices and in the crops and animals being farmed have had

collateral effects that have changed the balance and intensity of different selective forces. This has been particularly apparent in plants where increasing nutrient status (particularly nitrogen) generally favours the growth and development of insect and fungal pests – the numbers of which are frequently then further exacerbated by increased plant density (this increases humidity and thus conditions for fungal spore germination; and reduces inoculum loss during transmission) and genetic uniformity of crops. As selection by humans shifted to a conscious understanding of genetics, the focus also increasingly centred on accumulating single major gene traits because these could be more readily manipulated. While human selection has been a major driving force in the types of changes outlined above, subject to the vagaries of fashion, it has often tended to be highly directional favouring more and more extreme manifestations of the traits in question. In the realm of biotic interactions involving pests and pathogens, these approaches have often precipitated the equivalent of an ‘arms race’ between humans and these natural enemies of their crops.

Importantly, in contrast to many other evolutionary issues in agro-ecosystems, interactions between disease causing organisms and our crops and livestock are characterised by much more dynamic and unpredictable reciprocal evolutionary change. For example, during the 20th century, breeding for rust resistance in cereals through the deployment of single major genes for resistance, placed major selection pressure on relevant pathogen populations leading to the rapid emergence of new pathotypes with novel pathogenicity profiles capable of overcoming the recently deployed resistance. Indeed, this reciprocal process became so rapid and predictable that it became known as ‘man-guided evolution of the rusts’ (Johnson 1961).

Clearly then, developments in our understanding of evolution and genetics have had unintended effects as well as having a huge impact on the process of conscious plant and animal improvement. In recent decades, technological advances, particularly in molecular biology, have further accelerated this process. Traditionally in the context of agricultural breeding, to understand relationships between domesticated species we look to the concept of the gene pool to understand the closeness of relationship between any two species and the potential for utilising and combining desirable traits. Those in the primary (landraces and immediate wild progenitors) and secondary (closely related species) gene pools, because of their sexual compatibility have been used for some time as sources of beneficial traits. However, until the dawn of the molecular revolution, access to valuable traits in the tertiary gene pool (more distantly related species) was exceptionally difficult while

access to the quadrinary gene pool (organisms from other kingdoms) was impossible.

As noted above, the process of domestication is one of the most obvious ways in which human-driven selection has driven evolution in agriculture. The article by Moyle and Muir (2010) provides a fascinating overview of research on tomato and its wild relatives, in particular highlighting how such studies can provide insight into the mechanisms underlying traits of functional importance (e.g. adaptation to water stress). These studies also exemplify the genetic trade-offs that constrain high yield to a narrow set of environments. O’Neill et al. (2010) illustrates these trade-offs within a summary of the evolutionary history of *Bos taurus* cattle, as adaptation to stress-free temperate conditions generated breeds with little resistance to diseases common in tropical regions. They advocate explicit consideration of genotype \times environment \times management interactions in future breeding efforts. Such approaches may be critical to future livestock systems which must increasingly meet the twin goals of economic and environmental sustainability. A similar story is told within the article by Van Tassel et al. (2010), which describes how man-guided adaptation of plants to crop field situations has favoured shorter-lived species with unusually high allocations to sexual reproduction. Given the high environmental costs of this mode of production, these authors argue that there is a need and growing promise in the development of useful perennial plants for agriculture.

Traits that differentially affect group versus individual fitness have particular importance in agricultural production where domesticated plant and animal populations are generally grown at high densities. Aggressive behaviour in chickens and pigs, for example, can be individually advantageous, but result in reduced yield overall. Wade et al. (2010) present a theoretical framework for and evidence of successful efforts to use the principles of group selection to evolve less aggressive domesticated pigs and chickens with positive effects on farm yield. Similar conflicts between individual and group yield mediate production in cropping systems and two examples of these are presented by Denison et al. (2010) and Weiner et al. (2010) who focus on complementary aspects of competition for light in agricultural fields.

Focusing on maize as an example, Mercer and Perales (2010) explores the issue of crop genetic resources as maintained in landraces, the evolutionary potential for crop adaptation to changing climates, and some of the problems associated with *ex situ* conservation of crop genetic resources. Crop weeds have direct economic impacts on productivity, but are also of evolutionary interest in several contexts (e.g. herbicide resistance, shifts in weed life history, cross-species gene transfer), particu-

larly given that they demonstrate many of the ecological characteristics of crop species. A comparative analysis of weedy species that have evolved from domesticated plants suggests that useful insights can be gained with regard to traits that correlate with invasiveness (Ellstrand et al. 2010).

Despite the generally simpler communities represented by agro-ecosystems relative to natural plant and animal communities, strong interspecific interactions still constrain yield and influence man directed and unconscious evolution in agro-ecosystems. Principal among these interactions are the pathogens (Burdon and Thrall 2008), with the source of individual pathogen populations being a persistent question. Wang et al. (2010) integrate molecular, experimental and field studies to demonstrate that *Fusarium* wilt disease of cotton in Australia has most likely evolved locally from related fungal strains associated with native cotton hosts. The negative effect of pathogens and other natural enemies can be ameliorated through crop interactions with other symbionts, including endophytic fungi, though these fungi can themselves carry a yield penalty. Alternative frameworks for understanding conditions in which endophytic fungi improve yield are developed by Saunders et al. (2010) and Gundel et al. (2010). While Saunders and colleagues focus on determinants of endophyte dynamics such as order of colonisation, Gundel et al. (2010) examine patterns of plant breeding system and plant-endophyte compatibility. Plant yield is also determined by interactions with soil microorganisms and while there is increasing recognition of the role of soil biota as drivers of ecosystem function and productivity, there is still relatively little knowledge of how agronomic management practices (e.g. crop rotation, tilling practices, fertiliser applications) might impact on soil communities. Verbruggen and Kiers (2010) address this by focussing on agronomic management practices that influence underlying evolutionary forces that determine the diversity of arbuscular mycorrhizal fungi in farming systems, and how management might be shifted to enhance the benefits provided by these mutualisms.

Over the past decade, research into, and the deployment of GM technologies has increased rapidly, particularly in the developing world. Concomitant decreases in the costs of developing and implementing such approaches, together with advances in our technical ability to insert or modify specific genes or gene pathways will further contribute to shifts towards the use of these approaches. GM technologies provide one of the few examples where evolutionary principles (pyramiding of genes, crop refuges) have been explicitly applied in a preemptive fashion to minimise risks (another is seen in the use of varietal mixtures for disease control in cereals). In this issue, we highlight this topic with two papers which

focus on management strategies aimed at delaying the evolution of resistance to Bt toxins in transgenic crops such as maize and cotton. Carriere et al. (2010) provide an excellent overview of the success of these approaches over the past 15 years; they conclude that, while refuges have been generally successful, better understanding of source-sink dynamics and improved ability to manipulate resistance costs in pest species may be important avenues for future research. Downes et al. (2010) examine the specific case of Bt cotton in Australia, where it has been widely deployed, and where Bt resistance has been explicitly and successfully managed since the initial release of transgenic cotton.

The studies presented here represent only a fraction of the diversity of evolutionary issues of relevance to agro-ecosystems. With regard to human-driven selection of yield-associated traits in crops there are many other issues associated with changes in plant structure and architecture, genome duplication during domestication, and life history traits such as flowering time; tillering rates etc. that have practical significance. While articles in this issue highlight some research on species interactions in agriculture, overall the evolutionary potential of feedbacks across the agro-ecological interface is under-studied, particularly given likely changes in agricultural land-use (diversification, intensification, increased area under production, greater use of GM technologies). Such feedbacks include increased pest and herbicide resistance, pathogen evolution, weediness, and more generally the consequences of durable pest control (e.g. opportunities for previously minor pathogens/pests to emerge). In at least one case (Bt resistance in crop pests), there has been explicit development of management approaches based on evolutionary principles. New opportunities for evolutionary analysis also arise from recent advances in our ability to quickly characterise patterns of soil biodiversity (e.g. next generation DNA sequencing, microarrays) at multiple spatial scales and with rigorous replication – the necessary foundation for exposing the cryptic genetic variation that underpins soil community function.

Agriculture is thus the source of diverse selective forces, and modern agriculture – its species and practices, is the outcome of a continuous process of change that has dramatically changed physically and genetically all components of agro-ecosystems. Further advances in the genetic potential of crops and livestock will continue to be dominated by conventional breeding strategies made increasingly efficient by advances in marker technologies. In addition though, the introduction of genes from other species via molecular manipulation (GM technologies) will become increasingly common but generally restricted to introducing changes that are unattainable via conventional approaches. Overall therefore, recognition and

application of ecological and evolutionary principles will be an increasingly important part of the overall development and management of agriculture, particularly in the context of climate change (new plants and animals), and the imperative for greater sustainability (shifts in land management). As such, we suggest that biologists might do well to consider agro-ecosystems as useful models for the scientific investigation of evolutionary processes.

Literature cited

- Burdon, J. J., and P. H. Thrall. 2008. Pathogen evolution across the agro-ecological interface: implications for management. *Evolutionary Applications* 1:57–65.
- Carriere, Y., D. W. Crowder, and B. E. Tabashnik. 2010. Evolutionary ecology of insect adaptation to Bt crops. *Evolutionary Applications* 3:561–573.
- Denison, R. F., J. Fedders, and B. Harter. 2010. Individual fitness versus whole-crop photosynthesis: solar tracking tradeoffs in alfalfa. *Evolutionary Applications* 3:466–472.
- Downes, S., R. J. Mahon, L. Rossiter, G. Kauter, T. Leven, G. Fitt, and G. Baker. 2010. Adaptive management of pest resistance by *Helicoverpa* species (Noctuidae) in Australia to the Cry2Ab Bt toxin in Bollgard II® cotton. *Evolutionary Applications* 3:574–584.
- Ellstrand, N. C., S. M. Heredia, J. A. Leak-Garcia, J. M. Heraty, J. C. Burger, L. Yao, S. Nohzadeh-Malakshah *et al.* 2010. Crops gone wild: evolution of weeds and invasives from domesticated ancestors. *Evolutionary Applications* 3:494–504.
- Gundel, P., M. Omacini, V. O. Sadras, and C. M. Ghersa. 2010. The interplay between the effectiveness of the grass-endophyte mutualism and the genetic variability of the host plant. *Evolutionary Applications* 3:538–546.
- Johnson, T. 1961. Man-guided evolution in plant rusts. *Science* 133:357–362.
- Mercer, K., and H. R. Perales. 2010. Evolutionary response of landraces to climate change in centers of crop diversity. *Evolutionary Applications* 3:480–493.
- Moyle, L., and C. D. Muir. 2010. Reciprocal insights into adaptation from agricultural and evolutionary studies in tomato. *Evolutionary Applications* 3:409–421.
- O'Neill, C. J., D. L. Swain, and H. N. Kadarmideen. 2010. Evolutionary process of *Bos taurus* cattle in favourable versus unfavourable environments and its implications for genetic selection. *Evolutionary Applications* 3:422–433.
- Saunders, M., A. E. Glenn, and L. M. Kohn. 2010. Exploring the evolutionary ecology of fungal endophytes in agricultural systems: using functional traits to reveal mechanisms in community processes. *Evolutionary Applications* 3:525–537.
- Van Tassel, D. L., L. R. DeHaan, and T. S. Cox. 2010. Missing domesticated plant forms: can artificial selection fill the gap? *Evolutionary Applications* 3:434–452.
- Verbruggen, E., and E. T. Kiers. 2010. Evolutionary processes drive mycorrhizal functional diversity in agricultural systems. *Evolutionary Applications* 3:547–560.
- Wade, M., P. Bijma, E. D. Ellen, and W. Muir. 2010. Group selection and social evolution in domesticated animals. *Evolutionary Applications* 3:453–465.
- Wang, B., C. L. Brubaker, B. A. Summerell, P. H. Thrall, and J. J. Burdon. 2010. Local origin of two vegetative compatibility groups of *Fusarium oxysporum* f. sp. *vasinfectum* in Australia. *Evolutionary Applications* 3:505–524.
- Weiner, J., S. B. Andersen, W. K.-M. Wille, H. W. Griepentrog, and J. M. Olsen. 2010. Evolutionary agroecology – the potential for cooperative, high density, weed-suppressing cereals. *Evolutionary Applications* 3:473–479.