

MINI-REVIEW: ECOLOGICAL SOLUTIONS TO GLOBAL FOOD SECURITY

Looking at past domestication to secure ecosystem services of future croplands

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Summary

1. Food security faces challenges that must be addressed from multiple perspectives. Ecology and agronomy contribute to that endeavour, allowing improvement in management practices. However, not only management affects food provision but also crop traits modulate key ecosystem services (ESs), including sustained yields.

2. Here we highlight that understanding how crop traits evolved under domestication, affecting ESs delivery, should help to breed future crops. We address the effects of crop evolution (from initial domestication to current times) on crop traits and key ESs: crop yield and its stability over time, soil carbon sequestration, soil nitrogen retention and water provision.

3. Synthesis. There is evidence that crop domestication affects the delivery of ESs. However, most of these evolutionary effects are understudied. Accordingly, we identify research gaps and necessary actions, including (i) assessing whether performance in polyculture is lower for modern crop mixtures than for mixtures of wild progenitors, and breeding for more efficient crop polycultures; and (ii) investigating how crop evolution impacted on plant effects on soil carbon sequestration and nitrogen retention, and how such effects contribute to yield stability. The provision of cropland ESs, and thus food security, will benefit from exploring those avenues from an ecological perspective.

Key-words: artificial selection, biodiversity, crop evolution, crops, food security, litter decomposition, traits, water use, yield

Introduction

Securing food provision involves geopolitical, economic, societal and agricultural actions. We face the double challenge of enhancing sustainability of food production in the developed world, and fostering yields in developing regions. Both endeavours, augmenting yields and guaranteeing sustainability, are provisioning ecosystem services (ESs) of croplands, which rely on supporting and regulating ESs (Power 2010). Carbon (C) sequestration, regulation of water and nutrient cycling, or diversity and composition of cropland biological communities support and regulate the provision and stability of yields (Power 2010). Ecology has contributed extensive knowledge to devise agronomic practices that optimize the delivery of cropland ESs (see other papers in this issue). However, management is not the only driver of cropland ESs. We advocate that looking at crop evolution from the standpoint of trait-based, community and ecosystem ecology can offer complementary insights. We base our expectation on two lines of evidence: (i) plant traits exert strong effects over ESs relevant in croplands (Lavorel &

Garnier 2002) and (ii) those traits evolved during plant domestication and further breeding (Milla *et al.* 2015; Fig. 1). This paper presents a novel framework synthesizing how crop evolution affects the delivery of ESs (Fig. 2). We show the yet scarce evidence on how the provision of ESs, including yield and its stability, is affected by crop evolution. Additionally, we propose research actions that can guide ESs-oriented breeding for future crops (Table 1).

Yield and yield stability

Yield is the focal provisioning service of croplands. Domestication and breeding have improved the yield of wild plants, their nutritional quality and their adaptability to agricultural practices (Meyer, DuVal & Jensen 2012). Since the mid-1960s, yield of staple foods has grown at impressive, though linear, rates. Yet, current demographic growth requires exponential gains in yield to accommodate increasing food demands, which are no longer being met (Connor, Loomis & Cassman 2011).

The results of ecological research are an under-explored source of knowledge to help breed crops that optimize the sustained provision of yields. A complete coverage of that

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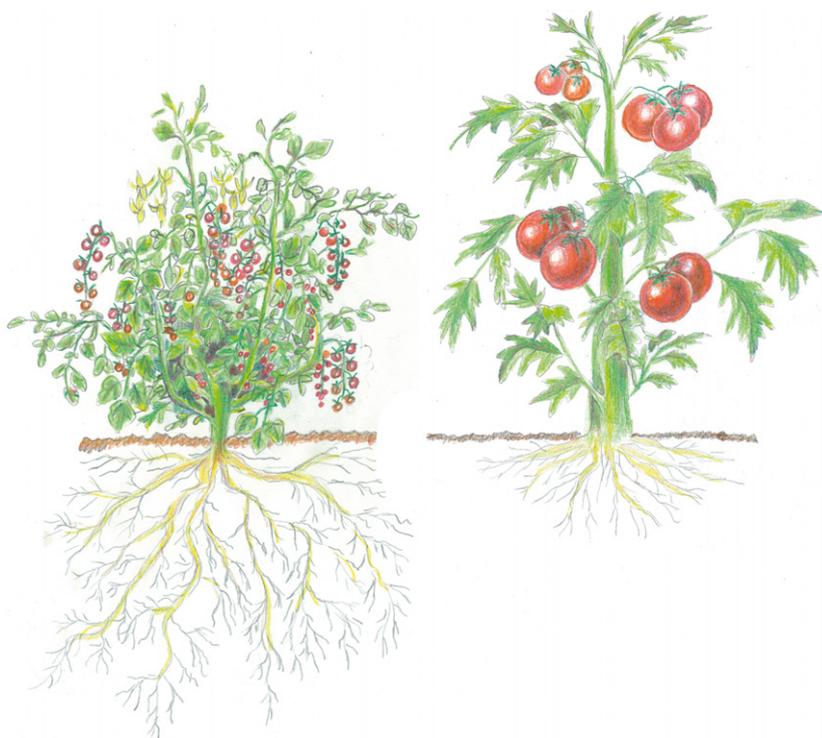


Fig. 1. Domestication and further crop evolution have changed plant phenotypes. Crops and their wild progenitors show contrasting traits, including size of organs, patterns of biomass allocation to plant functions, growth habit and phenology. Those and other traits might influence yield and other ecosystem services of croplands. In the picture, caricature drawings of *Solanum pimpinellifolium* L. (wild progenitor of tomato, left), native to the dry coastal lowlands of Ecuador and Peru, and of *Solanum lycopersicum* L. (domesticated tomato, right). Drawings by Nieves Martín-Robles. [Colour figure can be viewed at wileyonlinelibrary.com]

potential is outside the reach of this mini-review. However, we illustrate that promising transfer with the interaction between crop evolution and biodiversity effects on productivity. Plant diversity promotes productivity and stability in natural ecosystems (Reich *et al.* 2012; see Isbell in this issue). However, biodiversity effects are more variable in mixtures of crops (Trenbath 1974; Hauggaard-Nielsen *et al.* 2008). Biodiversity experiments and intercropping trials use different approaches, which might partly explain such discrepancy. Yet, crop evolution might have played a critical role in the delivery of biodiversity effects in crop mixtures. A recent study showed lower plant productivity in grassland mixtures composed of genotypes selected under monoculture than in mixtures of genotypes with a polyculture selection history (Zuppinger-Dingley *et al.* 2014). Genotypes raised under polyculture showed higher trait disparity than those with a history of monoculture. Only eight generations of selection in monoculture made grassland species less suited to perform in mixtures. Given that crop plants have been under monoculture for much longer time spans, poor complementarity in crop mixtures might dampen the benefits of biodiversity effects. Evolution in monocultures probably selects for enhanced competitive traits and less collaborative behaviour in stands. In fact, crops show traits typical of strong competitors (Milla *et al.* 2014). Strong competition promotes *tragedy of the common* scenarios, where collective performance suffers due to individual overinvestment in resource competition (Anten & Vermeulen 2016). Intensifying breeding against competitive traits can overcome past selection for competitive plants. This breeding will help to release genotypes and species whose yields and stability benefit from biodiversity effects (Litrice & Violle 2015; Prieto *et al.* 2015). Moreover, plant diversity regulates the delivery of multiple ESs beyond productivity, such as

soil C and nutrient cycling (Soliveres *et al.* 2016), which feeds back on the long-term sustainability of yields (Fig. 2). Therefore, wider adoption of multiline cultivars, polycultures or rotation practices should benefit increase yield stability (Prieto *et al.* 2015). Experiments investigating the consequences of crop evolution on biodiversity effects, and the underlying traits, are thus needed (Table 1).

Carbon sequestration

Soil C stocks typically decline after agricultural conversion (Guo & Gifford 2002). Croplands occupy 40% of land surface and the largest amount of terrestrial C is stored in soils. Thus, enhancing soil C sequestration rates is a major challenge for agriculture (Lal 2004). Agronomic practices like organic, diversification or no-till farming can promote soil C sequestration (Lal 2004). However, the potential of breeding to enhance C sequestration has received less attention. Importantly, we know that above- and below-ground plant traits influence soil C cycling in natural areas (De Deyn, Bardgett & Cornelissen 2008), which can facilitate plant breeding programmes oriented to promote soil C sequestration. Expectations are promising because plant traits with an impact on soil C cycling, like specific leaf area (Cornwell *et al.* 2008) or rooting depth (Kell 2011), are affected by breeding (Anten & Vermeulen 2016). In this line, García-Palacios *et al.* (2013) found that leaf litter of crops has become more labile after domestication. Furthermore, residues from domesticated crops decompose faster and promote lower concentrations of labile C forms in soil than residues from their wild progenitors (García-Palacios *et al.* 2013). However, not only plant inputs but also soil microbes, control the residence time of C in the

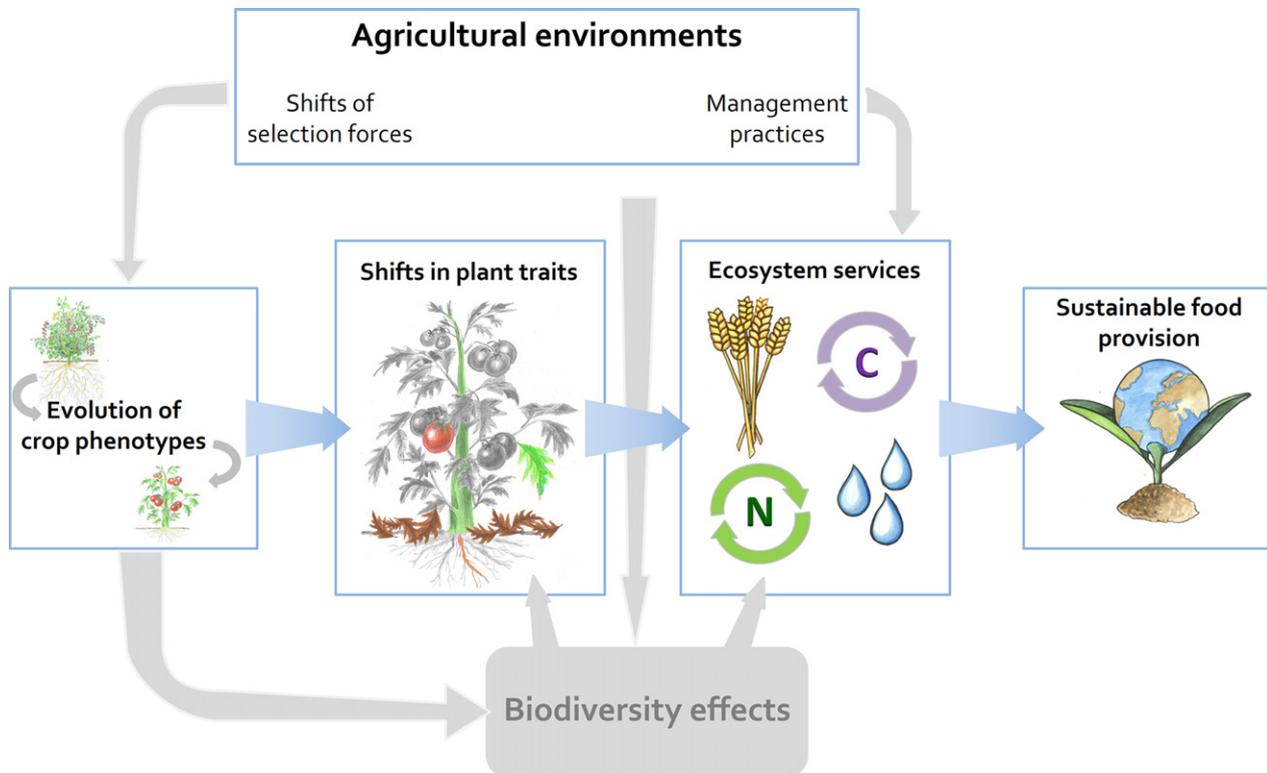


Fig. 2. Evolution under domestication, jointly with cropland management, control sustainable food provision. Sustainable supply of food is guaranteed through the promotion of cropland ecosystem services (ESs) such as carbon (C) sequestration, regulation of water and nitrogen (N) cycling, yield and yield stability. Managing the crop environment adequately contributes to that endeavour. However, plant traits also exert strong controls over ESs, and that control has evolved during domestication. Additionally, biodiversity is a key modulator of the delivery of ESs, but it is unknown how biodiversity effects have evolved under cultivation. Thus, advancing our understanding on the ecological consequences of domestication, and how we can promote beneficial effects through breeding, is of relevance for global food security. Drawings by Nieves Martín-Robles and Elena Granda. [Colour figure can be viewed at wileyonlinelibrary.com]

Table 1. Research gaps and recommended ecological research approaches

Research questions	Recommended approaches
Has past domestication hindered the ability of crops to perform in mixtures?	Experiments investigating the consequences of crop evolution on biodiversity effects, and the traits underlying these effects
Can crop residues and crop mixtures foster soil C sequestration?	Manipulative and observational studies assessing physiological constraints between crop tissue recalcitrance and yield
Has crop evolution changed N release and immobilization patterns from decomposing crop litters?	Simultaneous assessment of N dynamics in decomposing leaf, root and stem residues of monocultures and mixtures, as well as consequences for crop yield
Can adaptive plasticity of crops or their wild progenitors be used to increase yield and its stability?	Experiments addressing whether phenotypic plasticity and its adaptive value have evolved after domestication

soil (De Deyn, Bardgett & Cornelissen 2008). Soil microbial biomass shifts might be accompanied by changes in fungal: bacterial ratios and soil C cycling. In sum, historical reductions in the soil organic matter pools of croplands might be a consequence of agricultural management, and also of using genotypes with chemically labile residues and shallow roots. Breeding for: (i) increased recalcitrance of shoot and root residues, (ii) crop mixtures promoting fungal-dominated soil food webs and (iii) extensive and deeper root systems, will lead to slower soil C cycling and hence higher C sequestration in agricultural lands (De Deyn, Bardgett & Cornelissen 2008; Kell 2011). However, recalcitrance is typical of plants

with poor palatability (Cornelissen *et al.* 2004), which might compromise yield quality. Therefore, diversifying the lability patterns of crop residues by using recalcitrant varieties, via cover crops or rotations, may enhance soil C sequestration while maintaining the yield function of the harvested focal crop.

Soil nitrogen retention

Croplands are harvested at regular intervals, which requires the restoration of soil fertility. Addressing that need via inorganic fertilization has triggered major environmental impacts

(Davidson *et al.* 2012). Nitrogen (N) is lost via leaching and denitrification, as crops use on average <50% N from synthetic fertilizers (Galloway & Cowling 2002). Alternatives such as manure-based organic farming increase fertility while reducing N losses (Skinner *et al.* 2014). Efficient crop residue management is also an alternative to promote tightly coupled soil N cycling, because N release is slower than from inorganic fertilization, contributing to synchronized soil N availability with plant N demand (Tilman 1998). Residues from domesticated crops release nutrients to the soil faster than their wild progenitors, increasing soil N availability more rapidly (García-Palacios *et al.* 2013). Farmers could match N availability to N demand selecting diverse crop varieties with litter traits similar to domesticated (faster litter N release) or wild (higher litter N immobilization) genotypes. Such diversification enhances the variability of crop residue inputs, and may contribute to promote tight N cycles preventing N losses in agricultural soils. Enhancing soil fertility while reducing soil N losses is a major challenge for crop sciences (Davidson *et al.* 2012), and contributions with that aim may need proven strategies such as manure fertilization (Skinner *et al.* 2014) or crop varieties with increased longevity and length of root systems (Kell 2011), complemented with diversified crop residues across time and space. Thus, knowledge on how domestication has affected nutrient provision in croplands can complement current breeding programmes aimed to promote efficient soil N cycling.

Provision of water

Agriculture takes the highest proportion of the freshwater used by human populations (Frenken & Gillet 2012). Therefore, maximizing yields while making the most efficient use of water in croplands is a priority. Plants can improve water use efficiency (WUE) through traits that balance C and water use, or through adaptive plasticity in such traits. Adaptive plasticity is particularly relevant for water use, because fine-tuning physiology and morphology at short time intervals matches the high temporal and spatial heterogeneity inherent to water supply (Nicotra & Davidson 2010). Domestication has frequently been accompanied by shifts in traits involved in water use, such as leaf size, stomatal conductance or root architecture. Canalization of those traits, that is the reduced expression of their phenotypic variation, might benefit or hamper water use and yield, depending on the homogeneity of the environmental context. However, canalized phenotypes may not be adaptive when water is supplied heterogeneously. For instance, the increased size of stomata observed in several domestication processes (Milla, de Diego-Vico & Martin-Robles 2013) can be adaptive in constant, humid environments, but may result in low WUE when water supply is varying or limiting. Indeed, in spatially and temporally variable environments, a plastic genotype is more advantageous than a canalized one (Matesanz, Gianoli & Valladares 2010). Although many efforts have been devoted to breeding crops for future drier conditions (Cattivellia *et al.* 2008), a poorly explored avenue is to select for genotypes able to express

adaptive reaction norms in contrasting conditions rather than uniform phenotypes, that is breeding for adaptive plasticity (Bloomfield, Rose & King 2014). As the effects of crop evolution on plasticity remain unknown, a first step to implement this approach is to determine the impacts of genetic bottlenecks linked to domestication on the phenotypic responses of crop genotypes to environmental heterogeneity (i.e. genetic variation for plasticity). Trait means and their plasticity might, or might not, be genetically correlated. Therefore, assessing whether strong selection associated with breeding has limited or fostered plasticity in water use traits is a research gap. Furthermore, the adaptive value of phenotypic plasticity in agricultural environments remains largely unexplored. It is yet not known, for instance, whether and how plasticity of water use traits contributes to yield stability. We advocate the use of breeding experiments, using plasticity as the target of selection (van Kleunen *et al.* 2007), to assess its potential effects on crop resilience to climate change and associated effects on water use.

Conclusion

Global food security requires yield to be maintained long term, which involves optimizing supporting and regulating ESs like soil C sequestration, N retention, sustainable use of water or the promotion of biodiversity. Plant ecological research is providing an appreciation of how the delivery of those ESs in croplands has been affected by crop evolution. Current evidence indicates that evolution under domestication may have decreased the ability of crops to perform in mixtures, and that crop residues have evolved to be more labile and promote fast soil nutrient cycling. We need a deeper understanding on how plant-mediated controls of cropland ESs have changed as a result of past breeding, to develop guidelines on how to breed new genotypes that optimize the delivery of ESs. In Table 1, we suggest actions that will move forward the field, and can be performed from ecological research projects. Specifically, we identify as a core priority the investigation of whether and how biodiversity effects on productivity and nutrient cycling have changed during crop evolution (Table 1). Addressing these research gaps will bring new opportunities to increase and secure global food provision.

Authors' contributions

R.M., P.G.-P. and S.M. conceived the ideas and outlined the contents of the review. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility

Our manuscript does not use data.

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