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Title: Reproductive traits and evolutionary divergence between Mediterranean crops and their wild relatives

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Abbreviations

SC: self-compatibility; SI: self-incompatibility

Abstract

Changes in reproductive traits associated with domestication critically determine the evolutionary divergence between crops and their wild relatives, as well as the potential of crop plants to become feral. In this review, we examine the genetic mechanisms of plant domestication and the different types of selection involved, and describe the particularities of domestication of Mediterranean field crops with regard to their reproductive traits showing illustrative examples. We also explore gene flow patterns between Mediterranean field crops and their wild relatives, along with their ecological, evolutionary and economic implications.

Domestication entails multiple selective processes, including direct selection, environmental adaptation and developmental constraints. In contrast to clonal propagation in perennials, sexual reproduction and seed propagation in annuals and biennials have led to a distinct pathway of evolution of reproductive traits. Thus, the initial domestication and further breeding of Mediterranean field crops has brought about changes in reproductive traits such as higher mean values and variance of seed and fruit sizes, reduced fruit and seed toxicity, non-shattering seeds, and loss of seed dormancy.

Evolution under domestication is not a linear process and bi-directional gene flow between wild and crop taxa is a frequent phenomenon. Thus, hybridization and introgression have played a very important role in determining the genetics of current cultivars. In turn, gene flow from crops to wild relatives can lead to introgression of crop genes into wild populations and potentially alter the characteristics of natural communities. In conclusion, plant evolution under domestication has not only changed the reproductive biology of cultivated taxa, its effects are multifaceted and have implications beyond agriculture.

Introduction

Near-Eastern agriculture originated *ca.* 10600 years ago in a core area located in south-eastern Turkey and northern Syria (Lev-Yadun *et al.* 2000). From there, it expanded to the rest of the Mediterranean region. As a result of its long history and prevalence in the landscape, farming is arguably a major force that has shaped plant and animal evolution in the Mediterranean Basin (Thompson 2005).

Domestication is a process that involves obtaining living organisms with desirable and distinct forms as a result of human choice and further selection (Abbo *et al.* 2012). The suite of traits that marks the divergence of a crop plant from its wild progenitor is defined as the 'domestication syndrome' (Harlan 1971). A domestication syndrome may include combinations of several different traits that become fixed within the genome (Doebley *et al.* 2006). Similar domestication traits may arise independently multiple times, often under the control of different genes (Meyer *et al.* 2012).

In the case of plants, many of the traits included in the domestication syndrome are related to reproduction, including changes in reproductive strategy, increased fruit or seed size and non-shattering of seeds (Meyer *et al.* 2012). Two main themes in plant reproductive biology are the balance between sexual and asexual reproduction and the evolution of breeding systems (Thompson 2005). Concerning the former, plants, including annuals, often have more than one reproductive strategy, including sexual breeding systems and asexual strategies (Harper 1977). In domesticated plants, however, evolution may be constrained because only one of these reproductive strategies is usually exploited for propagation (Meyer *et al.* 2012). On the other hand, the evolution of breeding systems has long attracted attention because it determines gene transmission and has a crucial effect on the levels of genetic variability in a population. Therefore, the breeding system of plants has been a trait of primary interest for farmers. For example, self-compatibility and asexual reproduction are often favored to preserve useful trait combinations. However, in other instances, plant breeders have valued male sterility because all the seeds produced are outcrossed, and thus likely to benefit from heterosis (Frankel & Galun 1977).

The changes in reproductive traits associated to domestication have critically affected the evolution of crops by conditioning reproductive success and gene flow. Thereby, they determine the evolutionary divergence between crops and their wild relatives and, in several cases, the processes by which some crops have “de-domesticated” and become feral (*e.g.*, Lan *et al.* 2005; Burger *et al.* 2007; Burger & Ellstrand 2014; Jiang *et al.* 2014).

In this review, we aim to describe the changes in reproductive traits brought about by the domestication of Mediterranean crops. We delimit the Mediterranean region in bioclimatic terms extending over an area *circa* 2300000 km² along the 18 countries that border the Mediterranean Sea, and including the Macaronesian region off the Atlantic coast of Morocco (Blondel & Aronson 2004). We consider the timeframe between the origin of agriculture in the Mediterranean around 10600 years ago and the present. Rather than providing an exhaustive review of all the species domesticated in the region, we analyze common processes and patterns developed during and after initial domestication and illustrate them using some charismatic and well-characterized field crop examples. We also assess the significance of reproductive traits in controlling evolutionary divergence between crops and their wild relatives, as well as their association with feralization. In short, we a) examine the genetic mechanisms and types of selection involved in crop domestication, b) describe the particularities of domestication of Mediterranean crops showing illustrative examples, and c) explore the gene flow patterns between Mediterranean crops and wild relatives, and their ecological, evolutionary and economic implications.

Changes in reproductive traits induced by domestication

Genetic mechanisms of crop domestication

The much greater genetic variation found in the wild progenitors of the majority of crops compared to domesticates suggests that most crops derive from a single or a few domestication events (Zohary 1996, 1999; Meyer & Purugganan 2013). This implies that founder effects, derived from the initial stage of domestication, and bottlenecks, involving a small fraction of the genetic variability of the parental population, played an important role in domestication (Ladizinsky 1985; Doebley *et al.* 2006; Olsen & Gross 2008). Bottlenecks are inevitable consequences of early crop evolution when desired

traits are selected intentionally. Zohary (2004) noted that the use of two methods of crop maintenance, through seed and clonal propagation, necessarily leads to two contrasting modes of selection and evolution under domestication. Seed propagation (with a few apomictic exceptions) involves sexual reproduction and, thus, recombination-and-selection every sowing cycle. In contrast, in clonally propagated crops, the number of sexual cycles separating domesticated populations from their wild progenitors can be very small (Zohary & Hopf 2000; McKey *et al.* 2010).

In sexually propagated crops, domestication usually involved greater inbreeding (Rick 1988; Zohary 2004), except for species in which selfing was already the predominant way of reproduction (*e.g.*, cereals and some pulses). The level of inbreeding is often negatively associated with population size, *i.e.* genes promoting self-pollination can be favored in small populations maintained in isolation. Genes selected by early farmers are usually recessive or additive, and have a higher chance of being expressed in the progeny of self-pollinated parents. Moreover, self-pollination allows the fixation of desired forms. Not surprisingly, the majority of grain-crops domesticated in the Mediterranean are predominantly selfers (Zohary & Hopf 2000). Self-pollination can take place within a flower (autogamy) or between flowers of the same genet (geitonogamy) in both wind and insect pollinated plants. In the most extreme case of autogamy, self-pollination is complete and takes place by direct contact of the anthers against the stigma of the same flower in flowers that do not open (cleistogamy) (Traveset & Jakobsson 2007). A clear advantage of self-pollination is that it can facilitate fertilization and thus seed and fruit production under lack of pollinators, which can occur when the new crop is moved out of the range of its natural pollinators (Rick 1988). In contrast, in crop progenitors that could be propagated clonally, domestication did not affect self-incompatibility or increase inbreeding, because plants with desirable properties can produce large populations of exact copies of their parents. If one or a few genotypes are taken from wild populations and maintained through clonal propagation, selection is essentially a one-step process. Consequently, many clonally propagated perennial species are highly heterozygous (Petit & Hampe 2006) and maintain a greater proportion of total genetic variation in cultivation than sexually reproducing crops.

Other genetic processes associated with or leading to domestication are intentional or spontaneous hybridization and polyploidization, which can sometimes occur simultaneously (*e.g.*, allopolyploidy). Hybridization is an important domestication mechanism for both clonally and sexually reproducing plants. Clonal reproduction can permanently capture hybrid genotypes, even F1 hybrids, and any associated traits (*e.g.*, lack of seeds in sterile hybrids), while F1 hybrids must be recreated every year in annual sexually reproducing crops. Polyploidization can increase plant vigor and the size of useful organs. It is important to note, however, that sexual reproduction of polyploids is almost entirely limited to selfing, particularly in the case of allopolyploids (*e.g.*, *Triticum aestivum*, *Brassica napus*), and may lead to non-viable seeds (Dempewolf *et al.* 2012).

Human-mediated selection of reproductive traits: direct selection to maximize crop output

Humans intentionally selected the wild plants that fit their early agricultural needs (Hancock 2004). In the Near East and Mediterranean regions, grain cereals and pulses dominated the early choices of farmers (Zohary & Hopf 2000). Managed wild legumes and grasses that yielded more seed or more stable grain production over the years increased in their relative frequencies (Abbo, Lev-Yadun, *et al.*

2009). Thus, direct selection by humans in the Mediterranean profoundly affected the reproductive output of plants (*i.e.*, grain yield).

Grain yield is a function of seed size and number. Seed size and the number of ovules per fruit have limited variability (Harper *et al.* 1970), but high heritability (Sadras 2007). In contrast, fruit number and, consequently, seed number tend to be more plastic and responsive to changes in the environment (Andrade *et al.* 2005). Selection in cereal grain crops constrained variation in seed number by favoring plants with determinate growth. Following domestication, but usually several millennia later, breeding improved yield by increasing seed size, especially in Mediterranean pulses but much less in cereals (Kluyver *et al.* 2013). Remarkably, the resulting grain crops actually exhibited increases in the two components of seed production, *i.e.*, both in number and size (Evans 1993). Although this seems to challenge the existence of a fixed trade-off between seed size and number (Preece *et al.* 2017), it should be noted that trade-offs are only measurable if established at a common resource baseline. In the 20th century, when hay lost its critical role in feeding horses as a result of mass production of cars, grain crops were bred to increase proportional allocation to reproduction (*i.e.* harvest index; Evans 1993). Furthermore, domesticates are generally larger (Milla *et al.* 2014; Preece *et al.* 2017), which may provide more resources for both flower induction and grain filling processes (Paul-Victor & Turnbull 2009). Thus, yield improvements due to increased seed number and size have probably been facilitated by other changes occurring alongside domestication although already within the genepool of the domesticated crops.

The evolution of other reproductive traits such as synchronization of reproductive phenology within populations, increased endosperm to embryo ratio, or loss of natural seed dispersal resulting from domestication have also contributed to higher yields or facilitated harvest practices (Harlan 1992; Golan *et al.* 2015). Loss of natural seed dispersal (*i.e.*, non-shattering), in particular, was key to the very existence of cereal crops. For example, in wheat and other cereals, non-shattering of mature seeds not only facilitated grain harvest, but also bound humans and their crops, since domestication implies reproductive dependence of the domesticate on the domesticator species (Milla *et al.* 2015). In legumes, the critical domestication trait seems to be the loss of seed dormancy (Ladizinsky 1987).

Indirect selection of traits correlated with human targeted features and/or with environmental adaptations

Human-mediated directional selection is a powerful driving force for evolutionary change, as it operates consistently over generations, in contrast to the widespread fluctuating selection that dominates evolution in most other natural settings (Ridley 2004). Adaptation to the agricultural environment is another driver that accounts for phenotypic change in crops (Milla *et al.* 2015). As agricultural habitats are environmentally different from the habitats where the progenitors of crop plants thrived before domestication (Denison 2012), they can pose new challenges to plant performance, such as shifts in soil fertility, the frequency and intensity of disturbances, and the presence and abundance of both mutualist and antagonist species (Turcotte *et al.* 2014; Chen *et al.* 2015). Seed dispersal of crop plants provides an example. Although non-shattering of seeds was probably directly selected by humans to facilitate harvest (Maeda *et al.* 2016), it may also have been indirectly selected as an adaptation to the agricultural environment, *i.e.*, by making seeds more available to humans, which became the primary seed dispersers of agricultural habitats.

Other relevant reproductive traits may have changed without the direct intervention of early agriculturalists. Seeds of legumes, including several of Mediterranean origin, have lower levels of carotenoids than their wild progenitors (Fernández-Marín *et al.* 2014). In wheat, changes in fatty acid or amino acid profiles have also been documented alongside domestication (Beleggia 2016). Although they probably evolved without willing human action as adaptations to the agricultural environment, these changes in seed chemistry might have relevant consequences for current human diet.

Other driving forces for evolution under cultivation are constraints on trait variation. These are biophysical, physiological, developmental, or genetic limitations that, given values for trait *X*, hinder the expression of the potential range of variation of trait *Y* (Milla *et al.* 2015). The predominance of selfers among Mediterranean grain cereals and pulses (Zohary & Hopf 2000) might be partly due to trait correlations. Annual grasses tend to be selfers more frequently than perennials, and the frequency of selfers among annuals is higher in crops than in wild grasses (Glémin & Bataillon 2009). Self-fertilization accelerates domestication by facilitating the fixation of recessive traits or maladaptive traits in the wild, which accelerates the evolution of crops (Glémin & Ronfort 2013). Annuals do not allocate resources to long-term storage, favoring reproductive output, and thus seed yield, in the short term. However, we still lack evidence of whether selection for selfing is correlated to the selection of annual life cycles (Glémin & Ronfort 2013).

Domestication thus entails multiple selective processes, which are likely to be interconnected. For instance, domestication-associated increases in seed size might arise as a function of several drivers, including direct selection, environmental adaptation and developmental constraints (Milla *et al.* 2015). However, at this point, we cannot quantify the relative importance of each evolutionary force involved in plant domestication. Clearly, experiments where the different factors are studied both in isolation and in different combinations, and their relative effects measured, would be enlightening. Experimental evolution is a promising tool in this context (Kawecki *et al.* 2012).

Plant domestication vs. further crop diversification

Thus far, we have assimilated crop evolution to the events that shape the transition from wild to cultivated plants as a whole. However, the evolution of crops occurs in different stages, including initial domestication and fixation of desirable alleles, further diversification and adaptation to diverse habitats and cultures, and more recent deliberate breeding based on scientific knowledge (Hancock 2004) (Fig. 1). The genetic processes involved in those stages are different, with bottlenecks already dominating early domestication (Ladizinsky 1985), genetic divergence shaping later evolution under cultivation (Meyer & Purugganan 2013), and a recent loss of genetic diversity in crops due to widespread adoption of elite genotypes replacing traditional landraces (*i.e.* local varieties of domesticated species adapted to their natural environment). Modern Mediterranean landscapes are largely dominated by a relatively small set of genotypes that ensure high yield across years and environments but that have caused a severe reduction in overall diversity in the region (Abbo *et al.* 2003).

In Mediterranean seed crops, various reproductive traits were favored at different stages of crop evolution. Seed coat softening, non-shattering of mature seeds and changes in inflorescence architecture started in the early stages of domestication (Meyer & Purugganan 2013) and were improved progressively, sometimes in parallel with increases in seed size (Tanno & Willcox 2006). Other traits, like insensitivity to photoperiod, took place as crops underwent geographical diversification (Meyer & Purugganan 2013). Not only typical trait scores, but also variance in reproductive traits differs among domestication stages. For instance, the range of seed size became more disparate during crop diversification stages, becoming as wide as to include those of their wild progenitors in the case of wheat or chickpeas (Abbo *et al.* 2014). Therefore, the influence of crop evolution extends beyond the initial stages of domestication, with crop diversification promoting greater variance in reproductive traits.

Domestication in the Mediterranean

Domestication and plant phenotypes: a Mediterranean field crop perspective

The most striking difference between the farming systems originated in the Mediterranean and those of other regions is their over-reliance on big-seeded annual grasses and pulses (Abbo *et al.* 2010; Fuller *et al.* 2014). The earliest Near Eastern agriculture was based on seven cereal and pulse grain-crops, all of which were annuals: diploid einkorn wheat (*Triticum monococcum* L.), tetraploid emmer wheat (*T. turgidum* L.), barley (*Hordeum vulgare* L.), lentil (*Lens culinaris* Medikus), pea (*Pisum sativum* L.), chickpea (*Cicer arietinum* L.) and bitter vetch (*Vicia ervilia* (L.) Willd.). Additionally, flax (*Linum usitatissimum* L.) might be considered the first fiber crop of the ancient Near East, although it is simultaneously an oil crop (Zohary & Hopf 2000; Abbo *et al.* 2010). Compared to proto-agriculturalists from other regions, the first Mediterranean farmers seem to have benefited from a relatively large diversity of annual staple crops (Blumler 1998).

Even though early Mediterranean farms were relatively diverse, they only included a small subset of the taxonomic pool that had been exploited previously. Many other plant species represented an important dietary element of hunter-gatherer groups, including small-seeded grasses (Weiss *et al.* 2004). However, early domestication efforts favored a relatively small pool of large seeds, of which the flora of the Fertile Crescent seems to be particularly rich (Blumler 1998). Some authors have proposed that the earliest farmers favored high-yielding grains and pulses to optimize their efforts (Weiss *et al.* 2004; Gremillion *et al.* 2014). However, recent research indicates that the preference for high-yielding annuals might not suffice to explain the selection of taxa (Milla *et al.* 2015; Preece *et al.* 2015). Indeed, other grasses and pulses that were not domesticated are equally or even more productive (Preece *et al.* 2015). At this point, the question of why certain large-seeded species were domesticated, while others were not, remains unanswered. Adaptability of the first crops to the ecological conditions of early agricultural fields might have been as important, if not more so, than morphological or nutritional properties (Fuller *et al.* 2010; Cunniff *et al.* 2014). Larger seeds might have facilitated the establishment and growth of seeds buried in densely planted plots (Harlan *et al.* 1973; Cunniff *et al.* 2014). Similarly, other reproductive traits, particularly those involved in dispersal and mating, also facilitated the agronomic use of Mediterranean plants and their mass selection (Larson *et al.* 2014).

Loss of dispersal (*i.e.*, shattering) is considered one of the key diagnostic traits of the domestication syndrome of field crops. Indeed, many species seem to have lost their shattering capacity under cultivation. In Mediterranean crops, this process occurred quickly, partly due to the standing genetic variation for dispersal traits in the ancestral populations, or in the case of crops like chickpea and fenugreek (*Trigonella foenum-graecum* L.), to the existence of non-shattering wild relatives (Fuller & Allaby 2009; Abbo *et al.* 2014). However, this trait is not necessarily favored in some of the earliest domesticates. For instance, vetches (*Vicia* spp.) have dehiscent valves even in modern cultivars. This is probably attributable to their use, as these fodder or forage crops are often harvested before full seed maturation and in systems where spontaneous reseeding can be a useful feature (Ladizinsky 1979). This highlights the close association of early Mediterranean agriculture with animal husbandry, as many domesticates have commonly been used to feed both livestock and humans.

As mentioned above, selfing facilitates the breeding and handling of different genetic lines, and self-compatibility (SC) is often favored in crops (Zohary 2004). Mediterranean domesticates encompass a wide variety of SC species. In some cases, domestication seems to have entailed the evolution of SC crops from self-incompatible ancestors, as in cabbages (*Brassica oleracea* L.), endives (*Cichorium* spp.) or beet (*Beta vulgaris* L.; Rick 1988). However, the wild relatives of all of the first grain-crops domesticates were already self-compatible, a feature most likely unique to the Mediterranean (Zohary & Hopf 2000).

Reproductive traits in representative families of Mediterranean crops

Although the reproductive traits of crops are largely conditioned by their phylogenetic origin, they also depend on the use and applications given by humans. The reproductive traits of Mediterranean field crops of the most representative taxonomic families in terms of agricultural relevance are detailed below.

Poaceae

In the different parts of the world where domestication took place, cereals were among the first plants to be domesticated. The features common to most domesticated cereals are an erect habit with rather tall stems and large spikes, annuality, deterministic growth, relatively synchronous spike-ripening and, except for maize, a high degree of self-pollination. Domestication and evolution under domestication led to non-shattering of spikelets upon maturation, lack of seed dormancy, larger grains (although with some exceptions, *e.g.*, *Triticum pravicoccum* Kislev) and transition from difficult (hulled) to easy threshing (free-threshing) forms.

Three cereals played a major role in the emergence of Near Eastern agriculture: diploid einkorn wheat (*Triticum monococcum* L.), tetraploid emmer wheat (*T. turgidum* L.) and barley (*Hordeum vulgare* L.) (Zohary & Hopf 2000; Lev-Yadun *et al.* 2000). The wild progenitors of these species, wild einkorn (*Triticum monococcum* subsp. *boeoticum* = *Triticum boeoticum* Boiss.), wild emmer (*T. turgidum* ssp. *dicoccoides* (Körn.) Thell.) and wild barley (*Hordeum spontaneum* C. Koch), still grow in parts of the Eastern Mediterranean in sympatry with the crops (Zohary & Hopf 2000; Abbo, Saranga, *et al.* 2009).

The spikes of wild cereal progenitors disarticulate at maturity into awned spikelets that can penetrate the soil. Some seeds can remain dormant in the soil even after one or two seasons (Volis *et al.* 2004; Volis 2016). In both wheat and barley, ancient selection favored individuals with non-brittle spikes that readily germinated upon wetting. Furthermore, several domesticated forms of wheats evolved later towards free-threshing, where the products of threshing upon maturation are grains instead of grains enclosed in spikelets.

Oats (*Avena sativa* L.) were also domesticated in the Mediterranean, but their importance was not recognized by man as early as in the case of wheat and barley. Consequently, oats apparently persisted as a weed-like plant harvested together with wheat or barley for centuries or even millennia prior to being cultivated as a crop. Domestication of oats followed a path common to the other cereals towards non-shattering and high-yielding forms with large, non-dormant seeds.

Fabaceae

Legumes are found among the original crop species in almost every center of domestication. In the Mediterranean, four of the “big seven” grain crops were pulses (bitter vetch, chickpea, lentil and pea), a group that could be enlarged to include the fava bean (*Vicia faba* L.) that was domesticated in the Neolithic (Abbo *et al.* 2013). Domestication of these and other legumes benefitted from the existence of self-compatibility and, in some cases, some indehiscence of the wild progenitors. However, selection under cultivation has significantly altered the size and composition of the seeds to increase their nutritional value and reduce the content of secondary compounds (Abbo, Saranga, *et al.* 2009; Abbo *et al.* 2014).

Brassicaceae

There are several cultivated members of the mustard family of circum-Mediterranean origin, mostly in the genus *Brassica*. A wide diversity of vegetable, root and seed crops has been generated from just four ancestral *Brassica* species, *B. nigra* (L.) W.D.J.Koch (black mustard), *B. napus* L. (rapeseed), *B. oleracea* (cabbages, cauliflowers and kohlrabi) and *B. rapa* L. (turnip and bok-choy). Many of these taxa are SI, and their domestication and cultivation benefitted from the generation of SC lines. In the case of *B. oleracea*, selfing made it possible to propagate lines with modified inflorescences that ultimately resulted in the different forms of cauliflower and broccoli (Prakash *et al.* 2012).

Alliaceae

Vegetative propagation has not only been selected for in perennial or long-lived taxa. The genus *Allium* includes several annual or biennial species in which clonal reproduction has been crucial for domestication and cultivation. One of the most characteristic reproductive traits of *Allium*, in both wild and cultivated plants, is the presence of basal bulblets and bulbils which play an important role in vegetative propagation. The outcrossing breeding system of most *Allium* species along with the short viability of their seeds have favored their vegetative propagation in cultivation (Fritsch & Friesen 2002).

Onion (*Allium cepa* L.), garlic (*Allium sativum* L.), shallot (*Allium oschaninii* O.Fedtsch.) and leek (*Allium ampeloprasum* L. var. *porrum*) are the most widely cultivated *Allium* crops in the Mediterranean basin. Onion is propagated by seeds, bulbs or bulbils. The wide variation in bulb characteristics (shape, color of the membranous skins and the fleshy scales, and ability to produce daughter bulbs in the first season) indicates intensive selection on these traits in cultivated forms.

Domestication has also developed great variability in ecophysiological patterns, including adaptation to bulbing in a wide range of photoperiodic and temperature conditions, and to bolting and flowering in a broad range of climates (Hanelt 1986). Unlike onion, garlic became completely sterile after domestication because of polyploidization and thus is only propagated from cloves. The lost ability for sexual reproduction has led to lower morphological and genetic variation, irrespective of ecological differences within the large area where it is cultivated (Fritsch & Friesen 2002). Nevertheless, relevant variation can be found in bulb color and size, and in clove number and size, as a result of selection by farmers (Paredes C *et al.* 2008).

Asteraceae

The clustering of single flowers into the compound inflorescence of Asteraceae is beneficial for domesticating seed crops, since many seeds are clustered together in the capitulum on top of a single stalk, which allows for effective harvesting. Most wild Asteraceae are SI outcrossers, which may have reduced the probability of domestication. However, self-incompatibility is easily lost during or soon after domestication, as seen in other outcrossing groups such as tomato and peppers (Rick 1988). For instance, the domestication process of *Lactuca sativa* L. led to selfing, to the absence of early bolting, to increased seed size and to non-shattering seeds (De Vries 1997), as well as to a significant decrease of its chemical defenses (Dempewolf *et al.* 2008).

Divergence and gene flow between crops and wild relatives

Once domestication has taken place, the genetic relationship between crops and their wild relatives depends on the balance between introgression and divergence (De Wet & Harlan 1975). Gene flow effects between crops and their wild progenitors can be both positive (increase in diversity and adaptation) and negative (hampering fixation of alleles, generation of crop weeds or, in recent years, spread of transgenes).

Gene flow from wild relatives to crops

Hybridization and introgression between crops and their wild relatives have played a very important role in shaping modern cultivars (Arnold 2004). Wild-crop introgression was an essential component in the domestication process of many species (Olsen & Schaal 2007) and continues to play a relevant role in increasing the genetic diversity of modern crops (*e.g.*, variation conferring resistance to abiotic stresses, fungal and bacterial diseases, or pests such as nematodes and insects; Arnold 1992; Hajjar & Hodgkin 2007).

Wild to crop natural introgression is particularly important in the centers of plant domestication, where landraces grow sympatrically with their wild relatives. This introgression occurs when wild relatives are allowed to thrive in or around crop fields and part of the harvest is stored as seed for further sowing (Zizumbo *et al.* 2005; Barnaud *et al.* 2009). Interbreeding results in wild-domesticated plant complexes comprising individuals with varying degrees of introgression (Zohary 1959; Jarvis & Hodgkin 1999), called hybrid swarms. This leads to new gene combinations potentially important for the evolution of domesticated species (Harlan 1965; Van Raamsdonk & Van der Maesen 1996).

The domestication of several Mediterranean crops involved hybrid swarms. Spontaneous hybrid swarms of wild two-rowed and cultivated six-rowed barley are sporadically encountered at edges of barley cultivation and in disturbed contact areas in Israel (Zohary 1959, 1964). These swarms contain parental forms and a diverse range of intermediates and recombinants. A brittle six-rowed barley form initially described as a distinct species, *Hordeum agriocrython* Åberg (*H. spontaneum* K. Koch) is a remarkable example of hybridization between wild and cultivated barley. Although initially considered a wild species and ancestor of cultivated barley, it is actually a hybrid derivative that occurs in hybrid swarms (Zohary 1959). Wild emmer wheat with variable intermediate phenotypes are also observed sporadically in Israel, especially at the field edges as a result of hybridization with *T. turgidum* cultivars (Kamm 1974). Mixed cultivation of diploid, tetraploid and hexaploid wheats is a common traditional practice in the Middle East and the Transcaucasus (Dorofeev 1966; Matsuoka *et al.* 2008). This creates conditions for interbreeding between parental species, F1 and later-generation hybrids, and backcrosses to one or both parental species. Even one of the most important cereal crops, common wheat, *T. aestivum*, originated from a cross between domesticated tetraploid emmer wheat and wild diploid relative *Aegilops tauschii* (Matsuoka 2011).

Today, usage of the wild relatives of crops is an important component of breeding programs for most crops (Kovach & McCouch 2008). The wide range of biotic and abiotic adaptations found in wild relatives is a great genetic resource to mitigate the effects of climate change on agriculture, and help guarantee food security (Brozynska *et al.* 2016).

Gene flow from crops to wild relatives

Crop fields have experienced inexorable expansion from the origins of agriculture to the present, currently taking 11% of the globe's land surface (Bruinsma 2003). Consequently, the relative size of crop and wild populations has shifted, and with it the main direction of introgression. Early farming systems were repeatedly shaped by gene transfer from wild relatives into the crops, while gene flow from agricultural fields into wild relatives has become a prominent feature in many modern settings.

Changes induced by the domestication process can be expected to hamper gene flow from crops to wild relatives. When gene flow does occur and hybrids are produced, one could expect short persistence and low relevance of this genetic exchange due to the different ecological settings and selection pressures experienced in man-managed habitats vs natural ecosystems (Jenczewski *et al.* 1999). After all, selection associated with domestication generates traits considered to be maladaptive in natural ecosystems (Ellstrand & Hoffman 1990). However, several studies have shown that these expectations do not always hold true.

Gene flow from crops to wild relatives is thought to be mostly pollen-mediated (Ellstrand & Hoffman 1990). Consequently, a set of requisites must be met for gene flow to take place: 1) presence of populations of wild relatives within the pollen dispersal range of the crops; 2) overlapping flowering periods; 3) cross compatibility and fertile progeny, and 4) spontaneous backcrossing of the hybrid progeny to the wild relative populations (Gepts & Papa 2003). Lastly, a critical fifth requisite for this gene flow to have an evolutionary effect on wild relative populations is the long-term survival of the transferred crop genes (Gepts & Papa 2003).

The first three requisites lead to hybridization. There is an extensive record of crop–wild relative hybridizations in a wide range of taxa, suggesting that the morphological differences in reproductive traits between crops and wild relatives are insufficient to preclude successful reproduction (Ellstrand *et al.* 2013). Moreover, close co-occurrence of crops and wild relatives is not mandatory for hybridization. Gene flow events up to hundreds of meters away from the cultivated source have been reported, notably for *Medicago sativa* (Jenczewski *et al.* 1999).

Some works have documented the presence of crop-specific alleles in wild populations growing near cultivated relatives (*e.g.*, Bartsch & Ellstrand 1999). A few experiments have also measured hybridization rates between crops and wild relatives (Ellstrand 2003). In general terms, these studies show that spontaneous hybridization takes place in most cases where crops co-occur with wild relatives. Ellstrand *et al.* (1999) reported that 12 of the world's 13 most important crops were found to hybridize with their wild relatives. Later reviews (Ellstrand 2003; Andersson & Vicente 2010) gathered evidence that at least 48 crops hybridize with one or more wild relatives. Some recorded hybridizations in Mediterranean crops involve *Hordeum* (Zohary 1959), *Raphanus* (Klinger *et al.* 1992), *Brassica* (Lefol *et al.* 1996), *Beta* (Boudry *et al.* 1993), *Triticum* (Guadagnuolo *et al.* 2001), and *Medicago* (Jenczewski *et al.* 1999), among others.

The fourth and fifth requisites for effective gene flow lead to introgression, *i.e.*, the permanent incorporation of crop genes into the wild relative populations (Ellstrand *et al.* 2013). Introgression has been found in several Mediterranean crops regardless of their breeding system. Among Mediterranean outcrossing crops, *Daucus carota* L. (carrot) and *Medicago sativa* L. (alfalfa) embody examples of introgression in insect-pollinated species (Jenczewski *et al.* 1999; Rong *et al.* 2010). Magnussen & Hauser (2007) found that wild carrot populations in close proximity to cultivated carrot fields were genetically more similar to cultivated carrot than wild carrot populations located farther away, suggesting that introgression had changed the genetic structure of the wild populations. Hauser & Shim (2007) showed that hybrids between cultivated and wild carrots could survive and reproduce outside cultivation, allowing them to cross and backcross with the wild carrot populations. Similarly, Jenczewski *et al.* (1999) showed that crop-to-weed gene flow occurred between cultivated and wild populations of *Medicago* in Spain and that neutral alleles were maintained over time. Other examples of introgressed crop alleles in wild relative populations of outcrossing insect-pollinated Mediterranean crops include *Brassica napus*, oilseed rape (Andersson & Vicente 2010), *Cichorium intybus* L., chicory (Kiær *et al.* 2007), and *Cynara cardunculus* L. var. *scolymus*, artichoke (Leak-Garcia *et al.* 2013).

Crop to wild introgressions are not limited to outcrossing species. Although cultivated lettuce and the cross-compatible wild relative *Lactuca serriola* L. are predominantly selfing, substantial cross-pollination by insects has been observed along with introgression (D'Andrea *et al.* 2009; Uwimana *et al.* 2012).

The consequences of the introgression of domesticated traits are generally limited because the resulting crop–wild hybrids tend to exhibit low fitness and are generally maladapted (Stewart *et al.* 2003). However, some crop–wild hybrids have established successfully. Two of these that have been studied in detail are hybrid radishes and beets (Ridley *et al.* 2008; Bartsch 2010). Radish (*Raphanus sativus* L.) and its wild relative *R. raphanistrum* L. often hybridize naturally (Stace 1975). The California wild radish displays a combination of traits from *R. raphanistrum* and *R. sativus* parental

taxa, including variation in flower color, but also has new, seemingly adaptive traits, such as thicker fruit walls that might provide additional protection against herbivores (Heredia & Ellstrand 2014). This hybrid seems to have displaced both parents from the wild in their introduced range in N. America (Burger & Ellstrand 2014).

Beet is predominantly outcrossing and wind pollinated, and spontaneous hybridization easily occurs between the crop and its wild progenitor, *Beta vulgaris* ssp. *maritima* (L.) Arcang. (Ellstrand 2003; Bartsch 2010). Molecular studies have shown that *B. vulgaris* ssp. *maritima* populations growing near beet seed multiplication sites were introgressed with domesticated alleles (Viard *et al.* 2004; Andersen *et al.* 2005; Ellstrand *et al.* 2013). Crop–wild hybrid seeds are indistinguishable from beet cultivar seeds and are inadvertently sown in sugar beet fields. However, the resulting individuals display a differential suite of traits (*i.e.*, annuality, seed dormancy, SC) that make them highly effective colonizers (Arnaud *et al.* 2010; Ellstrand *et al.* 2013).

Even when hybrids are maladapted, gene flow from crops into wild populations can have stark consequences for the stability of the wild stock. Repeated introgression can result in genetic assimilation, where crop genes replace wild relative genes, and demographic swamping, where hybrids are less fertile than their wild parents, and wild-hybrid populations shrink. Using models of a wild population recurrently receiving pollen from a genetically homogeneous crop, Haygood *et al.* (2003) found that conditions for genetic assimilation are not stringent, and progress towards replacement can be fast, even for a low-fitness crop gene. Demographic swamping can give rise to ‘migrational meltdown’, where a small increase in immigration can lead to both the fixation of a low-fitness crop gene and drastic shrinkage of the wild population. This phenomenon has already been described, albeit outside the Mediterranean region: natural hybridization with cultivated rice has been implicated in the near extinction of the endemic Taiwanese taxon, *Oryza rufipogon* ssp. *formosana* Masam. & Suzuki (Kiang *et al.* 1979).

The ecological implications of gene flow from crops to wild relatives may be especially relevant when dealing with transgenic GMO. Evidence of transgene introgression is currently known at least in rice (Chen *et al.* 2004; Wang *et al.* 2006), cotton (Wegier *et al.* 2011), and canola (Légère 2005; Warwick *et al.* 2008), indicating that it may occur at a low frequency but may be widespread in different crop species. Even if gene flow between wild and cultivated relatives results in a transgene escape, its spread will depend on the relative fitness enhancement attributable to the nature of the engineered trait, as well as on other factors such as hybrid fertility, particularly during seedling establishment (Arnaud *et al.* 2003).

Feralization of crops and acquisition of weedy habits

The process of domestication is usually regarded as a continuum, with purely wild taxa on one end of the spectrum and fully domesticated crops on the other. However, this perspective ignores the existence of self-sustained populations of crop descendants, which can be important elements in certain natural communities (Harlan 1965; Baker 1974; Larson *et al.* 2014). Some of these provide interesting examples of adaptation to new habitats and illustrate how hybridization and strong selection can foster trait divergence in just a few generations (Gressel 2005; Ellstrand *et al.* 2010).

Mediterranean crops that have become weeds in other parts of the world
Semi-wild wheat of Tibet. Only found in the Qinghai-Tibet Plateau of China, *T. aestivum* subsp. *tibeticum* J.S.Shao is an hexaploid wheat that originated from the de-domestication of common wheat (Tsunewaki *et al.* 1990; Ayal & Levy 2005). Tibetan semi-wild wheat seems to have diverged from its cultivated ancestor conforming to Baker's predictions for the acquisition of a weedy habit (Baker 1974) and has regained spontaneous dispersal (*i.e.*, spike shattering) and seed dormancy (Lan *et al.* 2005; Jiang *et al.* 2014).

Feral rye in N. America. Feral rye (*Secale cereale*) spread throughout western North America after the introduction of the crop (Burger *et al.* 2006). Semi-wild or feral forms of rye occur mostly in the Near East and Central Asia. However, the differentiation of these forms has taken place in direct contact with the wild ancestor(s) of the crop, with which they are fully inter-fertile (Hagenblad *et al.* 2016). Conversely, American feral rye has diverged rapidly away from its wild relatives, and phenotypic divergence has accelerated following the reduction in cultivation of rye (Burger *et al.* 2007; Burger & Ellstrand 2014). In this case, feralization resulted in increased ability to disperse seed, smaller seed size and later flowering (Burger *et al.* 2007; Burger & Ellstrand 2014).

Avenues for future research

Throughout this review, we have highlighted topics that have received research attention. However, other issues need to be addressed to understand how domestication and plant breeding influence the reproductive biology not only of crops but also of closely-related taxa. In particular, we highlight the need to investigate correlated evolution of traits, effects of domestication for purposes other than direct human use, evolutionary applications, and impacts of current shifts in agricultural markets and practices.

The evolutionary effects of domestication on plant traits are often regarded as unidirectional, *i.e.* domesticates are taxa evolving away from their wild ancestors. However, as highlighted above, domestication is only one of the potential paths in an otherwise reticulate evolutionary process that sometimes also encompasses important shifts towards wild forms (feralization). The relative frequency and likelihood of these shifts to and from the wild remain to be explored systematically, and a general framework to understand feralization is still lacking (*i.e.*, whether one can define a "feralization syndrome").

Domestication research has focused on crops that sustain food provision for humans, but crops are also selected for other purposes. For example, as illustrated by *Vicia*, breeding for fodder might have led to different selection patterns than those found in selection for human feeding, which remain to be explored. It is still unclear whether domestication for alternative purposes has forced yet unknown particular adaptations and whether it might facilitate or hinder gene flow between wild and cultivated forms.

The study of the evolution of reproductive traits in crops provides an excellent opportunity for the study of parallel evolution (Olsen & Wendel 2013) because domestication has generated a suite of traits that are shared across many crop species. These independently evolved traits can be studied at various levels of phylogenetic divergence (*e.g.*, grain shattering in cereal crops; Paterson *et al.* 1995;

Lin *et al.* 2012) and can provide understanding into the mechanisms that underlie the generation of novel phenotypes, as well as the evolutionary constraints and the likelihood of specific evolutionary paths.

Finally, the current widespread cultivation of commercial varieties in highly fragmented Mediterranean landscapes brings about a completely new evolutionary scenario with respect to their wild relative counterparts. The study of the evolutionary impacts of these large, genetically uniform populations and their accompanying agricultural practices on wild species is still in its infancy (Turcotte *et al.* 2017) and brings about interesting challenges for research.

Conclusions

The reproductive traits of crops have originated as a result of the interaction of several selective forces, including direct human preference, adaptation to the agricultural environment and trait correlations caused by developmental constraints. The mode of propagation by either sexual reproduction through seeds or clonal propagation has conditioned the pathways of crop evolution. Plant domestication and especially subsequent evolution under domestication in the Mediterranean has selected for specific reproductive traits, linked to higher reproductive output through larger seed size and number, limited seed shattering and selfing.

Selection under cultivation has further promoted the divergence of crops from their wild relatives, while the porous fertility barriers between crops and wild relatives have enabled a genetic exchange that has been used as a source of genetic variability for crops. Conversely, the introgression of crops into wild relatives has led to the emergence of both new and intermediate forms in wild populations. Some of these forms often exhibit reproductive traits inherited from the crop ancestor that make them successful as weedy/wild populations.

Crop cultivation can be regarded as the introduction of a plant in a new habitat (Thrall *et al.* 2011). When this coincides with opportunities for introgression into wild-relative populations, new genetic diversity arrangements can be generated. The combination of new selective pressures and novel diversity provides opportunities for rapid evolution, even on contemporary timescales.

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Figure 1

Patterns of evolution of reproductive traits under domestication in field grain crops. **A.** Wild plant populations encompass individuals of various cohorts, from dormant seeds of previous generations (circles below the horizontal line) to dispersing seeds of current year plants. **B.** Early domestication reduces or completely eliminates seed dormancy, increases self-compatibility (SC, here represented by smaller flowers), reduces spontaneous seed dispersal (*i.e.*, shattering), the amount of reproductive structures such as glumes or fruit protective tissue (*i.e.*, chaff) and herbivore deterrent compounds producing toxicity or bitterness, and favors bigger seeds. **C.** Crop evolution under domestication further accentuates the changes fostered by initial domestication. It also induces a significant increase in mean seed size and variance, triggers diversification of seed morphology and selects for synchronous flowering, more compact growth, and larger fruits or infrutescences. **D.** Modern breeding, by means of targeted genetic improvement and concomitant loss in genetic diversity increases biomass allocation to reproductive structures, ensures predictable reproductive output and reduces the duration of the life cycle. Feralization (not shown) would lead to the transition from B, C or D to A. However, whether the strength and direction of the changes associated to domestication and feralization are symmetrical remains an open question (Zeven 1998; Abbo *et al.* 2014; Preece *et al.* 2017).

