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Patterns and processes in crop domestication: an historical review and quantitative analysis of 203 global food crops

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Summary

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Domesticated food crops are derived from a phylogenetically diverse assemblage of wild ancestors through artificial selection for different traits. Our understanding of domestication, however, is based upon a subset of well-studied 'model' crops, many of them from the Poaceae family. Here, we investigate domestication traits and theories using a broader range of crops. We reviewed domestication information (e.g. center of domestication, plant traits, wild ancestors, domestication dates, domestication traits, early and current uses) for 203 major and minor food crops. Compiled data were used to test classic and contemporary theories in crop domestication. Many typical features of domestication associated with model crops, including changes in ploidy level, loss of shattering, multiple origins, and domestication outside the native range, are less common within this broader dataset. In addition, there are strong spatial and temporal trends in our dataset. The overall time required to domesticate a species has decreased since the earliest domestication events. The frequencies of some domestication syndrome traits (e.g. nonshattering) have decreased over time, while others (e.g. changes to secondary metabolites) have increased. We discuss the influences of the ecological, evolutionary, cultural and technological factors that make domestication a dynamic and ongoing process.

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I. Introduction

It is estimated that 2500 plant species have undergone domestication worldwide, with over 160 families contributing one or more crop species (Zeven & de Wit, 1982; Dirzo & Raven, 2003). Much of our understanding of the processes driving domestication comes from a subset of well-studied crops, particularly crops of major economic importance and model crops (i.e. crops that have had their genomes analyzed and are transformable). These crops have been critical for developing our fundamental understanding of domestication as a continuum of ongoing processes. In particular, they have been critical for revealing the underlying genetic mechanisms responsible for the suite of phenotypic changes associated with domestication that comprise the domestication syndrome. They have also contributed to our knowledge of useful crop breeding traits, such as pathogen resistance, and of fundamental biological processes, such as polyploidization. However, information on such well-studied crops contributes disproportionately to the literature on domestication. In order to explore global trends and historical patterns in domestication, large datasets are required that consider a broad selection of species, including understudied crops and crops of minor economic importance, in addition to well-studied major global crops. Often, the data relevant to the history of use, selection and domestication of a particular crop are scattered across the literature of diverse disciplines. For many minor food plants, information relevant to domestication history may be difficult to access, if it is available at all. Most reviews have not included all the major agricultural regions but rather have concentrated on regional subsets of crops (Duke & Terrell, 1974; Harlan, 1992), or focused on specific groups, including recent studies of the Asteraceae (Dempewolf *et al.*, 2008) and Poaceae (Glémin & Bataillon, 2009), and on previously neglected groups such as vegetatively propagated crops, perennials, and underutilized crops (Padulosi *et al.*, 2002, 2011; McKey *et al.*, 2010; Miller & Gross, 2011).

This review considers information on 203 major and minor crop plants compiled across 36 categories, including center of domestication, changes in phenotype and use from the wild to the cultivated forms, uses, exploited organs, and conservation status. The threefold objectives of this paper are: to identify and interpret patterns in domestication by identifying trends across numerous categories of data on crop domestication and use; to test current and classic theories in domestication against this large sample; and to identify promising areas for further research based on the critical questions and gaps in the literature identified by this study. Data summaries and key analyses are presented and discussed in this review, while more detailed information, further analyses and crop bibliographies are provided as Supporting Information (Tables S1–S6). Updated versions of crop bibliographies (Tables S2, S4, S5) are maintained at: www.crop-domestication.com.

1. Historical context

The transition from hunter-gatherer societies to settled agriculture (the 'Neolithic revolution'; Childe, 1949) occurred independently over a dozen times in different regions around the world from *c.* 10–12 000 yr ago (ya) to as recently as 3000–4000 ya (Diamond, 2002; Diamond & Bellwood, 2003). Theories to explain the origins and development of agriculture have considered factors ranging from changes in climate and population expansion to cultural practices and religious beliefs (Harlan, 1992).

Current works continue to explore when, where, why and how wild plants became our modern food crops, while also considering the new technical, ethical and environmental challenges of emerging agricultural technologies (Murphy, 2007; Vaughan *et al.*, 2007; Ellstrand *et al.*, 2010; Thrall *et al.*, 2010; Cuevas-Badallo & Vermaas, 2011; Domingo & Giné Bordonaba, 2011; Ekici & Sancak, 2011). In recent years, scientists have used molecular techniques to test and apply theories of crop origins put forward 150 yr ago by Darwin (1868) and De Candolle (1884) (Doebley *et al.*, 1995; Gepts, 2004; Zohary, 2004; Fuller, 2007; Gregory, 2009; Brown, 2010). New works have increasingly recognized the importance of combining the relevant data from several fields to inform observations on crop domestication (Kroll, 2000; Nesbitt & Tanksley, 2002; Zeder *et al.*, 2006; Vaughan *et al.*, 2007; Wang *et al.*, 2008; Purugganan & Fuller, 2009; Richards *et al.*, 2009; Meyer *et al.*, 2012).

Although recent innovations are causing drastic modifications to the domestication pathways for many species (Vaughan *et al.*, 2007), domestication has always been a dynamic process. New artificial selection pressures have arisen throughout the history of crop cultivation driven by many factors, including new uses for existing crops (e.g. grain crops adapted for biofuel production) and the movement of crops to new environments. These have continually reshaped the evolution and geographic distribution of crops over time.

II. Key concepts and definitions

1. Food crop

To meet our criterion of being a food crop, a plant species must have been used at some time as a food, spice, edible oil, beverage, or fasting aid with nutritional value (e.g. khat). In the cases of some of the crops we selected, food uses are secondary, such as fiber crops with oil seeds (e.g. cotton, flax, hemp).

2. Reproductive strategy

Many wild plant species are characterized by more than one reproductive strategy, including sexual breeding systems (e.g. outcrossing or self-fertilizing), and asexual strategies (e.g. vegetative or clonal propagation). Under cultivation, however, only one of these strategies is usually exploited as a propagation method for a

given species. Here, we refer to crop reproductive strategies based on the strategy primarily used under cultivation.

3. Domestication syndrome

The suite of traits that marks a crop's divergence from its wild ancestor(s) is defined as the 'domestication syndrome' (Harlan, 1971, 1992; Hammer, 1984). A domestication syndrome may include combinations of several different traits, including seed retention (nonshattering), increased fruit or seed size, changes in branching and stature, change in reproductive strategy, and changes in secondary metabolites. The domestication syndrome may evolve over thousands of generations, as desirable traits are selected for in the agricultural environment and become fixed within the crop genome (Fuller, 2007; Fig. 1). The domestication syndrome may also evolve within a short time-frame, as in the cases of crops domesticated within the last 100 years or so (e.g. kiwi, cranberry).

Similar domestication traits may arise independently multiple times, often under the control of different genes. For example, the loss of a shattering mechanism of seed dispersal via a brittle rachis has arisen in many crops, particularly grasses (Allaby *et al.*, 2008); in barley, two independent domestication events targeted this trait via two different genes (*Bt1* and *Bt2*) (Takahashi, 1955; Fig. 1).

4. Degree of domestication

Domestication traits arising through artificial selection are desirable to farmers and consumers. For instance, they can ease harvest work and enhance taste and nutritional qualities. Often, domestication selects against traits that increase the plant's defensive or reproductive success in natural environments. Artificial selection

can therefore work in opposition to natural selection, and domesticated crops have reduced fitness, or, in some cases, an inability to survive outside of cultivation (Gepts, 2004; Pickersgill, 2007; Allaby *et al.*, 2008; Purugganan & Fuller, 2011).

Selection can be unconscious or conscious. In unconscious selection, likely the driver of many early domestications, the act of moving plants from the wild into man-made environments alters selection pressures, leading to increased fitness of phenotypes that have low fitness in the natural environment. Human management, including planting and harvesting techniques, creates further selection pressures (Fuller *et al.*, 2010). In conscious selection, desirable phenotypes are selected, while less desirable phenotypes are neglected or actively removed until their frequency decreases in the population (Zohary, 2004).

Here, 'domesticated' refers more generally to plants that are morphologically and genetically distinct from their wild ancestors as a result of artificial selection, or are no longer known to occur outside of cultivation. We define 'semidomesticated' as a crop that is under cultivation and subjected to conscious artificial selection pressures. Although named cultivars may exist, these are not yet clearly morphologically or genetically distinct from their wild counterparts. Finally, 'undomesticated' refers to uncultivated plants that continue to be wild-harvested with no conscious artificial selection pressures and no discernible morphological and/or genetic differentiations that could be used to distinguish them as a domesticate (e.g. Brazil nut).

5. Center of domestication

Vavilov defined eight 'centers of origin' according to certain criteria: high varietal diversity, co-occurrence of wild ancestors with their domesticates, and a long history of crop use (Vavilov, 1926, Vavilov, 1951; Harlan, 1971; Vavilov, 1992; Table S3). The

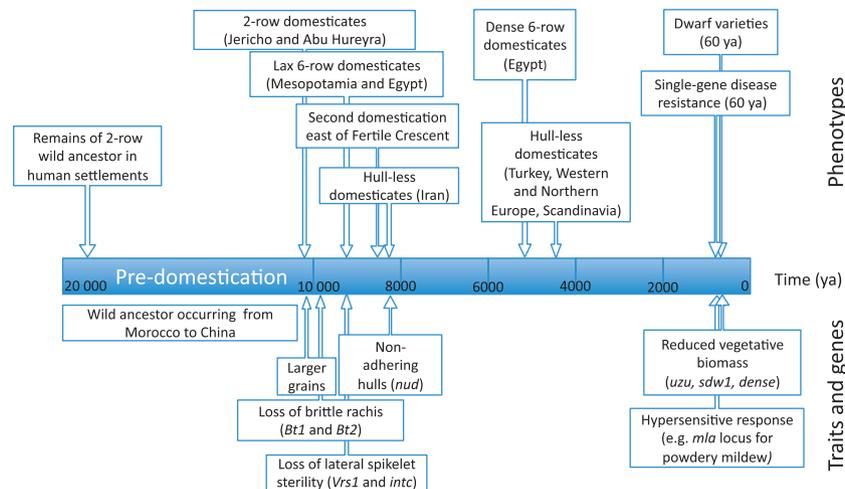


Fig. 1 The domestication history of barley (*Hordeum vulgare* ssp. *vulgare*) from its wild ancestor (*Hordeum vulgare* ssp. *spontaneum*), shown as a continuous process along a timeline. There is a long period of initial use and exploitation of the wild ancestor during the pre-domestication period, followed by the fixation of key domestication syndrome traits such as larger grains and nonshattering and finally the development of resistant and dwarf varieties in the past century as examples of ongoing domestication. There is an approximate 4000 yr time interval between the detection of hull-less types in Iran and the diffusion of this phenotype throughout Europe and Scandinavia. Information regarding the phenotypes of domesticates found in different locations are presented above the timeline, and the corresponding traits and genes that are modified to produce these phenotypes are presented below the timeline. At least two independent domestication events are posited for barley, based on genetic evidence. Such a thorough understanding of domestication processes is established for very few crops, usually because of limits in the available evidence in the archaeobotanical record. (ya = yr ago).

distribution of crop plants and wild relatives has since proven to be more complex than originally proposed and not all crops exhibit centers of high varietal diversity (Harlan, 1992). Recent archaeological work has further modified the definition of centers of origin, revealing small independent centers of origin within previously established centers. For example, India, originally considered as one center of origin, actually contains five independent centers of origin (Fuller, 2009). Other broad regions are now also recognized as important areas of domestication activity, including Near Oceania (Brandes, 1958; Allaby, 2007), Amazonia (Clement, 1999a,b; Clement *et al.*, 2010), Eastern North America (Zeven & Zhukovsky, 1975; Smith, 2006), and the river deltas of Western Africa (Harlan, 1971; Portères, 1976). Therefore, because centers of origin are difficult to define and delimit, we

favor the term ‘center of domestication’ to encompass broad areas with domestication activity. These include Vavilov’s original eight centers of origin and the four more recently proposed centers.

6. Single vs multiple origins

A crop species has a ‘single origin’ when it was domesticated once from the wild ancestor(s), followed by dispersal. A crop has multiple domestication events, referred to as ‘multiple origins’, when domestication occurred independently, from the same ancestor(s), in different locations or times. A domesticated species with multiple origins can have many forms with different common names (e.g. *Brassica oleracea*; Table 1). In contrast, different

Table 1 The 203 crop species reviewed in this study

Family	Crop common name	Species/species complex
Actinidiaceae	Kiwi	<i>Actinidia deliciosa</i> Chev. Liang and Ferguson
Agavaceae	Agave	<i>Agave tequilana</i> Weber
Amaranthaceae	Amaranth	<i>Amaranthus caudatus</i> L., <i>A. cruentus</i> L., <i>A. hypochondriacus</i> L.
	Beet	<i>Beta vulgaris</i> L. ssp. <i>vulgaris</i>
	Callaloo	<i>Amaranthus tricolor</i> L.
	Huauzontle	<i>Chenopodium berlandieri</i> Moq. ssp. <i>nuttalliae</i>
	Quinoa	<i>Chenopodium quinoa</i> Willd.
	Spinach	<i>Spinacia oleracea</i> L.
	Anacardiaceae	Ambarella
	Cashew	<i>Anacardium occidentale</i> L.
	Jocote	<i>Spondias purpurea</i> L.
	Mango	<i>Mangifera indica</i> L.
	Peruvian Peppertree	<i>Schinus molle</i> L.
	Pistachio	<i>Pistacia vera</i> L.
Annonaceae	Biriba	<i>Rollinia mucosa</i> (Jacq.) Baill.
	Cherimoya	<i>Annona cherimola</i> Mill.
	Pawpaw	<i>Asimina triloba</i> (L.) Dunal
Apiaceae	Anise	<i>Pimpinella anisum</i> L.
	Carrot	<i>Daucus carota</i> L. subsp. <i>sativus</i>
	Celery	<i>Apium graveolens</i> L. var. <i>dulce</i> and var. <i>rapaceum</i>
	Cumin	<i>Cuminum cyminum</i> L.
	Dill	<i>Anethum graveolens</i> L.
	Parsely	<i>Petroselinum crispum</i> (Mill.) Nyman ex A.W. Hill
	Araceae	Giant taro
	Malanga	<i>Xanthosoma sagittifolium</i> (L.) Schott
	Taro	<i>Colocasia esculenta</i> (L.) Schott
Arecaceae	Açaí	<i>Euterpe oleracea</i> Mart.
	African oil palm	<i>Elaeis guineensis</i> Jacq.
	Areca nut	<i>Areca catechu</i> L.
	Coconut	<i>Cocos nucifera</i> L.
	Date Palm	<i>Phoenix dactylifera</i> L.
	Peach palm	<i>Bactris gasipaes</i> Kunth subsp. <i>utilis</i> or subsp. <i>gasipaes</i>
	Sago palm	<i>Metroxylon sagu</i> Rottboell
	Asteraceae	Artichoke
	Chicory	<i>Cichorium intybus</i> L.
	Endive	<i>Cichorium endivia</i> L.
	Jerusalem artichoke	<i>Helianthus tuberosus</i> L.
	Lettuce	<i>Lactuca sativa</i> L.
	Safflower	<i>Carthamus tinctorius</i> L.
	Sumpweed	<i>Iva annua</i> L. var. <i>macrocarpa</i>
	Sunflower	<i>Helianthus annuus</i> L. var. <i>macrocarpus</i> (DC.) Cockerell
	Teff	<i>Eragrostis tef</i> (Zucc.) Trotter
Basellaceae	Ceylon spinach	<i>Basella alba</i> L.

Table 1 (Continued)

Family	Crop common name	Species/species complex
Berberidaceae	Mayapple	<i>Podophyllum peltatum</i> L.
Betulaceae	Hazelnut	<i>Corylus avellana</i> L.
Bixaceae	Annatto	<i>Bixa orellana</i> L.
Brassicaceae	Cabbage and derivatives	<i>Brassica oleracea</i> L.
	Cress	<i>Lepidium sativum</i> L.
	Horseradish	<i>Armoracia rusticana</i> G.Gaertn., B.Mey. & Scherb.
	Maca	<i>Lepidium meyenii</i> Walp.
	Radish	<i>Raphanus sativus</i> L.
	Rapeseed (Canola)	<i>Brassica napus</i> L. var. <i>oleifera</i> Delile
Bromeliaceae	Pineapple	<i>Ananas comosus</i> (L.) Merr.
Burseraceae	Pili nut	<i>Canarium ovatum</i> Engl.
Cactaceae	Dragonfruit	<i>Hylocereus undatus</i> (Haw.) Britton & Rose
	Pitaya	<i>Stenocereus queretaroensis</i> (Weber) Buxbaum
	Prickly pear	<i>Opuntia ficus-indica</i> (L.) Mill.
Cannabaceae	Hemp	<i>Cannabis sativa</i> L.
	Hops	<i>Humulus lupulus</i> L.
Capparidaceae	Caper	<i>Capparis spinosa</i> L.
Caricaceae	Papaya	<i>Carica papaya</i> L.
Celastraceae	Khat	<i>Catha edulis</i> Forsk.
Convolvulaceae	Kangkong (water spinach)	<i>Ipomoea aquatica</i> Forsk
	Sweet potato	<i>Ipomoea batatas</i> (L.) Lam.
Cucurbitaceae	Bitter melon	<i>Momordica charantia</i> L.
	Bottle gourd	<i>Lagenaria siceraria</i> (Molina) Standl.
	Cucumber	<i>Cucumis sativus</i> L.
	Loofah	<i>Luffa aegyptiaca</i> Mill.
	Pumpkin (giant pumpkin)	<i>Cucurbita maxima</i> Duchesne
	Squash and pumpkin	<i>Cucurbita pepo</i> L.
	Watermelon	<i>Citrullus lanatus</i> (Thunb.) Matsum. & Nakai
Cyperaceae	Tiger nut	<i>Cyperus esculentus</i> L.
Dioscoreaceae	Indian yam	<i>Dioscorea trifida</i> L.
	Mountain yam (Japanese)	<i>Dioscorea opposita</i> Thunb.
	Ube/yam	<i>Dioscorea alata</i> L.
	Guinea yam (White yam)	<i>Dioscorea rotundata</i> complex: <i>D. rotundata</i> Poir. and <i>D. cayenensis</i> Lam.
Ebenaceae	Chocolate pudding fruit	<i>Diospyros nigra</i> (J.F. Gmel.) Perrier (formerly <i>D. digyna</i> Jacq.)
	Persimmon (Japanese)	<i>Diospyros kaki</i> Thunb.
Ericaceae	Blueberry (highbush)	<i>Vaccinium corymbosum</i> L.
	Cranberry	<i>Vaccinium macrocarpon</i> Ait.
Euphorbiaceae	Cassava	<i>Manihot esculenta</i> Crantz ssp. <i>esculenta</i>
Fabaceae	Carob	<i>Ceratonia siliqua</i> L.
	Chickpea	<i>Cicer arietinum</i> L.
	Common bean	<i>Phaseolus vulgaris</i> L.
	Cowpea	<i>Vigna unguiculata</i> (L.) Walp.
	Fava bean	<i>Vicia faba</i> L. var. <i>minor</i> , <i>V. faba</i> L. var. <i>major</i>
	Hyacinth bean	<i>Lablab purpureus</i> (L.) Sweet
	Lentil	<i>Lens culinaris</i> Medik.
	Mung bean	<i>Vigna radiata</i> (L.) R. Wilczek
	Pea	<i>Pisum sativum</i> L.
	Peanut	<i>Arachis hypogaea</i> L.
	Soy	<i>Glycine max</i> (L.) Merr.
	Tamarind	<i>Tamarindus indica</i> L.
Fagaceae	Oak	<i>Quercus</i> spp.
	Sweet chestnut	<i>Castanea sativa</i> Mill.
Ginkgoaceae	Ginkgo	<i>Ginkgo biloba</i> L.
Gnetaceae	Eru	<i>Gnetum africanum</i> Welw.
	Spanish joint fir	<i>Gnetum gnemon</i> L.
Grossulariaceae	Black currant	<i>Ribes nigrum</i> L.
Iridaceae	Saffron	<i>Crocus sativus</i> L.
Irvingiaceae	Dika	<i>Irvingia gabonensis</i> (Aubry-Lecomte ex O'Rorke) Baill.
Juglandaceae	Pecan	<i>Carya illinoensis</i> (Wangenh.) K. Koch
	Walnut	<i>Juglans regia</i> L.
Lamiaceae	Basil	<i>Ocimum basilicum</i> L.
	Lavender	<i>Lavandula angustifolia</i> Mill.

Table 1 (Continued)

Family	Crop common name	Species/species complex	
Lauraceae	Mint	<i>Mentha spicata</i> L.	
	Sage	<i>Salvia officinalis</i> L.	
	Avocado	<i>Persea americana</i> Mill.	
	Bay laurel	<i>Laurus nobilis</i> L.	
	Cinnamon	<i>Cinnamomum verum</i> J. Presl.	
Lecythidaceae	Sassafras	<i>Sassafras albidum</i> (Nutt.) Nees	
	Brazil Nut	<i>Bertholletia excelsa</i> Humb. & Bonpl.	
Liliaceae	Asparagus	<i>Asparagus officinalis</i> L.	
	Garlic	<i>Allium sativum</i> L.	
Linaceae	Onion	<i>Allium cepa</i> L.	
	Flax	<i>Linum usitatissimum</i> L.	
Lythraceae	Pomegranate	<i>Punica granatum</i> L.	
Malvaceae	Baobab	<i>Adansonia digitata</i> L.	
	Cacao	<i>Theobroma cacao</i> L.	
	Cola (Kola)	<i>Cola nitida</i> (P.Beauv.) Schott & Endl.	
	Cotton	<i>Gossypium hirsutum</i> L.	
	Durian	<i>Durio zibethinus</i> Murr.	
	Okra	<i>Abelmoschus esculentus</i> (L.) Moench	
	Small leaved white cross berry	<i>Grewia tenax</i> (Forssk.) Fiori	
	Tossa jute	<i>Corchorus olitorius</i> L.	
	Moraceae	Breadfruit	<i>Artocarpus altilis</i> (Parkinson) Fosberg
		Fig	<i>Ficus carica</i> L.
		Mulberry	<i>Morus alba</i> L.
		Sycamore fig	<i>Ficus sycomorus</i> L.
	Musaceae	Banana	<i>Musa acuminata</i> Colla. and <i>M. balbisiana</i> Colla.
Enset		<i>Ensete ventricosum</i> (Welw.) Cheesman	
Myrtaceae	Clove	<i>Syzygium aromaticum</i> (L.) Merr. & L.M. Perry	
	Guava	<i>Psidium guajava</i> L.	
Oleaceae	Malay apple	<i>Syzygium malaccense</i> (L.) Merr. & L.M. Perry	
	Olive	<i>Olea europaea</i> L. ssp. <i>europaea</i> var. <i>europaea</i>	
Orchidaceae	Vanilla	<i>Vanilla planifolia</i> L.	
Oxalidaceae	African wood-sorrel	<i>Oxalis pes-caprae</i> L.	
	Cucumber tree	<i>Averrhoa bilimbi</i> L.	
	Oca	<i>Oxalis tuberosa</i> Molina	
	Starfruit	<i>Averrhoa carambola</i> L.	
	Pandanaaceae	Pandan	<i>Pandanus amaryllifolius</i> Roxb.
		Sesame	<i>Sesamum indicum</i> L.
	Pinaceae	Pinyon pine	<i>Pinus edulis</i> Engelm.
		Black pepper	<i>Piper nigrum</i> L.
	Piperaceae	Hoja santa	<i>Piper auritum</i> Kunth
		Barley	<i>Hordeum vulgare</i> L. ssp. <i>vulgare</i>
Bread Wheat		<i>Triticum aestivum</i> L.	
Corn		<i>Zea mays</i> L. ssp. <i>mays</i>	
Millet		<i>Panicum miliaceum</i> L.	
Millet (foxtail)		<i>Setaria italica</i> (L.) P. Beauvois	
Millet (pearl)		<i>Pennisetum glaucum</i> (L.) R. Br.	
Oat		<i>Avena sativa</i> L.	
Rice (African)		<i>Oryza glaberrima</i> Steud.	
Rice (Asian)		<i>Oryza sativa</i> L.	
Rye		<i>Secale cereale</i> L.	
Sorghum		<i>Sorghum bicolor</i> (L.) Moench ssp. <i>bicolor</i>	
Sugar cane		<i>Saccharum officinarum</i> L.	
Wild rice (American)		<i>Zizania palustris</i> L.	
Wild rice (Manchurian)		<i>Zizania latifolia</i> Turcz.	
Polygonaceae		Buckwheat	<i>Fagopyrum esculentum</i> Moench.
Proteaceae		Macadamia	<i>Macadamia integrifolia</i> Maiden & Betche and <i>M. tetraphylla</i> L.A.S.Johnson (and hybrids of the two)
	Blackseed	<i>Nigella sativa</i> L.	
Ranunculaceae	Jujube	<i>Ziziphus jujuba</i> Mill.	
Rhamnaceae	Almond	<i>Prunus dulcis</i> (Mill.) D.A. Webb	
Rosaceae	Apple	<i>Malus domestica</i> Borkh. (syn. <i>Malus pumila</i> Mill.)	
	Apricot	<i>Prunus armeniaca</i> L.	

Table 1 (Continued)

Family	Crop common name	Species/species complex
	Cherry	<i>Prunus avium</i> L.
	Peach	<i>Prunus persica</i> Miller
	Quince	<i>Cydonia oblonga</i> Mill.
	Red raspberry (European)	<i>Rubus idaeus</i> L. ssp. <i>idaeus</i>
	Strawberry	<i>Fragaria x ananassa</i> Duchesne ex Rozier
Rubiaceae	Coffee	<i>Coffea arabica</i> L.
	Noni	<i>Morinda citrifolia</i> L.
Rutaceae	Citron	<i>Citrus medica</i> L.
	Grapefruit	<i>Citrus paradisi</i> Macf.
	Lemon	<i>Citrus limon</i> (L.) Burns
	Mandarin	<i>Citrus reticulata</i> Blanco.
	Sichuan peppercorn	<i>Zanthoxylum bungeanum</i> Maxim.
	Sweet orange	<i>Citrus sinensis</i> (L.) Osbeck
	White sapote	<i>Casimiroa edulis</i> Llave & Lex.
Sapindaceae	Ackee	<i>Blighia sapida</i> Kon.
	Guarana	<i>Paullinia cupana</i> Kunth var. <i>sorbilis</i> (Mart.) Ducke
	Lychee	<i>Litchi chinensis</i> Sonn.
Sapotaceae	Cainito (Star Apple)	<i>Chrysophyllum cainito</i> L.
	Shea	<i>Vitellaria paradoxa</i> C. F. Gaertn.
Schisandraceae	Star anise	<i>Illicium verum</i> Hook.f.
Solanaceae	Cannibal's tomato	<i>Solanum viride</i> Sprang.
	Cayenne pepper	<i>Capsicum frutescens</i> L.
	Chili pepper	<i>Capsicum annum</i> L. var. <i>annuum</i>
	Cocona	<i>Solanum sessiliflorum</i> Dunal
	Eggplant	<i>Solanum melongena</i> L.
	Gboma eggplant	<i>Solanum macrocarpon</i> L.
	Pepino	<i>Solanum muricatum</i> Aiton.
	Potato	<i>Solanum tuberosum</i> L.
	Scarlet eggplant	<i>Solanum aethiopicum</i> L.
	Tomato	<i>Solanum lycopersicum</i> L.
Theaceae	Tea	<i>Camellia sinensis</i> (L) O. Kuntze var. <i>assamica</i> and var. <i>sinensis</i>
Vitaceae	Grape	<i>Vitis vinifera</i> L. ssp. <i>vinifera</i>
Zamiaceae	Bread tree	<i>Encephalartos altensteinii</i> Lehm.
	Grahamstown cycad	<i>Encephalartos caffer</i> (Thunb) Lehm.
Zingiberaceae	East Indian Arrowroot	<i>Curcuma angustifolia</i> Roxb.
	Ginger	<i>Zingiber officinale</i> Roscoe
	Turmeric	<i>Curcuma longa</i> L.

species that were independently domesticated from different wild ancestors can share a common name (e.g. Asian and African rice) but are considered many single origin events. Researchers determine the number of origins based on multiple lines of evidence, including archaeological, genetic, and linguistic data. For crops where there is insufficient evidence in the literature to determine the number of origins, the default assumption in this review is of a single origin, because this is the most parsimonious explanation. Further research may, however, reveal that some presumed single origin crops did, in fact, have multiple origins.

III. Methods of review and analysis

1. Selection of species for review

The crop species in this review were selected through a screening of multiple sources including the peer-reviewed literature on domestication and economic botany, literature reviews (including

reviews of specific categories of crops (e.g. trees)), and selected databases (Tables S1, S2). An initial 100 food crop species were identified from these sources to include crops from all continents, to minimize bias towards well-studied and/or familiar areas. There was no consideration for familiarity, importance of the crop, or the amount of data available. We selected an additional 80 species with the added criterion of phylogenetic distribution in plant families to ensure that no single family represented > 7% of the dataset. If too many crops from a single family were included, we randomly selected species to be removed from the dataset. To avoid bias from disproportionate representation of crops of current major economic importance, we identified an additional 23 crops of minor global economic importance but high local importance in developing regions from the economic botany, domestication, and development literature addressing underutilized crops.

The final dataset is composed of 203 crops spanning 68 families, representing 43% of the estimated number of families in

which domestication has occurred (Dirzo & Raven, 2003; Table 1). These species and families were grouped into phylogenetic clades for subsequent analysis based on the most current angiosperm phylogeny (Soltis *et al.*, 2011). This dataset includes a large selection of 'minor' crop plants that are locally important. We consider crops as minor if the area devoted to their cultivation is not included in FAOStat (<http://faostat.fao.org>). By this criterion, 47% of the dataset crops are minor. Forty-three percent of the crops are considered to be underutilized, based on inclusion in the Global Facilitation Unit for Underutilized Species database (Table 2).

2. Literature review

We collated information on crop domestication history, uses, and specific traits, including ploidy level, reproductive strategy, and life cycle. Our references are mostly peer-reviewed publications and academic sources, but also include some gray literature and well-referenced online databases, particularly for minor and understudied crops (Table S1). In total, we compiled information from over 800 references that have been organized as a table that is searchable by crop (Table S2). We categorized this information using predefined parameters (Table S3). We assigned a confidence score to each crop representing the overall availability and quality of data regarding the place of origin, time of domestication and wild ancestor identity, including how well data were supported with archaeological remains and whether evidence was contested (Tables S4, S5).

Using the FAO World Information and Early Warning System (WIEWS), we compiled data for the conservation status of crops using the number of institutions worldwide housing *ex situ* collections of each crop, and the total number of accessions and subspecies available in these institutions (Tables 2, S4, S5). WIEWS records are subject to some imprecision because they are reported on a voluntary basis and are not continually updated. Therefore, we also tabulated *ex situ* conservation data from the databases of a subset of prominent germplasm centers in the Western hemisphere (NORDGEN, USDA ARS-GRIN and Svalbard) and the network of CGIAR germplasm centers (SINGER) (Tables 2, S1). Although discussion of trends in *ex situ* conservation are beyond the scope of this review, the results of correlation analyses of *ex situ* conservation status with other domestication traits are presented (Table S6).

3. Data analysis

The compiled and categorized data for all 203 crops were coded as a binary matrix (Table S4). Our initial analysis of these data used Logic Forest (LF), a package in R statistical software (R Development Core Team, 2011), to identify correlations of interest across the multiple categories of data in the matrix. LF, which performs an ensemble classification of multivariate regressions, was designed to identify predictive variables in large and noisy datasets, and has a superior performance to logic regressions in identifying important predictors (Wolf *et al.*, 2010). We treated data in each category as an outcome with possible

Table 2 The number of crops assigned to the different categories and subcategories of information considered in this review (detailed definitions of categories and subcategories are available in Supporting Information, Table S3)

Category	Subcategory	Number of crops	
Classification	Monocot	41	
	Dicot	156	
	Gymnosperm	6	
Lifecycle	Annual ¹	85	
	Biennial ¹	13	
	Perennial ¹	150	
	Tree-like	76	
	NonTree	75	
Ploidy	Diploid ¹	165	
	Polyploid ^{1,2}	71	
	Allopolyploid	12	
	Autopolyploid	24	
Reproductive strategy	Unknown	6	
	Self-fertilizing ¹	95	
	Outcrossing ¹	102	
	Vegetative ¹	115	
Center of domestication	West Africa Delta	14	
	Eastern North America	15	
	Abyssinia	14	
	Central America	25	
	Central Andean	13	
	Central Asian	9	
	China	24	
	Indo-Burma	27	
	Mediterranean	30	
	Near East	27	
	Near Oceania	20	
	Amazonia	15	
	Domestication information	Domesticated ¹	160
Multiple proposed		38	
Outside native range		23	
Autochthonous		169	
Date known or proposed		184	
Semi-domesticated ¹		37	
Undomesticated ¹		15	
Wild ancestor		158	
Known/proposed		158	
Earliest date known/proposed		169	
Traits of the domestication syndrome	Nonshattering	32	
	Fruit characteristics	91	
	Aerial (vegetative characteristics)	93	
	Secondary metabolite	133	
	Seed characteristics	78	
	Reproductive strategy	54	
	Life cycle shift	29	
	Change in ploidy	37	
	Conservation/ utilization	Model	66
		Minor	95
Underutilized		87	
<i>Ex situ</i>		188	
Global (WIEWS)		149	
	GRIN	149	
	CGIAR	75	

¹These are nonexclusive categories, i.e. one crop may be assigned to more than one category.

²For some polyploid crops, insufficient information was available to distinguish between allopolyploidy and autopolyploidy.

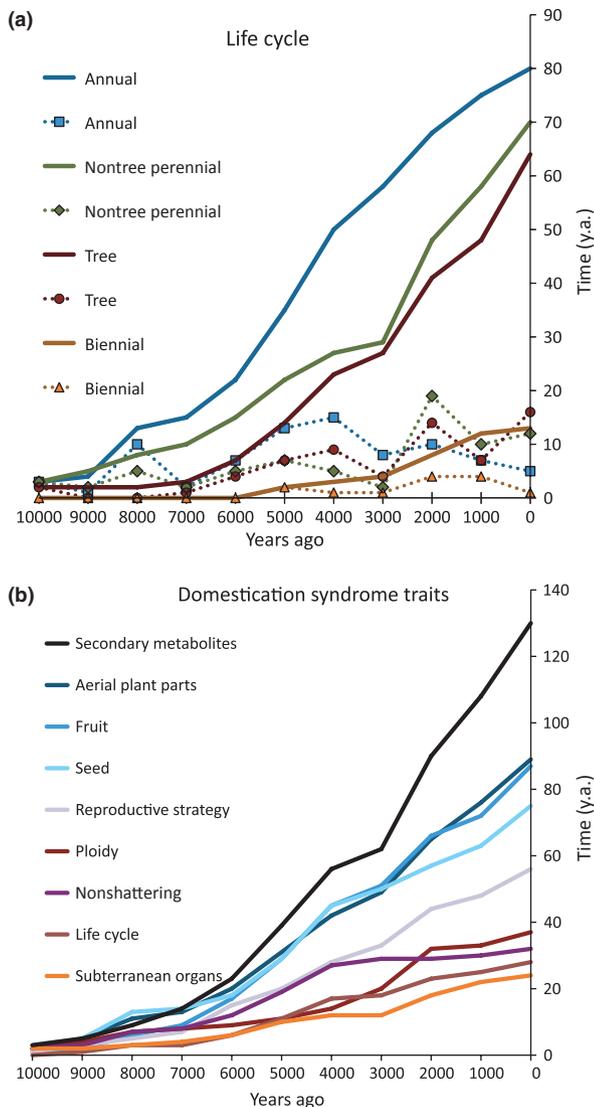


Fig. 2 The number of occurrences of life cycle types and domestication syndrome traits for 203 food crops as a function of the time at which domestication occurred. (a) The number of occurrences of different life cycles are shown both cumulatively (solid lines) and by interval within each 1000 yr period (dotted lines), from the earliest domestication events until the present. Temporal trends in the distribution of the different life cycles show that the appearance of domesticated annuals increases from 9000 to 4000 yr ago (ya), and then starts to slow. The broad dissemination and adoption of early domesticated grains, such as barley, corn and wheat, may have relaxed selection intensities on local cereals. An increase in the cultivation and domestication of trees and nontree perennials coincides with the decline in addition of new annuals in the last 3000 yr, and the two periods of sharp increase 6000 and 3000 ya coincide with innovations such as vegetative propagation through cuttings and later scion grafting. The first domesticated biennials appear in our dataset only in the last 5000–6000 yr, and their rise between 1000 and 3000 ya corresponds with the peak of trade and activity of the Roman empire throughout the Mediterranean, where many biennials were domesticated. (b) The occurrence of domestication syndrome traits in crops domesticated in different 1000 yr time intervals. Domestication traits involving a change in plant secondary metabolites are the most common in every 1000 yr time period of the last 7000 yr; the occurrence of some traits (e.g. changes in subterranean organs; life cycle; nonshattering types) have slowed or leveled off, most notably the trait for nonshattering, whose leveling off corresponds with a decline in the rate of addition of new annuals beginning 4000 ya.

predictors (i.e. other variables) and used LF to assign a predictor importance (PI) value representing the strength of either positive or negative correlations among the predictor and outcome variables. Some categories of data were removed from specific analyses if they were obviously redundant or linked (e.g. ‘diploid’ as a negative predictor for ‘polyploid’; Table S5). Crops with missing data in some categories were excluded from certain analyses. We also excluded undomesticated crops from regressions when testing questions specific to domesticated plants. Results of the LF analysis were compiled in a heat map showing the strength of positive and negative predictors among the different categories in the dataset (Table S6). These results were used to identify potentially interesting relationships among categories and to guide further exploration of the data using classical statistical tests.

Estimates of the time required for a crop to transition from its wild to its domesticated forms were calculated by subtracting the date of the earliest record of its domesticated form from the earliest date of exploitation of the wild ancestor. These data were available for 142 crops, based upon archaeobotanical evidence or written records. This method was used for consistency in determining domestication periods, even though more precise methods have been used, particularly for model crops (Allaby *et al.*, 2008; Fuller *et al.*, 2011b).

We generated maps of the density of domestication events during different time intervals, overlaid on floristic regions as defined by Takhtajan (1986), using ArcGIS (ESRI, Redlands, CA, USA). Takhtajan’s floristic regions were chosen over more fine-grained divisions (e.g. WWF ecoregions) because their scale and boundaries are frequently similar to those of proposed centers of domestication. Plots of the data were made in Microsoft Excel or in R statistical software.

IV. Trends identified from the review of 203 crops

Because domestication is an ongoing process, this analysis included crops in varying stages of domestication. The crops included: 160 domesticated, 37 semidomesticated and 15 undomesticated crops (some crops fell into two categories, e.g. a crop that is mostly wild-harvested, but also has semidomesticated populations; Tables 2, S3–S5). Crops exhibited a wide distribution within categories, including uses, plant organs used, geographic origins, life history traits, and domestication syndrome traits. Most crops were exploited for several organs and for many different uses. The crop domestication syndrome consisted of 2.8 traits, on average. Eighty-four percent of the crops had between two and five domestication syndrome traits, while some crops were defined by as many as seven (Tables S4, S5). The confidence scores for availability and quality of the data regarding the place of origin, time of domestication and wild ancestor identity reveal major gaps in the literature: just 30% of the crops had high confidence scores (Table S5). Ten percent of the studied crops were under dispute with regard to their origins or wild ancestor.

In the following sections, a series of core topics related to domestication are explored. Both LF regression and an evaluation of the data distribution are applied to re-examine domestication hypotheses and test models from the classic and recent literature,

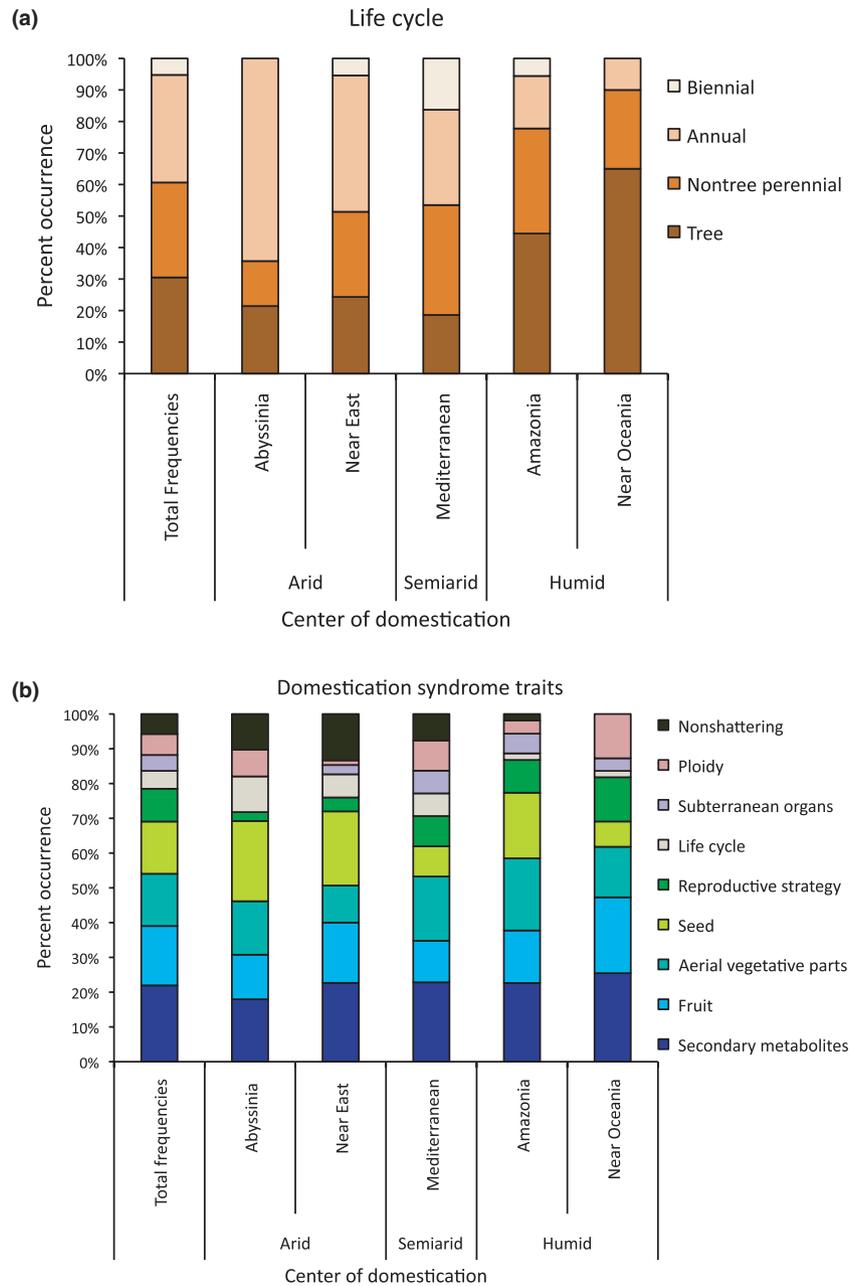


Fig. 3 The distribution of crop life cycles and domestication syndrome traits among different regions, plotted as the percent frequency of occurrence in the domesticated crops for each region. Selected regions are grouped by distinct climatic zones: arid, semiarid, and humid. (a) The distribution of annual, biennial, nontree and tree perennials in domesticated crops of different regions. Annuals are most prevalent in regions of arid climate, biennials are most prevalent in semiarid climates, nontree perennials exhibit relatively consistent proportions, and trees are most prevalent in humid climates. These results are consistent with expected proportions of such life cycles in the regional flora. (b) The distribution of domestication syndrome traits according to selected centers of domestication. Not all traits are found in the crops of all regions. No changes in seed shattering were observed in crops from Near Oceania. No changes to subterranean structures such as roots were observed in crops from Abyssinia (contemporary Ethiopia). Differences between different climates were identified: arid regions featured a smaller proportion of changes to fruits and reproductive strategy, and a greater proportion of the trait affecting seed morphology, consistent with the larger frequency of annual domestication (shown in a). Changes in secondary metabolites are the most common domestication trait observed in all regions.

and to explore potential novel patterns and trends. LF output for all categories, including robust trends not discussed in the text, is available as a heat map displaying the PI values for each variable (Table S6). The strongest and most potentially interesting results from our analysis are discussed in sections organized around life cycles, ploidy, reproduction, spatial-temporal trends, and uses.

V. Life cycle

The cumulative number of annuals domesticated per 1000 yr time period reveals that domestication events of annuals increased in number from 9000 to 4000 ya, with a peak at 8000 ya, followed by a steady increase, culminating in a second peak at

Table 3 Comparison of the rate of domestication, the number of traits of the domestication syndrome, and the range of crop wild ancestors for different categories of crops, using unpaired, one-tailed, Student's *t*-tests

Variable tested	Group A			Group B			Test result		
	Group definition	<i>n</i>	Mean (SE)	Group definition	<i>n</i>	Mean (SE)	<i>t</i> -value	df	<i>P</i> -value
Time from exploitation to domestication	Trees	39	3767 (467)	Annuals	32	2638 (305)	-2.02	63	0.0235
Time from exploitation to domestication	Vegetative root plus perennial fruit crops	77	3147 (318)	Annual seed crops	43	2424 (322)	1.48	118	0.1400
Number of traits of the domestication syndrome	Trees	76	2.54 (0.17)	Annuals	85	3.41 (0.17)	3.54	158	0.0003
Number of traits of the domestication syndrome	Perennial fruit crops	81	3.13 (0.16)	Annual seed crops	49	3.60 (0.22)	-1.92	128	0.0286
Number of traits of the domestication syndrome	Vegetative root crops	23	3.00 (0.34)	Annual seed crops	49	3.60 (0.22)	-1.32	70	0.0873
Number of floristic regions where the wild ancestor occurs	Crops with single domestication events	150	1.66 (0.08)	Crops with multiple domestication events	38	2.29 (0.21)	-3.36	186	0.0009

Bold *P*-values indicate significance at 95% confidence.

5000–4000 ya (Fig. 2a). The domestication of annuals has since exhibited a decrease over the past 4000 yr (Fig. 2a). This could be because most of the annual plants amenable to domestication in the regions settled by humans had already been domesticated by this time. It could also be explained by the broad dissemination of major annual seed crops (wheat, barley, rice and corn) decreasing reliance on minor grains, leading to the loss of minor domesticates or a reduced need to domesticate more annuals. One example of this is sumpweed, which was domesticated in North America as a seed crop and then abandoned when corn replaced it in local diets 700–1000 ya (Gepts, 2004).

Biennials appear in the dataset beginning nearly 6000 ya and increase in every subsequent 1000 yr time period (Fig. 2a). Their later occurrence is consistent with the need for more sophisticated crop management techniques and a sedentary lifestyle, because plants must be reserved for an additional year, rather than harvested, to obtain seeds for propagation (Sauer, 1993). Biennials are associated with the circumboreal floristic region in the LF results. Humans domesticate the plants that are available and amenable to domestication in the region where they live. The circumboreal region is suitable habitat for biennials because many have a life cycle that requires vernalization and are therefore more likely to occur in regions with a distinct winter season (Amasino, 2004). The appearance of domesticated biennials is also positively associated with the Mediterranean floristic region in the LF results, peaking between 3000 and 1000 ya, coinciding with the rise of major civilizations in Ancient Egypt, Ancient Greece and the Roman Empire in the Mediterranean basin and in Europe (Figs 2a, 3a, Table S5). It is possible that the domestication of many crops with a biennial life cycle in the Mediterranean region was facilitated by knowledge dissemination throughout the region via the extensive trade networks that existed among these civilizations.

An increase in domesticated perennials coincides with a decline in the rate of annual domestication (Fig. 2a). These findings are consistent with conclusions by Miller & Gross (2011) that trees and other long-lived perennials (collectively refer to as 'trees' throughout this review; long-lived perennials also include banana and palms) were domesticated later than annuals. Few trees were domesticated before 4000 ya, and over 50% of the included tree crops were domesticated in the last 2000 yr (Fig. 2a). The number of domesticated tree crops increased in two waves, with the first starting 6000 ya, with a peak 4000 ya, and a second wave starting 3000–2000 ya and continuing into the present era (Fig. 2a). The two waves of domestication observed in perennials may be linked to the dissemination of propagation techniques. It has been proposed that the first wave in fruit domestication (both nontree perennials and trees) in the Old World coincides with the domestication of species that can easily be propagated vegetatively using simple techniques such as cuttings or suckers (e.g. olive), while the second coincides with the discovery and dissemination of scion grafting (e.g. carob; Zohary, 2002; Hsina & El-Mtili, 2009). The two waves of domestication for trees coincide with this time-frame, particularly the second wave beginning 3000–2000 ya, which is the time-frame for the development of scion grafting techniques in the Mediterranean basin. In fact, of all the trees with a domestication syndrome that featured a change in reproductive strategy to mainly vegetative propagation, 76% were domesticated during one of the two waves (Tables S4, S5).

We tested whether crops with different life cycles exhibited significant differences in domestication rates and in the average number of domestication traits. According to Pickersgill (2007), 'vegetatively propagated root crops and perennial fruit crops show fewer domestication syndrome traits than annual seed crops, and domestication may occur more slowly because fewer sexual generations occur in a given period of time'. We found

perennial fruit crops do indeed exhibit significantly fewer domestication syndrome traits than annual seed crops (Table 3). However, vegetatively propagated root crops do not exhibit significantly fewer traits than annual seed crops (Table 3). Regarding the rate of domestication, there was no significant difference in the mean time to domestication between vegetative root crops and perennial fruit crops compared with annual seed crops (Table 3). However, in analyses comparing all trees to annuals, the time to domestication was significantly longer and there were significantly fewer domestication syndrome traits in trees (Table 3), consistent with trends described by Miller & Gross (2011). While this result is reasonable, it is also possible that some traits of the tree domestication syndrome are still uncharacterized, producing biased results.

VI. Ploidy level

Polyploidy has been an important factor in angiosperm evolution, underlying episodes of adaptive radiation in many plant families (Soltis & Soltis, 1999) and in the angiosperms as a whole (Soltis *et al.*, 2009 and references therein). It is estimated that 15% of speciation events in the angiosperms involve polyploidization (Wood *et al.*, 2009). A number of traits associated with polyploidy, such as larger seed size, increased disease resistance, and decreased allocation to reproduction are advantageous in domesticates (Lewis, 1980; Levin, 1983). Some crops, like wheat, have been derived from wild ancestors through a process of allopolyploidization, conferring desirable characteristics of both ancestors on the new species. Other crops have been domesticated or improved via autopolyploidization (e.g. potato). Autopolyploids typically have larger cells and organs than their diploid progenitors as a result of doubling of the DNA content, while allopolyploids are variable in this regard (Ozkan *et al.*, 2003). The alteration of plant traits may also confer a fitness advantage in certain habitats, allowing species to adapt to marginal environments beyond the natural range of their diploid ancestor (Ramsey, 2011). This could enable domesticates to adapt to disturbed agricultural environments that are not suitable for the wild ancestor. Furthermore, polyploidization provides a mechanism for sympatric speciation, by providing reproductive isolation of the new species from the co-occurring diploid form (Soltis *et al.*, 2007). This may allow the rapid divergence and fixation of traits that are of interest for cultivation by limiting gene flow between wild and cultivated forms. Despite the importance of increased ploidy in the domestication syndrome of such major crops as wheat and potato, little is known about the frequency

and importance of ploidy changes in domestication syndromes across a broader sample of crops.

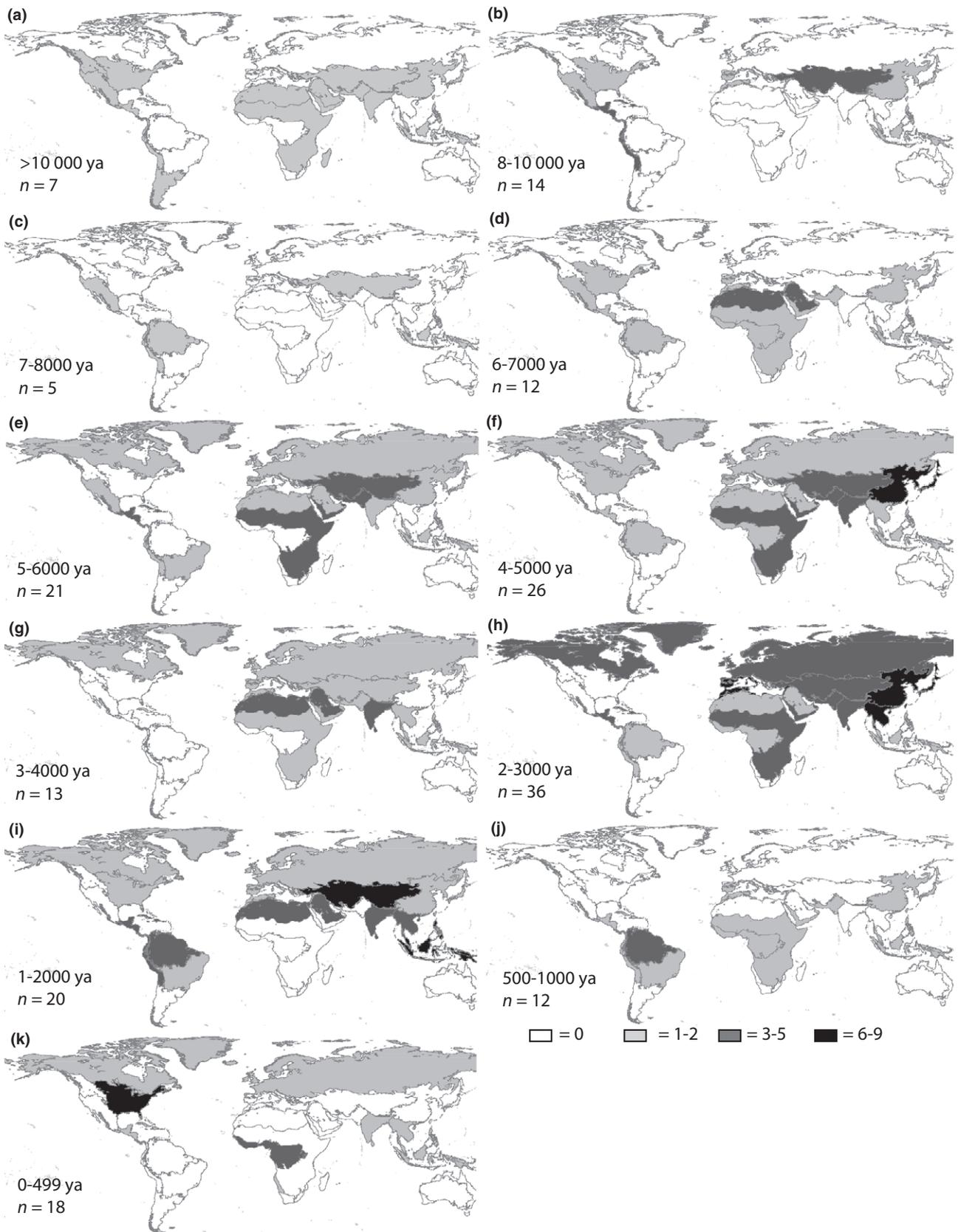
Of the crops with known ploidy ($n = 199$), our dataset includes 64% diploid crops and 17% polyploid crops, while 19% of the crops have both diploid and polyploid varieties (Table 2). This last proportion is slightly larger, although comparable, to the number of angiosperm species that include multiple ploidy levels (12–13%; Wood *et al.*, 2009). We examined how many polyploid angiosperm crops underwent polyploidization during the process of domestication and identified 37 crops (19%). Therefore the frequency of these ploidy changes is similar and only slightly higher than the frequency observed in speciation events among angiosperms, which is 15% (Wood *et al.*, 2009), suggesting that ploidy changes do not distinguish evolution under domestication. Of these, 51% were the result of autopolyploidy and 24% were the result of allopolyploidy, while 10% may have arisen from a combination of both and the remainder were of unknown origin or the result of ploidy reduction (Tables 2, S4, S5).

Perennial crops were the most common category of domesticates with ploidy changes as a domestication trait (78%). Of these, 90% were mainly propagated vegetatively under cultivation, and therefore would not have suffered decreased reproductive output in the event of genome duplication (Ramsey & Schemske, 2002). This is further supported by the observation that, of the crops with a domestication syndrome involving a ploidy change, nearly half (43%) also exhibited a change in reproductive strategy from outcrossing or self-fertilizing to vegetatively propagated. This is a trend previously noted for fruit trees (Zohary & Hopf, 2000).

The proportion of crops with a domestication syndrome involving both a ploidy change and a reproductive strategy change was significantly higher than the null expectation ($\chi^2 = 6.418$, $df = 1$, $P = 0.011$). A remaining 38% of crops with a ploidy change in their domestication syndrome were already propagated vegetatively in their wild form. Human intervention facilitating the propagation of crops with increased ploidy is also supported by the simultaneous increase of ploidy changes and reproductive strategy changes in crops domesticated between 3000 and 2000 ya. This coincides with a wave of domestication of perennials (Fig. 2a,b).

The outcrossing crops in our dataset exhibit a lower frequency of changes in ploidy as a domestication syndrome trait compared with self-fertilizing and vegetatively propagated crops (Tables S4, S5). Furthermore, in the dataset as a whole, only 19% of crops with either a self-fertilizing or an outcrossing reproductive strategy had a change in ploidy occurring under domestication that was not associated with a transition to vegetative propagation (bread

Fig. 4 The geographical locations of new crops domesticated worldwide represented grouped in 2000 yr time intervals from > 10 000 yr ago (ya) to the present ($n =$ total number of crops). The map is subdivided according to Takhtajan's floristic regions and reflects contributions from the different centers of domestication. Shading of regions represents the number of crops domesticated in that region in each time period. Higher numbers of domestication events (represented by darker shading) often correspond with the peaks of major civilizations throughout history, such as the Yellow Emperor period in China (f); the New Kingdom of the Egyptian Empire (g); the spread of the Eastern Han from China to Indochina (h); and the early Roman Empire (h). The last 1000 yr are broken into two 500 yr intervals (j, k) and reflect the influence of the Columbian exchange and contemporary breeding efforts, especially in North America (k). Near Oceania is active in domestication during every time interval (a–k); Mexico was an important site from over 10 000 to 5000 ya (a–e) but had no subsequent domestications in our dataset (f–k). More recently, recognized centers of domestication such as Amazonia and West Africa have had numerous low-intensity periods of domestication.



wheat, noni, oat, okra, rapeseed, soy, and sumpweed). Model cases of changed ploidy in sexually reproducing crops, such as wheat, are therefore exceptional, as vegetatively propagated crops domesticated either for edible vegetative tissue or for fruit, not seed crops, are most strongly associated with ploidy changes.

VII. Reproductive strategies

Our dataset included a relatively even distribution of outcrossing, self-fertilizing and vegetatively propagated crops (Table 2). Similar proportions were also found in a review of 124 crops by Simmonds (1976, 1979). There is considerable variation in reproductive strategies for a number of crops: of the total 203 crops, both self-fertilizing and outcrossing strategies characterized 25 crops, both self-fertilizing and vegetative propagation strategies characterized 32 crops, and both outcrossing and vegetative propagation strategies characterized 66 crops.

A number of crops exhibit a change in reproductive strategy between their wild and domesticated forms, either from outcrossing to self-fertilizing or from sexual reproduction to vegetative propagation. This is considered an important feature of crop domestication because, similar to a change in ploidy level, it is a mechanism for establishing reproductive isolation, allowing farmers to maintain desired phenotypes. It also allows for the production of desirable fruits with few or no seeds (Gepts, 2004). Both of these types of change in the reproductive strategy used under cultivation are frequently documented in this dataset. These changes occurred in 27% of the crops reviewed.

Shifts from outcrossing to a self-fertilizing system are considered a relatively common domestication syndrome trait for fruit and seed crops (Gross & Olsen, 2010; Roumet *et al.*, 2012). Overall, however, our data do not support this theory as common: results of LF analyses showed a negative association between self-fertilizing crops and changes in reproductive strategy (Table S6). Furthermore, this transition characterized under 20% of the self-fertilizing crops, indicating that most were already self-fertile in their wild state. This likely contributed to making them favorable candidates for domestication.

VIII. The domestication syndrome

We quantified differences in the frequencies of domestication traits characterizing different groups of crops. The most common domestication syndrome traits are changes in secondary (or specialized) metabolites (e.g. loss of bitter or toxic compounds, pigment changes), occurring in 66% of crops, followed by changes to the morphology of aerial vegetative parts, and changes to fruits (Fig. 2b; Table S3). Although loss of shattering is a classic domestication trait (Salamini *et al.*, 2002; Purugganan & Fuller, 2009), it only occurred at a low frequency (16%). Beginning *c.* 4000 ya, annual domestication began to decline (Fig. 2a), and, correspondingly, changes to seed morphology decreased in frequency and loss of shattering stabilized (Fig. 2b). Perennial crop domestication increased 2000–3000 ya and, correspondingly, domestication traits related to aerial vegetative parts, fruit

morphology, and secondary metabolites also increased sharply (Fig. 2a,b).

One caveat to discussion of these trends, however, is that our perceptions of domestication may be distorted by the plant groups and organs that are best conserved in the archaeobotanical record. Carbonized seed remains from the burning of food waste, starch analyses from early tools, and identification of phytoliths disproportionately reflect certain groups, in particular grasses, pulses and tubers (Smith, 1968). In contrast, traits shown to be prominent in recent times, such as changes to fruit morphology and changes to secondary metabolites, are less easily captured in the archaeological record. This may, in part, account for their lower observed prevalence in earlier periods.

In our dataset, many domestication syndrome traits occurred at different frequencies in different regions (Fig. 3b). Changes in secondary metabolites, fruit, aerial vegetative parts, and seed morphology were common across all regions. However, traits closely linked with particular plant life cycles often differed with the influence of climate and ecology on the respective regional floras. Regions with arid climates, such as the Near East and Abyssinia, are characterized by a large degree of domesticated annuals and high frequencies of seed morphology and nonshattering as domestication syndrome traits. Regions with humid climates, such as those of Near Oceania and Amazonia, do not have crops with nonshattering traits, corresponding to the lower occurrence of annuals. They also have fewer crops with a change in life cycle compared with arid regions; this is consistent with a year-round growing season (Fig. 3).

Further differences in domestication syndrome trends can potentially be explained by harvesting techniques, technologies and preferences specific to geographical regions. For example, in South Asia, sickle harvest of Asian rice resulted in fixation of the nonshattering trait (*sh4*; Li *et al.*, 2006; Ishikawa *et al.*, 2010). However, in West Africa, African rice was harvested by swinging a basket; as this method favored shattering phenotypes, nonshattering was never selected for (Carney, 2001; Linares, 2002). In some cases, similar crops were domesticated for different food organs in different regions. For example, amaranth provides a grain in Mesoamerica but is exploited as a pot herb in Africa (Grubben, 2004); and lettuce is used for edible leaves in the Mediterranean but was selected for an enlarged edible stem in China (Whitaker, 1969). Overall, we find that there is a high diversity of suites of domestication traits in food crops. This is contrary to the classical concept of the domestication syndrome; that there is a limited number of generally observed patterns of convergent evolution in crop plants (Hammer, 1984). Although the concept of a 'syndrome' can be a useful tool for education, it can oversimplify patterns in nature. This has previously been argued in the case of the 'pollination syndrome' (Ollerton *et al.*, 2009).

IX. Spatial and temporal trends

Archaeological evidence supports 24 separate regions where crop domestication occurred independently (Purugganan & Fuller, 2009). On the basis of floristic regions, our data supported

28 regions where crop domestication occurred (Fig. 4; Tables S4, S5), and 27 regions where one or more domesticates had probable origins as exploited wild species (Tables S4, S5).

The patterns of domestication activity in the different centers of domestication are extremely variable over time (Fig. 4). Peaks in domestication activity in our dataset coincide with the rise of major civilizations. The highest rates of domestication in Egypt occur during the prosperous New Kingdom period of the Egyptian empire (Fig. 4g). There was a spike in domestication events in the Mediterranean during the period of the early Roman Empire, which accounts for one-third of the crops domesticated worldwide during that interval (Fig. 4h). The two peaks of domestication in China coincide with the spread of Chinese civilization, religion, and medicinal knowledge associated with the Yellow Emperor starting near the Yellow River (4–5000 ya; Fig. 4f), and the spread of the Eastern Han into the northern Mekhong river valley of Indochina (2000–3000 ya; Fig. 4h). There is also a peak in domestication in Indochina during this interval. Relatively few crops have been domesticated in North America compared with other regions (Table 2). Although many of these (e.g. cranberry, wild rice) were used in their wild form for long periods, domestication in this region only peaked in the last 500 yr, during and after the ‘Columbian exchange’ (Gepts & Papa, 2002; Fig. 4k). Many are the result of modern breeding programs (e.g. cranberry, highbush blueberry, pecan). This provides a contemporary example of domestication as an ongoing process driven by diffusion of technology.

The regions of Amazonia and West Africa, were strongly associated with both ‘underutilized’ and ‘semidomesticated’ crops in LF results (Table S6). Light management and traditional harvesting of semidomesticated forest products in the Amazon and West Africa has meant that their production and distribution has been relatively restricted (Harlan, 1992; Clay & Clement, 1993). The low visibility of many crops domesticated in these regions could account for the relatively recent acceptance of Amazonia and West Africa as centers of domestication (Heller *et al.*, 1997). Today, in both regions, a number of species are entering plant breeding programs with an increased focus on previously undomesticated crops in West Africa (e.g. baobab, dika; Van der Stege, 2010), and improvement upon domesticated and semidomesticated crops in Amazonia (e.g. açai, guarana; Clement, 1999a,b; Brondizio, 2008; Clement *et al.*, 2010).

The marginality model posits that domestication is frequently driven by the reproductive isolation between wild and domesticated forms caused by the removal of a plant from its native range (Binford, 1968; Flannery, 1969; Verhoeven, 2004). We tested this model using the data for region of origin of the ancestor and center of domestication of the crop and found that only a small proportion (12%) of crops were domesticated outside of their native range, making this model an exception rather than the rule in explaining domestication (Table 2). Many of these exceptions are recently domesticated crops such as grapefruit and kiwi, driven by contemporary movement of germplasm. Kiwi was domesticated in New Zealand, although it had been exploited as a wild crop for thousands of years in China (Ferguson & Seal, 2008), and grapefruit, a hybrid of *Citrus sinensis* from South East

Asia and *Citrus maxima* from Indonesia, was domesticated in Barbados in the 1820s (Kumamoto *et al.*, 1987).

The question of whether a crop has been domesticated once vs multiple times is frequently an ongoing debate (see Section II.6, ‘Single vs multiple origins’; Zohary & Spiegel-Roy, 1975; Olsen & Gross, 2008; Fuller *et al.*, 2011a,b). The detailed analyses needed to differentiate single from multiple origins have not been performed for many crops. Furthermore, the genetic signature of multiple origins can be obscured by historic bottlenecks, gene flow, genetic drift, and admixture (Allaby *et al.*, 2008), and conclusions are strongly dependent on the sampling strategy and the abundance of molecular data available (Smith, 2006; This *et al.*, 2006; Blackman *et al.*, 2011; Molina *et al.*, 2011). Multiple origins have been proposed for only 38 (19%) of the crops analyzed. In the grasses, however, it appears that multiple origins have occurred more frequently.

One-third of the crops with proposed multiple origins originate in the Mediterranean region, a region contiguous with three other regions supporting crop domestication, including two centers of origin as defined by Vavilov (Abyssinia, Near East). This high proportion of crops with multiple origins may reflect the role of trading networks between North Africa, the Near East and Northern Europe that played an early role in the dissemination of crops and technical knowledge. One example of this is Nubian cotton (*Gossypium herbaceum* L.): the Roman textile market was purchasing cotton from India and that trade may have influenced Nubian farmers to domesticate their local cotton (Van der Veen, 2011; Palmer *et al.*, 2012).

For the major domesticates, multiple origins were rare in Eurasia but common in the Americas. It has been proposed that ease of crop diffusion along the east–west axis of Eurasia, combined with narrow ranges of the wild ancestors, limited multiple domestication events. In comparison, the Americas had slower crop diffusion along a north–south axis (Diamond, 2002). In our larger dataset, however, there were only slightly more crops with multiple origins in the New World (28%) than in the Old World (22%), suggesting that the difference in axes of the continents is not a sufficient explanation for the number of crops with multiple origins. These multiple origin crops, however, have wild ancestors that occur in a significantly larger number of floristic regions than crops with single domestication events (Table 3). This supports the theory that a broad distribution of the wild ancestor is a likely factor predisposing a species to multiple domestications, although further investigation of this question is required.

Recent evidence from archaeological data, modeling, and evolutionary genetics supports a protracted transition model, which maintains that domestication occurs gradually over time at rates comparable with evolution under natural selection (Tanno & Willcox, 2006; Purugganan & Fuller, 2009, 2011; Fuller *et al.*, 2011b). Our estimates of the time to domesticate a plant species fall in line with expectations of a protracted model (Fig. 5; Allaby *et al.*, 2008). Furthermore, the time interval between initial exploitation of the wild ancestor and domestication decreases as the time of first use of the common ancestor progresses toward the present (Fig. 5). Although this trend is undoubtedly

influenced by the greater availability of more recent archaeobotanical material and by the inherent bias in using the present day as the frame of reference, it merits further investigation. A number of factors relating to selection could accelerate the domestication rate over time; in particular, transitions from unconscious to conscious selection, increasing knowledge and innovation in agricultural practices and technologies, and the development of modern breeding practices. In addition, stronger barriers to gene flow between wild and domesticated forms caused by increased environmental patchiness and increased long-distance travel could facilitate more rapid fixation of domestication traits.

X. Utilization of plant parts

A large number of our food plants were originally exploited for purposes other than food or in addition to being a food. The eggplant was likely originally used as a medicine and hide-tanner (Daunay *et al.*, 2001), and saffron was used as a body paint, dye, and perfume (Mousavi & Bathaie, 2011). Wild olive trees in the Mediterranean basin were valued for their wood, with a high oil content that made it resistant to decay and allowed it to burn while wet, before the fruits became exploited as food (Salavert, 2008; Breton *et al.*, 2009; Belaj *et al.*, 2010). The toxic cyanogenic glycosides in cassava that must be removed before consumption were useful for stunning fish, and cinnamon was likely first used in embalming practices (Baumann, 1960). Others species were originally exploited for different organs than their current cultivated forms. For example, the carrot was first cultivated for seeds that were used as both a spice and a medicine (Simon, 2000).

Comparisons between early and current crop uses identified dynamic, persistent and interconnected uses. In the dataset, 62% of the crops exhibit more current uses than early uses. This may reflect the paucity of sources on early uses for many crops, but may also reflect ongoing domestication efforts to optimize utility. The largest increases were observed in the alcohol, fodder and cosmetic use categories; each category was nearly double the early use value. Fuel or oil, poison, food, and fiber increased over time as well, but to a lesser extent. Only two categories had fewer current uses than early uses: currency and ritual use. Despite these shifts in use, a high degree of continuity between the early and current uses of most crops is noticeable. This is supported by LF results (Table S5).

We hypothesized that shifts in the primary use organs of a crop would cause changes in other organs, and further, that there would be a correlation between some organs used for food and nonfood uses of other organs. We found that plants with edible seeds were positively associated with use as fiber, and crops with a domestication syndrome trait of seed retention were associated with use of leaves and use as fiber. Therefore, results suggest that over the course of domestication for nonshattering grains, nonfood harvest residues were adapted for other household uses, such as fiber, and then later as fodder when animal husbandry and domestication followed cultivation of grasses in many regions (Clutton-Brock, 1989; Verhoeven, 2004; Vigne, 2011). Fiber crops showed the least difference between early and current

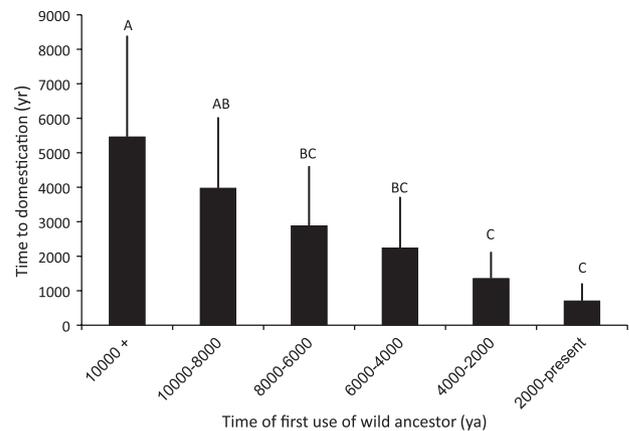


Fig. 5 Mean time to domestication (+ SE) for crops, as a function of the 2000 yr time period when the first use of the crop wild ancestor was recorded. Sample sizes for the different periods are, from left to right: $n = 40$, $n = 16$, $n = 15$, $n = 32$, $n = 23$, $n = 10$. Letters denote significant differences between 2000 yr periods based on results of a one-way ANOVA ($F_{5,138} = 17.79$, $P \ll 0.0001$) and pairwise comparisons using Tukey's HSD. There is a clear, progressive decrease in mean time to domestication, in particular between crops domesticated 8000 yr ago (ya) or more and more recent crops, indicating more rapid fixation of domestication traits, even though not all 2000 yr time periods are significantly different from one another.

use categories: 71% of crops with early uses for fiber are still used for fiber, suggesting that the discovery and reliance upon these useful materials (e.g. for rope) happens early in the selection process, and that this use remains important over time. Some of the earliest domesticated fiber plants, such as flax, cotton, and hemp, are still important in the global textile industry despite the emergence of synthetic alternatives.

The connections between food and medicine are well documented and many cultures do not distinguish explicitly between these two uses (Balick & Cox, 1996; Pieroni & Price, 2006). The prevalence of medicinal uses is strongly reflected in the crops we sampled: 69% of the food crops are currently used for medicinal purposes, and 59% were used as medicine early in their exploitation history, although this figure is certainly underrepresented as a result of limited information regarding early medicinal use (Table 2). A small number of crops (14%) were initially used as medicine but only later incorporated into the diet as a food; such histories illustrate the multiple values of food plants to our health aside from providing basic nutrients. These crops are predominantly spices such as annatto, bay laurel, clove, ginger, sage, and turmeric, or stimulants including kola, guarana, and tea. There is evidence that organoleptic preference for flavoring food in different cultures was developed in conjunction with the health needs of the people (Sherman & Hash, 2001; Nabhan, 2004). In addition, the strong correlation between medicinal and ritual uses in both early and contemporary eras points to the high cultural value of medicinal foods (Table S6).

XI. Conclusions

This review is an effort to consolidate, analyze and interpret available information on crop domestication in order to quantitatively

understand the changing traits, uses and geographic distributions characterizing a wide range of crop plants in various stages of domestication. The patterns detailed in this review support some established models and theories, contradict others, and identify recent trends in crop domestication as well as knowledge gaps. Because these conclusions are based largely on correlations across a large dataset, our intention is primarily to identify promising directions for further research, rather than to draw definitive conclusions regarding specific pathways and mechanisms of crop evolution. Conclusions and perspectives from this analysis include the following:

- Reliance on a small number of model crops, especially grasses, identifies trends in domestication syndrome traits that may be exceptions rather than rules. Loss of shattering, transitions from outcrossing to self-fertilizing, and ploidy changes in sexually reproducing crops are observed less frequently than expected.
- The marginality model, by which crops are domesticated after removal from their native range, is not common (12%), and many of these cases are recent domesticates produced by agricultural research centers.
- Multiple origins have been proposed for only a small subset of this dataset (19%), and these events are associated with trade networks, and range of the ancestor.
- Trees were domesticated in two waves, associated with increases in ploidy and shifts to vegetative propagation strategies.
- Trees were domesticated at a slower rate, and exhibit significantly fewer domestication syndrome traits, compared with annuals.
- Domestication syndrome traits vary by center of domestication, corresponding in part with local climates and plant life cycles.
- Suites of domestication syndrome traits differ between crops with surprisingly few common patterns, perhaps because of different temporal, geographic, and evolutionary factors.
- The most common domestication syndrome trait is changes to secondary metabolites affecting flavor, pigments and toxicity.
- Centers of domestication exhibit fluctuations in domestication activity over time, often corresponding with factors such as the expansions of major civilizations and increased trade.
- Decreasing intervals between initial exploitation of the wild ancestor and the appearance of domesticated forms demonstrate an ongoing trend towards more rapid fixation of domestication traits.
- A large proportion of global food crops (69%) are currently used medicinally.
- There are major gaps in the literature for many crop species, particularly with regard to ancestors, region of origin and domestication dates.

Crop varieties and wild relatives, while increasingly threatened by progressive climate change, habitat loss and agricultural intensification, can help to provide the genetic diversity necessary for adapting to future climate risk and meeting food security needs (Fowler & Mooney 1990; Jarvis *et al.*, 2008). This diversity can be secured through complementary *in situ* and *ex situ* conservation strategies (Fowler & Hodgkin, 2004; Mercer & Perales, 2010; Bellon *et al.*, 2011; Jensen *et al.*, 2012). Currently, many

research efforts are expanding the genetic base of our major food crops by incorporating new traits from a number of sources with an emphasis on using and conserving the gene pools present in crop wild relatives (Doebley, 1992; Gepts, 1993; Haussmann *et al.*, 2003; Meilleur & Hodgkin, 2004; Brown & Hodgkin, 2007; Sadiki *et al.*, 2007).

In North America alone, an estimated 3–5000 species of wild plants were once used as food, but today 90% of the world's food needs are met by just over 100. (Fowler & Mooney, 1990; Prescott-Allen & Prescott-Allen, 1990). The cultivation and commercialization of neglected and underutilized species is increasingly recognized as a viable development strategy with benefits such as managing climate risk, enhancing agrobiodiversity and improving rural livelihoods (Padulosi *et al.*, 1999; Williams & Haq, 2002; Giuliani, 2004; Wil, 2008). The compilation of available information regarding crop use, domestication history, and wild relatives can help to guide both *in situ* and *ex situ* conservation efforts to maintain diversity. Comprehensive knowledge of the state of agricultural biodiversity, along with the historical trends that have shaped and driven it, is critical in guiding our efforts to promote, conserve and utilize our rich heritage of global food crops.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 Online databases accessed to supplement crop information from the literature (updated periodically at www.cropdomestication.com)

Table S2 Literature cited for each of the 203 reviewed food crops (updated periodically at www.cropdomestication.com)

Table S3 Definitions, rationales and abbreviations used for coding categories and subcategories

Table S4 Boolean matrix of domestication data for 203 food crops (updated periodically at www.cropdomestication.com)

Table S5 Annotated matrix to supplement the Boolean matrix of domestication data (Table S4) with more specific dates for plant exploitation and domestication, life cycle, ploidy, and geographic center of domestication (updated periodically at www.cropdomestication.com)

Table S6 Searchable and sortable heat map of Logic Forest importance values

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