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**How the Neolithic Revolution Has Unfolded:  
Invention and Adoption or Change and Adaptation?  
Addressing the Diffusion Controversy about Initial Domestication**

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***Abstract***

It is widely agreed that initial domestication of plants and animals can be considered as the major innovation underlying the Neolithic revolution. There is however a controversy about how it has unfolded. One view supports it was an invention with subsequent adoption, and stresses the role of human intention in a rapid transition, geographically focused. The other view contends it was change and subsequent adaptation, and highlights the role of chance and co-evolution in a protracted and spatially diffused process. Thanks to recent developments of archaeobotany and archaeozoology, we evaluate both views and conclude that the latter is more relevant.

**Keywords:** domestication, origins of agriculture, Neolithic revolution, innovation, diffusion controversy.

**JEL codes:** N50, O30, Q10.

## 1. Introduction

The Neolithic revolution has attracted the attention of scholars for decades and is still at the center of several controversies (Svizzero, 2017a). Most contributions have been on either the causes of the advent of agriculture, or its consequences (Svizzero and Tisdell, 2014a). Both questions are in fact multidimensional. For instance, the Neolithic revolution has had several and various consequences, such as on the level of human population (Bocquet-Appel, 2009), on sedentism and the gradual disappearance of the hunting and gathering way of life (Svizzero and Tisdell, 2015), on surplus and social stratification (Svizzero and Tisdell, 2014b; Tisdell and Svizzero, 2017a), to say the few. Similarly the causes of the Neolithic revolution have been labeled in different (but quasi-similar) ways, such as "origins of agriculture" (Price and Bar-Yosef, 2011), or "the transition from foraging to farming" (Weisdorf, 2005), or "the neolithization process". This is because any attempt to consider the "causes" of the Neolithic revolution is automatically leading to different but overlapped queries such as "why", "when", "where", and "how", and authors give various relative importance to these previous queries. What is certain is that the "why" question has attracted more attention than the others, maybe because it is more elusive and therefore more suitable to diverse interpretations. Symmetrically, the "how" has attracted less attention than the other questions (Gopher et al., 2001), maybe because studying how the Neolithic revolution has unfolded is different (even though it is related) than studying the causes *per se* of this revolution. For instance, when surveying economic models of the transition to farming, Weisdorf (2005: 568) pointed out that *"Two aspects are common to nearly all the contributions. First, how agriculture was invented is generally not an issue."*

### ***Domestication and the Linear Model of Innovation***

In the academic literature, what is widely acknowledged about the "how" question is that the advent of agriculture was a revolution since major changes have occurred (Childe, 1936). As such it can be treated like more recent revolutions, such as the industrial revolution (from the eighteenth century) and the information-communication current revolution. These recent revolutions highlight the role of innovation (i.e. technological change in the present cases) and can be described, for instance, through a sequence consisting in three stages, invention-innovation-diffusion (also called "the linear model of innovation",<sup>1</sup> Godin, 2017), a sequence

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<sup>1</sup> Although the "linear model of innovation" has been heavily criticized in the academic literature and that other more elaborated models exist, we still refer to it because it is simple, and also it is still widely used (e.g. by the OECD).

already highlighted by Schumpeter (1939) in the economic literature. For the Neolithic revolution, it is often claimed that it can be characterized by a "Neolithic package" including four components: sedentism and houses, craft specialization (including pottery), polished and ground stone tools, and agriculture (based on domestication of plants and animals) (Verhoeven, 2011: 77). Of course the latter component is the most important. On the one hand, it means that from the Neolithic period food was produced and thus it clearly states the radical change with the pre-Neolithic way of life based on predation of wild resources. On the other hand, plant and animal domestication is technological in essence since it explains through which process people get their food. Then we claim that, to the "how" question of the Neolithic revolution, the usual (and implicit) answer present in the academic literature considers the domestication of plants and animals as (the main) technological change of this epoch which can be analyzed according to the sequence invention-innovation-diffusion.

Broadly speaking, an "invention" refers to the occurrence of an idea for a product or process that has never been made before. In the present case, pre-Neolithic people were all foragers, i.e. they used various techniques (hunting, fishing, gathering...) for their food procurement but they did not produce their food. Using domesticates - plants and animals - through cultivation and husbandry in order to produce food resources is a process that had never been made before the Neolithic (by definition of the latter). Furthermore, an "innovation" implies the implementation of idea for product or process for the very first time. The moment of innovation is the time when technological change has become widespread and embedded within communities (Van der Veen, 2010: 7). When, from the Early Neolithic, people have started to adopt farming and to abandon (or decrease their reliance on) foraging, they have contributed to the practical implementation of a new idea, i.e. that using systematically (and not experimentally) domesticates to produce food resources was an alternative strategy for feeding the population. Finally, this innovation has been diffused, i.e. used on a larger scale, both in biological as well as in spatial terms. Indeed, beyond the 'classic' eight 'founder crop' package (einkorn wheat, emmer wheat, barley, lentil, pea, chickpea, bitter vetch, and flax) and the four domesticated animals (sheep, goat, cattle and pig) underlying the emergence of agriculture in the Near East, domestication has been subsequently extended to other species (e.g. perennial trees, chicken). This new technology has also spread geographically, towards new regions (and new biomes), such as Europe and the Indian subcontinent, when the southwestern Asian center of domestication is considered.

## *The Diffusion Controversy*

During the last two decades advances in archaeobotany and archaeozoology have increased our ability to detect the context, timing and process of domestication in a wide array of different plant and animal species around the world (Fuller, 2007; Larson et al., 2014; Zeder, 2006, 2012, 2015). These advances have therefore provided answers to the "how" of the Neolithic revolution (for recent surveys, see e.g. Meyer et al., 2012, and Langlie et al., 2014). They have at the same time shown that the linear model of innovation could be interpreted according to two alternative views. Both views are clearly opposite when one considers the diffusion stage of the sequence. Indeed, the diffusion can be viewed as a simple imitation of the original invention, i.e. an adoption of the innovation by new people/regions. This is, for instance, how Schumpeter (1939) considered the diffusion when he dealt with innovation in an economic perspective. On the contrary, the diffusion of an innovation can lead to adaptation (to a new environment, broadly speaking), and thus to re-invention. The opposition of both views can then be labeled "the diffusion controversy" and is in fact quite common in social sciences. For instance it was already present among late nineteenth anthropologists (e.g. Boas, 1896) about the origins of "civilization", or more precisely about what was the process behind progress? (Godin, 2014). Such "diffusion controversy" is nowadays also present about the Neolithic revolution, or more precisely about the initial domestication. The latter, as any agricultural innovation, can indeed be viewed as, either invention and adoption, or change and adaptation (Van der Veen, 2010).

When domestication is considered as a process of invention and (diffusion through) adoption (Abbo et al., 2012; Abbo and Gopher, 2017), it therefore stresses the importance of human intention (Abbo et al., 2014a), the rapidity of the process, considered as a "one-event" (Hillman and Davies, 1990), the geographical focus of the process to a unique center or "core area" (Lev-Yadun et al., 2000; Abbo et al., 2010), and its implementation to several species roughly at the same time, i.e. to the so-called founder crop and animal package.

On the contrary, when domestication is viewed as the result of change and adaptation (Asouti & Fuller, 2013, Fuller et al., 2015), human intention is reduced since the process results from the entanglement of culture and nature (Fuller, 2010; Fuller et al., 2010). Moreover the domestication process is slow or protracted, due to a long period of pre-domestication cultivation during which wild plants were cultivated and wild animals were tended (Gepts, 2004; Tanno & Willcox, 2006; Fuller, 2007; Purugganan & Fuller, 2009, 2011); it has

multiple origin centers (Willcox, 2005; Brown et al., 2009; Fuller et al., 2011), and only one or few species were domesticated at the same time.

### ***The Place and Role of Human Behavior***

The aim of the present paper is to evaluate both views of initial domestication, i.e. should we consider it as an invention followed by adoption, or as change and adaptation? By doing so we also emphasize the place and the role of human behavior since it is central in any innovation process. Indeed, it is human behavior, through its decisions and the following up actions, which controls the occurrence of each stage of the domestication process of plants and animals. Such micro-founded approach finds support in the recent developments related to the origins of agriculture, the latter contrasting with early explanations. Indeed early explanations (the oasis hypothesis, the natural habitat hypothesis, the population-pressure hypothesis, the edge hypothesis, the social competition hypothesis, and more, Price and Bar-Yosef, 2011) had a common thread since they all stressed one main explanation which in addition was defined at a macro level (e.g. climate change, population pressure, social competition), i.e. human behavior was implicit or secondary in these early theories. By contrast more recent developments have focused on multi-causal factors and on micro-founded approaches (Gallagher et al., 2015; Svizzero, 2016, 2017b). Indeed, Human Behavioral Ecology has given rise to two distinct approaches, Optimal Foraging Theory (including the Diet Breadth Model, Winterhalder and Kennett, 2006) and Niche Construction Theory (Smith, 2007; Zeder, 2016, 2017). Although they are different, both approaches consider that human behavior (human's decisions and actions) is at the center of social evolutions such as the Neolithic revolution.

Throughout this paper, and beyond its central question previously presented, we also have to focus our attention on the role and place of human behavior. Indeed, even though the label "innovation" is assumed to be relevant in order to describe the Neolithic revolution, to which extent the initial domestication of plants and animals results from human's decisions? Were these decisions taken consciously or not with respect to their consequences on the domestication process? Even though decisions were intentional, have they systematically led to the desired outcome? If human behavior is considered to be at the center of the domestication process, what was the goal(s) of Neolithic farmers and which pathway(s) has finally led to the domestication? Recent developments of archaeozoology and archaeobotany

related to initial domestication of plants and animals allow us to shed new light on how the Neolithic Revolution has unfolded, and thus to provide answers to the previous queries.

## **2. Domestication as a Milestone of the Human-Environment Ongoing Interaction Process**

In the academic literature, most authors (if not all) agree that the Neolithic revolution cannot be considered as an invention. However, and according to the previously given definition of invention, the reasons they provide are not fully relevant. Let us for instance consider two quotations related to this rejection:

Weisdorf (2005: 568) states, about the economic literature on the Neolithic revolution, that : *"First, how agriculture was invented is generally not an issue. Regardless of whether this is explicitly stated, all articles seem to agree (...) that the first domesticates 'probably appeared near latrines, garbage heaps, forest paths and cooking-places where humans unintentionally had disseminated seeds from their favourite wild grasses, growing nearby'."*

Diamond (1997a: 105) states that *"What actually happened was not a **discovery** of food production, nor an **invention**, as we might first assume. There was often not even a conscious choice between food production and hunting-gathering. Specifically, in each area of the globe the first people who adopted food production could obviously not have been making a conscious choice or consciously striving toward farming as a goal, because they had never seen farming and had no way of knowing what it would be like."*

Both quotations deny to consider the initial domestication as an invention because they assume it was an unforeseen outcome and the unintended consequence of human behavior.<sup>2</sup> Even though they both are probably right, they however do not demonstrate that it was not an invention; in fact what they claim is that it was an unforeseen invention. In other words, even though an outcome is unforeseen/unintended, it should be considered as an invention if it is new compared to what existed previously. If we want to reject the domestication as an invention, we have to show that it has not led to a product or a process that had never been made before.

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<sup>2</sup> As claimed for instance by the dump heap hypothesis.

If, as previously highlighted, we "restrict" the Neolithic revolution to its hallmark, i.e. the initial domestication of plants and animals, then it is possible to demonstrate that the latter was not an invention but a simple milestone in the human-environment ongoing interaction process. Indeed, as clearly stated by Niche Construction Theory (NCT) (Odling-Smee et al., 2003; Smith 2007; Zeder, 2016, 2017), humans have always interacted with their environment (living species and landscapes), modifying and shaping the latter in order to satisfy their needs. This interaction is as old as humans are and it is a never-ending process. What characterizes this process is that human domination of the nature is increasing with the passage of time. Along this process some events or periods can be, at first sight, considered as revolutionary or as an invention, such as the fabrication of (stone) tools (by *Homo habilis*), the mastery of fire (by *Homo erectus*) and the domestication (by *Homo sapiens*). However such view must be qualified. Indeed, the common feature of these three previous examples of "invention" is that it was a protracted process, i.e. a slow and gradual evolution in which the time of invention can hardly be identified. Let us consider stone tools for instance. During the Lower Palaeolithic and before the appearance of *Homo habilis*, people have used stones for various purposes (e.g. for breaking nuts, as some apes still do); however these stones were not tools. Indeed, in order to be considered as tools, stones have first to be shaped by humans and then to be used for some purposes. According to archaeological records, the oldest stone tools in the life span of the genus *Homo* are provided by the Oldowan industry. These tools were very simple (compared for instance to tools of the Acheulean industry) but they were already more elaborated than stone tools found in Africa and that predate the genus *Homo*. In other words, stones have been used and also shaped as tools for a very long time. It is thus impossible to determine when the first stone tools have been created; considering the creation of stone tools as an invention is a pure convention which is quite often present in the academic literature. The same conclusion holds for the domestication of plants and animals. Indeed human have always tried to modify their environment and this has led to a protracted process of evolution. Many authors have tried to present such evolution as a succession of stages but since the process is very long and continuous, these stages also appear as a pure convention. For instance Harris (1989) classic model of evolution considered four stages, consisting in (1) foraging, or wild food gathering and hunting, (2) cultivation of wild plants, or pre-domestication cultivation, (3) systematic cultivation of wild plants, and (4) agriculture based on domesticated forms. However, and as pointed out by Abbo et al. (2012: 244), Harris (2007) revised his 1989 model and depicted three (rather than four) modes of food procurement and production. These are: wild-food procurement (foraging), wild food



production (pre-domestication cultivation) and agriculture (based mainly on domesticated crops). The previous example shows that the boundaries between stages are always blurred, and therefore the number of stages can vary according to the topic the author wants to stress. Such feature comes from the fact that the human-environment is a continuous and long-term process and therefore it is impossible to identify without ambiguity turning points, and *a fortiori* inventions. In other words, the domestication was not an invention but should be considered as a milestone of the human-environment interaction process. As we did previously for stone tools, let us now illustrate such claim by the evolving relationships that human have had (and still have) with (wild and then domesticated) cereals.

### **3. Change Rather than Invention: An Illustration through Human Interventions in the Life Cycle of Wild Cereals**

As most of the plants existing nowadays, cereals have appeared in their wild form from the end of last Ice Age. Although they were not ubiquitously present on earth, it is very likely that in places where they were present, people had consumed them. This is for instance what the (Terminal Pleistocene, Upper Palaeolithic) 23,000 years old site of Ohalo II indicates (Nadel et al., 2012). Thus, before the Neolithic and even the Epipalaeolithic, such consumption has necessarily led to some interaction between people and cereals. Such interaction could have had first unintentional consequences; for instance when gathering some ears rather than others, because their shape or color was more attractive. However such interaction has evolved towards a form of management of wild cereals. Weeding, eliminating plants competing for sunlight (or shadow) or water, irrigating by channeling water (...) can all be considered as proto-agriculture actions (Pryor, 2004). All these human actions, and even simply reaping ears, are leading, intentionally or not, to selective pressures which affect the evolution of plants (of cereals in the present case). In other words, the domestication process is as older as the human-environment interaction and since it is a continuous and long-term process, it is vain to try to identify precisely when and how it has started.

Given the previous conclusion, one may however argue that from foraging to farming, there is a turning point, i.e. when people have "invented" how to sow seeds. Once again we may demonstrate that this alleged turning point is in fact a simple milestone of a continuous process. Indeed, and still by considering the relationship human have had with wild cereals, we may claim, based on archaeological records, that pre-Neolithic foragers already had a

perfect knowledge (i.e. similar to the Neolithic farmers' knowledge) of proto-agriculture activities (weeding, irrigating..), harvesting techniques (beating basket, ground collection), and processing stages (threshing, winnowing, pounding, grinding, as testified by grinding stones, mortar and pestles found on pre-Neolithic sites). What seems to be the "big" difference between foragers and farmers is then about sowing. Let us first consider what happens in the wild, i.e. without human intervention. Wild cereals have spikelets (or panicles) which shatter when they are fully ripe. Even though most of the spikelets that have shattered are predated (by insects, rodents and birds) or get moldy, due to their morphological features, the remaining are self-burying into the soil. After a variable period of dormancy (several months or more), and according to natural influences (about temperature, moisture), the seeds are germinating, leading to seedlings, and after few months to ears. This is the life cycle of annuals wild grasses, which can be perpetuated forever (if natural conditions remain suitable) without human intervention. What happens now when human intervene? In this life cycle, harvesting is the essential human intervention, compared to the pre-harvesting as well as the post-harvesting activities. However, several harvesting techniques are possible (basket beating, uprooting, hand-plucking; Hillman and Davies, 1990), including the ground collection of seeds (Kislev et al., 2004). When pre-Neolithic foragers have collected seeds from the ground, they may have noticed that the more they collected the seeds, the less the next harvest would be.<sup>3</sup> In other words, they may have understood that during their dormancy period, the self-buried seeds were naturally "stored" into the soil for the next year. Thus, by deciding the ratio of the spikelets (present on the ground or that had not yet shattered) they harvested, the foragers also decided implicitly how much seeds would be (naturally) sown. The "production" of wild cereals was therefore under human control before domestication, and even before cultivation has occurred. What they may have noticed next, is that rather than leaving some seeds naturally stored into the soils, they could gather and store themselves these seeds in order to be sown subsequently. These human interventions have not modified the nature of the wild cereals life cycle. What has been modified, is a matter of degree or scale, but not a matter of nature or kind. Indeed, human interventions have allowed, on the one hand that a larger ratio of shattering spikelets can be stored for next sowing (this is a reduction of natural predation) and, on the other hand, that the next sowing can reach new plots of land (beyond the plots of land that can be reached in a short period of time by natural spread of seeds, such as through wind dispersion or animal propagation). For wild cereals, it

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<sup>3</sup> The same observation could have been deduced from hunting mammals belonging to a given herd: beyond a given rate of predation, the herd disappears.

is therefore the scale of the "production", as well as its spatial range, which have been modified by human interventions, and both modifications cannot be considered as inventions.

#### **4. The Domestication Syndrome: a Relative Concept**

A (large) number of authors have suggested definitions of domestication over the years but there are still no widely accepted meanings (Price and Bar-Yosef, 2011: S165) and there exist various definitions of domestication (for a complete review see Zeder, 2006, 2015). As pointed out by Larson and Burger (2013: 198, Box 1), "*Because domestication, similar to any evolutionary process, involves long-term and continuous change, the use of static terms is arbitrary and domestication definitions are almost as numerous as species definitions*". However all definitions of domestication, whether dealing with plants or animals, recognize that domestication involves a relationship between humans and target plant or animal populations.

The domestication of plants and animals resulted in countless forms and varieties, adapted to all kinds of environments and climates. Although plant and animal breeding created such a diversity, even among domesticates which descent from a single wild progenitor, many traits are shared by all of them. Because the types of selected traits were similar across different species (plants and animals), this has given rise to the concept of the domestication syndrome (Hammer, 1984). It can be defined as the characteristic collection of phenotypic traits associated with the genetic change to a domesticated form of an organism from a wild progenitor form.

Despite the different pathways that may lead to animal domestication, the occurrence of phenotypic alterations associated with domestication in animals is often similar in diverse and unrelated groups. In mammals, the 'domestication syndrome' (Zeder, 2012) is defined by the following features: increased docility, increased skillfulness in using human cues (gestures and glances), increased fecundity, reduction of tooth size, shortening of the rostrum, reduction of brain size, floppiness of the ears, curliness of the tail and depigmentation of skin and fur.

The domestication syndrome differs for different kinds of crop plants, according primarily to how they are reproduced, by seed or by cuttings, and what plant organ is the target of selection (grain, fruit, tuber) (Harris and Fuller, 2014). Harlan and his colleagues (1973) belong to the first who summarized common features of the domestication syndrome for

cereals. For grain crops, the domestication syndrome usually includes six morphological and physiological traits which are today well defined (Fuller, 2007): reduction/elimination of natural seed dispersal, reduction in seed dispersal aids, loss of germination inhibition, increase of seed size, synchronous tillering of plants and ripening of seeds, more compact growth habit.

The previous definitions, concerning animals as well as plants, clearly shows that the domestication syndrome is a relative concept. Indeed, all traits associated with the syndrome are relative, such as for instance "the increase of fecundity", or "the increase of seed size". In other words, although the domestication process has led to the increase of grain size for crops, it has been a continuous (and long-term) process; it is therefore impossible, by studying some grain crops provided by archaeological excavations, to determine precisely whether these grains were domesticated or not, and thus to say whether an invention has occurred. In fact the domestication syndrome - and therefore the start of the Neolithic revolution - does not defined a threshold or a turning point (that will be needed to demonstrate the existence of an invention) but is a pure convention among scientists. Moreover several scientists consider the domestication syndrome as an ill-defined concept. Some consider that it is necessary to establish additional identification criteria (e.g. for domesticated emmer wheat; Weide, 2015). Others (Abbo et al., 2014b) introduce the concept of 'crucial domestication traits', defined as traits imperative for domesticating a plant and necessary for its cultivation. They propose that only traits showing a clear domesticated-wild dimorphism represent the pristine domestication episode, whereas traits showing a phenotypic continuum between wild and domesticated gene pools mostly reflect post-domestication diversification.

## **5. Domestication as a Trial and Error Process**

Even though we have demonstrated in the previous section that domestication could not be considered as an invention, let us assumed (for demonstrating purpose) it could be. According to the linear model of innovation, the question is therefore about the next stage of this model, i.e. when the invention ceases to be experimental and is implemented, i.e. is considered as an innovation. Under such scheme, the invention is considered as a "success story", i.e. it becomes an innovation when it meets its market.

### ***Compared Productivities Support Change Rather than Innovation***

Such view is present in the academic literature about the transition from foraging to farming (North and Thomas, 1977; Smith, 1993; Diamond, 1997a; Weisdorf, 2005). Indeed it is often assumed that people who were late pre-Neolithic foragers and early farmers were able to compare the productivity of their labor associated with either foraging or farming, and to choose which activity (predation or production) was the more productive to get food resources. Even though both activities could have coexisted for a while in mixed economies (Smith, 2001), and except some rare cases of reversion to foraging (Smith, 1993; Bellwood and Oxenham, 2008), it is usually assumed that farming (i.e. the use of domesticates) has been progressively adopted by formerly hunter-gatherers. In other words, due to its superiority (measured in terms of labor productivity), domestication has been adopted (and thus has ousted foraging), i.e. has met its market and then can be considered as an innovation.

The previous view must however be challenged for various reasons. There are chronological and methodological flaws in such narrative. Indeed, it is as if late foragers were able to compare two systems and thereafter to choose the better, while at the very beginning of cultivation domestication was unknown for them (and thus was not a goal). Moreover, and as shown by Tisdell and Svizzero (2017b), it is likely that, due to the ubiquity of sharing in their society, foragers used average productivity in order to assess any economic system while farmers based their decision on marginal productivity of labor. Moreover, and beyond these chronological and methodological problems, it is unclear that in its Early Age farming was more productive than foraging. Some authors (Bowles, 2011; Barker, 2011) have used archaeological and ethnographic data to demonstrate the superiority (in terms of productivity) of foraging, or similarly than a higher productivity was not a necessary condition for farming to occur (Gallagher et al., 2015). Other authors (Diamond, 1997b; Berbesque et al., 2014) have used indirect evidence - such as the health (stature) of foragers compared to early farmers - to reach the same conclusion.

### ***The Lack of Pattern in the Domestication Process***

Recent developments of archaeobotany and archaeozoology tend to support the same conclusion, i.e. that in its Early Age farming was less productive than foraging and therefore that its hallmark, domestication, cannot be considered as an innovation. In other words, the commodification of domestication (considered as an invention) was not a success story as it should be required for the latter to be considered as an innovation, but was more likely the

outcome of a trial-and-error process. Let us illustrate this claim by considering how some Near-eastern species (plants and animals) have been domesticated or not.

Indeed, early farmers have tried to domesticate some plants (e.g. *Vicia peregrina*, rambling vetch; Melamed et al., 2008) and animals (e.g. gazelle ; Zeder, 2016), but after a while, and for various reasons, they have abandoned, even though some of these species (e.g. *Gazella gazella*, the mountain gazelle) were dominant in the diet of (e.g. Levantine) pre-Neolithic hunter-gatherers. Conversely, some plants (e.g. *Vicia faba*, Faba bean; Weiss, 2012) and animals (e.g. *Sus crofa*, pig) have been domesticated and extensively consumed (until nowadays) but we still do not know exactly how (when and where) it has unfolded. While the Near-eastern wild progenitors of crops were cultivated from the very beginning of the pre-domestication period (and by the same groups of cultivators), their domestication has occurred for some of them after two to four millennia (e.g. emmer wheat, einkorn, barley; Larson et al., 2014: 6142), while for others (rye, oat) it was several millennia later that domestication occurred, in Europe (Weiss, 2012). Moreover it seems that the latter species had been domesticated early (in the Near East) and possibly several times (chronologically), but that their domestication had been lost after a while. To some extent, the fact that some animals get feral, i.e. return to the wild after their domestication, can be viewed as a failure of the domestication process. Even in the food-production Neolithic package, there is among species an important diversity concerning the pace of domestication as well as the ordering of traits occurrence. For instance, the increase of seed size occurred before the loss of shattering for cereals, whereas it was the converse for legumes (Fuller, 2007). Variability of the pace of domestication was also present within species (e.g. for cereals; Allaby et al., 2017). While the fruits of some wild perennial trees (fig, almond, olive, grape) were consumed as much as wild cereals and pulses long before the Neolithic (as demonstrated from Ohalo II; Snir et al., 2015), their domestication has occurred several millennia after the domestication of annual grasses. Indeed, for all of the woody perennial domesticates, their early domestication and subsequent spread depended completely on the ease with which the species could be vegetatively (e.g. by cutting and later by grafting) propagated (Cox, 2009; Van Tassel et al., 2010).

## **6. The Limits Induced by the Entanglement of Natural and Artificial Selection**

These examples of success and failures encountered by early farmers do not reflect the lack of rationality of the latter but rather the inherent uncertainties they were facing about the domestication process. Indeed, the evolution of plants and animals is influenced by natural selection, meaning that the individuals which are best fitted for the complex and changing conditions they are exposed generally survive and procreate their kind. This evolution is in addition also influenced by artificial selection, i.e. by selective pressures implemented by human actions in order to favor some traits, such as the supply or predictability of a food resource provided by the domesticate. Both selections, natural and artificial, are therefore present at the same time or entangled, and this may lead to undesired outcomes in various circumstances.

First, both selections may not have convergent influences and may even have opposite effects. For instance, the lack of the natural dispersal mechanism is lethal for wild cereals and legumes. Yet, since it facilitates the harvest, such trait is highly prized by human selection.

Second, when artificial selection focuses on a specific trait, it also has - as a by-product - some influences on other traits, the so-called "selective sweep" (Cox, 2009). For instance, the domestication of mammals (e.g. cattle) has led to a reduction of their body size while the aim of early breeders was to get the largest amount of meat per animal, an objective they have reached indirectly through the increase of animal fecundity.

Third, the intensity of artificial selection cannot be increased indefinitely. Early cultivators ignored that the amount of selection that a population can withstand, without dropping to unsustainably low demographic levels, is limited. Indeed selection comes at a cost in that some organisms must die before reproducing each generation for their genes to be selected against the wild-type allele, therefore causing a reduction in the overall population size (Allaby et al., 2015). Even though nowadays artificial selection associated with domestication is increasingly being considered as being similar to the process of natural selection, it is in fact different. One critical difference between the two may be the severity of the population bottleneck caused by the cost of selection that would be tolerable. In the case of cultivation, too severe a bottleneck would result in an economic collapse of the agrarian system. This result explains why agricultural expansion was repeatedly associated with collapse in new environments, shortly after arrival. Such collapses can also have been reinforced by ignorance

of Liebig's law of the minimum (1840), i.e. the fact that the growth of plants is limited by the scarcest factor (or the limiting factor).

Fourth, and even though natural and artificial selection could be fully consistent in some circumstances, some cultural practices or preferences might have actually influenced the domestication process (Asouti and Fuller, 2013). They may have worked against domestication since, for instance, the higher yields per plant provided by domestication are paid for by an added activity and labor demand. Fuller et al. (2010) consider that the threshing of domesticated cereals (featured by non-shattering spikelets), rather than wild cereals, required additional labor, and thus the domestication has led to some "labor traps". Thus it is conceivable the early cultivators strategically chose practices that worked against the morphological changes that are recognized in domesticated plants as they attempted to balance food needs and labor costs. Another example of cultural influence on the post-domestication selection process is provided by tastes, for instance the preference for sticky cooked cereals (such as glutinous rice) in east Asian cultures (Purugganan and Fuller, 2009).

## **7. Unconscious Selection and the Role of Chance**

In the four cases previously presented, it was implicitly assumed that artificial selection was intentional. However, and as pointed out initially by Darwin (1868), selection by human can also be unconscious (unintended, or also "automatic"), i.e. as resulting from human activities not involving a deliberate attempt to change the organism (Zohary, 2004). One of the most famous, but still disputed, example is about the technique used by early cultivators for reaping wild cereals (Hillman and Davies, 1990; Maeda et al., 2016). Indeed, wild cereals have spikelets which shattered when fully ripe, except spikelets present in very low frequency and associated with a recessive mutant. When the ratio of these non-shattering spikelets increases and that they become dominant in the population, the latter is considered as domesticated. When spikelets are fully ripe, if the harvester beats plants into a basket, he collects only the wild phenotype and therefore he unconsciously works against the domestication. On the contrary, if the harvester uproots the plants or uses a sickle, he collects some spikelets with the wild phenotype and all the spikelets with the domestic phenotype; in this case he unconsciously introduces a selection fostering the domestication of cereals.



The recent reevaluation of the speed of cereal domestication has led to a renewed discussion of unconscious vs. conscious selection (Abbo et al., 2012, 2014a, 2017; Fuller, 2007, 2010). In fact, as illustrated by this debate, what is important is the place and the role of human intention in the domestication process. As shown by the following definitions of domestication, such place and role of human intention are highly variable among various authors:

For Price and Bar-Yosef (2011: S165), domestication is defined by "*Morphological or genetic changes in plant and animal species.*"

For Harris and Fuller (2014), "*Domestication is most clearly defined as a biological phenomenon, that is, by traits in crops that result from adaptation to cultivation and by which they differ from close wild relatives.*" Both authors also define "*Cultivation is an activity through which humans become directly involved in the management of the lives and life cycles of certain plants.*"

Abbo et al., (2012: 242) state that : "*Domestication in biological terms, refers to the major genetically-based phenotypic features that characterize the plants selected by man (e.g., non-brittle rachis, free germination, changes in bio-rhythms, etc.). Domestication, in cultural terms, is an event/episode based on a decision and follow up action by which the active person selects certain species and particular stocks within species for growing. Thus, domestication involves obtaining desirable plants with distinct phenotypes by educated and conscious human choice-making.*"

Of course if one assumes that selection was either conscious or not, this automatically implies consequences on other debates related to domestication. For instance, with conscious selection from the early beginning of cultivation - or the superiority of "human mind", as stated by Abbo et al., (2014a) - then one has also to assume that domestication was a one event (rather than a protracted process) with one center of origin (rather than multiple centers).

However, it seems vain to try to determine whether, at a given epoch, selection was intentional or not. What seems more likely is that at the beginning of cultivation, selection was unconscious simply because early cultivators did not know what domestication was or could be, and thus it was not a goal for them. Then, with the passage of time it is likely that selection became more and more conscious. In other words, artificial selection should be

considered (as we have previously claimed for domestication) as a long-term and continuous process featured by an increasing intentionality. With unconscious selection largely present at its beginning, and still present in its later development but to a lesser extent, domestication is to a large extent the result of chance (Fuller et al., 2010), and then cannot be considered as an innovation since chance is a feature only of invention.

## **8. Diffusion by Adaptation Rather than by Adoption**

The diffusion of domestication, considered as an innovation, can be analyzed from two different but complementary points of view. First is the biological diffusion, i.e. from the founder crop and animal package to other species. Second is the geographical diffusion, i.e. the spread of farming from a domestication center (e.g. the Near East) to other regions (e.g. Europe and the Indian sub-continent). Of course both diffusions are intertwined because, for instance, the spread of farming to new regions has led early farmers to encounter new species which could be suitable for domestication. Because the diffusion process is twofold, biological and spatial, it cannot be a mere adoption or imitation of the initial domestication. Rather it is an adaptation, implying the re-invention of domestication when for instance domesticates were introduced in new biomes (e.g. the introduction of cereals in Central and Northern Europe), or when wild species - present in the same biome of the founder crop package - were subsequently domesticated (e.g. Near-eastern perennial trees).

### ***The Multiple Goals of Early Farmers***

When plant and animal domestication is under consideration, we automatically assume that the goal of early farmers was related to their diet, i.e. that they undertook domestication in order to improve the supply, the quality and the predictability of food resources provided by these domesticates. However this belief must be qualified, and by doing so we demonstrate that early farmers had multiple goals, a feature not consistent with a process of diffusion through imitation.

First, and even though they were cultivated for the human diet, some crops were not cultivated for their yield, but rather for their nutritive properties. For instance, chickpea stands as an exception among the wild progenitors of the founder grain crops since its wild progenitor (*Cicer reticulatum* Ladiz.) is a rare species reported from only locations in south-eastern Turkey. Because chickpea has been domesticated despite the difficulties implied by its

scarcity as well as the sophisticated agro-techniques its cultivation required, this leads Kerem et al. (2007) to conclude that it should be its nutritional quality which has attracted early farmers.

Second, the diet was not the only goal of early farmers, as demonstrated by the presence of flax (*Linum usitatissimum*) in the founder package, since it is a fiber crop. Similarly some plants could have been domesticated for non-diet goals, such as for medicine purpose, or for craft production (e.g. for basketry).

Third, although they were domesticated, the cultivation of some plants is remained confidential for a while for cultural reasons. For instance Barker (2011) reports that in Borneo the consumption of rice was restricted to ceremonies during several centuries, hindering its diffusion and use as a major crop.

Fourth, the first animal as well as the first plant ever domesticated were not used for the diet. Indeed, the dog (*Canis familiaris*) was the first domesticated species of animal and have special attributes, such as an inclination to bond with humans. Gray wolves, the source species, are asserted to have first evolved into dogs in East Asia c. 15,000 BP, during the latter stages of the most recent Ice Age (Savolainen et al., 2002). Since dogs have been domesticated especially during the Pleistocene-Holocene transition, i.e. by hunter-gatherers, one may surmise that it was for numerous uses since a dog could serve as a sentry that barked when hostile people or animals were approaching, and members of many breeds were able to assist in hunting. It was only in emergencies that dogs were considered as a source of meat. Similarly the bottle gourd (*Lagenaria siceraria*) is one of the oldest domesticated plants in the world - possibly the oldest. Even though its geographical origin is still disputed (Africa vs Asia), it is well established that New World peoples possessed and valued domesticated bottle gourds 10 000 year ago, before there is evidence for cultivation of any other crop (Langlie et al., 2014). Despite being bitter, the seeds and young fruits are edible. However their domestication was motivated by a goal different from the diet one. Indeed gourds would obviously have been useful as containers, rattles, and net floats.

Thus, the dog and the bottle gourd share the same background since they both have been domesticated by pre-Neolithic hunter-gatherers. Moreover they both lead to the same conclusion since they have not triggered a domestication process of other species which could have led to the emergence of an agricultural economy. In other words their domestication were both isolated innovations.

### ***The Multiple Pathways Towards Domestication***

For animals as well as for plants it is possible to identify three different pathways which have led to the domestication. Even though Zeder (2012, 2016, 2017) also identifies three pathways, we present here our own vision (a variation of Zeder's one) of these three pathways.

The first is the "proximity pathway"; it concerns animals and plants which, for various reasons and without human intention, were living in close proximity of human habitats, and such proximity has led, for some of these species, to their domestication. For animals, this commensal pathway includes, for instance the dog, the cat, to some extent the mice, and possibly the pig, i.e. animals which were attracted by the human's refuses present around human's settlements. Various plants are also concerned, such as weeds which proliferate in disturbed soils such as the neighborhood of camp sites, but also ruderal species, and plants thriving on human's refuses (according to the dump heap hypothesis).

The second is the "prey (for animals) or harvest (for plants) pathway" which, contrary to the previous one, has been initiated by human. The main idea has been first clearly articulated by Rindos (1984) who considered domestication as a co-evolving mutualism between humans and plants/animals. Indeed, the relationship between early farmers (and even hunter-gatherers) and wild species (plants and animals) was a predator-prey relationship. However this relationship has evolved and for some species, the initial predation is become a form of cooperation. However it has not necessarily led to domestication. Indeed, in order to result in domestication, a sustained, multi-generational relationship must develop from which both humans and target species gain mutual, though not necessarily symmetrical, benefits (Zeder, 2016). The eight crops and four animals of the founder Neolithic package have been domesticated according to this pathway.

The third is called the "direct pathway" because human intention to domesticate some species was clearly established from its beginning. For animals, it concerns for instance horses, donkeys and llamas, i.e. animals that have been domesticated in order to be used as beasts of burden, even though they could be used as a source of meat in some circumstances. For plants, this pathway should include perennial trees (fig, olive, grape) since the domestication of fruit crops relied heavily on the invention of vegetative propagation. Indeed, by contrast to annual plants (and their reproduction based on seeds), the vegetative propagation allows the

selection of specific traits which can be reproduced indefinitely and identically through cloning.

## **9. Conclusion**

Initial domestication of plants and animals has led to the advent of agriculture and subsequently to major consequences, mainly to the emergence of civilizations. As such it can be considered as a macro-innovation. However it is the result of an ongoing, long-term and gradual interaction process between human and the environment and therefore it cannot be considered as an invention or a discovery. It is rather the cumulative effects of small-scale changes which, under some circumstances, have led to domestication. These small changes have sometimes been delayed and some have even failed, showing that the domestication process is not an innovation, according to its usual meaning, i.e. the successful implementation of an invention, but rather the outcome of a trial and error process. The latter can be explained by the fact that artificial selection could have been hindered by natural selection and the evolutionary potential or evolvability of targeted organisms, and was partly unconscious even after the pre-domestication cultivation episode. When the domestication, considered as a technological change, has spread to new species and new regions, the early farmers were motivated by various goals and have undertaken different pathways in order to reach them. This multiplicity, of goals and of pathways, stresses that the diffusion of domestication was not a mere imitation or adoption, but rather an adaptation.

Thus the present analysis supports the view that domestication, considered as the hallmark of the Neolithic revolution, is the result of a protracted process of changes followed by adaptations. Although these changes, or number of improvements co-occurring in separate areas of the farming system, may be introduced gradually, they deserve the term revolution once they reach a critical mass such that their impact on society may be of a significant magnitude. The implications of this protracted transition are manifold. For one thing it means that over the course of a domestication process of 3000 years, social and environmental circumstances are likely to have changed. Thus, whatever motivations might have been there at the beginnings of domestication may no longer have played a role later in the process. In other words, even though it is certain that the place and the role of human behavior are central into this domestication process, the importance of human intention in this innovation process remains a matter of conjecture.

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