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Opinion

What is domestication?

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The nature of domestication is often misunderstood. Most definitions of the process are anthropocentric and center on human intentionality, which minimizes the role of unconscious selection and also excludes non-human domesticators. An overarching, biologically grounded definition of domestication is discussed, which emphasizes its core nature as a coevolutionary process that arises from a specialized mutualism, in which one species controls the fitness of another in order to gain resources and/or services. This inclusive definition encompasses both human-associated domestication of crop plants and livestock as well as other non-human domesticators, such as insects. It also calls into question the idea that humans are themselves domesticated, given that evolution of human traits did not arise through the control of fitness by another species.

Highlights

The study of domestication has seen enormous strides in recent years, but the concept of domestication has been unclear.

The core nature of domestication is as the coevolution between domesticator and domesticate.

Evolutionary and ecological studies with both human-associated domestication and non-human domesticators can help us understand the nature of this phenomenon.

Defining domestication

The domestication of plants and animals by *Homo sapiens* is thought to be one of the most important developments in the history of humans [1,2]. About 11 000 years ago, at the start of the **Holocene** (see Glossary), many human societies intensified their transition from hunting and gathering to the cultivation of plants and herding of animals, leading to the domestication of crops and livestock [1,2]. A large component of modern human culture is sustained by the plants and animals that underpin our survival, owing in no small part to the domestication of numerous species undertaken by ancestors of farming/pastoralist societies.

It has been observed that 'domestication is one of those terms…long used…[but] struggling to find a satisfactory definition' [3]. This may come as a surprise, as there is an instinctual consensus on what domesticate species are: the plants and animals found under the care of humans that provide us with benefits and which have evolved under our control. Humans, however, were not the only species associated with domestication and termites, ants, and beetles have been shown to have domesticated various fungal species (Figure 1) [4]. Moreover, the term domestication is sometimes mistakenly applied in relation to entities as diverse as **commensal** species, weeds, transposable elements, and even humans (Box 1). When one looks carefully at the concept of domestication, and how it differs from other interspecies relationships, one suddenly appreciates how the use of this term can so easily be misdirected.

There is certainly no lack of attempts to define domestication and tease apart its core characteristics and there have been several discussions on differing approaches to defining this process [3,5–10]. Previous definitions of domestication may (or may not) include: (i) the idea of evolutionary change; (ii) control of the process by humans, including the invocation of human intentionality; (iii) the concept of **mutualism**; (iv) benefits derived by humans; (v) the action of artificial selection; and (vi) enumeration of common domesticate phenotypes [3,5–10].

These past definitions have their strengths but also crucial shortcomings. Many, for example, privilege a human-centered conception of domestication [5,11], which minimizes its biological context while also marginalizing non-human domesticators [6]. There are definitions in which

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domestication is narrowly described as the control of the domesticate by the domesticator, devaluing the reciprocal nature of the ecological interaction. And for definitions that rely on a checklist of specific traits/phenotypes (referred to as the domestication syndrome) [12,13], these conflate the outcome (domestication traits and species) with the process (domestication) and are relevant to only a handful of cases.

In crafting a definition of domestication, the thoughtful analysis provided by Zeder [7], whose own definition leans heavily on ideas by Rindos and others [14–18], can serve as a starting point. Synthesizing these and other perspectives [3,5,6,8–10], a broad biological definition of domestication is that it is a **coevolutionary** process that arises from a mutualism, in which one species (the domesticator) constructs an environment where it actively manages both the survival and reproduction of another species (the domesticate) in order to provide the former with resources and/or services (Figure 2). This allows for increased fitness for the interacting organisms within the mutualistic relationship, leading to the evolution of traits that ensures the stable association of domesticator and domesticate across generations.

This biological definition has several advantages. It firmly centers domestication as an explicitly evolutionary process that arises from an ecological interaction (mutualism) [3,7,14–20]. This definition incorporates the language of fitness components (survival and reproduction) and highlights the **niche construction** role of the domesticator [21,22]. Unlike Zeder, however, it does not attribute the goal of the process as providing a more predictable resource supply to the domesticator [7], which may not be clearly applicable across all instances of domestication. Finally, this conception of domestication is agnostic to the identities of the interacting species and to the precise mechanisms by which the mutualism is established and stabilized by coevolution.

The interactions associated with domestication are similar to other mutualisms, but with two key differences. First, unlike other mutualisms, the domesticator establishes the environment where it actively controls the fitness (survival and reproduction) of the domesticate. Second, this control is exerted by the domesticator primarily so it can utilize the resources or services provided by the domesticate.

Glossary

Agriculture: a system of cultivating domesticated plants and practicing animal husbandry to obtain food, resources, and other services.
Coevolution: a process in which two or more species interact and evolve reciprocally through selection.
Commensalism: biological interaction between two species where one species gains benefits while the other neither gains benefit nor is harmed.
Holocene: current geological epoch that began ~11 650 years ago, after the last glacial period.
Mutualism: ecological interaction between species where each species derives a net benefit.
Neolithic: the latter part of the Stone Age, with a wide-ranging set of cultural developments, including the rise of agriculture, that independently arose in different parts of the world.
Niche construction: the process by which an organism alters its own (or another organism's) environment, often for their benefit, and possibly leading to evolutionary change.
Prosociality: behaviors that are intended to benefit other individuals.

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Figure 1. Examples of domestication. (Left) Humans with rice, *Oryza sativa*. (Right) Leaf-cutter ant *Atta cephalotes* carries a leaf back to its nest that will serve as substrate for its fungal crop. Left photograph by IRRI (CC BY-NC-SA 2.0), right photograph by Scott Bauer/USDA (CC BY 2.0).

Box 1. Ferals, weeds, and other peri-domesticates

A number of species are sometimes referred to as domesticated, even though their fitness is not under the control of a domesticator. In principle, these species are better understood as peri-domesticates (i.e., in the vicinity or fringe of domestication). Peri-domesticates are adapted to living in the environments provided by (or associated with) the domesticator, or are wild species that descended from domesticated taxa.

Commensal species are classic examples associated with humans, including house mice and fruit flies, and it is sometimes thought that commensality may have served as an intermediate step towards domestication [25,74]. Another category are feral individuals that were once domesticated but have left the mutualism and whose fitness is no longer under the control of the domesticator [75,76]. This process has been described as 'de-domestication' [77] and feral dogs, cats, pigs, and horses are good examples, as are fruit tree species that colonize wild areas or grow in abandoned orchards. Some feral organisms revert completely to the wild, others become commensal, and a few evolve as weeds.

Weedy species are a special case of peri-domestication, as these organisms can be considered cheaters within the domestication relationship. Weeds grow and exploit the agricultural environment developed by humans [78] and, in so doing, negatively impact the fitness of domesticated crop species by competition. Weeds can evolve from wild species, some via Vavilovian or crop mimicry [79]; examples include false flax (*Camelina sativa linicola*) that grows in flax fields [79] and the *Echinochloa* sp. barnyard grasses that compete with rice [80]. Others, such as weedy rice [81], evolve as ferals from crops. Weedy species are not confined to human-associated domestication, as attine ants have been shown to identify and remove the microfungi *Escovopsis* sp. from their fungal gardens [82,83]. In all these cases, the continued growth and survival of the weedy species depends on it evading domesticator control and their proliferation reduces fitness of both domesticator and domesticate.

One should note that there are also examples of species, such as epazote (*Chenopodium ambrosioides*) [84] and columnar cacti (*Escontria chiotilla* and *Polaskia chichipe*) [85] in Mexico, that are described as weedy, but studies suggest they have been subjected to human management and selection. Although not quite domesticate species, these illustrate how weedy species (and indeed other peri-domesticates) can become subject to increasing human intervention in their life cycles and possibly cross the threshold into domestication.

This biological conceptualization of domestication also raises the question of when to consider a species as 'domesticated' or as a 'domesticate species'. The term may be appropriately reserved for those species that have evolved to specialize in thriving under the active management of the domesticator and therefore become dependent on the latter as opposed to living in the wild. The issue, however, as to what threshold of evolutionary transformation and dependency a species must cross before they can be recognized as a domesticate, needs more scrutiny.

Human-associated domestication

Of all the examples of domestication, human-associated domestication is undoubtedly the best known, not least of which is because of its central role in the ecology of modern *H. sapiens* [1,2,23–25]. Most human-associated domestication began in earnest starting in the Holocene about 11 000 YBP, when humans in different parts of the world transformed their behavioral ecology of food acquisition from largely hunting and foraging to controlling the survival and reproduction of heretofore wild populations by cultivation, herding, and animal husbandry. This

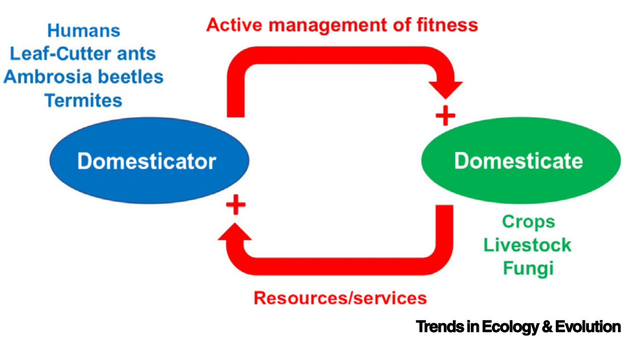

Figure 2. Domestication from mutualism. The active management of fitness of the domesticate by the domesticator ensures provision of resources and/or services by the former to the latter, resulting in increased fitness of both interacting partners (+). Examples of domesticators and domesticates are shown.

transition began the process of domestication; in food plants, for example, the annual cycles of sowing, harvesting, and processing by humans led to novel selection pressures that over the next 2000-4000 years eventually led to crop domestication [14–16,23].

It is estimated humans have domesticated about >1000 plant [26,27] and possibly around 40–50 animal (i.e., mammal, bird, fish, and insect) species [28], as well as about a dozen fungal and bacterial species [29]. While food remains the primary resource that domesticate species supply to humans, these mutualistic taxa also provide material (e.g., cotton, flax, silk) and services (e.g. sentry duty and hunting by dogs [30], transport by horses, and mouse eradication by cats [31]) to *H. sapiens* (but see Box 2).

Within the context of this mutualism there is an increase in fitness both in humans and their associated domesticate species. Interestingly, domesticate species have been thought to be biologically unfit due to their disadvantages in the wild. This overlooks the reality, however, that the wild is not the natural environment for domesticate taxa and, in its proper ecological niche (i.e., with humans), crops and other domesticates possess remarkable fitness [13,16,32]. For example, there is a massive increase in census population size and species range of domesticated *Zea mays* ssp. *mays* (maize); from its origins in the western lowlands of Mexico, maize is now planted in ~197 million hectares (ha) across the world [33]. Similarly, wheat has moved from its origins in the Near East to be planted in ~216 million ha and *Oryza sativa* (Asian rice) from the Yangtze Valley in China to ~165 million ha worldwide [33].

Human fitness has also arguably increased as a result of its relationship with domesticate species. Paradoxically, studies have shown that reliance on domesticate species have led to greater health problems in humans, possibly from more reduced dietary diversity and increased population densities [34,35]. Moreover, recent work has suggested that agricultural societies did not grow faster than contemporary hunter/gatherer groups [36,37]. This is in contrast, however, to studies that suggest a **Neolithic** demographic transition of rapid population growth following the adoption of **agriculture**, associated in part with increased human fertility by two births per woman in the transition from foraging to farming [38]. Preindustrial agricultural societies were believed to be 100 times denser than hunter/gatherer groups [39] and the latter was largely replaced by agriculturalists as they expanded around the world. Today it is estimated that there are likely only ~10 million hunter/gatherers among a human population of >7.5 billion people [40].

Domestication is evolution, it has certainly transformed domesticate crop and animal species. For cereal, legume, and some oil crops, this may include reduced seed dormancy, diminished seed dispersal, and more compact plant architectures [6,24,41,42]. In domesticate mammals, these traits include reduced aggression, changes in craniofacial morphology, and prolongations of juvenile behavior [13,43]. There is also growing appreciation that domesticate species evolve to be more attractive and desirable to their human domesticators (e.g., higher sugar content, attractive coloration), a phenomenon most pronounced in the domestication of ornamental species (Box 2). In so doing, domesticates ensure their fitness advantage in their relationships with humans [14,44].

Domestication is coevolution and there are reciprocal and correlated evolution in humans as a result of the domestication process, mostly associated with dietary changes brought about by the mutualistic association. Known evolutionary changes include adult lactase persistence in dairying cultures [45,46], increased amylase gene copy number in cereal growing societies [5,47], and other metabolic genetic modifications correlated with dietary shifts [48,49]. In the context of the mutualism with domesticate species, however, humans adapted largely by cultural

Box 2. Why domesticate flowers?

There is a long history of the cultivation of plants for ornamental purposes, in the Fertile Crescent, China, Mexico, and South America, including the maintenance of pleasure gardens [86]. Moreover, the presence of floral ornaments and plants in various tombs (including with Egyptian pharaohs 3300 years ago [87] and a Natufian grave before 11 700 years ago [88]) are indications that these ornamental plants were possibly imbued with symbolic and religious significance.

The domestication of floral crops and other ornamental species that are selected and maintained for aesthetic purposes (Figure I) presents a special difficulty in our understanding of domestication. Unlike food plants, these ornamentals are usually selected for sensory traits that include flower and/or leaf color, leaf shape, fragrance, leaf texture and variegation, and overall plant form [89]; most were domesticated only in the last 500 years [86]. The conundrum of the domestication of ornamental plants rests on why they were domesticated and what fitness advantage they confer on their human domesticators.

There are several possibilities. First, many of these may have been initially domesticated for other purposes, for food or medicine, for example, before their continued use as ornamentals [86,89]; this may explain their original use, however, but not the reason for later maintenance. Second, these ornamentals may serve as prestige goods [87] that in turn may lead to social signaling, which could aid in resource acquisition and mate attraction. Third, studies in neuroscience suggest aesthetic sensory stimuli can stimulate brain activity in the medial orbito-frontal cortex, which may have psychological and cognitive advantages [90], and flowers elicit positive psychological responses [91]; perhaps this led to fitness advantages to the human domesticators. Finally, it may be that the stimulation of pleasure responses in humans becomes a goal in itself even in the absence of fitness advantages. If true, the domestication of ornamental plants for aesthetic purposes could represent a distinct type of domestication, what one could describe as hedonistic domestication.

Interestingly, the same question could also be raised for the domestication of pet species, many of which serve as human companions but not as a source of food or other material resources. The domestication of species for these types of nonmaterial purposes need further scrutiny, including the development of biological models that can be further examined.

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Figure I. Hedonistic domestication. The painting entitled *Irises* by Vincent van Gogh, 1890. Ornamental species such as flowers were selected for their aesthetic characteristics. Irises were one of the earliest garden flowers.

evolution and have developed farming, culinary, and other traditions that are inherited across generations and diffused across human populations [8,50,51].

One distinctive feature of human-associated domestication is the role of intentionality. Certainly there is human agency and intentionality in the acts of cultivation and/or animal management, the behavioral prerequisites that lead to domestication. There is also the role of intentionality in conscious (also described as methodical) selection of specific plant and animal variants, accompanied by the deliberate intent to propagate specific phenotypes [52,53], which is also a popular feature ascribed to domestication and subsequent post-domestication evolution [23,54]. Whether Neolithic humans predicted that domestication (the evolutionary process) would occur when they engaged in farming is doubtful. It has also become apparent that unconscious (or automatic) selection [14,15,52–55], arising from domesticate populations living in an environment of human cultivation, herding, care, harvesting, and processing, also plays a strong role in domesticate evolution. Indeed, it is widely accepted that human-associated domestication during the Neolithic and later evolutionary diversification is brought about by both conscious and unconscious selection, the latter more akin to natural selection [23,54,55], and that conscious intentionality, while important, may not be all-encompassing. This has changed, however, in contemporary humans as well as more recent examples of domestication, when knowledge of genetics and evolution can bring conscious selection and greater intentionality to the process [56,57].

Insects and other domesticators

While human-associated domestications are the best-known examples, it has long been recognized that numerous other species engage in farming that has led to domestication. This is most widespread in insects, where farming of domesticate fungi has evolved independently in at least three groups: the ants (Hymenoptera), beetles (Coleoptera), and termites (Blattodea) [4].

The best-studied insect-associated domestication is that of the attine ants (subfamily Myrmicinae), which evolved between 57 and 61 million years ago, and include the leaf-cutter ants of the Central and South American tropical rainforests [4,10,58]. This monophyletic group of ants number approximately 220 species and the majority cultivate parasol mushrooms in the Leucocoprineae [58]. The ants plant sessile fungal cultivars, manage growth conditions by regulating temperature and moisture and fertilizing the fungal gardens, protect their crop from other herbivores, parasites, and disease, and harvest the cultivated fungi for food [4,58]. This coevolved domestication system has turned ants into obligate fungivores, as experimental removal of the fungal crop results in reduced reproduction and increased mortality among ants [58]. For the fungi, the ants increase their fitness relative to the free-living state by increasing their proportion across generations, providing for geographic dispersal and protecting the fungi against parasites and pathogens [58]. In the higher attine ants, the fungal cultivars are obligate mutualists and cannot grow in a free-living state [58]. It should be noted that fungi may not be the only ant domesticates; some ants tend to hemipteran insects like aphids and treehoppers in a system reminiscent of human animal husbandry [4,10].

Other examples of insect-associated domestication include the ambrosia beetles of the weevil family Curculionidae, which have also domesticated species of fungi in the orders Ophiostomatales and Microascales. Fungal farming evolved at least 14 times in the beetle subfamily Scolytinae and once in the subfamily Platypodinae, where all but two of the ~1400 species practice fungi agriculture [4,59]. There are also approximately 330 termite species in the subfamily Macrotermitinae that grow fungi from the genus *Termitomyces* as food [4,60], with a single origin of fungal cultivation in termites occurring between 25 and 40 million years ago [4].

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Beyond insects, other examples of farming hint at possible candidates for non-human domestication. The damselfish *Stegastes nigricans* manages farms of the filamentous red algae *Polysiphonia* on coral reefs, protecting them from invading grazers and weeding out other algal species [61]. There are also reports that the shrimp species *Mysidium integrum*, which are found in these damselfish algae farms, could be considered domesticated [62], although this is unlikely as the shrimp life cycle does not appear to be controlled by the damselfish. The social soil amoeba *Dictyostelium discoideum* has also been reported to farm *Burkholderia* bacteria for food [63]. The marsh snail *Littoraria irrorata* creates wounds in *Spartina* plants, where fungi grow and are consumed by the snails [64]. In all these examples, there are certain elements that may suggest the possibility of domestication or at least incipient domestication.

Are humans domesticated?

The question of whether humans are domesticated has a long history and Darwin considered this question briefly in *Descent of Man* [65]. The idea of human domestication, especially the concept of 'self-domestication', has gained momentum in recent years based on the assertion of similarities in traits between humans and domesticate mammals, including evolution of smaller body sizes, shortening of the face and a reduction in tooth size, reduced sexual dimorphism, and a reduction in cranial capacity [66–69]. More importantly, these morphological changes are accompanied by a decrease in reactive aggression and increase in docility and **prosociality** [68,69]. Finally, the concept of self-domestication has been extended to include bonobos [70].

Invoking the term 'self-domestication' as applied to humans (and bonobos) is problematic. Darwin dismissed the idea of human domestication, as he understood that humans had not been subject to the control of its fitness, which is one of the critical hallmarks of domestication [65]. Moreover, the idea of self-domestication is untenable, since domestication as a biological concept is rooted in a mutualistic interaction with another species. Finally, defining domestication based on shared phenotypic similarities is also fraught with problems, given that such similarities could also arise outside the context of domestication [71,72].

While there are some trait similarities between *H. sapiens* and domesticate animals, in humans these do not appear to have evolved as a direct result of the mutualistic interaction with domesticate species. Such phenotypic similarities may arise from parallel/convergent evolution [71,72], possibly associated with secondary effects of the domestication process (for example, increased population density or sedentism) [68,69] but arguably do not directly spring from the human/crop, human/livestock, and human/pet mutualisms. Those who have remarked on these similarities need to explore other mechanisms to explain these evolutionary convergences.

Concluding remarks

Here, I have attempted to provide a broad but rigorous biologically centered definition of this unique phenomenon. In this overarching biological conception, domestication has the following critical elements. It is: (i) an evolutionary process, (ii) arising from mutualistic ecological interaction, (iii) involves constructing an environment where there is control of the fitness of one species by another, (iv) occurs so that the domesticator can garner resources and/or services from the domesticate, (v) leads to fitness benefits that accrue to both partners, and (vi) is agnostic to the interacting species. The pace of domestication is governed by the strength of the selection exerted by the domesticator (and the environment it provides) and the genetic and ecological characteristics of the target domesticate.

This definition has the advantage that it is grounded in evolutionary and ecological concepts, first recognized by Darwin [52,53] and later on championed by others [7,10,14–25]. Like any

Outstanding questions

What are the ecological and evolutionary pathways that lead to domestication?

To what extent do the partner species rely on the mutualism for their survival and reproduction?

Does every individual domesticated organism have to impart a fitness benefit to the domesticator?

How do we determine whether a species is domesticated?

In human-associated domestication and subsequent diversification, what are the relative roles of conscious versus unconscious selection?

How do we understand domestication and selection for aesthetic traits?

definition, it struggles for both inclusivity and exclusion and there may well be cases that present some ambiguity. Indeed, domestication has understandably come to mean many other things and undoubtedly its varied usage will continue. It is expected, however, that the biologically oriented view presented here can provide a more precise conceptualization of domestication, help sharpen discussion of cases as they arise, and focus attention on major issues surrounding fundamental aspects of this phenomenon (see Outstanding questions). With a comparative, evolutionary, and ecological framework [1,2,10,16,19,26,27,73], there is an opportunity to understand the nature of this coevolution and the dynamics of this unique mutualism.

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Declaration of interests

No interests are declared.

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