



A universally applicable definition for domestication

Kathryn A. Lord^{a,b,1} , Greger Larson^c , Robin G. Allaby^d , and Elinor K. Karlsson^{a,b}

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The process of domestication is commonly perceived as a human achievement, and domestic species are typically assumed to be those under human control. Domestic species have emerged from a greater diversity of interactions than this perspective allows, and none of the many definitions proposed for domestication can readily, reliably, and consistently distinguish domestic and nondomestic populations. Here, we propose that the process of domestication should instead be defined solely as evolution of a nonhuman population in response to an anthropogenic niche and that a domestic population is one that cannot sustain itself outside of an anthropogenic niche. As a result, this definition does not require comparisons with a presumed and largely unobservable ancestor. Instead, it focuses on the observable relationship between a nonhuman population and humans. It also avoids making assumptions about how domestication happens, thus enabling an exploration of the mechanisms underlying the process of adaptation to an anthropogenic niche. By applying this definition to plants, animals, and microbes, we illustrate its utility for investigating the evolution of the relationship between humans and other species and for anticipating which species are likely to survive in an increasingly human-influenced world. Domestication is simply an evolutionary process resulting from the interaction between two species, one of which is human. As we work to protect Earth's biodiversity, this definition allows us to understand why, in response to the conditions human societies create, some species survive and thrive, while others struggle and go extinct.

natural selection | anthropogenic | biodiversity | symbiosis | extinction

People have interacted with a wide variety of plants and animals as they dispersed across the globe. However, relationships we refer to as domestic appear in the archaeological record only within the last ~20,000 y—just ~3% of our species' existence (1). Since then, our interactions with domestic species have reshaped the planet, and agriculture and rangelands now covering a third of Earth's unfrozen land surface (2). Humans, livestock, and pets now comprise 94% of the global mammalian biomass (3). Domestication underpins modern human societies and is a contributor to climate change (4, 5). Despite its enormous impact, there is little agreement regarding how to define either the state of being a domestic species or the process of domestication.

The False Dichotomy of Artificial and Natural Selection. It is often presumed that domestication is distinct from other forms of evolution. This dichotomy originated with Charles Darwin (6) who used contemporary animal breeding practices to illustrate how selection and differential survival of offspring led to shifts in measurable traits through time. While this

was a persuasive analogy for the efficacy of selection, its unfortunate legacy has been to falsely dichotomize domestication as something that occurs through a process of intentional, "artificial" selection that is necessarily distinct from the processes that shape the rest of the natural world.

Problems with Previous Attempts to Define Domestication

Most attempts to define what a domestic organism is, whether plant, animal, or microbe, are based on notions of human control, intentionality, and exceptionalism. Domestic animals are often defined as those whose lives, including feeding, hazard avoidance, and reproduction are controlled by humans (7–13), and domestic plants as those that require cultivation and human propagation (14, 15).

Most Populations Considered Domestic Are Not Under Human Control. Many agricultural plant species, including blackberries, barley, and alfalfa, are also weeds that cause economic losses and ecological damage by growing where they are unwanted (16). Large populations of dogs, cats, pigs, deer, horses, goats, and donkeys thrive despite intensive efforts to cull or sterilize them (17–20) (Fig. 1A). Free-living pigs are estimated to cause \$800 million per year in damages in the United States alone (21). While some free-living populations are established by individuals who have strayed from human control, this should not be the default assumption, particularly when the global free-living population is much larger than the controlled population. For example, between 76 and 83% of all dogs live outside of direct human control (22).

Conflating Current Utility with Historical Origin. Criteria for domestication that center upon intentionality and control are often predicated on the assumption that modern relationships between humans and other taxa are reflective of their historic relationships. Certainly within evolutionary biology, this assumption has been shown to be invalid.

Author affiliations: ^aGenomics and Computational Biology, University of Massachusetts Chan Medical School, Worcester, MA 01655; ^bMedical and Population Genetics Program, Broad Institute of MIT and Harvard, Cambridge, MA 02142; ^cThe Palaeogenomics and Bio-Archaeology Research Network, School of Archaeology, University of Oxford, Oxford OX1 3TG, United Kingdom; and ^dSchool of Life Sciences, University of Warwick, Coventry CV4 7AL, United Kingdom

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¹To whom correspondence may be addressed. Email: kathryn.lord@umassmed.edu.

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Fig. 1. Populations that thrive in areas of human disturbance. Four examples of domestic populations include (A) dogs (Image credit: G. Cimarelli), (B) house sparrows (Image credit: E. Pracht), (C) some populations of fruit flies (Image credit: D. Genereux), and (D) some populations of *Arabidopsis* (Image credit: M. Nordborg).

Presuming that the modern state of domestic populations can be applied to the process that led to them would, to paraphrase Gould, be the equivalent of conflating current utility with historical origin (23). Today, nearly all chickens are raised for consumption, but the initial stages of chicken domestication were driven not by human exploitation but by the arrival of dry rice agricultural practices, which attracted red junglefowl (24). It took more than 500 y for chickens to become part of human diets (25). This pattern of shifting relationships with domestic populations, often driven by changes in lifeways or cultural taboos, is common.

The presence of useful traits in a domestic population is not on its own evidence of intentional selection. For example, even though large grain size in plants benefits humans by increasing crop yields, an analysis of archaeometric grain measurements suggests that it is not associated with selection for yield (26). Instead, large grain size emerged from competitive behavior between seedlings in the anthropogenic niche.

Attempts to Avoid Assumptions of Control and Intentionality.

Recent pathway-focused frameworks for domestication try to avoid assumptions of control and intentionality, but still look backward from modern taxa assumed to be domestic using definitions of control. In animals, the codification of a framework that describes multiple distinct pathways for domestication (12, 27) includes a commensal pathway that explicitly allows for some taxa to be attracted to anthropogenic niches, rather than being the deliberate targets of human intention. In plants, seven distinct ecological pathways into domestication have been described (28, 29).

Some authors have proposed defining domestication within existing evolutionary processes like mutualism and coevolution (30–34). However, many populations considered domestic may not be in a mutualistic relationship with

humans. A mutualistic relationship improves the evolutionary fitness of both species when considering all aspects of the interspecies relationship (*SI Appendix, Table S1*) (35). This is difficult to prove since even if humans benefit in one way (e.g., increased food supplies), other less-noticed facets of the interspecies relationship may counterbalance this, yielding no net increase in fitness. For humans, agriculture increased carbohydrate intake, worsening dental health and leading to vitamin and mineral deficiencies (36). Farming of animals introduced new pathogens (37). The measles virus most likely emerged from a spillover of the rinderpest virus from domestic cattle into humans (38) and subsequently spread to infect nearly every human in childhood (causing short-term mortality and long-term immune dysfunction) until the advent of vaccines (39, 40).

Coevolution may be even more difficult to demonstrate than mutualism. Coevolution requires reciprocal evolutionary change in the human population in response to the evolutionary changes in the domestic population (41). For example, selection in human populations for lactase persistence, which facilitates the digestion of milk in adulthood, may be a response to cattle and camel domestication (42). However, detecting selection within the timeframe of domestication (<20,000 y), particularly in long-lived humans, is extremely difficult (43), and even when selection is detected in both species, it may not be reciprocal. The extra copies of the starch processing gene amylase in some human populations have been proposed to reflect adaptation to a starch-rich diet concurrent with agriculture, but other research shows the selection-predated agriculture by hundreds of thousands of years (44–46).

The use of coevolution as a criterion for domestication is also ambiguous since the term is sometimes used to describe a relationship that requires only cultural change in humans (12, 34, 47) rather than a biological process. Using the term

“codevelopment” instead would avoid this ambiguity (12) but does not eliminate the burden of showing a reciprocal relationship between the cultural change in humans and the evolutionary change in the domestic population.

All Definitions Require Comparisons to an Unobservable Ancestor. It is almost never possible to directly compare domestic populations to a wild ancestor. The sole exception is long-term evolutionary studies that maintain stocks of the progenitor populations. A study that selected for rapidly growing budding yeast for ~10,000 generations used samples stored at early time points to show that mutations in the adenine biosynthesis pathway confer dramatic increases in fitness that persisted over time (48). More often, the wild representative of the ancestral population is either unknown [as with yams (*Dioscorea alata*) (49)] or is extinct.

Even when a wild population is extant, it is as genetically diverged from the ancestor as the domestic population, has also evolved due to selection and drift, and is unlikely to be a suitable phenotypic proxy for the ancestral wild population. Comparisons between modern domestic and wild populations are also complicated by porous genetic boundaries. For example, modern western Eurasian pigs were initially derived from Near Eastern wild boar, but they interbred so extensively with European wild boar that they lost virtually all their Anatolian ancestry (50). In the 19th century, East Asian pigs were imported into Europe. Most commercial pigs today have substantial (>30%) ancestry from East Asian sources (51).

An alternative approach is to compare domestic populations to archaeological remains of the wild ancestor, but determining whether an organism was wild or domestic from archaeological context alone is difficult. Evidence of use is not the same as evidence of control (or mutualism). For example, only one of two genetically similar yeast strains isolated from ancient Egyptian beer brewing vessels possessed genetic changes consistent with adaptation for beer production, even though both were sampled from similar contexts, suggesting that one strain was not domestic (52). More generally, the domestication process is multigenerational and thus resists simple dichotomous characterization (53). Even the use of a wide variety of morphological, genetic, isotopic, and contextual approaches to distinguish wolves and dogs, for example, has failed to clearly establish the domestic status of early archaeological canid remains (54).

Defining Domestication Through Morphological Proxies. Some have used a suite of observable traits (e.g., animal color, size or shape, and plant architecture), collectively described as the domestication syndrome, to distinguish domestic individuals. However, numerous studies question whether the syndrome exists as a useful unifying theme (55–61). Validating the domestication syndrome requires first defining which populations are domestic, so that the syndrome traits can be compared between domestic and wild populations. Using the syndrome to define domestic populations presents a circular reasoning challenge.

Proliferating Domestication Neologisms

In the absence of a clear definition for domestication, neologisms have proliferated. We documented 13 neologisms which have collectively been incorporated into 38 distinct

definitions (*SI Appendix, Table S2*). Many attempt to address the ambiguity inherent within the terms domestic, domestication, and domesticated. If the term domestication was clear and universally applicable, there would be no need to append the word to create neologisms for specific contexts.

Many of these new terms have multiple usages. For example, usages of “semidomestic” include 1) wild populations being bred in captivity (deer mice, mango ginger, and fence-post trees) (62, 63); 2) useful domestic populations no longer under human care (feral lima beans and passion fruit) (63); and 3) populations under partial or indirect human care (reindeer, elephants, and mongoose) (64–66). Self- and autodomestication are both used to describe evolutionary change in populations adapting to the anthropogenic niche, but not under human control (67, 68). Self-domestication is also used to describe an increased frequency of alleged domestication-related traits in populations that live entirely independent of humans, such as bonobos (69), while autodomestication is also used to describe the taming through habituation of populations who normally live independent of humans, such as big-horned sheep (70). The need to adopt a neologism rather than using more conventional terminology is often unclear. “Self-domestication,” for example, is used to describe the evolutionary process of a population adapting to a new niche through natural selection (67).

These neologisms have also been applied to humans to describe behavioral evolution outside the context of a relationship with any other species. This is particularly problematic as these neologisms often carry an implied value. For example, being more (hyperdomestic) or less (hypodomestic) domestic is variously equated with either being more civilized or less fit (degenerate) (71).

A Formal Definition of Domestication

We propose that domestication be defined simply as evolution in response to an anthropogenic niche. It is the process in which a nonhuman population adapts to an environment created through human activity. Like all other evolutionary processes, it acts on individual populations. Using this definition, all self-sustaining populations of any species can be positioned on a continuum ranging from those that are wild and thrive in the least human disturbed areas, to those that require regular human disturbance (Fig. 2). In ecology, a disturbance is a temporary change in environmental conditions, and human or anthropogenic disturbance is a disturbance caused by human activity (72). Along this continuum, we propose that the term “domestic” should refer solely to those populations that are obligate synanthropes and have adapted to an anthropogenic environment to the extent that only sink populations (in which the death rate is higher than the birth rate) exist outside of that niche.

A population’s domestication status is therefore based only on its relationship with an anthropogenic niche and not in comparison to an unobservable ancestor. If a population thrives amid human disturbance, it can be classified as a human exploiter. If there is also evidence it cannot survive independently of an anthropogenic niche, it is classified as obligate synanthrope. Once a population transitions to obligate synanthrope (domestic), subsequent manipulation (e.g.,

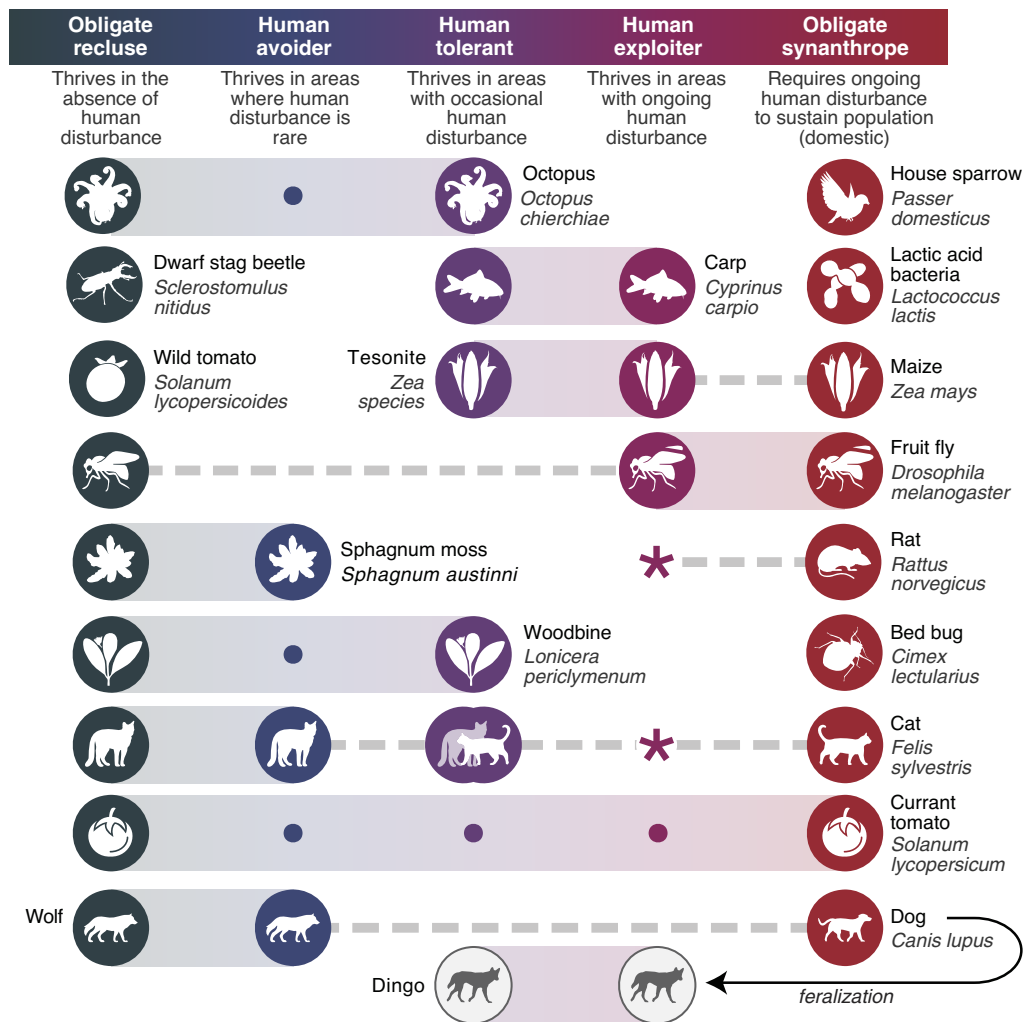


Fig. 2. The domestication spectrum. Under the new definition, populations can be categorized along a spectrum of domestication types that are defined by their relationship with the anthropogenic niche. Circles and gradients indicate where populations are observed. Dashed lines demarcate categories where no populations are observed. Overlapping circles with silhouettes represent admixture between wild and domestic subspecies. Asterisks indicate populations observed only through human translocations. Expanded version in *SI Appendix, Fig. S1*.

lab animals, breeds, and elite crop lines) does not make it “more” or “super” domestic (73) (*SI Appendix*).

This definition addresses the legacy of ambiguity and proliferating exceptions and modifications that have consistently plagued all definitions of domestication. It can be applied to any population of organisms, including microbes, plants, and animals. It eliminates the false dichotomy that has historically separated domestication and “natural” evolution, and avoids making assumptions about how the process of domestication unfolds. The only thing that sets domestication apart from other terms is that it specifically refers to those evolutionary processes that occur in response to an anthropogenic niche.

Evolution within the human context is not extraordinary; it functions just as it does in all other organisms. However, as humans, we have a particular interest in the evolutionary stories that involve us. This definition also obviates the need for qualifying the terms through neologisms, all of which can be defined either within the domestication spectrum or by existing terminology in evolutionary biology. Finally, it clarifies that domestication is not a concept that should be applied in the absence of a human-created environment or in the absence of a nonhuman organism. Humans define the anthropogenic niche and cannot be more or less adapted to it.

Assessing Domestication at the Species Level. This definition allows for domestication to be assessed within species by considering the distribution of populations along the spectrum of relationships with the anthropogenic niche (Fig. 3). In many species, populations are distributed broadly across the spectrum. However, in some species, like house cats, nearly all populations (representing ~98% of all cats) cluster at the obligate synanthrope end of the distribution, suggesting a species-level classification of domestic. House cats, whether family pets or free-living, are not found outside of anthropogenic environments in which they can avoid predators and access human-related food (74) with the exception of human-transplanted populations in places like Australia (75). This is demonstrated by a large-scale photo trapping study that collected data over the course of 4,000 nights in a Mediterranean forested area with scattered farms (76). Cats were only ever seen at farms still in use.

Applying the Definition

We propose that domestication spans a continuum that ranges from obligate recluse (those that thrive in the absence of human disturbance) to fully domestic populations. Any

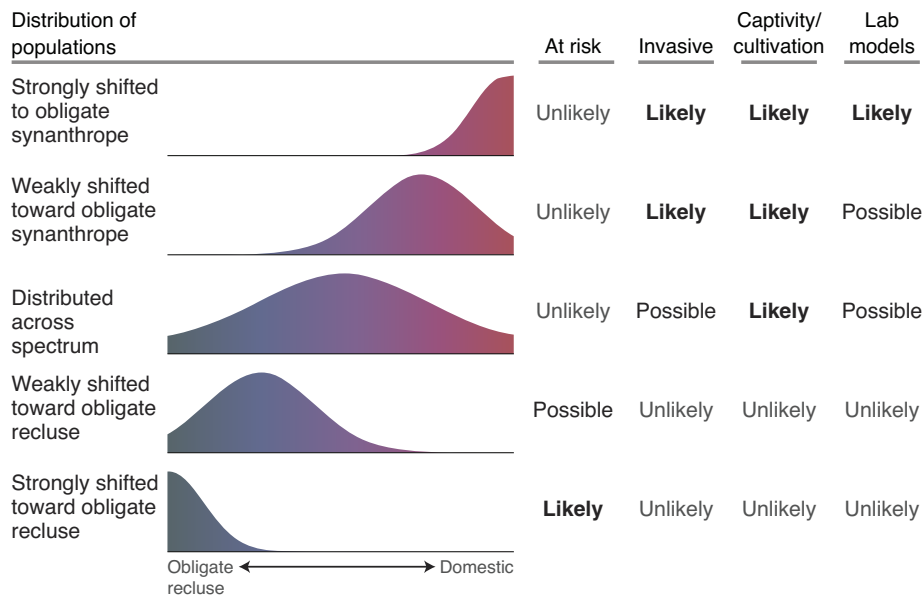


Fig. 3. Operationalizing the new definition for domestication to investigate ecological and conservation topics. We hypothesize that the distribution of populations within a species on the domestication spectrum may help predict whether the species is endangered, likely to be invasive in new environments, will tolerate captivity, and if it can be successfully established as a laboratory model.

self-sustaining population can be placed on this continuum based on the level of human disturbance it will tolerate. Below, we delineate five categories along this continuum to help operationalize this new definition. Populations may fall between categorizations and shift their position with successive generations.

Category 1. Obligate Recluse Populations Thrive in the Absence of Human Disturbance. These populations are increasingly rare as humans are ubiquitous and affect shape landscapes across most of the world. They include wolf populations that thrive in northern Canada where human disturbance is negligible (77). Similarly, the domestic tomato relative *Solanum lycopersicoides* does not tolerate agricultural disturbances and is now found only at undisturbed higher altitudes (78). The dwarf stag beetle (*Sclerostomulus nitidu*) requires late-stage dead logs that only occur in the absence of human disturbance and is now only found on one mountain (79).

Category 2. Human Avoider Populations Thrive Where Human Disturbance Is Rare. For example, the sphagnum moss *Sphagnum austinni* tolerated occasional human disturbance in the early Iron Age when used as a fuel source (80), but dwindled when agricultural activity and maintenance burning increased (81). Populations within a species can span a range of human relationships. Some African wildcat (*Felis lybica*) populations are human avoiders and thrive on ranches with low human population density (82) while others are obligate recluses and live in environments devoid of humans (83).

Category 3. Human Tolerant Populations Thrive in Areas with Occasional Human Disturbance. This includes animals who live near humans but emerge when humans are less active, and plants that thrive in areas with intermittent human disturbance. For example, coyote (*Canis latrans*) populations tend to spend daylight in areas with lower human density but move through areas of higher density at night (84). Individual coyotes will exploit food sources that put them in close

proximity with humans, such as eating pet food or preying on pets, if natural food sources are less available, but this results in poor health and increased risk of culling and is rare (85, 86). The plant woodbine (*Lonicera periclymenum*) thrives in hedgerows and forests with occasional human activity, but not in recently or heavily managed forests (87, 88).

Category 4. Human Exploiter Populations Are Synanthropic Opportunists. These populations thrive in environments with ongoing human disturbance. However, if the anthropogenic niche disappeared, they would persist. For example, stinging nettles (*Urtica dioica*) are self-sustaining in undisturbed areas with high-nitrogen soil, but thrive in the increased nitrogen of human-disturbed soil (89). The Asian subterranean termite (*Coptotermes gestroi*) is self-sustaining in old-growth forests but also thrives using human buildings as nests (90). Red foxes (*Vulpes vulpes*) can sustain their populations in nonanthropogenic environments. By moving closer to humans, they access new food sources and partition their ranges from less human-tolerant coyotes (91, 92) and grow to higher population densities (93).

Category 5. Obligate Synanthrope Populations (Domestic) Require Ongoing Human Disturbance. If the anthropogenic niche suddenly disappeared, these populations would be out-competed, predated, or simply unable to acquire the resources required to sustain their population. Lactic acid bacterial strains (*Streptococcus thermophilus*) required for fermented milk products have lost genes necessary to ferment nondairy carbohydrates (94). The common bed bug (*Cimex lectularius*) is both parasite and likely obligate synanthrope because both bat- and human-associated bed bug populations are found only in human structures (95).

We do not count organisms that require human bodies as domestic. For example, body lice (*Pediculus humanus humanus*) require human clothes and are domestic, but head lice (*Pediculus humanus capitis*) require human hair and are not (96).

Domestic Populations Are Not More or Less Domestic. Once a population is domestic, subsequent selection does not represent an ongoing process of domestication. A population that already requires an anthropogenic niche cannot evolve to become “more obligate.” Artificial selection in captive breeding programs can produce populations that are no longer self-sustaining and thus cannot be independently assessed on the domestication spectrum. Broiler chickens selected for growth rates and meat yield have impaired reproduction without intensive feed management (97).

The Spectrum Clarifies Exceptions

Domestication is distinct within an evolutionary context only because humans are one of the species involved. It has value as a term because it can help us understand how we affect the life around us, and how this has shaped both human culture and the wider world. A less prescriptive definition free of assumptions of intent, control, or utility accommodates situations that were previously awkward exceptions.

Ambiguous Terminology. Under this definition, domestication status is independent of whether or not a population is perceived as wanted, thereby avoiding ambiguity introduced by conflating domestic with “desirable.” For instance, even when intentionally grown crops and unwanted weeds are from the same population, only the crops have been described as domestic (16, 35). Rye is cultivated as a major crop but also classified as a noxious weed (98). Similarly, animals we want or control are called domestic but unwanted populations are described as human commensals or anthrodependent [e.g., house sparrows, body lice, and brown rats (99)] (Fig. 1B).

Similarly, domestication status does not differ between domestic pets and free-living animals from the same population. Free-living domestic animals, including those poorly socialized to humans, are dependent on an anthropogenic niche but are often erroneously described as feral (e.g., “feral” barn cats). Feralization is an evolutionary process by which a domestic population evolves to no longer require an anthropogenic niche (100). For example, the dingoes of Australia are descended from domestic dogs that evolved to survive outside of an anthropogenic niche (101) (Fig. 2).

Adaptation to Captivity Is Not Domestication. Domestication and adaptation to captivity are not synonymous, even though the two processes are indistinguishable when domestication is predicated on intentionality and control. Under our definition, a domestic population is one that is self-sustaining in an anthropogenic niche. In contrast, captive, cultivated, or cultured populations require ongoing and direct human care and are rarely self-sustaining. Captive populations are often sink populations that require the continual introduction of individuals from the noncaptive population (102). Captive environments lack the complex interactions and selective pressures of noncaptive anthropogenic environments such as cities (103).

Adaptation to captivity is distinct from domestication. Subpopulations from across the domestication spectrum can be maintained in captivity if human caretakers create an artificial environment sufficiently similar to their native habitat. For example, human-tolerant woodbine (*Lonicera periclymenum*) will not grow spontaneously in highly human-disturbed

areas like urban gardens, but can be grown as a cultivar (104). More human-tolerant populations may be easier to maintain in captivity because human caretakers are better able to replicate an anthropogenic niche. However, even populations that are human exploiters may not tolerate captivity if key components of their environment are missing. The achlorophyllous ghost orchid (*Epipogium roseum*) grows on the edges of gardens and in compost piles (105) but was difficult to first cultivate because it depends on a fungal symbiote (106).

While selection in a captive population can favor traits that are advantageous in a noncaptive anthropogenic niche, it often does not. For example, by favoring deformed skeletal morphologies, dog breeders created subpopulations that rarely produce healthy pups without veterinary intervention (107). Plant breeders, by selecting for a more palatable animal feed, created lupins that are less protected from herbivorous insects (108).

Thus, when we seek to protect species at risk of extinction by bringing populations into captivity, we do not “domesticate” them. Their breeding is often carefully controlled to retain genomic diversity and to reduce the effects of selection (109). Some adaptation is often unavoidable but does not necessarily result in populations better adapted to an anthropogenic niche. Fur-farmed foxes breed in captivity (61), but fur farm escapees can still thrive in the wild (110). Captivity can result in a reduced fear of humans (whether genetic or environmental) that can prove fatal. Reintroduced captive-born carnivores are more likely than wild-born individuals to die through human interactions when released (111).

Most Major Laboratory Models Were Already Human-Tolerant.

The individuals used to establish nearly all major laboratory models (Table 1) came from populations that already exploited or required an anthropogenic niche (Fig. 1A, C, and D) and thus may have been easier to maintain in captivity. For example, fruit flies were collected using fruit left on window sills (112) and sand fleas (*Parhyale hawaiiensis*) were sourced from the Shedd Aquarium’s filtration system (113). A common strain of laboratory rats is descended from rats captured at an Oscar Mayer company dump (114). Even the “wild” mice crossed into the laboratory populations were from commensal populations living in, for example, a pigeon coop (115). In contrast, populations that thrive further from human disturbance are often challenging lab models. For example, the most successful attempt to create an octopus model [*Octopus chierchiaie*; populations likely range from human avoiders to human tolerant (116)] lasted just three generations, with an 85% fatality rate due to escapes and inadequate diet and water quality (116). Even when a population can be maintained in captivity, the physiological effects may affect outcomes (117). For example, the brains of captive shrews [*Sorex araneus*; likely human avoiders (118)] have changes in gene expression linked to neurodegeneration (119).

Populations that Cannot be Domesticated. Distinguishing domestication from tolerance of captivity dispels the popular belief that some species like zebras are resistant to domestication (120). This idea is based primarily on short-lived, poorly executed captive breeding attempts that failed within one or two generations, and thus never tested domestication, which is an evolutionary process that unfolds over many generations. For example, the largest effort to intentionally

Table 1. The individuals used to establish nearly all major laboratory model organisms came from populations that were either human exploiters or domestic (SI Appendix)

Name	Source	Category
Dog	Breeders and dog pounds	Domestic
Fruit fly	Flies attracted to fruit on window sills	Domestic
Maize	Crop varieties	Domestic
Mouse	Fancy mouse breeders and caught commensal mice (e.g., from pigeon coop)	Domestic
Rat	Fancy rat breeders and caught commensal rats (e.g., Oscar-Mayer dump)	Domestic
Nematode (<i>C. elegans</i>)	Garden soil and from mushroom compost	Human exploiter
Sand fleas (<i>P. hawaiiensis</i>)	Filters at the Shedd aquarium	Human exploiter to domestic
Yeast (<i>S. cerevisiae</i>)	Commercial sources, rotting figs, and rotting bananas	Human tolerant to domestic
South African clawed frog (Xenopus)	Unknown commercial distributor in South Africa	Human tolerant to human exploiter
Zebrafish	Pet store in Oregon selling ornamental fish	Human tolerant to human exploiter
<i>Arabidopsis</i>	Collected by Laibach. Little information on where	Mostly human exploiters; potentially any

domesticate zebras (*Equus quagga*) failed when the vast majority died within a year without breeding (121). Rather than proving resistance to domestication, this experiment simply demonstrated that zebras, as obligate recluses (122), are harder to manage in captivity than horses. In contrast to conventional wisdom, we classify horses as human exploiters and not domestic because horse populations are self-sustaining outside of the anthropogenic niche (123, 124).

Domestication Through Translocation and Other Changes in Environment. Like any evolutionary process, domestication is an interaction between genetics and environment. Thus, the categorization of a population can change because its environment changes, as happens with human-mediated translocations. In their original Eurasian habitats, house cats (*Felis catus*) are domestic: we found no examples of self-sustaining cat populations outside of an anthropogenic niche. However, this changes when cats are translocated to places without their natural competitors. Australia has cat populations that are self-sustaining even in remote areas like the Gibson desert, albeit at much lower densities (125). Environmental change can also shift populations to obligate synanthropy. For example, most polecats (*Mustela putorius*) in farms and garbage dumps are human exploiters who take advantage of a high prey density in these environments but do not require it (126). In the coldest parts of their range, however, polecats require access to warm human structures in the winter to survive (127).

A population could shift to domestic if their nonanthropogenic niche is destroyed by human activity. Western honey bee (*Apis mellifera*) populations use both large hollow trees and human structures for their nests (128) but would become obligate synanthropes if their native habitat were destroyed and they were unable to use a different nonanthropogenic niche. Similarly, gourds and squashes adapted to the disturbance of ancient megafauna were rescued after the last ice age by anthropogenic disturbance (129).

Exploring the Relationship of Other Taxa with Humans Based on Archaeological Context. Circumstances in which different populations are found over time in relation to an anthropogenic niche can provide insights into how and why

populations went through the process of domestication. For example, house mice (*Mus musculus*) displaced Macedonian mice (*Mus macedonicus*) when humans moved to more permanent settlements at the beginning of the Natufian period, and this reversed when humans became more mobile again (130), suggesting the house mouse population was domestic (required an anthropogenic niche). Thus, the archaeological context itself provides information regarding the population's relationship with the anthropogenic niche.

Conclusion

Our new panspecies definition for domestication is grounded in evolutionary biology and resolves persistent differences in how domestication is defined. This new framing thus enables interdisciplinary investigations of the underlying biological and cultural processes that led to the emergence of domestic populations. It avoids prior assumptions about how and why domestication happens and obviates the requirement for control, utility, and human intentionality. It also accommodates the potential for domestication to vary between populations within a species. We clarify that domestication is a symbiotic relationship distinctive only because one of the two parties is human and is otherwise not fundamentally different from any other form of evolution. In other words, domestication is not an example of human exceptionalism but an aspect of evolution that is particularly relevant to our species.

This perspective allows us to ask and answer new questions about our relationship with other species in the past and future. Humans are reshaping ecosystems globally and millions of other species are being forced to adapt (131). Thus, anthropogenic habitats are model systems for investigating adaptation to rapid environmental change (132, 133). However, key questions remain. Why do some taxa adapt more readily to anthropogenic environments than others? Are less human-tolerant taxa unable to adapt, or simply adapting more slowly? Do wild taxa share traits that hinder adaptation? Likewise, do domestic populations share traits that facilitate it? Understanding the interactions between

human and nonhuman species will help us develop strategies to mitigate our impact and protect irreplaceable biodiversity. It also raises the uncomfortable prospect that, if domestication is adaptation to an anthropogenic world, we may face a future devoid of wild populations.

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