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Insularity and early domestication: anthropogenic ecosystems as habitat islands

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Over the past decade research into early domestication has been transformed by the genomics revolution and increased archaeological investigation. Despite clarification of the timing, locations and genetic processes, most scholars still envision evolutionary responses to human innovations, such as sickle harvesting, tilling, selection for docility or directed breeding. Stepping away from anthropocentric models, evolutionary parallels in the wild can provide case studies for understanding what ecological pressures drove the evolution of the first domestication traits. I contrast evolutionary trends seen among plants and animals confined on oceanic islands with the changes seen in the first cultivated crops and animals. I argue that the earliest villages functioned as habitat islands, applying parallel selective pressures as those on oceanic islands. In this view, the collective assemblage of parallel evolving traits that some scholars refer to as either an island syndrome or domestication syndrome results from similar ecological pressures of insularity, notably ecological release.

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Research into the origins of agriculture and the earliest domestication of plants and animals has been dominated by a humanist paradigm for the better part of the last century. Scholars have largely envisioned rational drivers for the cultural shift from foraging to farming; these often entail active and purposeful adaptation to external variables, notably climate change, population pressure, social institutions, such a prestige acquisition and feasting, or as a response to resource abundance (Flannery 1973, Cohen 1977, Hayden 1990, Zeder 2012). Additionally, researchers have envisioned evolutionary drivers that are tied into directed human action and innovation, for example animal domestication models often involve active selection for docile individuals and models for plants often incorporate seed selection. Even in cases where domestication theorists are willing to venture beyond active and intentional selection, they still tend to latch onto aspects of human innovation. For example, plant domestication scholars have focused on a perceived link between sickle harvesting and the evolution of tough rachises (Harlan 1975, 1995). In recent years, domestication scholars have begun to shed the humanist shackles and are now better placing the earliest evolutionary steps

in the domestication process within a framework of evolutionary ecology (Rindos 1984, Purugganan and Fuller 2009, Langlie et al. 2014, Larson et al. 2014, Kluyver et al. 2017, Purugganan 2019, Spengler 2020, Jones et al. 2021). As a result, scholars can look to the evolution of plants and animals in the wild as case studies or models for understanding evolutionary processes in the fields of the earliest farmers and vice versa.

Evolutionary ecologists from Darwin and Wallace to Mayr and Wilson have focused on islands, because: 1) oceanic islands function as expedited case studies in evolution; and 2) organisms on these islands tend to follow parallel or convergent evolutionary trends. In a now canonical text, MacArthur and Wilson (1967) first recognized that small ecological pockets (ecotopes or habitat islands) on a continental mainland can ecologically function like islands, and insular populations of plants and animals in these habitat islands are likely to follow parallel evolutionary trends. Since this revelation, evolutionary ecologists have been fixated on relationships between habitat size (i.e. island area), biodiversity and population size (Diamond 1975). Ultimately, modern theory in both ecology and evolutionary biology is built on a foundation of island studies. Nonetheless, there remains a disconnect in reasoning, whereas most scholars accept that city parks, nature preserves, unlogged patches, oases or hilltop forests are habitat islands, but they do not discuss a farm, village or the saved seed reserves of a community as also being habitat islands. Fitting domestication studies into a framework of island biogeography will allow researchers to envision the early farms and villages of the ancient world functioning, ecologically, as habitat islands. I promote this theoretical approach here by demonstrating that early evolutionary changes in plants and animals under cultivation directly parallel the evolutionary changes seen among insular populations on oceanic islands. Support for these proposed ecological links comes from the convergence of three recent trends: 1) the most-cited case study in animal domestication – the Siberian silver fox study – has been reanalyzed; 2) the interpretations of the most-cited case study in plant domestication, the sickle harvesting studies, have been called into question; and 3) there is a general trend away from humanist models of domestication, allowing for reevaluation of the ecology of early domestication.

Islands as ecological models

Most ecologists today recognize that 'islands are fascinating natural laboratories of evolution' (Benton et al. 2010; p. 438). This view is, however, not a novel revelation, and island biogeography has led the way in evolutionary theory since Darwin. While parts of the story may be apocryphal, Darwin clearly developed aspects of his ideas by looking at phenotypic differences between specimens of tortoises (*Chelonoidis niger*), mockingbirds (*Mimus* spp.) and eventually also finches (Geospizinae [Thraupidae]) from different islands in the Galápagos Archipelago (Darwin 1859, Grant and Grant 2002). Wallace (1881) produced the same conclusions regarding parallel trends in insularity by observing specimens of insects and birds from a wider array of oceanic islands. Since these seminal studies, island biogeography has continued to drive evolutionary theory. For example, Mayr (1942, 1963) developed his concepts of a founder effect and genetic bottlenecks by studying birds in the Solomon islands. Scholars today are still studying the patterns or evolutionary trends associated with island speciation and extinction rates, referred to by many ecologists as the species–area relationship and island rule (Foster 1964, Van Valen 1973, Lomolino 2001, Whittaker and Fernández-Palacios 2007, Lomolino et al. 2012, Faurby and Svenning 2016, Burns 2019).

Habitat islands

As with the focus on islands in evolutionary studies, the use of domesticated organisms as case studies in evolution also traces back to Darwin (1859, 1868); his pigeons (*Columba livia* ssp. *domestica*) paralleled his mockingbirds and finches. However, scholars view the island syndrome and the domestication syndrome as analogies rather than examples of the same evolutionary process. The insightful reference by MacArthur and Wilson (1967) to the fragmented forests of Cadiz Township, Wisconsin, changed conservation biology and evolutionary ecology, as it likened anthropologically fragmented forests to archipelagos. Another island ornithologist recognized the significance of the theory of island equilibrium and developed the concept further (Diamond 1970, 1975). Diamond (1975; p.130) stated: 'if one applies the island metaphor to natural habitats and to man-isolated species, island areas are shrinking and large islands are being broken into archipelagos of small islands'. The link between the species–area relationship (island effect) as an ecological principle on both oceanic and anthropogenic habitat islands was unequivocally illustrated by Newmark (1986), in his study of mammal extinctions in North American national parks. Over the past five decades, subsequent ecologists have recognized that human ecosystem engineering almost always involves fragmenting landscapes, whether through clearing forests, damming rivers, building roads and cities, or planting fields. Evolution on islands, whether oceanic or habitat islands, represents a considerable level of non-randomness, expressing pronounced evolutionary trends or patterns.

I have chosen to use the term 'syndrome' in this paper as a blatant misapplication of a medical disorder, given that nearly all scholars have consistently used it erroneously for decades. In the same vein, dwarfism and gigantism in this article follow convention, despite the critique by Gould and MacFadden (2004), which notes that they are also misapplications of medical concepts (they suggest using nanism and giantism). A deeper consideration of the use of the term syndrome would be timely, as a number of domestication scholars are now arguing that there is no such thing as a domestication syndrome, in the sense that not all organisms express all traits of the syndrome in the same way (Lord et al. 2019). What both domestication and island ecologists call

a syndrome is really a complex set of convergent or parallel evolving traits (Fuller and Allaby 2009, Fuller et al. 2014, Spengler 2020, Spengler et al. 2021). Assuming these traits are adaptive, a solid understanding of the ecological factors that have facilitated convergence should clarify the elusive why and how questions of domestication. Another prominent island biogeographer, Carlquist (1966; p.32), used the term 'insular syndrome', which could hypothetically encompass both domestication and island syndromes – scholars may wish to adopt his terminology.

Parallel evolution in plants

Island speciation

While most research into island speciation has focused on animals, notably mammals, angiosperms also express an island syndrome (Carlquist 1974, Whittaker and Fernández-Palacios 2007, Burns 2019). Traits of the island syndrome in plants include an increase in overall plant size (sometimes leading to lignification), increases in seed size, a loss of traits associated with dispersal mechanisms and a loss of defensive mechanisms, such as secondary metabolites (Lomolino 1984). All angiosperms possess features for seed dispersal (Tiffney 2004, Eriksson 2008); the plants that make the journey to oceanic islands often rely on either anemochory or exo- or endozoochory. Features that facilitate these dispersal mechanisms are often lost, such as a pappus. Most discussions about the ecological drivers for a loss of seed-dispersal mechanisms on islands focus on the sea-swept theory, whereas the high rates of seed loss due to dispersal (often referred to as cost of dispersal) drive plants to focus on greater local competitiveness as opposed to ability to colonize. A recent synthesis by Burns (2019) covers this topic in detail, but he ultimately postulates a pleotropic link between increasing seed size and a reduction in the functionality of dispersal mechanisms, as opposed to a direct selection against dispersal (an annex to the pleiotropy theory discussed below). In his synthesis, Burns (2019; p. 152) emphasizes that 'insular seed gigantism' is extremely prominent among island plants.

Several insular species in *Fitchia* spp. in the Polynesian islands appear to express significant increases in overall vegetative mass, and most of them have lost their seed-dispersal mechanisms (Carlquist 1974). Additionally, individuals on more remote islands seem to express more phenotypic change, presumably via serial bottlenecks. Several Polynesian Asteraceae, thought to originate in South America, have evolved much larger achenes and lost apertures for exozoochoric dispersal, a few have evolved lignified stems to support their weight (Carlquist 1966). North American *Bidens* sp. colonized several Pacific islands, losing the two retrorse barbs and evolving larger seeds. Carlquist (1966) suggested that the recently introduced *B. pilosa* is still in the process of evolving to lose its dispersal structure, but related species that colonized these islands much earlier have already lost these features, such as *Dendroseris litoralis* and *B. macrocarpa*. Carlquist

(1966) draws on species in *Oparanthus* spp. in the Marquesas and Rapa islands, which express parallel trends in evolution; these specifically appear to have lost wing-like dispersal structures. He references 18 species of *Scalesia* in the Galápagos, 24 species of *Lipochaeta* in the Hawaiian Islands and three species of *Centaurea* spp. in the Juan Fernandez Islands all of which express parallel trends, many losing pappus structures (Carlquist 1966). He notes cases on Socorro Island, Mexico, as well as across the southern Polynesian Islands, through the Hawaiian Islands, the Samoan Islands and the Marquesan Islands, including species in *Argyroxiphium* spp., *Dubautia* spp., *Wilkesia* spp. and *Fitchia speciosa*. He also notes a number of cases where the plants appear to have evolved perennial habits, which may be tied to a loss of zoochoric dispersal and a reduction in colonizing ability. A large-scale assessment of plants across New Zealand has also suggested that many evolved to lose ancestral features for seed dispersal (Thorsen et al. 2009, 2011). Increases in seed and overall plant size, leading to reduced dispersal potential, has also been noted in *Sonchus grandifolia* in the Chatham Islands (Wagstaff and Breitweiser 2002).

In one particularly informative study, ecologists looked at weed communities on 200 near-shore islands in Barkley Sound, Canada, focusing on *Hypochaeris radicata* and *Lactuca muralis* (Cody and Overton 1996). As a small archipelago comprised of small islands (ranging from a few square meters to roughly a kilometer), these islands may represent an ideal ecological analogy for the origins of agriculture. Both species expressed a reduction in pappus size under insular conditions, which the ecologists suggest may have evolved over as little as ten years. In a follow-up study, Cody (2006) noted continual increases in seed size, which in turn further reduced dispersal potential. Given that the seeds cannot colonize new islands without their pappus, the trait presumably evolved in parallel across all islands. As the phenotype for a reduced pappus was already in the broader population (mixed pappus and non-pappus morphs exist in mainland populations), it is possible that one gene for the trait exists, despite the independent trajectories towards a dominance of that morph on many separate islands (Fig. 1).

Domestication

In the same way that insular angiosperms on oceanic islands evolve to lose traits associated with seed-dispersal, the earliest steps in the domestication process for plants are all associated with a loss of wild seed-dispersal mechanisms (Rindos 1984, Spengler 2020, 2021). This process is clearly expressed in crops with mechanical dispersed progenitors, such as the large-seeded grasses and legumes (Fuller and Allaby 2009, Li and Olsen 2016, Wood and Lenné 2018). While often not discussed in scholarship, most crop progenitors have evolved for zoochory (Janzen 1984, Kuznar 1993, Kistler et al. 2015, Small 2015, Spengler 2019). This endozoochory followed two broad evolutionary patterns: 1) fleshy fruits (Janzen and Martin 1982, Tiffney 1984, Spengler 2019) and 2) foliage as fruit (Janzen 1984, Jaroszewicz 2013, Spengler and Mueller

2019, Mueller et al. 2020). At its core, these early steps in the domestication of angiosperms were ecological switches from a wild to an anthropogenic dispersal process, leading to corollary evolutionary changes. For example, in fleshy fruit crops, domestication involves an increase in pericarp and seed size; whereas in small-seeded herbaceous plants, the first traits of domestication were an increase in seed size, breaking of dormancy and thinning of the seed coat. Another trait of domestication expressed across nearly all early domesticated angiosperms is an overall increase in vegetative mass. While hypothetical, seed size increase may be a pleiotropic response to overall plant size increase, i.e. gigantism. The pleiotropy theory of seed-size increase under domestication has been well-articulated by Jones et al. (2021).

Studies have consistently illustrated that fragmentary and long-lived habitat patches can select for reduced dispersal abilities in weedy plant species (North et al. 2011). On landscapes with widely spaced habitat patches, an insular species can make a tradeoff between larger seeds that express greater local competitive ability or lighter seeds that express greater rates of colonization (Jakobsson and Eriksson 2003). Dimorphism in seeds usually allows for extended dispersal in both time and space (Venable and Lawlor 1980, Ellner 1986, Cruz-Mazo et al. 2010). Most early domestication in plants consisted of an increase in the frequency of one plant morph over another (as opposed to the evolution of a novel trait). Therefore, focusing on dimorphic plants, allows for a better visualization of the early steps in the domestication process for three reasons. First, several crops have dimorphic-seeded progenitors, including erect knotweed *Polygonum erectum* (Mueller et al. 2017); and many *Chenopodium* spp. (Williams 2019), all of which switch to a greater frequency of thin-testa (or hardened pericarp) morphs under cultivation. Second, these dimorphic species regularly shift between frequencies of morphs using both developmental and evolutionary mechanisms in the wild. Third, it makes it easier to imagine how a single trait could be selected in parallel across hundreds of insular populations with only one allele for that trait. As an example, *Leontodon saxatilis* produces two morphs in a single capitulum, one with a pappus for long-distance dispersal and the other with greater rates of dormancy (Brändel 2007). Plasticity studies in this species have shown that increasing the nutrient supply to the parent plant leads to more non-pappus seeds that produce plants that have greater numbers of inflorescences, as well as pappus seeds, which produce plants with greater numbers of seeds per inflorescence (Brändel 2007). Similar conclusions have been draw from studies of multiple species in *Scorzoneroides* spp. (Venable and Lawlor 1980, Ellner 1986, Cruz-Mazo et al. 2010). Plasticity studies in dimorphic-seeded *Hypochoeris glabra*, *Hedypnois cretica* and *Crepis aspera* also demonstrate that the percentages of one morph over the other can be directly altered by changing the density of competitive plants or available water and nutrients (Baker and O'Dowd 1982, El-Keblawy 2003). This may provide a natural feedback mechanism, if the plant in a population starts dropping too many seeds directly below the parent plant, they will develop to produce seeds that are

better for long-distance dispersal. Hypothetically, if a farmer artificially thinned out her crops, they would all produce more seeds that lacked traits for dispersal. Additionally, the wide reaction norms of plasticity in key domestication traits may suggest that developmental processes paved the way for the evolution of domestication traits (i.e. the Baldwin effect or Waddington's genetic assimilation).

As an example of how anthropogenic fragmentation can parallel island speciation, a study that contrasted urban and rural populations of *Crepis sancta* in Montpellier, France, noted that urban populations produced fewer seeds with pappus structures (a dimorphic traits). The ecologists in this study identified the evolutionary driver as the anthropogenic ecosystem itself, with small patches of the plants growing in sidewalk medians surrounded by concrete and asphalt (Cheptou et al. 2008). Follow-up research has verified that the fragmentary habitat drove evolution of a loss of the dispersal mechanism; effectively, the medians functioned like an archipelago of small islands (the authors favor the sea-swept theory: Dubois and Cheptou 2017). The small patches between sidewalks and roads represent islands of 5–10 m in area, and the researchers estimated that the windborne seeds from these plants were 55 percent more likely to land on concrete, and therefore, fail to establish, than those of their rural counterparts. Furthermore, using the Breeder's equation, the researchers estimated that the evolutionary loss of the seed-dispersal trait could have introgressed into the population in as little as five to 12 years (Cheptou et al. 2008). Like the archipelago in Barkely Sound, these *C. sancta* plants likely evolved this trait in parallel across many medians, as they would have lost their ability to colonize after adaptation to one. Equally as interesting, these ecologists also noted changes in the flowering time between the urban and rural populations (Lambrecht et al. 2016). Studies also shown that non-dispersing achenes germinated roughly four days earlier than the dispersing achenes (Dubois and Cheptou 2012). These temporal differences could cause reproductive isolation, creating a habitat island in both space and time. Many other studies have supported the observation that plants in fragmented landscapes follow similar evolutionary trends as ones on oceanic islands (Riba et al. 2009, North et al. 2011).

The leading theory for why cereal crops began to evolve tougher rachises is the sickle theory (Hillman and Davies 1990, Harlan 1992, 1995, Zohary 2004). This theory essentially states that early seed foragers, harvesting wild stands of wheat and barley (among other grasses), invented the stone-set sickle in order to facilitate grain harvesting. The sickle, in turn, allowed the farmers to collect greater quantities of grain, but the rough action of harvesting caused most brittle-rachised specimens to drop their seeds – presumably lost to seed predators. Eventually, after millennia of foragers/early farmers dropping the brittle-rachised seeds during harvest, the plants evolved to possess all tough-rachised individuals. This theory is presented in nearly every textbook on plant domestication, and it has overshadowed discussions, seemingly supported by a series of well-recognized experimental harvesting studies (Hillman and Davies 1990, Harlan 1992,

1995, Zohary 2004). While the sickle theory is often linked to the prominent experiments of domesticating wild cereals by Hillman and Davies (1990), they did not explicitly claim that it was the sickles driving evolution, but rather argued that it was the cultivation practice as a whole. In fact, Hillman and Davies (1990) specifically theorized that either reaping or uprooting a full plant would equally impose selective pressures for tough rachises – at the time, they were pioneering ideas of unconscious selection. Over the past few decades, the sickle theory has grown in popularity, despite the fact that it has several inherent flaws in reasoning. First, there are plenty of examples of crops that evolved tough rachises in the absence of sickle technology (e.g. East Asian rice; *Oryza sativa*). Second, as recently quantified by Maeda et al. (2016), sickle blades in the Fertile Crescent do not become prominent until well after the full introgression of the tough rachis trait, as attested by archaeological and archaeobotanical data. As an alternative approach, I pose and insularity or ecological release theory (or if archaeologists prefer to focus on the human actions it could be called a seed saving theory), whereas, the process of saving seeds to replant the next season caused the formation of an insular population. The insularity could have been either geographical, by planting the crops outside of wind–pollination range of their wild relatives, or temporal, by sowing a week or two later than the germination of any potential local relatives. Earlier flowering could also have been achieved in weedy species due to developmental plasticity and greater rates of growth among field and garden crops lacking competition for resources (Ecological release, as discussed below). Supporting and ecological release theory would not nullify the legendary wild cereal harvesting studies (Hillman and Davies 1990, Zohary 2004), it would simply add to them by suggesting a different interpretation of the evolutionary driver. Additionally, it would explain why, despite a lack of sickles, East Asian rice evolved tough rachises and why, despite heavy harvesting, Ojibwe wild rice *Zizania palustris* never evolved tough rachises.

When studying domestication, scholars often envision mono- or polyphyletic origins for a crop, depending upon how many mutations of that allele exist. However, most traits for domestication already existed in the progenitor population; hence, early domestication was almost always the selection for a segment of the existing population, as opposed to introgression of a novel mutation. In the brittle rachis case within cereals in the Fertile Crescent, the most widely cited and studied example of crop domestication in the ancient world, many estimates have been presented for a pre-domestication baseline of brittle verses non-brittle morphs in the progenitor population(s); often scholars rather arbitrarily claim that < 10% of the wild progenitor population possessed tough rachises prior to cultivation (Kislev 1989, Snir and Weiss 2014). However, the only measurable ancient assemblage of progenitor cereal rachises ever discovered comes from Ohalo II. Of 320 measured barley rachises from Ohalo II, 36% appear to be from a tough-rachised form and of the 148 wheat rachises, 25% represent a tough-rachised form (Snir et al. 2015). In this regard, these cereal populations are better thought of as dimorphic for their seed dispersal trait. The number of alleles for this trait in modern populations holds no bearing on the number of domestications that occurred and it is equally likely that ratios of morphs independently evolved across hundreds of insular populations (in the same way it theoretically did in Barkley Sound or Montpellier), as farmers started saving seeds (archipelago speciation).

Parallel evolution in animals

Island speciation

One of the features of the island syndrome in animals that has attracted the most attention since Darwin is the loss of flight, clearly expressed in birds, and arguably also observable in beetles and possibly a giant Hateg Island pterosaur (Whittaker and Fernández-Palacios 2007). The large stubby stature of the dodo *Raphus cucullatus*, kakapo *Strigops habroptilus*, island rail *Laterallus rogersi* or duck (*Cairina moschata*; *Anas platyrhynchos*) and chicken *Gallus gallus* ssp. *domesticus* may all be examples of convergent evolution. Flightlessness likely shares evolutionary drivers with the loss of seed-dispersal in plants, and could, therefore, either be part of a pleiotropic response to increased body size (pleiotropy theory) or part of the sea-swept theory (or a bit of both). Darwin suggested the latter, claiming that when trapped on an island, it is evolutionarily more advantageous for an organism to evolve to lose all dispersal ability than to evolve to be a better swimmer or flyer.

The loss of flight in birds is often linked to an increase in body size (paralleling the loss of dispersal in plants); as a general trend in island speciation, small-bodied animals evolve to be large and large-bodied animals shrink (island rule, also Foster's rule or island effect). Darwin recognized parallel size increases in island reptiles, birds and insects, with size reductions in large mammals. While evolutionary trends towards larger or smaller body sizes among insular populations were well-reported by the end of the nineteenth century (Darwin 1859, 1868, Wallace 1881, Nopcsa 1914), the empirical supporting data were not pulled together until the work of Foster (1964) and Case (1978). Foster (1964) compiled an assemblage of insular species (n = 116), specifically working on the Queen Charlotte Islands off the coast of British Columbia in Canada. He claimed to see 'a clear tendency toward gigantism in insular rodents while dwarfism is characteristic of insular lagomorphs (rabbits and allies), carnivores and artiodactyls (cloven-hoofed mammals)' (p. 234). Case (1978; p.1) added many additional examples to this list and stated, 'groups such as lagomorphs, bats, artiodactyls, elephants, foxes, raccoons, snakes and teiid and lacertid lizards are habitually represented by relatively smaller forms on islands. On the other hand, cricetid rodents, iguanid lizards, tortoises and bears often have races with larger body sizes on islands'. The term 'island rule' was originally coined by Van Valen (1973; p.35), who stated: 'the regular evolution of mammalian body size on islands is
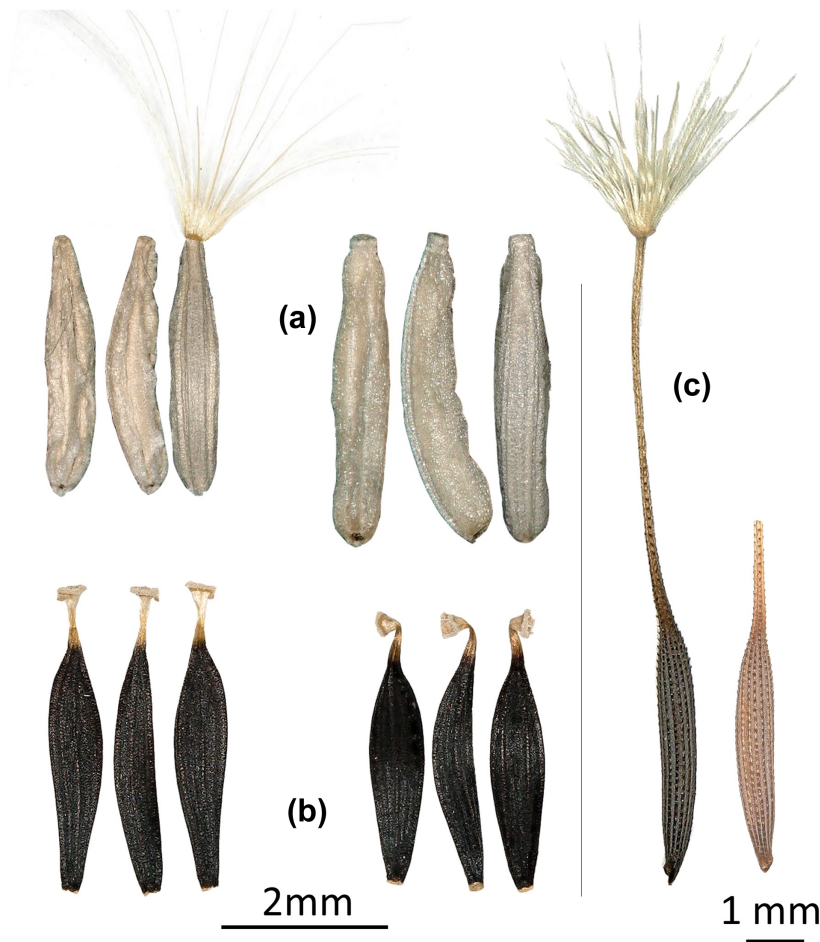
Figure 1. Three examples of dimorphic seeds that have case studies mentioned in the text showing that they have evolved to produce more of the non-dispersal forms: (a) *Crepis sancta*; (b) *Lactuca muralis*; and (c) *Hypochoeris radiacata*. All photos are the author's.

an extraordinary phenomenon which seems to have fewer exceptions than any other ecotypic rule in animals'.

All this said, it is essential to point out that there are scholars critical of the idea that there are evolutionary body-size trends among insular animals, especially for non-mammals (Meiri et al. 2011, Lokatis and Jeschke 2018). It is beyond the scope of my discussion here to enumerate the points of these critiques, but I will say that these scholars raise some valid concerns about biases and it is clear that further research is needed. Additionally, trends towards larger body sizes have been observed on continental mainlands, such as in the terror birds (Phorusrhacidae; see controversial Cope's law), and many large island species, such as tortoises are relic populations. A clearer understanding of contexts where the island rule does and does not apply could result from an integration of domestication and island ecological theory. Proposed examples of island dwarfism include, but are far from limited to, the hobbits *Homo floresiensis* from Liang Bua Cave on Flores in Indonesia, dwarf crocodiles on Tagant and Mauritania, dwarf hippos on islands across the Mediterranean, insular proboscideans (e.g. *Palaeoloxodon falconeri* on Malta; *Mammuthus exilis* in the Channel Islands)

and a dwarf sauropod (*Magyarosaurus* sp.) and two ornithopods (*Telmatosaurus* and *Zalmoxes*; Nopcsa 1914, Benton 2010, Lomolino et al. 2021).

Other aspects of the island syndrome in animals include the loss of secondary display organs and coat color changes, often expressing as leucism, melaism or piebaldism. Mayr (1942) focused on the loss of conspicuous male morphological traits in island birds, paralleling the loss of horns, tusks and conspicuous plumage in domesticated animals. One example of island leucism comes from Polynesian rats; an island ecologist recently reported aberrant coat colors on rats from 12 different islands, with individuals expressing all three morphisms: leucism; melaism; and piebaldism (Van der Geer 2019). No known mainland rat populations in the South Pacific express these traits; additionally, the rates of these pathologies were higher on islands further away from the mainland, likely reflecting the effects of repeated founder events or serial bottlenecks.

The most telling trait linking the domestication and island syndromes is the loss of fear responses, referred to by Darwin as Island Tameness. Most island ecologists link the evolutionary loss of hormonal fear responses on islands to

a lack of predators (i.e. Ecological release; Rödl et al. 2007, Cooper et al. 2014). It is feasible that the same release of predation drove hormonal changes in domesticated animals, as animals penned or maintained near a village lack predators. While there are too many examples of island tameness to address here, Darwin did describe the Falkland fox *Dusicyon australis* in considerable detail (Fig. 2). Darwin noted that the island foxes lacked all fear of humans and would walk up to sailors, who would then proceed to club them (Whittaker and Fernández-Palacios 2007, Austin et al. 2013). The animals also expressed coat color modifications, with white spots on their muzzles, lower limbs and tails, essentially paralleling changes in dogs. Another island fox (*Urocyon littoralis*) is native to six of eight Channel Islands: it appears so much like a domesticated dog in its behavior that archaeologists have even speculated that it might have been domesticated by ancient humans and brought to the island (Rick et al. 2009). Statistical studies of limbs and other features show that the Channel Islands foxes are not simply scale versions of mainland foxes, but have undergone evolutionary shortening of specific features (Young 2020).

Domestication

Leucism, dwarfism, gigantism, flightlessness, reduction of fear responses and loss of display organs are all traits well-represented among domesticated animals, albeit, not all at the same rate or in exactly the same ways. Additionally, it appears that different genetic pathways lead to some of these similar changes, all implying parallel or convergent evolution. From an ecological perspective, most discussions of early animal domestication are fixated on active human engagement in the evolutionary process – many archaeologists have started embracing the term 'human agency' as a way of recognizing that humans were probably not aware of the millennial-scale processes of organismal change, but without letting go of the entrenched humanist paradigm. In these discussions, animal domestication results from selection for docile animals, hunting or intentional trait selection (Zeder 2012, Larson and Fuller 2014). At their core, these ideas are all tied into the most well-recognized and cited study of animal domestication, the Siberian silver fox study, which seemingly illustrates how active selection for docility could drive evolution. The study consisted of experimental domestication work conducted on a population of silver morphs of *Vulpes vulpes* and started in 1959 at the Institute of Cytology and Genetics in Novosibirsk, under the directorship of Belyayev. The founder population consisted of 130 individuals, and the typically cited numbers of 20% of the human-tolerant lineage were expressing domestication traits that were not directly selected for within ten generations (Trut 1999, Kukekova et al. 2006). These secondary traits include dog-like attention seeking, barking, whining, submissiveness, tail-wagging, prancing and licking, as well as a suite of physiological changes, including floppy ears, coat color changes, a curly tail, shorter muzzles and hormonal shifts. This study has been taught, referenced, discussed and re-cited many times among domestication scholars, and it is almost dogmatically accepted that selection for more docile animals drove early domestication in mammals.

Recent investigative work by Lord et al. (2019) has traced the history of the foxes back before the inception of the study, showing that Belyayev obtained his founder population from a Canadian fur farm. Letters among representatives of the fur farm in the early 1900s show that

Figure 2. Four examples of foxes evolving traits of an insular syndrome: 1) the Falkland Islands fox; 2) the Channel Islands for; 3) a London fox and 4) a Siberian silver fox from the Belyayev study. Photo copyrights have been purchased.

the foxes were already expressing traits of domestication before being moved to Siberia. While these revelations do not nullify the Siberian silver fox study, it is still the greatest case study in animal domestication, but, like the sickle harvesting studies discussed above, the foundational interpretations need reconsidering. If, indeed, traits of domestication were appearing in the population, prior to selection for docility, then active selection for less aggressive individuals cannot be the driving cause for these trait changes – at least not the only cause. Whatever ecological factors drove evolution under captivity in these foxes, it must have been present among the Canadian caged foxes prior to this study. Essentially serving as linking case studies, there are plenty of examples of animals expressing traits of island or domestication syndromes due to confinement on continental habitat islands. Some good examples come from the leucistic deer *Odocoileus virginianus* confined in the WWII barracks by Seneca Lake in upstate New York or the Nara deer *Cervus nippon*, which have lost all fear responses around humans after centuries of confinement in the vicinity of Mount Wakakusa.

Other examples of insular fox populations can serve to better contextualize the processes observed in the silver fox study. Like the *Crepis sancta* in Montpellier, insular populations of foxes are developing as a response to anthropogenic ecosystems, and these foxes appear to be expressing similar traits of domestication as seen among the Canadian fur farm foxes and their descendants in Siberia, as well as in the Channel and Falkland Islands foxes. Gradually over the past four decades urban foxes have evolved novel traits, and in some cases physiological features, that made them well-adapted to life in urban settings. Genetic studies of some of these urban fox populations have shown strong genetic barriers between urban and neighboring rural fox populations, and ecologists have speculated that behavioral changes are driving isolation (Wandeler et al. 2003, Kimmig et al. 2019). Increasingly, ecologists and geneticists are studying this interesting phenomenon, as urban fox populations are appearing across western European, some Asian and even Australian cities, and they have only begun to evolve since the 1980s (Hewson 1983, Gloor et al. 2001, Wandeler et al. 2003, Yom-Tov et al. 2007, Plumer et al. 2014, Parsons et al. 2020). While many scholars have focused on rodent availability as the key driver for urban adaptations, the earliest recorded accounts of urban foxes happen in highly developed cities in western Europe, with notable cases in London dating back to the late 1960s. In fact, massive-scale poisoning and trapping campaigns in London between 1971 and 1973 failed to slow the spread of urban foxes. These extermination programs did provide copious crania for study, and recent reanalysis has shown cranial changes, notably reduced muzzle length and a smaller cranial capacity among the London foxes, in relationship to their neighbors just outside the city (Parsons et al. 2020). Body size changes have been noted in urban fox populations in Spain (Yom-Tov et al. 2007); diurnal resting and human avoidance changes have been observed in village fox populations in Switzerland (Hewson 1983, Meia and Weber 1993). One recent reassessment of the urban fox situation in Switzerland estimated that 28 out of 30 large cities in the country are now occupied by insular populations of foxes that are genetically isolated from wild foxes, a phenomenon that has only developed over the past 40 years (Gloor et al. 2001). The first recorded urban foxes in Estonia were noted in 2008, and by 2011 urban fox populations had established in 33 out of 47 towns (Plumer et al. 2014). Urban foxes have taken over many village dump heaps in the Spiti Valley of the Indian Himalaya (Ghoshal et al. 2015). Despite being introduced to Australia, urban foxes began to appear in Melbourne in the 1970s and by the early 2000s were recorded in Perth, Adelaide, Brisbane, Canberra and some Sydney suburbs (Marks and Bloomfield 2006).

The urban foxes may provide a far greater case study for domestication than the Siberian silver foxes, but these domesticated fox populations have been overlooked by domestication scholars. Note that the foxes evolved domestication traits without direct human selection for docility; in fact massive-scale eradication attempts had no discernable effect on curbing the evolutionary trends. This would seem to support models of domestication that suggest that ancient humans were not only unaware of the process, but had no control over it. The questions remain, why were foxes never domesticated in anthropogenic contexts prior to the end of the twentieth century and why are domesticated foxes appearing, seemingly independently, across three continents over just the past 40 years. I will pose a logical answer to these questions, but I recognize further research is needed. My response would be that the dump-heap or village forager niche had been filled across all villages globally since the development of the first villages. London began large-scale feral dog round-up and euthanasia programs in the late 1950s, with neutering beginning in the 1960s. The London foxes started appearing in the 1970s. Estonia began their feral dog eradication programs in the late 1990s, with the first urban foxes appearing in 2008. Similar correlations can be made across Europe, notably leaving eastern European and Central Asian villages and cities that still have large feral dog populations lacking urban foxes. Paralleling evolutionary processes in the wild, the evolution of new crops and animals is largely tied into the opening of new niches, and once a niche is occupied, it is unlikely that new organisms will evolve traits to occupy it. The origins of agriculture opened novel niches for plants and animals to rapidly evolve into, in the same way that colonization of an oceanic island would. A combination of insularity pressures and adaptation to the anthropogenic ecosystem drove evolution and closed the niches. The elimination of feral urban dogs opened the dump-heap forager niche for the first time in 10 000 years (Coppinger and Coppinger 2001, 2016); within a decade in multiple genetically isolated cases foxes started to rapidly evolve to fill that open niche and take on the behaviors and even pathogen loads of dogs.

Rethinking domestication

A unifying mechanism

The similarities shared among plants and animals expressing the domestication syndrome has led most scholars to assume that there is a single unifying process. Larson and Fuller (2014; p. 117) summarize this way of thinking as: 'the ubiquity of the domestication syndrome suggested the existence of a single domestication process; or at least there was little incentive to consider either differential stages from wild to domestic or the possibility that different animals followed unrelated pathways to reach the same domesticated status'. The concept of a domestication syndrome is, in itself, an expression of this perceived unifying mechanism (Harlan 1973, 1975). Social scientists tend to assumed that this unifying mechanism was tied to the cultural practices of cultivation, and the majority of domestication scholars have assumed that some form of directed breeding occurred in the past. Understandably, the fixation on a unified process and the suite of domestication traits that all seem to benefit human interests have fueled the humanist ideal of domestication as the great prehistoric human innovation. Geneticists have also searched for the unifying mechanism of early domestication, seemingly as a way to account for the lack of agreement among archaeologist on a unifying cultural mechanism. Four prominent unifying genetic or epigenetic mechanisms exist in the literature, most notably the neural crest hypothesis (Donoghue et al. 2008, Wilkins et al. 2014, Sánchez-Villagra et al. 2016), the paedomorphosis or neoteny hypothesis (Coppinger et al. 1987, Goodwin et al. 1997), the thyroid hypothesis (Crockford 2006) and the regulatory genes or pleiotropic cascade theory (Jensen 2006). The neural crest hypothesis has risen to the forefront in recent years, seemingly suggesting a single unifying genetic process of mammal domestication. If it is true, it would challenge the large-scale hunt for alleles associated with domestication traits.

Archaeologists have begun theorizing differing cultural pathways to domestication, most notably Zeder's (2012) three type model, which has been adopted and modified by subsequent scholars (Larson and Fuller 2014). Of these three types, commensalism is the only one with clear logical precedence and analogous examples from the wild. The prey pathway to domestication contradicts basic Red Queen dynamics, as heavy predation never leads to reduced aggression, intelligence, reactiveness or metabolic and hormonal responses. In fact, the prey pathway goes against ongoing observable evolutionary responses to human hunting (maybe slightly less so under the specific context of trophy hunting). The third type, the directed pathway, lacks any supporting evidence or even a proper case study; it is largely based on a narrative that inserts Enlightenment Era scientific discoveries into the context of prehistory. The one case study used to support this theory, the horse *Equus ferus* ssp. *caballus*, is highly problematic, as decades of intensive scientific research into horse domestication have failed to provide indisputable evidence for where, when or even why (for food or traction) the horse was brought under cultivation (William and Barrón-Ortiz 2021). Niche construction theory has also emerged as a sort of unifying process in domestication studies, but using the logic that all human behaviors can be clumped into one term – niche construction (Zeder and Smith 2009, Smith 2011). In this way, NCT simply serves as a flashy new banner to fit all cultivation or agricultural behaviors under, and does not contribute novel concepts to the debate (Spengler 2021).

I suggest that a unifying process may still emerge, but that it is hiding in the ecology of early domestication and not the genetic or cultural mechanisms. Despite the extreme complexity of the genetic and cultural mechanisms involved, domestication represents an astonishing degree of predictability; this non-randomness in evolution resembles evolutionary adaptations to island ecosystems. It may serve domestication scholars better to set aside the focus on active human engagement, such as through sickle harvesting, hunting or directed breeding, and to focus instead on secondary evolutionary responses to life in a village or farmstead, resulting from millennia of seed saving and maintenance of genetically isolated landraces or ecotypes. This said, the processes that actually drive parallelism on an island are still not agreed upon by ecologists. Arguments already in the literature to explain these evolutionary trends include, optimum body size models, relying on optimization criteria and net energy gain (Case 1978); predation release; competitor release (collectively called ecological release); and resource limitations or resource abundance. While the evolutionary drivers linking adaptive divergence on islands and in ancient farmers' fields may involve a combination of these factors, I would suggest that interested scholars begin their focus on ecological release.

Types of insularity	Plants	Animals
Oceanic islands	Increases in plant mass; increases in seed size; loss of seed dispersal mechanisms; moss of secondary metabolites	Docility; coat color changes; loss of display organs; reduced size; reproductive changes; increased stockiness
Anthropogenic habitat islands	Increases in plant mass; increases in seed size; loss of seed dispersal mechanisms	Docility; coat color changes; reduced size
Early domestication	Increases in plant mass; increases in seed size; loss of seed dispersal mechanisms; moss of secondary metabolites	Docility; coat color changes; loss of display organs; reduced size; reproductive changes; increased stockiness

Ecological release

There remain ongoing debates over which factors of insularity actually drive convergent evolution, but it appears likely that ecological release plays an important role. Ecological release is 'niche expansions and shifts when a constraining interspecific interaction is reduced or removed' (Herrmann et al. 2020). When an organism colonizes a new area that lacks predators or the predators (including parasites and herbivores) are extirpated from an area, then an organism experiences ecological release (Lomolino 2005). The same process occurs when competition for resources is reduced. The concept was first laid out in the 1940s by yet another island ecologists, Lack (1944). The term ecological release and the theoretical scaffolding that holds it up were developed by Wilson and his colleagues over the following decades (Brown and Wilson 1956, Wilson 1961, MacArthur and Wilson 1967). Evolutionary responses to ecological release are highly predictable and involve trends, as seen in the specific cases of island adaptation (Herrmann et al. 2020, Voje 2020). If the hypothetical link between canine control programs and the rise of urban foxes proves accurate, it might further support the ecological release theory. These same speculative parameters could be applied to the domestication of humans; human social behavior, cooperation, tool use and possibly the extinction of megafaunal predators may have all provided conditions of ecological release.

A few domestication scholars have theorized that seed size and vegetative mass vary allometrically; i.e. the pleiotropy theory (Kluyver et al. 2017, Jones et al. 2021). Additionally, some scholars have theorized links between loss of seed-dispersal mechanisms and increased seed size, such as in the thinning of the seed coat in *Chenopodium* spp. Paralleling these observations, one island ecologists recently pulled together an extensive summary of published case studies of island speciation and speculated a link between the evolution of a loss of the wild seed dispersal mechanism and an increase in overall seed size (Burns 2019). Linking the pleiotropy theory and ecological release to early plant domestication would suggest that plants evolved to be more locally competitive, as opposed to investing in colonizing potential, increasing overall plant mass and nutrient stores for offspring. The evolutionary increase in overall plant mass would have been facilitated by a lack of herbivory and high inputs of water and nutrients. Thinking about early domestication in plants and animals as being a result of ecological release, is, in many aspects, equivalent to thinking about them as invasive species. The earliest crops and cultivated animals to develop a mutualism with humans experienced anthropogenic-facilitated invasiveness, expanding their range, broadening their niche and driving a key set of evolutionary adaptations.

Archipelagos of the Anthropocene

Domestication scholars have debated over the role of founder effects in driving evolution (Ladizinsky 1985) and whether genetic bottlenecks occurred during the early stages of domestication (Iorizzo et al. 2013, Allaby et al. 2019). Some scholars envision seed saving as functioning like serial bottlenecks (Allaby et al. 2019), similar to island hopping species. Arguably, the scholars in these debates are already thinking about the early steps towards domestication as responses to insularity. However, such debates are mostly restricted to select domestication scholars. Additionally, certain Mendelian traits of domestication have held the spotlight in research, likely due to the simplicity and ease in which they can be presented. Geneticists should ask: would they expect to see the genetic signature of Mayr's founder effect or a genetic bottleneck if they thought about the early steps toward domestication as an archipelago of islands rather than an island? Like the evolution of a loss of seed-dispersal traits on all islands in Barkley Sound or all medians in Montpellier, in parallel, would the key domestication features evolve in parallel without a discernable bottleneck on a larger regional scale? In most cases, the earliest traits for domestication were already present in the founder populations, hence domestication was simply a shift in the frequency of a phenotype within a select population or assemblage of populations, as best illustrated in the dimorphic weed examples above. Genetic studies have at least partially supported this way of thinking, for example, by showing that the genetic material for barley came from wild barley populations spread across the Fertile Crescent as opposed to from a specific central population (Poets et al. 2015).

In at least some cases, plants and animals under cultivation clearly evolved in parallel independently in different isolated populations or lineages of populations. As some examples, recent genetic work on maize domestication has illustrated that the crop spread north and south out of Central America in a form that would have looked much like its progenitor population, but evolved in parallel to look like modern maize among multiple isolated lineages in the north and south (Kistler et al. 2018, 2020). Likewise, broomcorn millet traversed two continents by 3500 years ago, from its domestication region in northern China to reach Europe and genetic studies illustrate that at least two distinct lineages evolved in isolation over a considerable period of time (Hunt et al. 2018). Size measurements of ancient millet grains from Central Asia show that the plant was still producing relatively small seeds when it spread across Eurasia, but within a millennium, large-grained millet crops were being cultivated across Europe and East Asia (Spengler 2015). In a similar vein, cereal crops appear to have continued evolving larger grains in isolation across multiple parts of the ancient world; although, scholars have recognized a suite of complicating variables in these discussions, such as the potential for uniform plasticity responses (Fuller et al. 2017, Motuzaite Matuzeviciute et al. 2021). Ultimately, it may serve scholars better to think of evolution as parallelism of an organism across an archipelago of insular communities (habitat islands each equating individual ecotypes or landraces), as opposed to speciation among a single community. Better wild analogies for understanding the ecology of domestication may come from looking at the rapid evolution of Galápagos finches (Grant and Grant 2002), or the weeds in Montpellier

or on the islands of Barkley Sound. Even better ecological models for understanding early domestication may come from anthropogenic archipelagos, such as the parks of New York City, where studies of black-footed mice *Peromyscus leucopus* show separate trajectories towards domestication (Harris et al. 2013, Munshi-South and Nagy 2014) or isolated city park populations of lizards *Intellagama lesueurii* in Brisbane (Littleford-Colquhoun et al. 2017).

In this paper, I avoid genetic debates, suggesting that there is room for complex arrays of genetic and epigenetic processes leading to parallel or convergent trait evolution. Following this reasoning, one estimate suggests that there are more than 300 genetic loci and more than 150 identified coat-color genes that cause pigment changes in mammals (Cieslak et al. 2011). Genes associated with tameness in the foxes and rats of the silver fox study have been identified, notably *Tph1* and *Gabra5*, but it is clear that the overall loss of fear responses involves a more complex suite of evolutionary and developmental processes, which may include a migration of the neural crest cells during development (Sánchez-Villagra et al. 2016, Ahmad et al. 2020). In this sense, the focus on a few Mendellian alleles in domestication studies may provide a false impression of monophyletic origins. As the one-gene-one-disorder paradigm rapidly fades from theoretical research (Cerrone et al. 2019), the one-gene-one-domestication-trait view of domestication seems to be following. To reiterate, when scholars use the term syndrome – both in the sense of islands and domestication – they are not evoking the medical definition, but rather a suite of similar phenotypic traits that appear to evolve in parallel. If parallelism or convergence is not driven by a single genetic or cultural mechanism, then it is likely to be driven by a similar set of ecological factors (in an adaptationist sense).

If we accept that the evolution of the island and domestication syndromes is convergent, then domestication scholars studying animals should back away from (maybe not let go of completely) the focus on overhunting, selection of docile individuals and active breeding for specific traits, and instead consider the maintenance of small well-fed populations, protection from predation or herbivory and genetic isolation as key drivers of domestication. Likewise, domestication scholars studying plant evolution should let go of ideas of sickle harvesting, seed selection or conscious breeding and focus on seed saving as a means to maintain insularity and weeding, watering, fertilizing and protection from herbivory as causes of ecological release. As Burns (2019; p. 155) states 'seed sizes regularly increase in island organisms, providing a remarkable example of evolutionary convergence'. Size increases in plants and animals under insular conditions may be directly tied to ecological release and potentially cause cascading pleiotropic changes, including a loss of flight or dispersal abilities. It is beyond the scope of this discussion to conclude why the insularity syndrome exists, rather I hope to encourage future discourse by emphasizing the similarities and by suggesting that domestication scholars can benefit from an already robust literature on island speciation and island biogeographers can benefit from a plethora of case

studies in domestication. I also suggest that scholars look to the already well-discussed sea-swept model and the ecological release or pleiotropy models (increases in seed size are tied to increases in overall seed mass, whereas traits for seed dispersal are lost due to lack of effectiveness with larger seeds). Under the latter views, insularity syndromes are the result of a loss of predation and greater nutrient and water inputs, driving increases in overall plant mass, resulting in a pleiotropic cascade. Ultimately, in letting go of the fixation on human intentionality and innovation when modeling early domestication, scholars can benefit from rich collaborations between anthropologists/archaeologists and ecologists working outside anthropogenic contexts.

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