



Historical range expansion and biological changes of *Sus scrofa* corresponding to domestication and feralization

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Abstract

Globally, *Sus scrofa* is one of the most widely recognized species inhabiting earth alongside humans. Known by many names (wild boar, domestic swine, feral pig), *S. scrofa* is both an ecosystem engineer and an important agricultural species. Originating in Southeast Asia 5 million years ago, *S. scrofa* naturally expanded throughout Eurasia and into North Africa but now inhabits every continent, except Antarctica. The worldwide distribution of *S. scrofa* can be attributed largely to human-mediated transport occurring over the course of the past 500 years particularly during the European age of exploration. Biologically, the differences between wild, domestic, and feral populations can be traced to these historical events, which resulted in a marked increase in reproductive rates and growth rates among domestic populations that have generally been shown to regress when these populations become feral. Given the importance of this species ecologically and the great deal of available research describing it, this review summarizes existing literature on the global expansion and corresponding biological changes of *S. scrofa* within a historical and genetic context to allow for better understanding of the species.

Keywords Boar · Hog · Invasive · Native · Pig · Swine

Introduction

One of the most broad-ranging species on earth (Ruvinsky and Rothschild 1998), *Sus scrofa* is commonly known as Old World swine, Eurasian wild boar or hogs, domestic pigs or swine, and feral or wild pigs, hogs, or swine (Keiter et al. 2016). This broad range of names by which *S. scrofa* is recognized is indicative of the vast portion of earth it inhabits, which includes every continent except Antarctica, as well as the species' genetic and morphometric diversity. Globally, the range of *S. scrofa* is primarily limited by its inability to withstand harsh winters in polar climates and arid conditions in desert regions with only small pockets of refugia existing in

these areas (Alexander et al. 2015; Lewis et al. 2017; Long 2003; McClure et al. 2015). The ability of *S. scrofa* to survive in this wide array of climates is often attributed to their overall adaptability and flexible diet. An opportunistic omnivore, *S. scrofa* will consume most forms of vegetation including roots, stems, leaves, fruits, and nuts as well as obtain protein from carrion and macroinvertebrates (Cuevas et al. 2010; Diong 1982; Herrero et al. 2004; Massei et al. 1996; Parkes et al. 2015; Wehr et al. 2020; Wilcox and Van Vuren 2009). In habitats near humans, free-ranging populations frequently rely on agricultural crops as a food source but are also capable of obtaining the majority of their diet from human refuse (Hafeez et al. 2011; Schley and Roper 2003; Wurster et al. 2012; Zeman et al. 2016). Importantly, Ballari and Barrios-García (2014) found that diets did not vary significantly between wild and feral populations of *S. scrofa*.

Socially, *S. scrofa* live in large groups called “sounders” which are composed of matrilineal family groups with adult males generally being solitary (Gray et al. 2019; Maselli et al. 2014; Podgórski et al. 2014). However, it has previously been shown that during periods of parturition, these groups may become more fluid to aid in protection from predation and hunting pressure (Iacolina et al. 2009; Maselli et al. 2014). *S. scrofa* do not typically defend their home ranges from other

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sounders, and individuals from separate sounders generally have non-exclusive overlapping home ranges, which has the potential to facilitate gene flow (Graves 1984; Hampton et al. 2004b; Sparklin et al. 2009). These home ranges vary in size from 0.5 km² in habitats with high food availability to those as large as 58.7 km² in areas with fewer available food sources (Gray et al. 2019; Hampton et al. 2004a; Iacolina et al. 2009; Martins et al. 2019; McIlroy 1989; Morelle et al. 2015; Saunders and Kay 1991) and can be highly adaptable to habitats with increased human presence (Podgórski et al. 2013). Correlating to these home ranges, population densities range from 0 to 2 pigs/km² to densities as high as 12–47 pigs/km² in habitats with high food availability, such as southeast Asia in their native range or Hawai'i in their nonnative range (Ickes 2001; McIlroy 1989; Saunders 1993; Scheffler et al. 2012). Other environmental variables affecting these population densities include bottom-up controls such as precipitation and top-down controls in terms of depredation (Lewis et al. 2017).

Prior to the availability of contemporary genetic techniques, the phylogeny of Suidae was based solely on comparative morphology of skeletal remains compared to modern specimens, cytogenetic determination, and utilization of other morphometric characteristics (Allen et al. 2001). Today, the use of genetic tests allows for differentiation between lineages and tracking of historical introductions (see Aravena et al. 2015; Linderholm et al. 2016; Soria-Boix et al. 2017; Zhang et al. 2016). Given this recent bloom in phylogenetic work, the goal of this manuscript is to summarize the existing literature describing the history of global range expansion among *S. scrofa* and the corresponding changes to the biology of the species as it transitioned from wild to domestic to feral within this context. As such, this paper may serve as a reference for understanding differences between past, present, and future populations of the species globally.

Wild boar

Suides diverged as a unique clade separate from other Artiodactyla >34 million years ago in Southeast Asia (Frantz et al. 2016; Ruvinsky and Rothschild 1998). Further divergence of taxa within the *Sus* genus thereafter resulted from geographic isolation due to fluctuations in sea level (Frantz et al. 2016). The nine extant species of the *Sus* clade (*S. ahoenobarbus*, *S. bucculentus*, *S. barbatus*, *S. cebifrons*, *S. celebensis*, *S. philippensis*, *S. scrofa*, *S. salvinus*, and *S. verrucosus*) arose in different regions including the Malay Peninsula, Sumatra, Java, Borneo, and the Philippines between 3 and 5 million years ago (Choi et al. 2014; Frantz et al. 2013b, 2016; Larson et al. 2007; Mayer et al. 2019). Subsequently, the dispersal of wild populations of *S. scrofa* from southeastern Asia occurred 0.8–2 million years ago, until the species covered much of Eurasia (Frantz et al. 2016; Liu

et al. 2019). Following the dispersal of *S. scrofa* across Eurasia, wild lineages ancestral to Europe and Asia diverged between 500,000 and 1 million years ago (Fernandez et al. 2011; Giuffra et al. 2000; Groenen et al. 2012). Thereafter, interactions between the European and Asian populations occurred primarily in the northwest of modern Iran (Khalilzadeh et al. 2016).

Presently, the native range of *S. scrofa* in Asia occurs throughout the continent and across parts of Island Southeast Asia (Barrios-Garcia and Ballari 2012; Dobney et al. 2009). This native range includes regions ranging from the Malay Peninsula, westward through Southern Asia, including India and China, as well as northward along the eastern coast including genetically distinct populations in both Japan and the Korean Peninsula (Hongo et al. 2002). The only environmental limitations to wild populations' expansion into the rest of Asia are winter conditions in Russia where snow depth limits population expansions (Markov et al. 2019) as well as the arid climates of the Gobi Desert and Mongolian steppe (Barrios-Garcia and Ballari 2012; Kirilyuk et al. 2012) as predictively modeled by Lewis et al. (2017).

West of Asia, Middle Eastern *S. scrofa* populations occupy regions surrounding the Caspian Sea including, but not limited to, present day Turkey, Iran, and Kazakhstan. Limited in the far north by Siberian winters (Markov et al. 2019), *S. scrofa* expansion southward across the Arabian Peninsula is hindered by its aridity. Native Middle Eastern populations of *S. scrofa* are unique because they inhabit the crossroads between Asian and European populations (Giuffra et al. 2000). Specifically, northwestern Iran has been identified as an important center for genetic diversity among wild boar in that region, which contain alleles unique to the Middle East as well as alleles in common with both Asian and European populations (Khalilzadeh et al. 2016). Interestingly, the mountainous terrain and numerous large rivers characteristic of the region have not limited gene flow (Demirbas et al. 2016). However, while autosomal markers suggest minimal genetic differences between Middle Eastern and European populations (Ramirez et al. 2009), examinations of mtDNA indicate distinct genetic differences between the two regions (Khedertzadeh et al. 2019; Kusza et al. 2014).

In Europe, genetic delineations of native populations of *S. scrofa* have shown some disagreement in the arrangement of regional clades describing this species. However, these discussions typically organize the populations into two main populations with wild boar south of the Alps in Italy—E2—being genetically unique from the remainder of Europe—E1 (Giuffra et al. 2000; Kusza et al. 2014; Velickovic et al. 2015; Vilaca et al. 2014). Some studies additionally add third or fourth clades representing distinct genetics in Eastern Europe (Khedertzadeh et al. 2019; Kusza et al. 2014). Further, Khedertzadeh et al. (2019) grouped the wild boar of the Italian Peninsula with those of the Iberian Peninsula

deviating from prior research making this a topic warranting further consideration. Historically, these genetic distinctions were likely established by glacial expansion resulting in the Balkans, the Italian Peninsula, and the Iberian Peninsula serving as individual glacial refugia (Alves et al. 2010; Kusza et al. 2014; Vilaca et al. 2014). Thereafter, wild boar movement over the Italian Alps was likely limited while populations from the Balkans and the Iberian Peninsula were able to recolonize central Europe (Velickovic et al. 2015). Individually, populations across the three peninsulas have high levels of genetic diversity, which is likely the result of this most recent glacial maximum combining with mountainous terrain resulting in population fragmentation and bottlenecks (Alexandri et al. 2017; Alves et al. 2010; Scandura et al. 2008). However, while these bottlenecks result in a high degree of heterozygosity in European wild boar genomes (Bosse et al. 2015; Scandura et al. 2008), Asian populations of wild boar are generally more diverse and account for an overall greater percentage of the total diversity described across all wild boar (Bosse et al. 2015; Choi et al. 2014; Groenen et al. 2012).

Native populations of *S. scrofa* first expanded their range into Africa via the Strait of Gibraltar ~90,000 years ago (Blench and MacDonald 2006). During this expansion, wild populations spread along the Mediterranean and Atlantic coasts but were unable to expand further due to the Sahara Desert (Blench and MacDonald 2006). These first populations entered into present day Morocco, Tunisia, and Algeria with a genetic composition similar to that found among European

populations (Ramirez et al. 2009; Soria-Boix et al. 2017). However, wild *S. scrofa* populations did not immigrate into the eastern reaches of the African continent until traversing the Nile Corridor into Egypt, Sudan, and Ethiopia in the fourth century AD (Barrios-Garcia and Ballari 2012; Blench and MacDonald 2006). It has been surmised that, while human civilization had long been established in the region, the expansion of *S. scrofa* was not directly attributed to human-mediated dispersal (Blench and MacDonald 2006), but rather facilitated by land use change. Similar to populations in northwestern Africa, populations along the eastern coast of northern Africa are limited by the Sahara Desert.

Biology

Wild boar are usually mostly black admixed with brown, red, and white coloration, with upward curving canine teeth forming tusks among males (Graves 1984; Long 2003) (Fig. 1). The development of wild boar piglets begins in the womb (see Fulgione et al. 2017) and includes the development of taste and scent preferences allowing piglets to rapidly adapt to their environment after birth (Oostindjer et al. 2011). Once born, piglets are able to stand within minutes of birth and begin social interactions within hours (Graves 1984). Then, as juveniles, wild boar continue maturing quickly, and males can become sexually mature at 7 months of age while females may begin ovulating after only 4 months (Ahmad et al. 1995; Mauget 1981). This ability to reproduce at an early age is mirrored in the demographics of wild boar populations

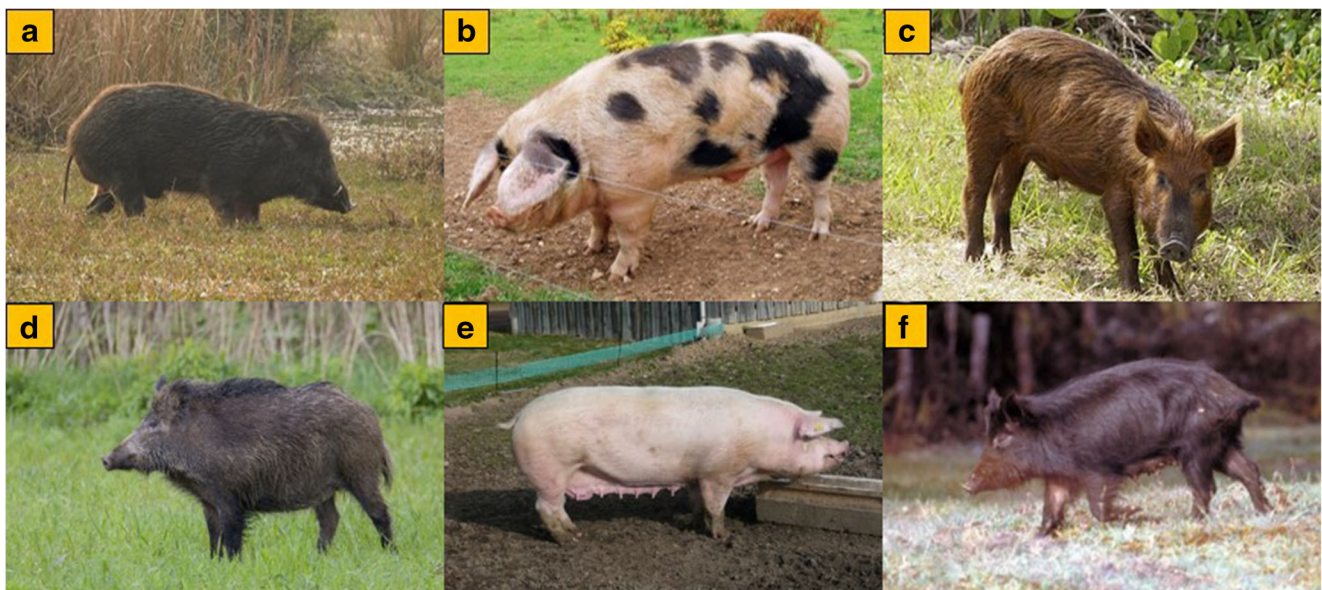


Fig. 1 Pictures of the various forms of *Sus scrofa*. **a** Male wild boar, Asia; **b** male Gloucester old spot domestic swine; **c** male feral pig, USA; **d** female wild boar, Europe; **e** female American landrace domestic swine; **f** female feral pig, USA. Important morphologic changes to note are the loss of defensive traits (dark coat color and tusks) in domestic swine in comparison to wild boar, and the return of these traits among feral pigs.

All pictures were obtained from the Wikimedia commons under the GNU free documentation license with the exception of **f**, which is available via the US Government. Original photographers are **a** Dr. Raju Kasambe, **b** Amanda Slater, **c** National Aeronautics and Space Administration, **d** Jerzy Strzelecki, **e** Zeilog, and **f** United States Geological Survey

that generally have a mean population age of only 2 years (Ahmad et al. 1995; Fernandez-Llario and Mateos-Quesada 2003). It is important to note that, while there is a large body of literature describing demographic characteristics of wild boar, interpretation of demographics must be contextual in terms of resource pulses (e.g., mast years: Gamelon et al. 2017) and in terms of hunting pressure, which has been shown to alter birthing dates and result in wild boar reproducing more quickly (Gamelon et al. 2011; Servanty et al. 2011).

Despite reaching sexual maturity quickly, wild boar continue to gain weight for their first 3 years until reaching maximum adult size (Pedone et al. 2014). At this point, average males weigh 80 to 120 kg with a great deal of variation dependent on food availability and habitat quality including males as large as 300 kg in some parts of Eurasia (Moretti 2014; Pedone et al. 2014; Ruvinsky and Rothschild 1998; Saunders 1993). Comparatively, the maximum size of females usually ranges from 45 to 100 kg (Fernandez-Llario and Mateos-Quesada 1998; Moretti 2014; Saunders 1993; Servanty et al. 2009). While female wild boar may begin ovulating as early as 4 months, it has been suggested that body weight is a more accurate predictor of sexual maturity (Ahmad et al. 1995; Servanty et al. 2009). Females generally reached sexual maturity at ~25 kg, which may be only one-third of their adult body weight (Servanty et al. 2009). Interestingly, young females became pregnant at the same frequency as larger females and produced the same number of piglets in Spain (Fernandez-Llario and Mateos-Quesada 2005) but not in Portugal (Fonseca et al. 2011) suggesting some unknown variable describing these patterns—future research on this topic is therefore suggested. Similar to body size, litter size is dependent on food availability and habitat quality (Geisser and Reyer 2005; Servanty et al. 2009). Also shown to mirror latitude in Europe (Bywater et al. 2010), this environmental dependency results in litter sizes of only 2 to 4 piglets under drought conditions, but under comparatively ideal conditions, litters may reach up to seven piglets (Ahmad et al. 1995; Fernandez-Llario and Carranza 2000).

As described above, native populations of wild boar range throughout Eurasia and parts of North Africa, and there is a significant amount of variation in the morphology and reproductive capabilities of wild boar throughout their range. As such, the numbers above should be viewed as useful descriptive averages and not steadfast rules for individual study systems. In particular, it has been suggested that sampling bias may alter important demographic information because populations existing under heavy hunting pressure are more frequently sampled due to higher availability of samples (Gamelon et al. 2011; Servanty et al. 2011).

Domestication

S. scrofa can be easily domesticated, and the traits of this species mirror those found among other domestic agricultural species including a gregarious matrilineal group structure and generally docile nature (Delgado-Acevedo et al. 2010; Graves 1984; Hampton et al. 2004a). Domestication of *S. scrofa* appears to have arisen in multiple centers between 5000 and 10,000 years ago (Choi et al. 2014; Frantz et al. 2016; Giuffra et al. 2000; Groenen et al. 2012; Larson et al. 2005; Ottoni et al. 2012; Ramos-Onsins et al. 2014). In Asia, the Tibetan Highlands and Island Southeast Asia have both been identified as likely areas of early domestication (Yang et al. 2011), as have the Mekong and lower Yangtze regions of China (Wu et al. 2007). Breeds of European origin are estimated to have been domesticated in the Fertile Crescent, with independent domestication occurring thereafter in central Europe (Caliebe et al. 2017; Giuffra et al. 2000; Ottoni et al. 2012; Ramos-Onsins et al. 2014; Scandura et al. 2008). Clear histories are difficult to obtain because of the inherent challenges of using archeological data to track the domestication process (Evin et al. 2013), but interested parties may be able to improve knowledge on this subject through modern genetic research.

Historical differences in husbandry practices between Asia and Europe delineated the two ancestral lineages. In Asia, pigs were generally raised in pens and fed human food waste resulting in a short, round breed well-adapted for pens. In contrast, European domesticated swine were generally herded through forests foraging on available food items and seasonal mast which resulted in a longer-legged breed (White 2011). Historically, the morphology of the Asian and European lineages differed enough that Charles Darwin suggested they were two different species (Giuffra et al. 2000).

Presently, > 100 breeds of domestic swine exist worldwide with frequent crossbreeding occurring to maximize production or develop unique phenotypes (Bosse et al. 2015; Maximov et al. 2019). However, it has been recognized that these high levels of crossbreeding may lead to the loss of individual breeds, which will require intentional preservation, such as those in the Henan Province of China (Qiao et al. 2019). Among the many breeds of domestic swine, some of the most well-known and therefore well-studied include the European Finnish Landrace and Asian large-white breeds (Li et al. 2014; Serenius and Stalder 2004). The dramatic phenotypic differences among breeds is likely the result of selective breeding and crossbreeding for specific traits over the past 200 years. These breeding practices have resulted in up to 20% genetic variation between European and Asian breeds indicative of the differences between the two regions (Bosse et al. 2014, 2015; Giuffra et al. 2000).

Biology

An initial step toward domestication is the selective adaptation of wild species to survive in anthropogenically altered habitats. This adaptation includes natural selection favoring higher reproductive rates and smaller body size to maximize the increased availability of resources in altered habitats (Tchernov and Horwitz 1991; Nikitin et al. 2014). After initial adaptation, manipulation of traits associated with domestication becomes clearer such as rapid reproductive and growth rates. Among domestic swine, genetic analyses have shown a high level of intentional human manipulation including morphological, behavioral, physiological, and reproductive alterations (Johnson and McGlone 2011; Rubin et al. 2012; Rutherford et al. 2013). Easily recognized results of these manipulations include the reduction of defensive characteristics commonly found in wild boar including replacing dark fur patterns with lighter patterns accented by belting or spotting and selective reduction of the canine teeth/tusks (Fig. 1; Table 1).

Some of the most important traits that have been manipulated in domestic swine are the demographic traits. In particular, domestic swine have been bred to reach maturity quickly (Lega et al. 2016). Presently, husbandry practices commonly raise domestic swine for slaughter at ~21 weeks of age. At this age, domestic swine reach body weights ranging from 95 to 120 kg (Beattie et al. 2000; Cannon et al. 1996; Van Bameveld 2003). However, breeding males and females are often much larger with commonly used breeds of swine weighing between 250 and 450 kg, with the largest pigs ever recorded weighing >750 kg (FAO 2009; Mizelle 2011). Typical slaughter weights are similar to those of fully mature male wild boar, which generally do not

reach these weights until their third year, and signifies the selective pressure implemented on domestic swine by humans. The maximization of litter size and piglet survival has similarly been selected for in animal husbandry. Individual litters can range from as few as 6 to more than 21 piglets depending on the domestic breed (Baxter et al. 2013) and litters can be born up to twice annually (Ali 1994). Typically, western breeds of domestic swine have 12–14 teats resulting in litters ranging from 8 to 12 piglets with 10–11 normally surviving (Andersen et al. 2011; Milligan et al. 2001). Comparatively, Chinese breeds average 18 teats resulting in larger litter sizes (Baxter et al. 2013; Ding et al. 2009). The number of teats is important to the survival of individual piglets and can be attributed in large part to milk access which correlates strongly with teat availability (Baxter et al. 2013; Ding et al. 2009; Milligan et al. 2001; Rutherford et al. 2013).

Feralization

The presence of feral populations of *S. scrofa* globally mirrors routes of global expansion and exploration by humans (Barrios-Garcia and Ballari 2012; Crosby 2004; Ramirez et al. 2009). Frequently, the release of domestic swine into the wild was accidental due to the escape of domesticated populations. However, in many regions, *S. scrofa* was intentionally introduced by European explorers as food sources for return trips (Fig. 2). These populations of feral pigs frequently exhibit greater environmental impacts because they reside in habitats maladapted to large omnivores (Barrios-Garcia and Ballari 2012; Campbell and Long 2009; Hess 2016).

Table 1 Biological characteristics of *Sus scrofa*. Important comparisons to recognize are the increased growth and reproductive rates present among domestic swine in comparison to wild boar. These characteristics, however, largely return to baseline levels among feral pigs. Please note that these are typical averages with high variability between regions particularly when considering the massive size to which some domestic swine have been raised (see Mizelle 2011) and the differences between breeding pigs and those raised for slaughter.

	Wild boar	Domestic swine	Feral pigs
Coloration	Black with brown, red, and white admixing	White with belts or spots of other colors common	Black with possible red or white stripes or spots
Mean population age	2 years	< 21 weeks	1.5 years
Mean adult body mass	45–120 kg	95–120 kg	30–120 kg
Maximum reported mass	~ 300 kg	> 500 kg	~ 250 kg
Age at completion of growth	3 years	21 weeks	3–4 years
Age at sexual maturity	4 months	4 months	5 months
Frequency of pregnancies	Annually/biannually	Annually/biannually	Annually/biannually
Number of offspring	2–7/litter	6–21/litter	4–8/litter

Additionally, there is a potential for the biased selection of populations with high hunting pressure because these populations are easier to study (Servanty et al. 2011). This bias may therefore result in differences in recorded demographics (Servanty et al. 2011), and this bias may explain differences between feral pigs and wild boar because feral populations are generally heavily hunted because they are considered invasive (Tchernov and Horwitz 1991)

In the Pacific, nearly every island throughout the region has supported feral pigs, with active populations still present on the majority of islands (Hess et al. 2019; Wehr et al. 2018). This includes numerous islands ranging from populations on the Indonesian Islands, on the Northern Mariana Islands, throughout Polynesia, and in Australia and New Zealand (Barrios-Garcia and Ballari 2012; Long 2003; Wehr et al. 2018). The history of these feral populations present throughout the Pacific is closely associated with human exploration. Two separate dispersals of *S. scrofa* into Oceania have been associated with human expansion to Wallacea (Larson et al. 2005, 2007) with subsequent domestic swine being spread by ancient Polynesians eventually reaching the Hawaiian Islands between 1000 and 1200 AD (Burney et al. 2001; Dye and Pantaleo 2010; Field and Graves 2008; Kirch 2011). *S. scrofa* did not, however, reach Australia and New Zealand until European exploration through Polynesia in the late eighteenth century, which brought European *S. scrofa* to nearly every island throughout the Pacific (Clarke and Dzieciolowski 1991; Gongora et al. 2004). Presently, *S. scrofa* inhabiting Australia are almost entirely composed of feral pigs originating from a mix of domestic swine from Asian and wild boar from Europe attributable to human dispersal at local scales (Spencer et al. 2006; Spencer and Hampton 2005).

Geographically, the only connections between the Americas and continents within *S. scrofa*'s native range are in the far northern regions where cold climates have prevented the natural spread of *S. scrofa* outside of Eurasia. As such, the spread of *S. scrofa* outside of its native range can largely be attributed to European exploration, which introduced *S. scrofa* to new regions globally throughout recent history (Fig. 2). For example, McCann et al. (2014) showed that at least fifteen different haplotypes of *S. scrofa* from at least thirty different locations worldwide are present in the USA alone, and these haplotypes largely represent introductions occurring after colonization. These North American populations cluster into eight primary groups with notable admixing of genes from different regions (Mayer et al. 2019; McCann et al. 2018). Largely, North American populations are limited by colder climates with only a few populations surviving in Canada (Brook and van Beest 2014; McClure et al. 2015). However, future monitoring of population expansion associated with climate change in North America will be important, particularly in the Northern United States and southern Canada. Elsewhere in North America, *S. scrofa* are

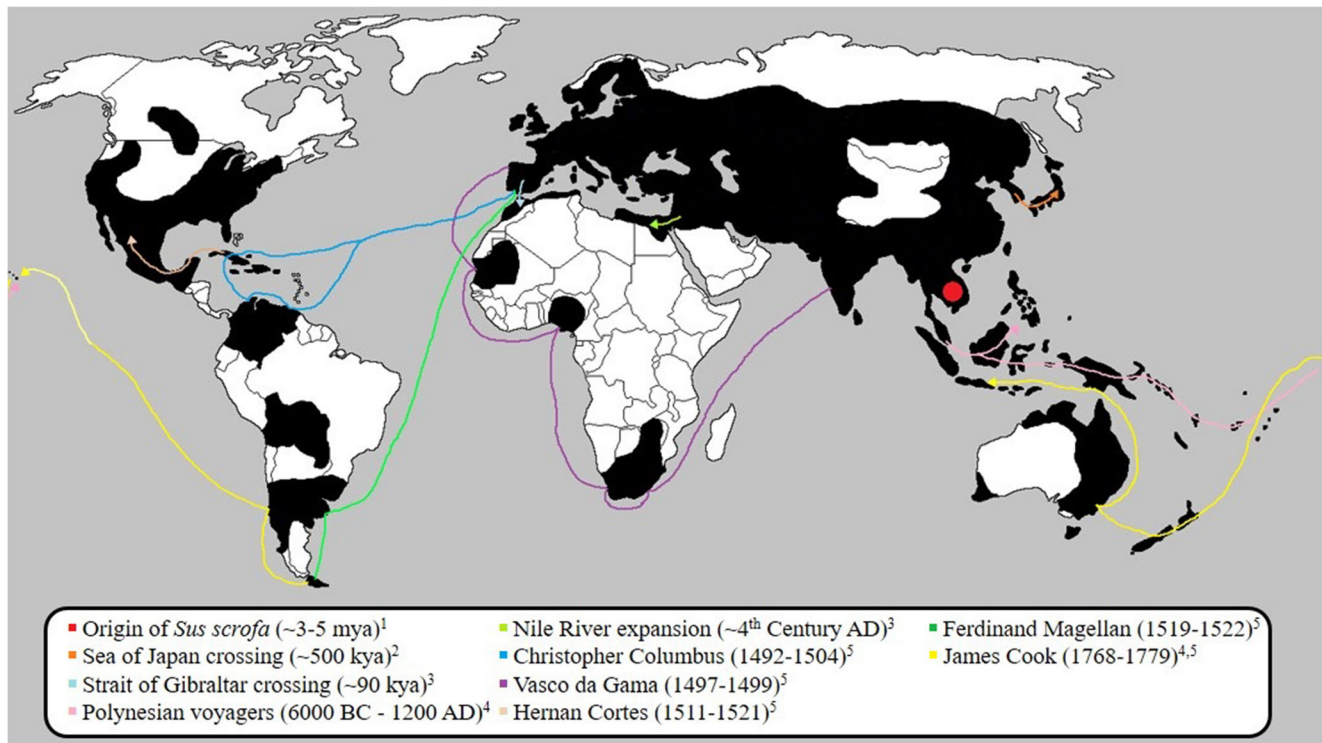


Fig. 2 Map of global *Sus scrofa* dispersal with the corresponding occurrence times labeled. Range expansion throughout Eurasia took place between 0.5 and 2 million years ago likely with significant changes in the range of *S. scrofa* following global climatic trends. Subsequent expansions of pigs are based on genetic analyses, historical climatic estimates, and travel records of historic voyagers. Further, these

times should be viewed as estimates, and only the initial arrival dates are listed with future expansion requiring time to pass, such as broad-ranging expansion and multiple introductions in North America (McClure et al. 2015). Regarding individual dispersals, see ¹(Frantz et al. 2016); ²(Watanobe et al. 2003); ³(Blench and MacDonald 2006); ⁴(Wehr et al. 2018); and, ⁵(Crosby 2004)

known to inhabit large portions of Mexico and Central America as well as numerous Caribbean islands associated with European exploration (Barrios-Garcia and Ballari 2012; Wilson and Reeder 2005).

In South America, feral populations currently exist in Argentina, Brazil, Chile, Columbia, Ecuador, Uruguay, and Venezuela and are primarily limited by the spread of introductions rather than environmental factors (Barrios-Garcia and Ballari 2012; Hegel et al. 2019; Novillo and Ojeda 2008; Wilson and Reeder 2005). Their initial introduction into these regions is almost certainly the result of intentional introductions by sailors as food sources (Crosby 2004). However, their proliferation and genetic diversity can be more generally attributed to trade (Ramirez et al. 2009), and there is wide agreement that the release of *S. scrofa* into the region has occurred on multiple occasions after domestic breeds from both Europe and Asia became feral either intentionally or accidentally (Aravena et al. 2015; Garcia et al. 2011; Ramirez et al. 2009).

Available information regarding feral pig populations in Africa is sparse. However, the range of *S. scrofa* on the continent certainly includes resident populations in South Africa, Zimbabwe, and Nigeria (Blench and MacDonald 2006; Long 2003). These locations mirror historical trade routes and indicate human introductions of the species, with genetic analyses suggesting *S. scrofa* in southern Africa are more closely related to far eastern breeds while those in western Africa are more closely related to European and North African populations (Ramirez et al. 2009). Similar to South America, the range of feral pigs in Africa appears to be limited by the locations of introductions and not by inherent environmental factors in these areas, a topic warranting future study.

Biology

Similar to their wild boar ancestors, juvenile feral pigs are often primarily black, but additional varieties include types with reddish striping or white spotting and/or belting. As adults, feral pigs have a sparse, coarse coat, which is usually all black with spotting and the occasional presence of white feet (Fig. 1). These traits, unique to feral pigs in comparison to wild boar, are generally indicative of prior domestication (Graves 1984; Long 2003; Tomich 1986). As was seen among wild boar, feral pig weight is highly dependent on environmental factors and food availability (Dexter 2003). As such, there is a wide range of body sizes found among feral pigs with typical mean weights ranging from 30 to 60 kg, and in some rare cases, weights have been reported of females reaching up to 90 kg and males reaching up to 250 kg (Giffin 1978). These decreases in body mass likely stem from remnant genetics of initial domestication pressures selecting for smaller body sizes and inbreeding resulting from small source populations as suggested by Nikitin et al. (2014) in combination with selective pressures for increased rates of growth and reproduction mirroring the high food availability and heavy hunting

pressure often found in areas where *S. scrofa* are nonnative. Further, biases stemming from research sampling occurring among populations specifically targeted for removal via recreational hunting or direct management could result in data below the global norm (Tchernov and Horwitz 1991).

Despite their ancestral relationship to domestic swine, feral pigs generally have similar reproductive rates to wild boar (Table 1). Among feral pigs, typical litter sizes are 4 to 8 piglets (Diong 1982; Hess et al. 2006; Snow et al. 2019; Taylor et al. 1998). This regression of litter sizes among feral pigs compared to domestic swine has been attributed to lower ovulatory rates among feral pigs (Hagen and Kephart 1980), but may also be due to lack of selective pressure existing among earlier populations of domestic pigs during the European age of exploration. In feral populations, older, heavier females became pregnant more often than their younger, smaller counterparts, with these older, larger females generally producing larger litters, but yearling females still regularly become pregnant (Snow et al. 2019; Taylor et al. 1998), a pattern partly in contrast to data examining wild boar reproduction. Once feral pigs become reproductively active, females typically become pregnant between 0.5 and 2 times/year, with 25–50% of females being pregnant or suckling at any point depending on climate and resource availability (Diong 1982; Hess et al. 2006; Sierra 2001; Snow et al. 2019; Taylor et al. 1998).

Conclusions

Natively occurring throughout Eurasia, wild boar have established themselves as a highly adaptable species capable of living in all but the coldest and most arid regions. Mirroring this adaptability, genetic analyses of wild boar indicate the Iberian Peninsula, Italian Peninsula, and the Balkans served as refugia during the last glacial maximum with genetic interchange occurring since then with the exclusion of some Italian populations (Velickovic et al. 2015). However, despite genetic, demographic, and morphometric variability being high in Europe, it has been accepted that the greatest diversity among wild boar occurs in southeast Asia near the origin of the species, as is often the case among all species (Bosse et al. 2015).

Following human expansion into areas overlapping with wild boar, the domestication of *S. scrofa* occurred on multiple occasions including parts of China, the Fertile Crescent, and central Europe (Scandura et al. 2008; Wu et al. 2007). Following the trends of other domesticated species, the domestication of *S. scrofa* resulted in domestic swine that reached adult size more quickly and was capable of producing much larger litters (Table 1). Selective breeding has since resulted in domestic swine with belted or spotted fur patterns and reduced tusk size.

Outside of Eurasia, the initial global range expansion of *S. scrofa* can largely be attributed to humans during the European age of exploration (Fig. 2). During this era, domestic swine were intentionally introduced to many regions and set free to provide a food source for explorers upon their return to an area. Since then, populations have largely been introduced elsewhere either intentionally to serve as a game species or via accidental release from domestic populations (Mayer et al. 2019). Accompanying this feralization of intentionally and/or accidentally released domestic swine is an overall return to the traits of wild boar (Table 1). The return of defensive characteristics—such as darker fur patterns and larger tusks (Fig. 1)—can be logically explained by selective pressures associated with predation and intra-species competition. However, the regression of increased growth and reproductive rates is less clear. Likely, the increased competition for resources in natural habitats compared to agricultural systems can explain some of this change. Further, it is possible feral pigs are more similar to wild boar because the greatest portion of selective breeding has occurred more recently than the European age of exploration resulting in *S. scrofa* released during that era being naturally more similar to wild boar than modern domestic swine.

Future work

The patterns described by this paper indicate that, largely, the demographic characteristics of feral pigs are most similar to those of wild boar indicating an overall regression in those traits. However, a growing field of research important in future studies is the examination of hybridizing wild boar and feral pigs within the native range of *S. scrofa*. In 2011, Scandura et al. stated that introgression of feral pig genetics into wild boar in Europe was minimal; since then, studies have begun to emerge indicating potential changes associated with this pattern of hybridization. For example, the hybridization of domestic swine with wild boar has been shown to increase reproductive rates (Fulgione et al. 2016), and it is possible other biological traits are being influenced by this hybridization warranting future research (Frantz et al. 2013a). An important hotspot of this hybridization, Bosnia and Herzegovina and the Balkans as a whole have been identified as areas with high proportions of wild boar exhibiting domestic swine genetics (Iacolina et al. 2018). The results of future work on this topic should allow improved understanding of the patterns described by this paper in regard to perceived regression of demographic traits among feral pigs being due to a lack of selective breeding rather than a true regression. Further, the results of these studies may hold pertinent information for land managers monitoring *S. scrofa* populations in regard to human-wildlife interactions.

Of additional importance to land managers is the future development of research examining the range expansion of

S. scrofa. In North America, feral pigs are showing major range expansions northward in correspondence to global climate change (McClure et al. 2015; Snow et al. 2017), a pattern reflected in Eurasia (Danilov and Panchenko 2012; Markov et al. 2019). In both areas, tracking these expansions will be important due to the known impacts of feral pigs on natural environments in combination with potential hybridization due to both intentional and unintentional releases (Barrios-Garcia and Ballari 2012; Danilov and Panchenko 2012; Morelle et al. 2016; VerCauteren et al. 2019). Additionally, future studies examining the expansion of feral populations in both South America and Africa will be interesting because populations in these regions have thus far likely been limited by human dispersal and not by environmental factors, but research on this topic is lacking. As such, their spread in these regions has the potential to serve as an important model for understanding the invasion process among large mammals. Further, genetic analyses of these populations will allow for improved insight into the history of introductions into these regions thereby providing a more useful baseline from which to track these expansions (e.g., Aravena et al. 2015).

Finally, recent publications by Barrios-Garcia and Ballari (2012) and VerCauteren et al. (2019) have provided detailed summaries of the impacts of feral pigs. These publications provide the reader with a distinct understanding of the numerous effects feral pigs have on native environments. However, knowledge gaps remain. For example, while this paper has attempted to summarize our knowledge of demographic patterns among feral pigs, our understanding of patterns regarding spatiotemporal variation of these traits is lacking among feral pigs (Snow et al. 2019) and producing more succinct broad-scale work on this topic will be useful (i.e. Lewis et al. 2017 for wild boar) as will similar work aiming to support management decisions at local scales (i.e., Risch 2019). Further, beyond the range and demographic variation described in this paper, a meta-analysis of spatiotemporal variation of the impacts of feral pigs on native environments is recommended to help explain differences in environmental impacts, such as the variable impacts on soils observed across multiple regions (Wehr et al. 2018, 2019). Toward the completion of such an analysis, it is important that researchers and land managers continue to collect data on the individual impacts of feral pigs to their local ecosystems to improve our understanding in both the current and expanding range of feral pigs.

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