1 Wild Boar *Sus scrofa* Linnaeus, 1758

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L. Corlatti, F. E. Zachos (eds.), *Terrestrial Cetartiodactyla*, Handbook of the Mammals of Europe,
https://doi.org/10.1007/978-3-030-24475-0_17

Common Names

English	(Eurasian) wild boar
German	Wildschwein
French	Sanglier
Spanish	Jabalí
Italian	Cinghiale
Russian	Кабан

Taxonomy, Systematics and Paleontology

The origin of *Sus scrofa* (Fig. 1) is in Asia, where a radiation of the genus *Sus* into several different taxa has occurred during the last 5 million years (Frantz et al. 2013a). In particular, an evolutionary engine for such suids (like the Rift Valley for hominids) was represented by the islands of South East Asia, where a vast number of related taxa occur nowadays. According to genomic data, the speciation of the Eurasian wild boar started during the Pliocene (4–4.5 million years ago (mya)), accompanied by its spread across the Asian continent and the radiation into regionally diverging populations (Frantz et al. 2013a). The spread of the species to the west was belated and its appearance in Europe, according to the first fossil records, goes back to the late Early Pleistocene around 900-800 thousand years ago (kya) (Cherin et al. 2020) during a period of great woodland expansion. During the Late Pleistocene, the wild boar was severely affected by cooling periods, restricting its range to southern regions. Converging paleontological and genetic data revealed refugial areas in southern Europe where the species survived during the last glaciation (Vilaça et al. 2014; Veličković et al. 2015). The following postglacial recolonization restored the species in almost the whole continent. An important role in the species' history was played by pig domestication, a long-lasting process that started in Asia about 10 kya and received a tremendous boost during the last centuries (White 2011). The relevance of pig domestication resides in the parallel evolution of the wild ancestor with its domesticated form, manipulated by humans. Their persistent contact and crossbreeding have shaped populations of the two forms over time (Frantz et al. 2013a) and still represent a powerful evolutionary force for the Eurasian wild boar.

High levels of intraspecific variation led to a repeatedly revised taxonomy. The first comprehensive assessment distinguished 16 subspecies, clustered into four groupings based on geographical and morphological criteria: Western, Eastern,

Fig. 1 Wild boar (photograph by and courtesy of I. I. Serval)

Indian, and Indonesian "races," the first one occurring in Europe (Groves 1981). Later on, Genov (1999) reviewed the variation in cranial morphology and confirmed the wild boar as a single polytypic species. This view was then questioned (Groves 2007) and more recently revised, elevating most of the 16 originally identified subspecies to species rank (Groves and Grubb 2011), although this splitting approach has received severe criticism. Under this classification, *Sus scrofa* represents a narrower taxon ranging from the Iberian Peninsula and Maghreb to Central Asia and is the only wild pig occurring in Europe. Here, four different subspecies were proposed on the basis of morphological and karyological data (Groves 2007):

S. s. scrofa Linnaeus, 1758: western subspecies (from Iberia to Belarus); variable size from south (smaller) to north (larger)
S. s. attila Thomas, 1912: from central Belarus and the Carpathians to Western Russia; a large subspecies
S. s. meridionalis Major, 1882: endemic to the islands of Sardinia and Corsica, formerly believed to include the wild boar inhabiting the south of Spain; a small subspecies
S. s. lybicus Gray, 1868: from the Balkans to the Near East; a small subspecies

Recent phylogeographic studies weakly supported this partition, confirming the genomic peculiarity of *S. s. meridionalis* from Sardinia (Iacolina et al. 2016) and suggesting some levels of differentiation for the populations inhabiting mainland Italy (where the endemic subspecies *S. s. majori* De Beaux and Festa, 1927 had been proposed in the past, see Scandura et al. 2008) and the southern Balkans (where several endemic lineages occur, Alexandri et al. 2012). On the other hand, no sharp genetic discontinuity emerged in Eastern Europe between putative *S. s. scrofa* and *S. s. attila* (Vilaça et al. 2014).

Current Distribution

The wild boar, also thanks to human action, has one of the widest distributions among terrestrial mammals and is abundant in many parts of its range. Such a broad range relies on the presence of individuals at different domestication stages, from wild to domestic, going through feral and hybrid forms. The species is now present on all continents but Antarctica, including many oceanic islands. In Europe, wild boar are present in most continental areas and on many islands (see Fig. 2). Being a thermophilic species, the northern boundary of its distribution is limited by snow depth and winter temperature, and in the last decades, it has notably expanded northwards in consequence of climate change (Danilov and Panchenko 2012). Island populations have been strongly influenced by humans. Historical populations occur in Corsica and Sardinia, where the species was introduced during the Neolithic. Once extinct, wild boar were recently reintroduced in Sicily and reappeared in Great Britain and Ireland, where the local populations proved to be represented by hybrid individuals, likely escaped from farms or illegally released (Frantz et al. 2012; McDevitt et al. 2013). In Cyprus, the species was illegally reintroduced in 1994, but went extinct again in 2004 (Hadjisterkotis and Heise-Pavlov 2006). Many other minor islands host populations of doubtful or admixed origin. In continental Europe, after a reduction in both distribution and abundance till the beginning of the twentieth century, especially after World War II the species experienced a strong recovery. Also thanks to milder climatic conditions, it has naturally recolonized regions like Estonia and Denmark, despite the attempts to prevent it in the latter country (Apollonio et al. 2010). A hybrid stock escaped from farms is the source of the present population in Sweden (Lemel et al. 2003), whose spread has recently reached southern Norway (Østfold county, VKM et al. 2018).

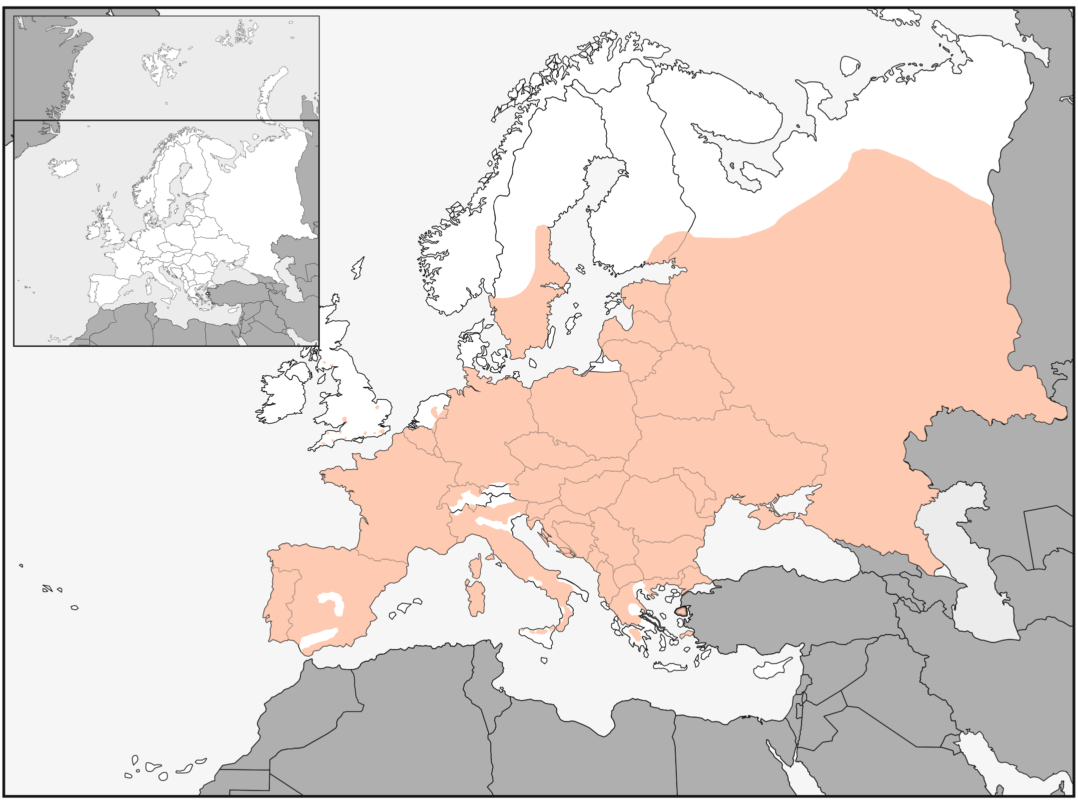

Fig. 2 Distribution map of the European wild boar, based on the IUCN Red List of Threatened Species. Version 2018–1 with kind permission. (Map template: © Copyright Getty Images/iStockphoto)

Description

Wild boar distribution covers a wide range of habitats and significant variation in coat color and size can be observed (Fig. 3). The general trend sees the smallest animals (maximum 70–90 kg) in the south and on Mediterranean islands, while larger animals (maximum *c.* 300 kg) are present in the northern and north-eastern parts of its range. Accordingly, other body measurements also show wide variation. One of the most striking is the head. Skull size has been a key trait for taxonomy, ranging in length between 30 and 47 cm across European wild boar (Keuling et al. 2018). Body length goes from 90 to 200 cm, but tail length (15–40 cm) and shoulder height (55–110 cm) are also highly variable (Keuling et al. 2018). The species is strongly built, with moderately short tail and legs, with the anterior legs longer than posterior ones, and the frontal part of the skull is more developed than the frontal area. Additionally, females are smaller than males, on average around 40% (Keuling et al. 2018). Coat color varies with age. Piglets are striped up to about 4 months, then they turn into a reddish color and, around one year of age, they display the adult pelage. The latter goes from brown to almost black and, with age, it can turn into grey.

Fig. 3 Wild boar from different areas in Europe. (**a**) Sardinia, Italy (photograph by M. Scandura); (**b**) Coto Doñana, Spain (photograph by J. Vicente); (**c**) Bulgaria (photograph by and courtesy of F. Morimando)

Table 1 Estimated tooth eruption. Teeth in parentheses might be absent

Age	Incisors	Canines	Premolars	Molars
Birth	$\mathrm{i}\,\frac{3}{3}$	$\mathrm{c}\,\frac{1}{1}$		
2 months	$\mathrm{i}\,\frac{1}{1}\,\frac{3}{3}$	$\mathrm{c}\,\frac{1}{1}$	$\mathrm{p}\,\frac{3}{3}\,\frac{4}{4}$	
2–4 months	$\mathrm{i}\,\frac{1}{1}\,\frac{2}{2}\,\frac{3}{3}$	$\mathrm{c}\,\frac{1}{1}$	$\mathrm{p}\,\frac{2}{2}\,\frac{3}{3}\,\frac{4}{4}$	
5–6 months	$\mathrm{i}\,\frac{1}{1}\,\frac{2}{2}\,\frac{3}{3}$	$\mathrm{c}\,\frac{1}{1}$	$\mathrm{p}\,\frac{2}{2}\,\frac{3}{3}\,\frac{4}{4}$	$\mathrm{M}\,\frac{1}{1}$
7–8 months	$\mathrm{i}\,\frac{1}{1}\,\frac{2}{2}\,\frac{3}{3}$	$\mathrm{c}\,\frac{1}{1}$	$\mathrm{p}\,\frac{2}{2}\,\frac{3}{3}\,\frac{4}{4},\,(\mathrm{P}\,\frac{1}{1})$	$\mathrm{M}\,\frac{1}{1}$
8–9 months	$\mathrm{i}\,\frac{1}{1}\,\frac{2}{2},\mathrm{I}\,\frac{3}{3}$	$\mathrm{c}\,\frac{1}{1}$	$\mathrm{p}\,\frac{2}{2}\,\frac{3}{3}\,\frac{4}{4},\,(\mathrm{P}\,\frac{1}{1})$	$\mathrm{M}\,\frac{1}{1}$
10–12 months	$\mathrm{i}\,\frac{1}{1}\,\frac{2}{2},\mathrm{I}\,\frac{3}{3}$	$\mathrm{C}\,\frac{1}{1}$	$\mathrm{p}\,\frac{2}{2}\,\frac{3}{3}\,\frac{4}{4},\,(\mathrm{P}\,\frac{1}{1})$	$\mathrm{M}\,\frac{1}{1}\,(\frac{2}{2})$
12–15 months	$\mathrm{i}\,\frac{2}{2},\mathrm{I}\,\frac{1}{1}\,\frac{3}{3}$	$\mathrm{C}\,\frac{1}{1}$	$\mathrm{p}\,\frac{2}{2}\,\frac{3}{3}\,\frac{4}{4},\,(\mathrm{P}\,\frac{1}{1})$	$\mathrm{M}\,\frac{1}{1}\,\frac{2}{2}$
15–18 months	$\mathrm{i}\,\frac{2}{2},\mathrm{I}\,\frac{1}{1}\,\frac{3}{3}$	$\mathrm{C}\,\frac{1}{1}$	$\mathrm{p}\,\frac{2}{2}\,\frac{3}{3},\ \mathrm{P}\,(\frac{1}{1})\,\frac{4}{4}$	$\mathrm{M}\,\frac{1}{1}\,\frac{2}{2}$
20 months *c.*	$\mathrm{I}\,\frac{1}{1}\,\frac{2}{2}\,\frac{3}{3}$	$\mathrm{C}\,\frac{1}{1}$	$\mathrm{P}\,(\frac{1}{1})\,\frac{2}{2}\,\frac{3}{3}\,\frac{4}{4}$	$\mathrm{M}\,\frac{1}{1}\,\frac{2}{2}$
22–28 months	$\mathrm{I}\,\frac{1}{1}\,\frac{2}{2}\,\frac{3}{3}$	$\mathrm{C}\,\frac{1}{1}$	$\mathrm{P}\,(\frac{1}{1})\,\frac{2}{2}\,\frac{3}{3}\,\frac{4}{4}$	$\mathrm{M}\,\frac{1}{1}\,\frac{2}{2}\,\frac{3}{3}$

Winter pelage, which includes a conspicuous dorsal mane in adult males, starts growing in the summer, the change is complete by the autumn, and it is then lost in late winter early spring. Upper and lower canines are well developed in the form of tusks. In males, upper canines curve out and upward and lower canines are long, protruding from the mouth and kept sharp by rubbing against the upper ones; they have a predominant role of defense. At birth, wild boar have eight primary teeth, while adults have 44 permanent teeth. Changes in dentition are commonly used to estimate age of individuals (Table 1).

Physiology

The wide distribution of the species highlights its ecological and physiological plasticity, enabling it to adapt and exploit the opportunities offered by a wide range of environments. Physiologically it is, therefore, a "generalist" animal. The wild boar is the ancestor of domestic pig (*Sus scrofa domesticus*, the most important animal species used for meat production worldwide), which has been often used as a model to biomedical research. This species has highly developed auditory and olfactory senses for the detection of predators, communication, and foraging. Wild boar do not differentiate all colors (Fulgione et al. 2017) and do not have a *tapetum lucidum* (residual light amplifier), and therefore, the ability to see in the dark is less relevant than the olfactory and auditory senses to perceive information about the environment. The tactile sense is well developed, especially in the oral and lip regions in order to detect food during rooting. A variety of scent glands secrete odorous compounds: preputial, anal, metacarpal, mandibular and salivary, tusk, lip, Harderian, and eyelid. Steroid pheromones in the saliva and preputial secretions inform on the reproductive status of males and may induce females in estrus to stand for copulation (Vandenbergh 1988). Digestion is rapid, adapted to the fast transition of food, and efficient for a large variety of nutrients (can be classified as dietary generalists), although the fermentation of cellulose, occurring in the *caecum*, is only partial. During late pregnancy and lactation, females experience higher protein and energy requirements, which may affect the survival of piglets (Vetter et al. 2015).

Wild boar prefer warm temperatures and do not tolerate extreme cold and hot dry environments. This species shows a limited metabolic capacity to produce heat without shivering and has very few sweat glands. Therefore, cold winters may impact survival, especially among piglets, since mass-specific metabolic rate is low and thermoregulatory costs cannot be compensated by the available resources when energetic food is scarce. In southern latitudes, hot summers, together with seasonal scarcity of food, can also impact survival. However, wild boar have developed behavioral thermoregulation strategies to cope with cold and hot conditions (Vetter et al. 2015). Climate change may favor wild boar population growth by buffering the negative effect of cold winters on survival and reproduction and increasing food availability (Vetter et al. 2015). Wild boar may store large amounts of fat, which helps to survive when food is scarce (Merta et al. 2014). Body condition (the amount of energy stored in organs and tissues) is especially relevant to health, reproductive performance, and population dynamics of the species (see section "Life History"). Consequently, kidney fat index and other measures of fat deposits (e.g., brisket, rump fat thickness) and different biometrical procedures (including regression approaches based on multiple biometric measures) have been used to assess it (e.g., Risco et al. 2018). Hematological and biochemical parameters in wild boar sera can be used to obtain insight into its metabolism and physiology. Nonetheless, reference values often differ among studies and with that of domestic pigs, evidencing a wide range of factors may affect them, such as environment, season, diet, age, and stressors (Casas-Díaz et al. 2015).

Genetics

Chromosomes

$2n = 36–38$, shared with domestic pigs. The number of chromosomes is variable because of a Robertsonian translocation involving chromosomes 15 and 17 (McFee et al. 1966). $2n = 36$ is the basic condition of western populations, whereas $2n = 38$ is typical of Asian wild boar (from South-East Asia to Turkey and Russia). Crossings between the two groups produce fertile hybrid individuals with $2n = 37$, which are common in admixed European populations (see Table S1 in Scandura et al. 2011a and references therein).

Phylogeny and Phylogeography

Phylogenetic relationships within *Sus scrofa* have been reconstructed by the analysis of mitochondrial DNA (mtDNA) and, more recently, by genome-wide analysis, contributing to disclose complex evolutionary interactions, including long-lasting introgressive hybridization with domesticated pigs and interspecific gene flow with other related suids in South-East Asia (Groenen 2016).

Whole-genome sequencing data provided a high-resolution phylogeny of the genus *Sus*, giving insights into the chronology of divergence between European and Asian populations, dated back to around 1 mya (Groenen et al. 2012; Frantz et al. 2013a). Genomic data are also informative on the demographic history of the European population, which reached a minimum during the last glacial maximum, around 20 kya, in parallel with the species' retreat to southern refugia (Groenen et al. 2012).

Different mtDNA clades are observed in the Eurasian wild boar, most of which occur in southern Asia (Larson et al. 2005), according to the abovementioned evolutionary history of the species. Only a few lineages are found in Europe, namely a pan-European clade (E1), an endemic Italian clade (E2), and an East Asian clade (A), whose occurrence in European wild boar is commonly attributed to genetic introgression from domestic pigs belonging to international commercial breeds (Scandura et al. 2011a; Vilaça et al. 2014). In fact, pig breed amelioration in past centuries involved the intentional crossbreeding of European pigs with Asian breeds (White 2011). Some Near Eastern (NE) haplotypes are also occasionally found in Eastern Europe and seem the result of natural gene flow (Alexandri et al. 2012). The overall phylogeographic pattern of the species in Europe is consistent with a major impact by Quaternary peri-glacial dynamics rather than by recent human-induced events (Scandura et al. 2008; Vilaça et al. 2014). Accordingly, a higher genetic diversity in southern peninsulas (i.e., glacial refugia) and a gradient of decreasing diversity northwards are observed (Alexandri et al. 2012; Vilaça et al. 2014; Veličković et al. 2015), as well as the signal of a postglacial population expansion (Scandura et al. 2008).

Genetic Diversity and Structuring

The genetic diversity of European wild boar is low compared to that of the Asian wild boar, mostly as a consequence of the ancient colonization history and of the bottlenecks undergone during the Quaternary glaciation (Groenen et al. 2012). Nonetheless, the genetic diversity of local populations can vary remarkably as a consequence of demographic fluctuations, degree of isolation, hybridization with domestic pigs, and human-mediated gene flow (Scandura et al. 2011a). Only a few studies have assessed genetic variation at a continental scale, while a number of investigations have explored local situations that are not directly comparable because of the use of different molecular markers and sampling designs. As expected on the basis of glacial/interglacial dynamics, southern peninsulas (Iberia, Italy, and Balkans) host a large amount of the overall diversity observed in European wild boar, showing endemic mtDNA lineages and haplotypes (Scandura et al. 2008; Alexandri et al. 2012; Vilaça et al. 2014; Veličković et al. 2015). High genetic variation in some wild boar populations may be affected by the local degree of anthropogenic introgression (see section "Hybridization"). At mtDNA, the effect of introgression from domestic pigs is reflected by the occurrence of Asian haplotypes, whereas at autosomal markers (i.e., microsatellites and single nucleotide polymorphisms (SNPs)), the assessment of the impact of introgression is more challenging. Therefore, genetic variation in wild boar populations should be evaluated with caution and only the richness of its endemic component can be interpreted as really informative under an evolutionary and conservation perspective. For example, populations like Castelporziano, Maremma, and Sardinia in Italy (Scandura et al. 2008; Iacolina et al. 2016), central Greece and the Dinaric region in the Balkans (Alexandri et al. 2012; Veličković et al. 2015), and Southern Iberia (Alves et al. 2010) show a remarkable proportion of endemic genetic variation.

Though the present status of the species depicts it as overabundant and almost continuously distributed in Europe (see section "Current Distribution"), the wild boar underwent a period of strong range fragmentation and local bottlenecks in the past centuries. This, along with the impact of land use modifications and human infrastructures, has left a detectable genetic signature in many European populations. As a result, many populations appear genetically structured (Scandura et al. 2011b; Goedbloed et al. 2013; Renner et al. 2016). Nonetheless, factors determining genetic discontinuities are not always easy to interpret and contrasting patterns of gene flow are observed in different areas (Renner et al. 2016).

Island populations deserve a separate mention, as most of them arose from one or multiple introductions in historical or more recent times. Consequently, their status varies greatly, as does their genetic variation, quite often diverging from the closest continental populations and possibly affected by hybridization with domestic pigs (McDevitt et al. 2013; Canu et al. 2018).

Hybridization

Hybridization, between the wild boar and its domestic counterpart, has been assessed in several European countries, using a variety of molecular and morphological markers. Wild x domestic hybridization levels vary greatly across Europe, from absent (Iberia, using mtDNA; Alves et al. 2003) to very high (England, using microsatellite and mtDNA; Frantz et al. 2012) and so does the geographic distribution of the phenomenon. For example, it was reported to be widespread in the Netherlands (Goedbloed et al. 2013) and Luxembourg (Frantz et al. 2013b), whereas in Greece and in Sardinia, it appeared to be limited to a few areas (Koutsogiannouli et al. 2010; Scandura et al. 2011b). Gene flow between the two forms is usually related to human practices, be it release of admixed individuals or free-ranging farming practices (e.g., McDevitt et al. 2013). Consequences of hybridization are not fully understood: Canu et al. (2016) argued that coat color changes due to crossbreeding can lead to a lack of camouflage that might increase the chances of being spotted by hunters or natural predators; Goedbloed et al. (2015) reported decreased resistance to pathogens, whereas Fulgione et al. (2016) noticed a fitness increase. Additionally, an improvement in meat quality was observed after introgression of wild genes into the domestic population (Matiuti et al. 2010). Nonetheless, the most commonly reported effects were alterations to the local gene pool, possibly leading to a loss of adaptation, increased population size or invasiveness, and morphological changes (Koutsogiannouli et al. 2010; Fulgione et al. 2016). An issue in assessing hybridization in natural populations is represented by the choice of diagnostic markers. Although mtDNA has been largely used, it can only enable the detection of alleles introgressed in the matriline, while autosomal markers (like microsatellites and SNPs) are needed to identify hybrid individuals and to correctly estimate their prevalence in the population. Furthermore, some quantitative trait loci (e.g., melanocortin 1 receptor, nuclear receptor subfamily 6, group A, member 1) can be useful to track the introgression of nonneutral domestic alleles (Frantz et al. 2013b; Canu et al. 2016). In addition to the wild x domestic hybridization, introgression between different putative wild boar subspecies has resulted from animal translocations, mostly carried out for hunting purposes (e.g., in Sardinia, Scandura et al. 2011b).

Life History

Growth

The two sexes exhibit a similar growth rate during their first year of life (reaching approximately 30–45 kg), after which males grow faster than females; they reach 90% of their asymptotical mass, respectively, at around 3 and 2 years of age (Spitz et al. 1998; Brogi et al. 2021). Growth continues throughout their lifetime, with local differences depending on variations in food availability. Such differences are less pronounced in males, which adopt compensatory strategies according to the environment, and affect more strongly females whose energy reserves are used to support pregnancy and lactation more than growth (Spitz et al. 1998).

Reproduction

The wild boar life history strategy is very uncommon among similarly sized ungulates, with a very high reproductive potential (Table 2). The reproductive biology of wild boar is a very complex process that depends on intrinsic and environmental factors, and involves highly plastic breeding tactics and allocation strategies in different ecological scenarios. Female wild boar have a higher reproductive effort than most other ungulate species. Therefore, they are highly dependent on food availability to compensate the energetic investment and ensure survival of both mother and litter. In hunted populations, most females normally do not live for longer than two or three mating seasons, reaching early sexual maturity (Gamelon et al. 2011).

Although changes in climatic conditions influence the reproductive pattern, the wild boar generally shows several estrus cycles per season (seasonally polyestrous) and normally does not mate during the summer to avoid giving birth in winter when low temperatures impair the survival of the piglets. The main breeding period typically occurs in autumn-early winter (between October and December) in temperate regions (Fonseca et al. 2004; Ježek et al. 2011), with peaks in November–December when most of the reproductive females come into estrus and males show increased testes size, testosterone levels, and semen quality (Kozdrowski and Dubiel 2004). Piglets are born in spring, but births may occur throughout the year (Maillard and Fournier 2004). In northern areas, the mating season is shifted, starting in November and may continue until January. In years with high availability of food resources, births are earlier and significantly more synchronized than in poor years (Maillard and Fournier 2004). In areas with a stronger climatic seasonality, with a short period of high food abundance, births are highly synchronous compared to areas with high food diversity all year round (Santos et al. 2006).

Female sexual maturity depends on age and body mass (Gethöffer et al. 2007): a female must reach a threshold body mass to be able to reproduce (typically between 25 and 35 kg,

Table 2 Wild boar life history traits

Trait	Parameter	Value
Gestation (days)	Mean (min-max)	115 (112 to 130)
Weaning (months)	Range	3–4
Litter size (nr)	Mean range (min-max)	3.05–6.91 (1 to 14)
Litters per year (nr)	Min-max	1
Mass at birth (g)	Min-max	670–1090
Proportion of breeding females (%)		
Juvenile (<1 year) Yearling (1–2 years) Adult (>2 years)	Min-max Min-max Min-max	0–90 35–100 65–100
Female age at 1st reproduction (months)	Mean range (min)	8–22 (4)
Female body mass at 1st reproduction		
(kg) (% adult body mass)	Mean range (min) Mean range	24.6–33 (17) 33.3–40
Age at natal dispersal (months)		
Female Male	Min-max Min-max	7–22 9–20
Dispersal distance (km)		
Female Male	Max Max	20 250
Longevity (yr)		
In captivity In the wild	Max Max	27 13

exceptionally 20 kg or less, Servanty et al. 2009; Table 2). Males may physiologically be able to mate at 10 months of age, possibly related to body mass, but normally gain access to females later. Once females become sexually active, they try to reproduce every year under any environmental conditions.

Fecundity ranges between 1 and 14 embryos, with average litter size highly variable among areas (e.g., Servanty et al. 2007; Bywater et al. 2010 and references therein). The mean litter size for adult boar in Europe is 6.28 (Bywater et al. 2010), the largest litters occurring in Central Europe, where their average size varies between 4 and 7 (Frauendorf et al. 2016; Náhlik and Sandor 2003; Servanty et al. 2007), compared to average litters between 3 and 5 in Southern Europe (Fonseca et al. 2004). Females produce one litter per year. Though hypothesized, there is no confirmation that under certain circumstances they can produce two litters (Bieber and Ruf 2005). The number of embryos increases with age, body size, and body condition (e.g., Náhlik and Sandor 2003; Fonseca et al. 2004; Frauendorf et al. 2016). Litter sizes and the proportion of pregnant females are higher in good mast years, which also result in earlier start of estrus and a higher proportion of females breeding during their first year of life (Groot Bruinderink et al. 1994). Furthermore, predictability of seasonal resources may relate to litter size increases with latitude (Bywater et al. 2010), whereas in Mediterranean ecosystems, rainfall positively affects breeding parameters (Fernández-Llario and Mateos-Quesada 2005).

Gestation is about 115 days, and piglets, which can see immediately after birth, remain close to the nest for 4–6 days. Sex ratio of foeti seems not to be biased (Keuling et al. 2013). Maternal condition (i.e., body mass) and resource availability appear to relate to litter size but, as known so far, not to the sex ratio in the litter (Servanty et al. 2007). Contrary to juvenile females, adult ones can adjust their relative allocation to littermates, according to the amount of available food resources. In mast years, a high variance in offspring weights is observed within litters that is matched by the variation in milk production among teats, leading to a lower rivalry among siblings. This way more piglets can be raised, maximizing female reproductive success (Gamelon et al. 2013).

Survival

Although wild boar over 10 years were reported living in nature, the average life expectancy is far lower (Gamelon et al. 2014). In fact, in hunted populations, the average life span may not extend longer than 24 months. Sexes display similar senescence rates (Gamelon et al. 2014). Yearly survival rates under different environmental and management conditions are variable (juveniles: 0.06 to 1.00 with an average in hunted populations of 0.46; yearlings: 0.11 to 1.00, on average 0.41 in hunted populations; adults: 0.03 to 1.00, on average 0.64 in hunted populations; see Keuling et al. 2013). Under good environmental conditions (namely tree seeding, access to crops and mild climate), yearly survival of juveniles may double (Bieber and Ruf 2005). Recruitment of piglets to the female population has been reported to be low; and only less than half of the piglets may survive till the end of September (Náhlik and Sandor 2003). Survival differs between areas, sex, and age (Keuling et al. 2013). Based on telemetry data, piglet survival averaged 0.5 (with 181 days reference period), and overall survival in hunted populations was similar over 1-year period (specifically 0.47 for female piglets, 0.44 for male piglets, 0.46 for yearling females, 0.29 for yearling males, 0.66 for adult females, and 0.59 for adult males; Keuling et al. 2013). In Spain, survival rates for adults ranged from 0.44 in hunting grounds to 0.66 in protected areas (Barasona et al. 2016).

Habitat and Diet

Habitat Selection

Wild boar are flexible in their habitat use, and their ecological plasticity explains the broad distribution and wide range of occupied habitats (Segura et al. 2014). Primary habitats of wild boar are characterized by well-developed vegetation and include forests, shrublands, marshes, and river valleys. Food and shelter availability are the main factors shaping wild boar occurrence (Segura et al. 2014) and highest densities are observed in highly productive areas dominated by rich deciduous forests and agricultural areas (Melis et al. 2006). Agricultural landscapes, which provide abundant shelter and food, have become important secondary habitats for this species in the last decades. Standing crops of maize, rapeseed, and cereals can provide optimal habitats utilized partially or exclusively during the cultivation period (Dardaillon 1986; Keuling et al. 2009; Thurfjell et al. 2009). Open and exposed farmlands outside of cultivation season are generally avoided, but linear vegetation elements, such as rows of trees/shrubs, within the fields can be utilized for movement all year round (Thurfjell et al. 2009). Grasslands and pastures shared with livestock provide attractive foraging habitats (Dardaillon 1986). Finally, wild boar have become increasingly present in urban and periurban areas of most European cities (Podgórski et al. 2013). Wild boar use natural corridors (river valleys, tree- and bush-covered areas) to enter and move within cities, while permanent presence is often observed in city parks and woodlands (Stillfried et al. 2017; Castillo-Contreras et al. 2018).

The effect of natural predators on the habitat use of wild boar is poorly understood. Presence of wolves (*Canis lupus*), the species' main natural predator, does not seem to be perceived as a high predation risk and evokes few behavioral responses in wild boar (Kuijper et al. 2014). Human hunting can have stronger impact on habitat use and can lead to home range shifts from exposed to refuge areas (Tolon et al. 2009), dispersion of resting sites (Scillitani et al. 2010), and greater randomness in habitat use as compared to nonhunting period (Saïd et al. 2012). Females tend to seek safe habitats away from disturbance, while males are more risk-tolerant and can remain hidden close to hunting activities (Saïd et al. 2012). Habitat use patterns may vary according to seasonally changing availability of resources, such as water, food, and shelter (Singer et al. 1981; Keuling et al. 2009). For example, dry season in the Mediterranean can drive wild boar from dried-up marshes into cultivated areas (Dardaillon 1986).

Movement Ecology

Foraging and social interactions are usually performed in a relatively small area (approx. 25 ha) where animals move short distances at low speed, rarely exceeding 1 km/h (Spitz and Janeau 1990). When travelling between habitat patches (foraging spots, resting sites), wild boar move directionally and at faster pace, that is, trotting at 1–10 km/h (Spitz and Janeau 1990; Briedermann 2009; Morelle et al. 2015). When fleeing, they can gallop in short burst of up to 40 km/h. Daily distances travelled are usually shorter than 10 km (Podgórski et al. 2013). Longer daily distances were observed in fragmented environments, where between-patch movements are frequent (e.g., urban areas; Podgórski et al. 2013), and during intensive hunts (Scillitani et al. 2010). Over a 24-h period, wild boar can cover 45–90% of its annual range (Podgórski et al. 2013). This indicates that home range size of wild boar is relatively small given the movement capacity of the species, which can be thus considered sedentary.

Wild boar exhibit remarkable intraspecific variation in home range size across a wide range of habitats. Size of annual home range varies between 400 ha to 6000 ha with an average size of about 800 ha (Boitani et al. 1994; Keuling et al. 2008; Podgórski et al. 2013). The smallest ranges are observed in urban areas and in rich habitats, while the biggest ranges occur in mountainous areas and poor habitats (Singer et al. 1981; Podgórski et al. 2013). Range shifts between habitats were observed in heterogeneous landscapes offering seasonally changing resources (e.g., mountains, field-forest mosaic) (Dardaillon 1986; Keuling et al. 2009; Thurfjell et al. 2009). Sexual differences in home range size are ambiguous, some studies reported larger home ranges in males (Morini et al. 1995), whereas others observed no sex-related differences (Boitani et al. 1994). During the rut, adult males roam widely in search of receptive females and may temporarily extend their home ranges (Singer et al. 1981), whereas movements of pregnant females decrease around parturition (Morelle et al. 2015).

The majority of young wild boar (70–80%) do not disperse further than 5 km away from their natal ranges (Truvé and Lemel 2003; Podgórski et al. 2014a). Longer movements (5–30 km) are observed less frequently and are undertaken more often by dispersing males than females. Natal dispersal is most frequent during the second year of age (Podgórski et al. 2014b). Occasionally, long distance movements of 50–250 km in straight line are performed by young animals, adult males, and adult females with offspring (Andrzejewski and Jezierski 1978; Truvé and Lemel 2003). Hunting disturbance, particularly intensive methods such as frequent drive hunts, may induce escape movements resulting in greater distances travelled, larger ranges, and dispersion from resting sites (Scillitani et al. 2010).

Diet

Wild boar are omnivorous and opportunistic in their food preferences and their diet reflects local and seasonal food availability. Plant matter constitutes over 90% of the diet on the annual scale and dominates in terms of frequency and volume over other food sources (Briedermann 2009; Barrios-Garcia et al. 2012). Plant food in the wild boar diet is very diverse and includes seeds, fruits, leaves, stems, shoots, bulbs, and roots (Schley and Roper 2003). Agricultural crops are heavily used when available, particularly during the summer and autumn when their nutritional value is at its peak. Consumed agricultural food items include cereals, vegetables, legumes, fruits, and others (Genov 1981; Herrero et al. 2006). Maize is one of the preferred crops (Herrero et al. 2006; Schley et al. 2008) and is commonly used as a bait by hunters (Schley and Roper 2003). When availability of agricultural crops or supplementary food is low, natural forage, such as herbaceous plants, browse, roots, and tree seeds (e.g., acorns, beechnuts, chestnuts), becomes an important dietary component (Groot Bruinderink et al. 1994; Herrero et al. 2005; Merta et al. 2014).

Diet composition is dominated by agricultural crops (>70% of stomach content volume) in wild boar living in the mosaic landscape of woodlands and farmlands (Genov 1981; Herrero et al. 2006; Merta et al. 2014) and, together with plant roots, constituted over 70% of the wild boar diet in the Mediterranean wetlands (Giménez-Anaya et al. 2008). Herbaceous plants, browse, roots, and tree seeds (up to 40% of the diet during mast years) make up most of the diet in mixed lowland forests and mountainous areas (Groot Bruinderink et al. 1994; Herrero et al. 2005; Merta et al. 2014).

Animal material is consumed by wild boar all year round and includes at least 40 animal species and genera. Wild boar consume animal matter frequently (occurs in 90% of analyzed stomach contents), but at low total volume (about 3% of the stomach content with >2% invertebrates and the rest vertebrates; Schley and Roper 2003; Herrero et al. 2006). Invertebrate prey includes mainly earthworms, insects, and snails, whereas consumed vertebrates are small mammals (rodents, shrews), fish, amphibians, reptiles, and birds (Schley and Roper 2003). Animal food can be obtained by wild boar by scavenging or predation (Herrero et al. 2006; Giménez-Anaya et al. 2008; Barrios-Garcia et al. 2012). Large mammals are consumed as carrion, whereas small mammals (rodents, shrews, hares, rabbits) are also taken directly as prey (Schley and Roper 2003). Wild boar eat eggs and chicks of ground nesting birds (Barrios-Garcia et al. 2012). The composition of animal items in the diet varies greatly among seasons. In the case of small mammals, it is higher in autumn and winter, whereas earthworms are mainly consumed in spring and summer (Schley and Roper 2003). The use of carrion can increase during autumn and winter due to the greater availability of carcasses (Briedermann 2009).

Behavior

Social Behavior

Wild boar societies are centered around family groups composed of one to several adult females and their offspring from the last or second last breeding season (Dardaillon 1988; Podgórski et al. 2014a). Most members of the groups are genetically related to each other at the level of first- or second-order relatives (Kaminski et al. 2005; Poteaux et al. 2009; Podgórski et al. 2014a). Size of social groups usually ranges between 5 and 10 individuals (Gabor et al. 1999; Poteaux et al. 2009; Podgórski et al. 2014a). Social groups are generally stable and coherent but may temporarily merge to form larger units (up to 30 animals) and single individuals may occasionally shift between groups (Poteaux et al. 2009; Podgórski et al. 2014a, b). Wild boar are not territorial and undefended home ranges of neighboring groups partly overlap, with individuals from different groups interacting regularly (Boitani et al. 1994; Podgórski et al. 2014b).

Male offspring leave maternal groups early in their life, usually around one year of age, and become solitary boars, rarely found within groups outside of the breeding season (Hirotani and Nakatani 1987; Dardaillon 1988). Adult males engage in dynamic and short-lived intraspecific relationships (Podgórski et al. 2014b), involving interactions with mating competitors or assessment of females' reproductive status and mating. During the rut, which takes place in late autumn and early winter, males temporarily join female groups for mating (Graves 1984; Dardaillon 1988). Female offspring show stronger fidelity to maternal groups and most of them do not disperse far (Hirotani and Nakatani 1987; Dardaillon 1988; Kaminski et al. 2005; Podgórski et al. 2014a). New groups can be formed following the permanent separation of yearling females from their maternal group or the split of a larger social unit

(Kaminski et al. 2005; Poteaux et al. 2009). Adult females maintain stable, long-lasting relationships and rarely shift between groups for long periods of time (Gabor et al. 1999; Poteaux et al. 2009; Podgórski et al. 2014b).

Mating Behavior

Breeding activity of wild boar is seasonal and the mating system is polygynandrous (Pérez-González et al. 2014). During the mating season, boars actively compete for access to estrus sows, which can mate with more than one boar within the 2–3 days of estrus, resulting in litters with multiple paternity (Poteaux et al. 2009; Gayet et al. 2016). Similarly, a single boar can fertilize several sows, which tend to synchronize their estrus locally (Canu et al. 2015). Farrowing takes place mainly in March and April (Gethöffer et al. 2007; Ježek et al. 2011; Rosell et al. 2012). Prior to parturition, pregnant females temporarily separate from their group and choose secluded sites for building a farrowing nest, in which piglets remain for a few days after parturition and then join the maternal group. Piglets are weaned at around 4 months of age but already at 4 weeks they start rooting and processing solid food (Špinka 2009). Due to synchronized estrus of sows within a group, multiple litters of similar age may be present in a group at the same time, and females may participate in cooperative nursing (Graves 1984).

Senses

Wild boar have a well-developed olfactory sense which is used in foraging, communication, navigation, and predator avoidance. Scent signals are used to locate food items at close distance (Suselbeek et al. 2014), assess predation risk (Kuijper et al. 2014), locate familiar individuals (Kittawornrat and Zimmerman 2011), stimulate reproductive activity (Kirkwood et al. 1983), and navigate within the home range. Wild boar also have a good auditory capacity and a rich repertoire of vocal signals used in social communication. There are around 20 types of calls, such as grunts, squeals, and trumpets, which may vary in amplitude, frequency, and modulation depending on the behavioral context (Špinka 2009). Vision is poorly developed and its role in communication is limited. Visual signals, usually displayed by competing or threatened animals, include ears and body positioning, erection of the dorsal mane, tail wiggling, bristle rising, and back arching (Graves 1984).

Activity

Wild boar activity typically lasts between 6 and 12 h a day. In natural and undisturbed conditions, wild boar are active during day and night, with alternating periods of activity and rest (Podgórski et al. 2013; Brivio et al. 2017). In human-dominated landscapes, wild boar have become largely nocturnal (Lemel et al. 2003; Keuling et al. 2008; Brivio et al. 2017). In urban environments, wild boar are mostly nocturnal, independently of the seasonal changes in day length, in order to minimize interference with humans (Podgórski et al. 2013). In rural areas, activity usually peaks around dawn and dusk and drops in the middle of the night. Seasonal variation in the activity patterns is generally low (Lemel et al. 2003; Keuling et al. 2008), but daily adjustments are observed in response to changes in temperature, precipitation, and humidity (Brivio et al. 2017).

Parasites and Diseases

Pathogens and Parasites

Their demography, ability to cross-breed with pigs, wide distribution, adaptability to a variety of habitats and to suburban areas, feeding habits, sociability, and high contact rates with many species, all expose wild boar to a plethora of pathogens. Their infectious and parasitic diseases have extensively been studied, mainly descriptively, because they are shared with: (1) humans (e.g., *Trichinella* spp.), (2) livestock-domestic pigs are susceptible to the same pathogens but other species might be involved (e.g., cattle – *Bos taurus* – Barasona et al. 2014); (3) endangered species (e.g., Aujeszky's disease with Iberian lynx – *Lynx pardinus* – Masot et al. 2016), and also because of pathogens' impact on its population dynamics (Barasona et al. 2016). The knowledge on wild boar diseases (based on long-term studies) has increased markedly during the last two decades. A recent review ranked the most frequently studied pathogens and host species in long-term studies on wildlife, and with respect to Europe and Asia wild boar was the most studied host (Barroso et al. 2021). Wild boar are thus relevant in the One Health context, due to their role as a true reservoir host for pathogens shared among wildlife, livestock, and humans (Fig. 4 provides details on the number of studies including wild boar as host species.

The list of infectious and parasitic diseases of wild boar is long and includes several zoonoses (see Ruiz-Fons et al. 2008; Jori et al. 2017 for a review). The most significant infectious diseases involving wild boar over the last two decades have been highly host-specific viruses: African swine fever (ASF) and Classical swine fever (CSF). There are also some remarkable multi-host pathogens such as tuberculosis (TB), foot-and-mouth disease virus, and zoonotic nematodes like *Trichinella* spp. Parasitic diseases, including ectoparasites, are normally of lower concern because many of them are usually adapted to one host species and rarely transmit to others. Wiethoelter et al. (2015) reported the top 10 diseases at the wildlife–livestock interface of which wild boar may host nine: two viruses (avian influenza and rabies), four bacteria (salmonellosis, TB, brucellosis, and

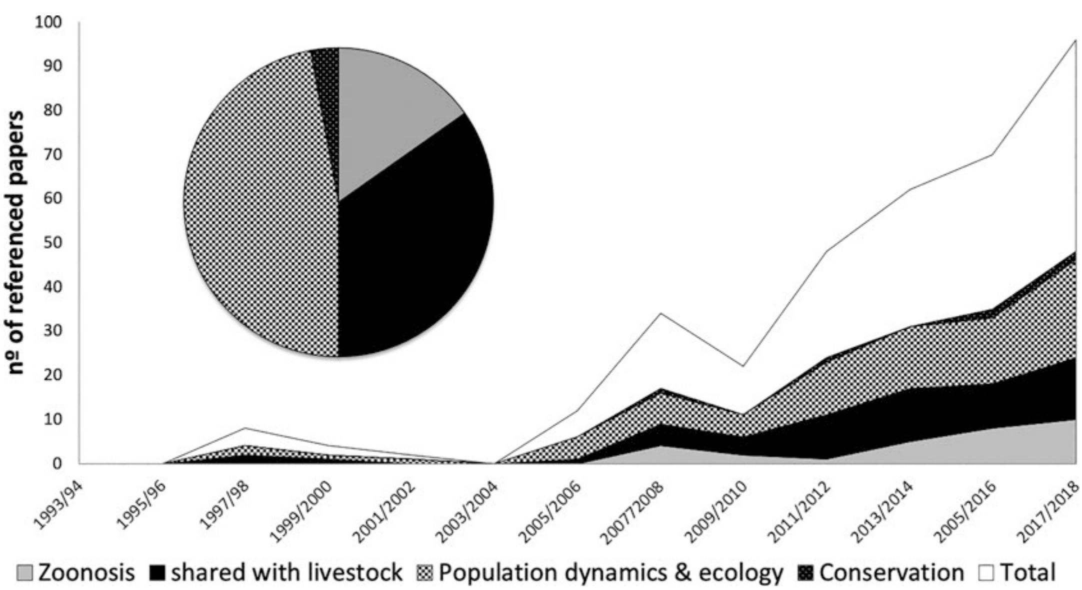

Fig. 4 Bi-annual number of georeferenced papers on long-term epidemiological studies including wild boar as host species in Scopus + Medline + Pubmed from 1993 to 2018. Databases were accessed on April 15, 2018. The keyword used was "wildlife diseases." We initially retrieved 6541 references, which resulted in 535 papers once duplicates and spurious results were removed and the following conditions applied: study longer than three consecutive years, annual sampling minimum of 10 individuals, same study area and populations over time, and wild animals in their natural environment (excluded lab and captive animals as well as clinical trials). Studies exclusively focusing on passive surveillance were also excluded. Finally, we filtered the papers which included, at least, wild boar as host species, and classified records according to the nature of the main conclusions: 1) zoonosis-related, 2) diseases shared with livestock, 3) population dynamics and/or ecology, and 4) conservation. Totals over the study period (proportions) are indicated in a pie chart

leptospirosis), one protozoon (toxoplasmosis), and two helminths (echinococcosis and trichinellosis).

Wild boar may function as a disease reservoir when they are able to maintain an infection in a given area in the absence of transmission from other hosts. In some cases, wild boar just maintain the infection secondarily to the main reservoir or are accidentally infected. The epidemiological role of wild boar is not easy to determine and requires compiling sound evidence about epidemiologic associations between reservoirs, genetic characterization of pathogens, and intervention studies (Naranjo et al. 2008). The possible transmission routes from and to other hosts are highly variable and can happen through both direct (contact with infected animals or carcasses, consumption of meat, oral, respiratory, conjunctival and transdermal routes, skin wounds) and indirect exposure (there is an indirect step or media: aerosols, consumption of contaminated food or water, through bites of arthropod vectors). Foodborne pathogens and antimicrobial resistance in indicator bacteria have been reported in urban wild boar, causing concerns for public health (Navarro-Gonzalez et al. 2013).

Pathogens can have direct or indirect (e.g., body condition mediated) impacts on the reproductive performance of wild boar (Ruiz-Fons et al. 2006), which can be partially compensated by an earlier return to estrus. Co-infections with multiple pathogens with different characteristics are frequent in wild boar, resulting in complex effects. For instance, some viral infections (e.g., porcine circovirus type 2) may impair the ability of wild boar to respond to other infections, including TB (Díez-Delgado et al. 2014). Population effects can also be relevant, as some diseases can lead to high mortality (e.g., CSF and ASF, Lange et al. 2012; Cortiñas Abrahantes et al. 2017). TB causes 30% of deaths in adult wild boar in endemic areas of Southern Spain (Barasona et al. 2016), which contrasts with a total natural death rate of 3% in Central Europe (Keuling et al. 2013).

Epidemiology

The factors involved in the maintenance and spread of pathogens by wild boar are varied and interdependent. Individual factors include sex, age, body condition, reproductive and immunological status, and genetics (e.g., genetic mechanisms are involved in susceptibility to TB, Queirós et al. 2018). Pathogen prevalence in wild boar is driven by changes in population densities and aggregation, sometimes caused by implementation of management practices (e.g., supplementary feeding, Vicente et al. 2013 for TB, Oja et al. 2017b for helminths and intestinal protozoa). Assessing how wild boar use their environment and how this affects interspecific interactions with wildlife and humans is therefore essential to estimate the risks for disease transmission and maintenance (e.g., Barasona et al. 2014, for scavenging: Carrasco-Garcia et al. 2018). The parallel growth of urban areas and wild boar populations in recent decades has contributed to increased interactions between wild boar, humans, and other animals alike. The removal of predators, recreational hunting (often under non-sustainable managements schemes resulting in overabundance; Gortázar et al. 2006), translocations, consumption and movement of wild boar meat and meat products without previous sanitary inspection, all increase the chances of spreading and sharing wild boar pathogens.

Population Ecology

Population Dynamics

Population dynamics of wild boar are driven by both natural and anthropogenic factors, and the most important natural drivers include mast of deciduous trees (such as acorns, beechnuts, and chestnuts), winter severity, and predation. Long-term data on wild boar population numbers in central and eastern Europe show that abundance of mast has a dominating positive effect on the population growth rates (Jędrzejewska et al. 1997; Bieber and Ruf 2005; Briedermann 2009; Vetter et al. 2015; Frauendorf et al. 2016). During the mast seeding years, when trees synchronously produce large seed crops, wild boar take advantage of the abundant food to accumulate energy reserves which enhances overwinter survival and subsequent reproduction (Jędrzejewska and Jędrzejewski 1998; Servanty et al. 2009; Canu et al. 2015; Frauendorf et al. 2016). Another natural factor strongly limiting wild boar numbers is winter severity, that is, the combination of average winter temperature and snow cover duration and depth. Deep snow and frozen soil make it difficult for wild boar to root and forage on vegetation and invertebrates. Harsh winters can cause marked declines in wild boar populations as a result of starvation and diseases which are responsible for most (73%) of natural mortality (Jędrzejewska et al. 1997; Jędrzejewska and Jędrzejewski 1998). This weather stochasticity mechanism shapes wild boar densities and dynamics across Europe, resulting in higher densities and faster population growth rates where winters are milder. Food abundance, however, can offset or even outweigh the negative effects of cold winters. Thus, winter severity will have weaker limiting effect on wild boar populations in highly productive regions or during mast seeding years (Melis et al. 2006; Vetter et al. 2015). The third and least important natural factor shaping wild boar numbers is predation. Wolves are the main natural predators of wild boar, contributing 50–100% to the predator-caused mortality across the species range, depending on the presence of other large carnivores that prey upon wild boar, such as brown bear (*Ursus arctos*) or lynx (*Lynx lynx*). However, impact of wolves on wild boar populations appears limited. Where wild boar and wolves co-occur, wolf predation makes up on average 16% (maximum 30%) of the natural mortality (Okarma 1995). Impact of wolves varies locally depending on the composition of ungulate communities and wild boar abundance. Wolf preferences may also change and wild boar can either represent the selected prey in some areas (Mattioli et al. 2011) or an auxiliary prey in others (Okarma 1995). The impact of natural predation is heavier on juveniles and yearlings (over 70% of kills), while adults can defend themselves effectively and are rarely attacked (Okarma 1995; Bassi et al. 2012).

Anthropogenic Impacts

Anthropogenic impacts on wild boar populations include direct effects of management and indirect effects related to climate change. Hunting is the main cause of wild boar mortality across Europe (Toïgo et al. 2008; Keuling et al. 2013). Hunting pressure can significantly affect life-history traits, for example, earlier age and timing of reproduction (Gamelon et al. 2011), and demographic structure of the populations by targeting mostly adults, in contrast to predation by wolves (Okarma 1995; Toïgo et al. 2008; Keuling et al. 2013). However, hunting does not seem to limit the currently observed growth of wild boar populations in Europe (Massei et al. 2015; Vetter et al. 2015). Supplementary feeding, which is common management practice across most European countries, can also shape population dynamics (Andrzejewski and Jezierski 1978). Food availability contributes to increased overwinter survival and buffers the negative effect of cold winters (Vetter et al. 2015). This effect will be greater at northern latitudes, where the limiting effect of cold winters is stronger. For example, wild boar densities in Estonia, where supplementary feeding was common (before the arrival of ASF), were much higher than in Finland, where climatic conditions were similar but supplementary food was never provided. Wild boar abundance in Estonia was strongly related to the number of supplementary feeding sites (Oja et al. 2014). Climate changes influence two major factors limiting wild boar population growth: winter severity and food abundance. First, winter temperatures increased throughout the twentieth century and these changes are associated with increased size of wild boar populations across central Europe (Vetter et al. 2015). The most likely mechanism driving this relationship is the increased survival during mild winters. Second, rising temperatures have also been shown to increase the frequency of mast seeding years (Bieber and Ruf 2005; Vetter et al. 2015), which have a positive effect on growth rates of wild boar populations (Bieber and Ruf 2005). Finally, changes in agricultural practices led to increased availability of energy-rich crops, such as maize, which is associated with higher reproductive output of wild boar and, often coupled with supplementary feeding in winter, contributes to population growth (Bieber and Ruf 2005; Servanty et al. 2009; Rosell et al. 2012).

Population Trends

Wild boar populations all over Europe have grown considerably during the last decades, despite large variation in climatic conditions and management across the continent (Fig. 5; Sáez-Royuela and Tellería 1986; Apollonio et al. 2010; Massei et al. 2015; Vetter et al. 2015). The increasing trend in wild boar numbers in Europe started in the 1960s and is continuing today (Sáez-Royuela and Tellería 1986; Massei et al. 2015). From 1982 to 2012, the average five-year population growth index, based on the hunting bag statistics from 18 European countries, varied between 1.4 and 1.7 (with 1 = no growth; Massei et al. 2015). This increase in population numbers is accompanied by geographical expansion towards the north (Apollonio et al. 2010). Other indices of wild boar abundance, such as crop damage, vehicle collisions, and environmental impacts, also show an increasing trend and confirm real growth in wild boar populations (Massei and Genov 2004; Schley et al. 2008; Apollonio et al. 2010; Morelle et al. 2013). Despite an increase in hunting bags (+150% from 1992 to 2012) and over 3 million wild boar annually

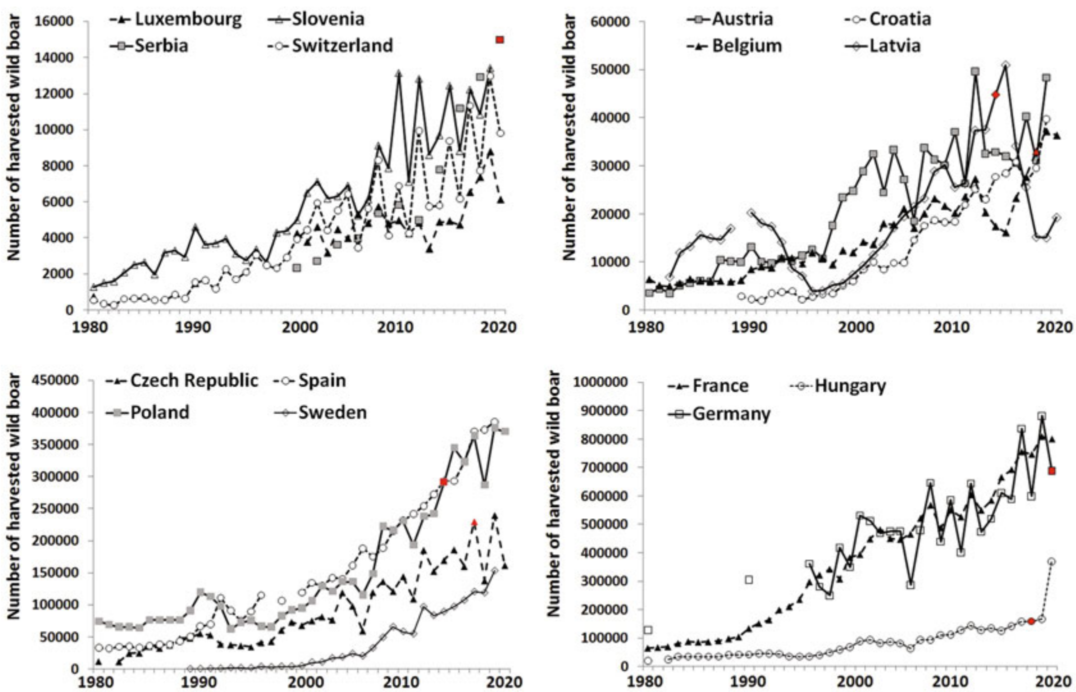

Fig. 5 Trends in wild boar hunting bags from selected European countries (1980–2020). Data provided from national/regional administrations to the Enetwild consortium (www.enetwild.com). Symbols in red indicate the year of the first African swine fever outbreak in the country

harvested in Europe, hunting seems to be not sufficient to limit wild boar population growth, which is thus expected to continue (Massei et al. 2015; Vetter et al. 2015). This is partly due to a declining number of hunters (−18% from 1992 to 2012) and their general unwillingness to reduce wild boar densities (Keuling et al. 2016). Other factors discussed above, such as increasingly milder winters and greater availability of natural and anthropogenic forage, are likely to continue to boost the growth of wild boar populations.

Conservation Status

The wild boar is the most abundant and widespread suid species in the world. Accordingly, it is classified as Least Concern by the IUCN (Oliver and Leus 2008). If the species, as a whole, is overabundant and does not raise any conservation concern, different situations may emerge at a local scale. The only threatened subspecies (or species, according to Groves and Grubb 2011) is *S. s. riukiuanus* Kuroda, 1924, living in Ryukyu Islands, Japan. The main, probably underestimated, issue in Europe is represented by the extensive anthropogenic hybridization leading to genetic homogenization and to the erosion of local genetic diversity. The current lack of sharp taxonomical units (see section "Taxonomy, Systematics and Paleontology") is likely to have been enhanced by human-mediated gene flow. Even where long-lasting isolation has favored genetic divergence, as in the case of the Sardinian wild boar, the introgression from commercial pig breeds and introduced non-native wild boar has impacted the local gene pool, jeopardizing the status of the *S. s. meridionalis* subspecies (Iacolina et al. 2016). At a regional scale, the genetic structure observed today often arises from different histories of releases by humans, hybridization, and human exploitation, artificially leading to diverging allele frequencies among local stocks (Goedbloed et al. 2013).

It is likely that the positive trend of the species has concealed the loss of native adaptive genetic variation across its European range. The ban of animal translocations and of the release of captive stocks, yet mainly associated to sanitary risks, will also help preventing further loss of adaptive potential.

Management

Introductions, Reintroductions, and Restocking

The Eurasian wild boar represents one of the most managed ungulate species in the world. Its present distribution is the result of introductions outside its native range, local extinctions due to overexploitation, restocking with animals translocated from other areas, farming, and escapes or releases of captive stocks. In Europe, the establishment of new populations by intentional introductions has only affected some minor islands (e.g., Canu et al. 2018), while previously extinct populations have been restored by reintroductions (e.g., in the Netherlands, Denmark, Serbia, Italy, and Greece; Apollonio et al. 2014) or by escapes from captivity (e.g., in Great Britain, Sweden, Ireland, and Slovenia; Apollonio et al. 2014). Restocking of depleted populations has been also a common practice in some areas (Apollonio et al. 2010) and has contributed to the recovery of the species across the continent. In many cases, human actions were not documented, and both the origin and number of released animals are unknown. Introductions and reintroductions were mostly successful, an exception being the wild boar in Cyprus, where the species was illegally restored in 1994, after a previous extinction, and died out again in 2004 (Hadjisterkotis and Heise-Pavlov 2006).

Impact, Conflicts with Humans, and Damage Control

Sus scrofa is listed by IUCN among the 100 worst invasive species in the world, because of its biology (i.e., rapid population growth rate) and overall impact on human activities and on the environment. Conflicts with humans are mainly associated with damages from feeding activity and the number of traffic accidents involving the species. The main impact is represented by crop damages that mostly affect cereals, especially maize, and are due not only to consumption but also to trampling (Schley and Roper 2003). In warm regions, heavy losses are also caused to vineyards and rice paddies (Calenge et al. 2004) and in continental regions to vegetables and grasslands (Schley et al. 2008). The main factors affecting the amount of damages are density of wild boar, distance of crops from natural refuges (e.g., woodlands), species cultivated, availability of natural food, and crop ripening period (Calenge et al. 2004; Schley et al. 2008; Thurfjell et al. 2009). Furthermore, damages are seasonally distributed according to geography and crop type (Schley et al. 2008). In Mediterranean areas, they peak in summer, induced by the shortage of water, whereas in temperate climates a maximum occurs in late winter, when food resources are scarce (Licoppe et al. 2013). Together with roe deer, the wild boar is responsible for most of the wildlife-vehicle collisions in Europe, especially in highly urbanized areas (Morelle et al. 2013). An annual peak in wild boar-caused accidents is observed in autumn-early winter, likely induced by an increased mobility during the rut and the hunting season (Morelle et al. 2013). Additional conflicts with humans arise from the habit to dig up the ground, looking for hypogeal food. Recreational areas like city gardens and parks or golf courses can be severely impacted by rooting, as can grazing areas for livestock (Licoppe et al. 2013). Besides, wild boar can occasionally affect livestock farming directly, by predation on lambs or new-born calves (Seward et al. 2004). Finally, a serious concern is represented by the transmission of diseases and zoonoses, which can affect livestock, pets, endangered wildlife, and humans (see "Parasites and Diseases").

In addition to the impact on human activities, at high densities, wild boar can represent a threat to local ecosystems, because of its trampling, rooting activity, and opportunistic feeding behavior (Massei and Genov 2004). Feeding on whole plants, fruits, bulbs, and tubers can alter the abundance and richness of plant species (Cuevas et al. 2012), and feeding on seeds and seedlings of forest trees can impact forest regeneration (Bongi et al. 2017). Predation on eggs and chicks can compromise the reproduction of ground-nesting birds (Oja et al. 2017a); grubbing and predation on earthworms, grubs, and small ground-dwelling mammals can modify animal communities and soil properties (Laznik and Trdan 2014).

Several methods are used to mitigate such impacts, differing in effectiveness, feasibility, costs, and social acceptance (Massei et al. 2011). Although not always true, a high impact by wild boar is often interpreted as a consequence of an overabundant population, so actions are undertaken to reduce their number. Traditional control methods include culling, as the main option, but also trapping (followed by suppression or translocation). In addition, methods of fertility control have been developed, based on immuno- or oral contraception (Massei et al. 2012). Other mitigation measures are intended to limit wild boar access to sensitive sites by metal fencing, electric fencing, diversionary feeding, and the use of chemical repellents and acoustic scarers. No eradication program has been successful in Europe, but experiences in the Americas suggest that a combination of different methods is more effective.

Hunting and Hunting Regulation

Besides being considered a pest, the wild boar is an important game species. It has been estimated that more than 3 million wild boar were harvested in 2012 in Europe (Massei et al. 2015). Traditional cooperative forms of hunting are based on drive hunts and are practiced especially in southern Europe (like the "braccata" in Italy and the "monteria" in Spain), while individual hunting (e.g., stalking, standing or high-seats) is more common in continental Europe. In some countries, harvest quotas are imposed by local authorities. Baits (mostly maize or other vegetables) are used in many areas as attractants during the hunting season. Hunting is generally allowed to licensed hunters from summer to early winter, with huge differences among countries; in some of them (e.g., in Portugal, Austria, Croatia, and

Estonia), wild boar hunting is allowed all year round, with possible restrictions to specific sex/age classes (Apollonio et al. 2010).

Although hunting is the main cause of wild boar mortality (around 85% of deaths, Keuling et al. 2013), it appears insufficient to counteract the positive trend of wild boar populations. Moreover, this population growth is paralleled by a general negative trend in the number of hunters which poses serious doubts on the capacity to effectively manage this species in the future (Massei et al. 2015).

Economic Value

Due to its size, abundance, current distribution, and the high level of interaction with human activities, the wild boar has enormous economic repercussions. In Poland alone, over a 5-year period, the compensation for damages amounted to 34.2 million €, whereas the revenue from the sale of the meat of shot animals amounted to 9.5 million € (Frackowiak et al. 2013). In Italy and France, the wild boar was reported as responsible for 90% of damages to crops and forests, causing an estimated annual loss exceeding 30 million € (Apollonio et al. 2010). A recent study, measuring the willingness-to-pay by hunters in Sweden, estimated at 113–529 SEK (10–50 €) the value of a wild boar, with large differences among hunter categories (Engelman et al. 2018). However, the value attributed to this game is context-dependent and may vary a lot among countries. Maximum values are reached by trophy hunting which is practiced in several countries, especially in central-eastern Europe. According to the International Council for Game and Wildlife Conservation (CIC) evaluation system, tusk size is the reference parameter to assess the quality of boar trophies. On this basis, a single harvested boar can be worth up to more than 1500 €.

Health Management

The control of wild boar diseases is a major challenge, especially for those shared with livestock, and takes advantage of the establishment of surveillance and monitoring schemes, together with health surveillance in domestic pigs. Suitable diagnostic tools, designed for pigs, are available. However, biosecurity measures should be implemented to prevent pathogen transmission, which can be bidirectional at the wild boar-livestock interface (Carrasco-Garcia et al. 2016). Additionally, wild boar management constitutes an essential aspect to prevent risk factors for many pathogens, since excessive densities and aggregation favor disease spread and maintenance (Gortázar et al. 2006; Cano-Terriza et al. 2018). Effective disease management requires tools from several fields which should be combined in an integrated control strategy. Different options can be applied and combined; however, a proper surveillance and monitoring scheme (for both disease and population; Sonnenburg et al. 2017) is always required to make the best decisions. Disease control can be achieved by different means, including (1) preventive actions (especially at the wildlife-livestock interface), (2) arthropod vector control, (3) host population control through random or selective culling, habitat management, or reproductive control (Massei et al. 2012), and (4) vaccination (Rossi et al. 2015; Díez-Delgado et al. 2018). Wild boar population control is performed through random or selective culling. However, despite a decline in population size of approximately 50% during the period 2014–2017, it did not prevent ASF spread in the Baltic States and Poland during the first years after detection (Cortiñas Abrahantes et al. 2017). Reproductive control is being researched (Massei et al. 2012), and field vaccination against certain pathogens has proved to be a potentially effective tool in some cases (for CSF, Rossi et al. 2015; for TB, Díez-Delgado et al. 2018) which should be integrated in control strategies. After a cost/benefit assessment, the alternative options of zoning or no-action should also be considered. Finally, the success of any disease control strategy in this species, which is part of the European hunting culture, also depends on stakeholders' collaboration and attitudes.

Future Challenges for Research and Management

The population growth and the spread of wild boar across Europe have brought the species to increase its interaction with humans, leading to a combination of worrying issues:

1. Urban wild boar: Once absent, wild boar are now a regular presence in the periphery and in green areas of cities like Berlin, Barcelona, and Rome. The management of these (peri-) urban populations is a real challenge, encompassing aspects like public education, species monitoring and control, public safety, and disease surveillance.
2. Population monitoring: An effective management of wild boar impact on human activities and natural systems, as well as the prevention of disease transmission, would require a reliable estimation of local population abundances and trends. However, estimating wild boar numbers is difficult to achieve because of their clumped distribution, social structure, use of resting sites in dense vegetation, and nocturnal activity. Although several methods have been proposed (see ENETWILD consortium et al. 2018), no standard exists so far and, in the common practice, science-based approaches give way to "guesstimates" or, quite often, to the use of (biased) hunting bag statistics. Nonetheless, great advances have been recently achieved by the ENETWILD consortium (https://enetwild.com/), which has produced suitability maps of wild boar occurrence and relative abundance in Europe by harmonizing hunting bag data. This project has also pointed out that hunting statistics can be suitable to determine wild boar density estimates, if a calibration with accepted rigorous methods is performed. This, however, deserves further research in a variety of contexts throughout Europe.
3. Hunting effectiveness: though hunting is recognized as a fundamental tool of population control, its effectiveness turned out to be constrained by social and legal aspects. In order to counteract more effectively the demographic trend and growing impacts of wild boar, new generations of specialized hunters and modifications to the current regulations are invoked (Apollonio et al. 2010; Massei et al. 2015). Professional hunting can also be of help in the future, especially in specific situations (e.g., in urban areas).

Given the present status and invasiveness of the species, the role of research on wild boar biology and management will be of utmost importance. Response to climate change, biological and ecological effects of different hunting regimes, biological consequences of the introgression of domestic pig genes, the genomic basis of the species' plasticity are among the most stimulating topics. Furthermore, a special effort should be devoted to technical aspects, like the development of more suitable and cost-effective monitoring procedures, the refinement of methods of population control (e.g., sterilization), or the development of vaccines against the most dangerous transmissible diseases (e.g., ASF). Finally, an important goal would be the dissemination of good practices and standards to reduce the current discrepancies among regions and countries in the management of the species.

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