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EXTERNAL SCIENTIFIC REPORT

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Wild boar ecology: a review of wild boar ecological and demographic parameters by bioregion all over Europe

ENETWILD-consortium, Pascual-Rico R, Acevedo P, Apollonio M, Blanco-Aguiar JA, Body G, del Rio L, Ferroglio E, Gomez A, Keuling O, Plis K, Podgórski T, Preite L, Ruiz-Rodriguez C, Scandura M, Sebastian M, Soriguer R, Smith GC, Vada R, Zanet S, Vicente J and Carpio A.

Abstract

The definition of the most relevant parameters that describe the wild boar (WB) population dynamics is essential to guide African swine fever (ASF) control policies. These parameters should be framed considering different contexts, such as geographic, ecological and management contexts, and gaps of data useful for the parameter definition should be identified. This information would allow better harmonized monitoring of WB populations and higher impact of ASF management actions, as well as better parametrizing population dynamics and epidemiological models, which is key to develop more efficient cost-benefit strategies. This report presents a comprehensive compilation and description of parameters of WB population dynamics, including general drivers, population demography, mortality, reproduction, and spatial behaviour. Beyond the collection of current available data, we provided an open data model to allow academics and wildlife professionals to continuously update new and otherwise hardly accessible data, e.g. those from grey literature which is often not publicly available or only in local languages. This data model, conceived as an open resource and collaborative approach, will be incorporated in the European Observatory of Wildlife (EOW) platform, and include all drivers and population parameters that should be specified in studies on wild boar, and wildlife in general, ecology and epidemiology at the most suitable spatio-temporal resolution. This harmonized approach should be extended to other taxa in the future as an essential tool to improve European capacities to monitor, to produce risk assessment and to manage wildlife under an international perspective.

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Key words: Wild boar ecology, population dynamics, bioregion Europe

Question number: EFSA-Q-2022-00047

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Acknowledgements: We acknowledge EFSA ALPHA and DATA units, and ENETWILD partners and Bernad A., Martínez A. and Tardón A. for reviewing this manuscript. We are grateful to ENETWILD collaborators (listed on http://www.enetwild.com/collaborators).

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Summary

Background and objectives: Wild boar (WB) is an ecologically very plastic species, with potentially rapid population growth rates. Overall, WB populations are still growing and expanding despite high mortality rates. This ability to adapt to a wide array of environmental and climatic conditions makes WB population dynamics highly variable across the European continent, requiring a deeper understanding of local and regional variations over its distribution range. In order to guide African swine fever (ASF) control policies, it is essential: (i) to define which basic parameters of WB population dynamics are most relevant, (ii) to understand them in a context-dependent manner, based on their variation in given geographical, ecological and management contexts (hereafter called "WB population bioregions"[1]) and conditioned by drivers, and finally (iii) quantifying their values and range, identifying gap areas or contexts, both management and epidemiological. The potential impact of the results obtained by this review on WB ecological and population dynamics parameters for ASF management in the EU are:

- Planning integrated and harmonized (comparable) monitoring of WB population dynamics trends and impacts over space and time under different scenarios.
- Monitoring the effects of ASF management actions under an adaptive approach, to inform future decision-making.
- Parametrizing population dynamics and epidemiological models to develop most efficient cost-benefit strategies.

The aim of the present report is to produce a comprehensive compilation and description of parameters on WB population dynamics throughout Europe.

Methodology: We compiled WB demographic parameters using a literature review on WB population dynamics and drivers throughout Europe. From each publication we extracted available data on parameters describing the basic aspects of wild boar population dynamics relevant to understand disease dynamics and improve science-based ASF management, i.e.: (1) description of publication (year of publication, journal, country); (2) general ecological factors or drivers (bioregion, predator presence, hunting pressure, supplementary feeding and ASF presence); (3) population characteristics (e.g. density, sex ratio, body size, group size, age structure by age…); (4) mortality (due to predation, diseases, hunting harvest, and others such as road kills); (5) reproduction parameters (e.g. litter size, proportion of pregnant females); and (6) spatial behaviour (e.g. proportion of dispersants, dispersal period, distance travelled, home ranges).

Results: One of the main difficulties to produce such a harmonized database was the wide diversity of parameters describing WB population dynamics and different methods applied (e.g., for relative abundance). Also, even for peer reviewed sources, there is lack of descriptive information or this is not sufficiently detailed and/or standardized about the specific context and main drivers determining population dynamics: spatio-temporal, management (e.g., population control, hunting), ecological and environment scenarios. All this may impede further use of data as they are not always comparable. A case example to illustrate the usefulness of such data collection is presented, analysing the relationship between WB population decrease (%, based on known densities) and pre-ASF density, considering only the countries where ASF is widespread and information available. This simple example provided insights into the possible impact of ASF

[1] Areas of Europe that result from reducing the dimensionality of the environmental variables into a set of linearly uncorrelated and independent components (ENETWILD consortium et al. 2021).

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and culling policies on WB populations, and what the scenario could be if ASF would spread all over Europe.

Conclusions:

- Beyond the collection of current available data, we provided an open data model to allow academics and wildlife professionals to continuously update population parameters with new and/or low accessible data (i.e., grey literature which is not public or only available in local languages). This data model, to be conceived as an open resource and collaborative approach, has been incorporated into the European Observatory of Wildlife[2] (EOW) platform.
- To overcome the lack, or when available, unharmonized information, our data model includes the main potential drivers and population parameters that should be specified in every study on wild boar (wildlife in general) ecology and epidemiology at the proper spatio-temporal resolution.
- Even when we mostly focused on recent data (mainly from 2010 onwards), the temporal frame of available data does not always represent the current situation. WB populations have been increasing during the last decade in the absence of ASF, and in certain regions the direct impact of ASF and/or reactive and proactive policies have led to very different scenarios. Therefore, recent data is needed.
- The immediate potential impact of making available the information we reviewed here on WB ecological and population dynamics parameters are (i) better understanding the impact of ASF and ASF-management on wild boar populations and (ii) to identify gaps in data, areas or management contexts to plan integrated and harmonized monitoring of WB population dynamics trends (e.g. EOW). In addition, (iii) reliable parameters are now available to feed population dynamics and epidemiological models.
- Next steps that have been identified are:
    - This harmonized approach should be extended to other taxa as an essential tool to improve European capacities to monitor, to produce risk assessment and to manage wildlife under an international perspective. The EOW aims hosting a virtual space in the web and promote this activity among wildlife professionals and academics.
    - To promote the use of common standards to record and publish ecological and population dynamics parameters.
    - To continue data collection in the case of WB, including those from grey literature.

[2] A network of "observation points" funded by EFSA which is provided by collaborators from all European countries capable to monitor wildlife population at European level in the long term (https://wildlifeobservatory.org/).

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1. Introduction

1.1. Background and Terms of Reference as provided by the requestor

This contract was awarded by EFSA to Universidad de Castilla-La Mancha, contract title: Wildlife: collecting and sharing data on wildlife populations, transmitting animal disease agents, contract number: OC/EFSA/ALPHA/2016/01 – 01.

The terms of reference for the present report (specific contract 9) were (deliverable D5.1): Wild boar ecology: to develop studies on basic aspects of WB population dynamics all over Europe (particularly the collection of ecological parameters by bioregion). This deliverable is due by November 2021.

1.2. Scope of the report

The ENETWILD consortium (www.enetwild.com) implemented an EFSA funded project whose main objective has been the collection of information regarding the geographical distribution and abundance of WB and other ungulates throughout Europe to subsequently create geospatial tools to be used in further risk assessment of diseases, such as African swine fever (ASF) in the case of wild boar (WB).

Currently, the lack of standardized information WB population dynamics covering the necessary range of biogeographical, management, socio-economic and cultural factors is impeding the use of such data at the European level, hampering risk assessments (ENETWILD et al. 2018a, b; 2019b, 2020). Biased, incomplete, or simulated parameters are normally used for these purposes, and their regional variation is not considered. The situation is further complicated by two factors:

- There exists a wide diversity of parameters to describe WB population dynamics and different methods are applied, which are not always appropriate and/or comparable (ENETWILD consortium et al. 2018a, 2019b, 2020).
- The temporal frame of available data does not always represent the current situation. WB populations have been increasing over during the last decade in the absence of ASF, and in certain regions the direct impact of ASF and/or reactive and proactive policies have led to very different scenarios (EFSA et al. 2020).

Compiling and generating valid up-to-date information on WB population dynamics is needed, following harmonised methods and filtering by standards of quality. Recent activity has been restricted to density and distribution data but not to population dynamics (ENETWILD consortium et al. 2019a, 2019b, 2020). There is a large body of literature describing basic aspects of WB population dynamics. However, this literature is extremely biased towards certain regions of its native range (Central Europe) and certain parameters (reproduction and spatial ecology). WB population parameters are largely determined by different drivers including natural and human-related extrinsic factors influencing ecological processes and population dynamics. Population models addressing the drivers that may affect WB populations depend on the local and regional variation, and the scarce literature mainly refers to Central European WB populations (e.g., Bieber and Ruf 2005, Vetter et al. 2020).

WB is ecologically very plastic, with potentially rapid population growth rates. WB populations still growing and expanding despite high mortality rates. They are also able to adapt to a wide array of climatic conditions (ENETWILD consortium et al. 2019b). All of this makes WB population dynamics highly variable across the continent, requiring a deeper understanding of local and

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regional variations over its distribution range. The essential steps to guide ASF control policies are: (i) defining which basic parameters of WB population dynamics are most relevant, (ii) understanding them in a context-dependent manner, based on their variation in given geographical, ecological and management contexts (hereafter called "WB population bioregions") and conditioned by drivers, and finally (iii) quantifying these parameters (once data gaps are identified). The potential impact of the results obtained by this review on WB ecological and population dynamics parameters for ASF management in the EU are:

- Better planning integrated and harmonized (comparable) monitoring of WB population dynamics trends and impacts over space and time under different scenarios and drivers occurring in Europe (e.g., protected areas, agricultural land, hunting grounds; management schemes such as artificial feeding or not), and epidemiological situations (pre-ASF, during or post-ASF; at a local outbreaks scale and over large frontlines and regions affected by ASF).
- Monitoring the effects of ASF management actions under an adaptive approach, that is, information is collected continuously, and this is used to improve biological (including the human dimension) understanding and to inform future decision-making. For example, changing hunting strategies to achieve the most effective method WB population reduction (Massei et al. 2011).
- Parametrizing population dynamics models (disentangling factors regulating population dynamics such as compensatory growth, density dependence, top-down control by predators, stochasticity) and epidemiological models (e.g., risk analysis, control options). Only science-based modelling should be accepted to guide policy, for instance, to develop most efficient cost-benefit strategies: control and eradication of ASF in different scenarios (ASF affecting large areas, local outbreaks, ASF-free zones) and epidemiological stages of ASF (epidemic, endemic).

In April 2021, the ENETWILD consortium proposed a number of research protocols for designing studies/pilot trials to evaluate and to improve effectiveness of WB management in relation to African swine fever virus (https://enetwild.com/wp-content/uploads/2021/06/ENETWILD_report_D3.1_SC8_approved_EFSA_for_publication_website-2-2.pdf). This previous report presented twelve research objectives (ROs) grouped into six categories, the first of which addressed aspects of WB ecology, i.e., studies on basic aspects of WB population dynamics and assessment of the factors that determine the presence of WB near outdoor pig farms. Following recommendations by RO1 ("Studies on basic aspects of WB population dynamics all over Europe" the aim of the present report is to produce a comprehensive compilation and description of data on WB population dynamics throughout Europe. This will facilitate further understanding of disease dynamics, improve science based ASF management, and will help to identify and prioritize data gaps over the (bio)regions and contexts of Europe. This will also be useful to determine the main drivers of WB population dynamics and to propose the approach and design of short-term field research to address these gaps.

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2. Methodology

2.1. Bioregions

For summarizing and grouping population and ecological parameters of WB, we considered the European bioregions determined by ENETWILD consortium et al. (2021) (see Figure 1). Bioregions are areas of Europe that result from reducing the dimensionality of the environmental variables into a set of linearly uncorrelated and independent components (see Pittiglio et al 2018). Bioregion has been included as predictor factor in previous ENETWILD wild boar abundance models, allowing the inclusion of new predictors which help to solve regional or local misleading predictions.

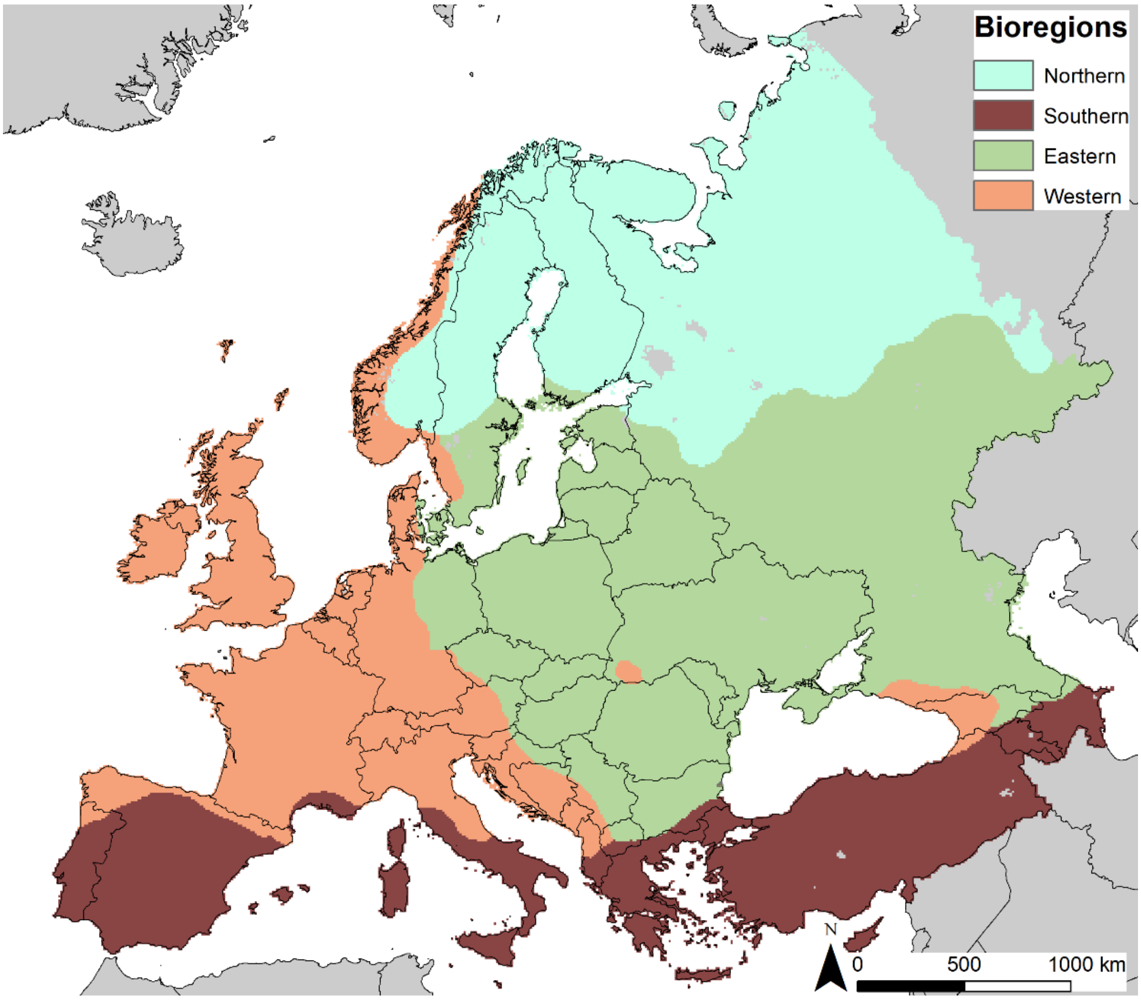

Figure 1: Map showing the bioregion classification used to subgroup the data for modelling purposes (ENETWILD consortium et al. 2021).

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2.2. Comprehensive compilation and description of data on WB population dynamics throughout Europe following a standardised data model

We compiled and described data on WB population dynamics and drivers (e.g., management strategies) following the standardized data model (proposed by ENETWILD, https://enetwild.com/wp-content/uploads/2021/06/ENETWILD_report_D3.1_SC8_approved_EFSA_for_publication_website-2-2.pdf). Data collection following these standards guarantees that sufficient information (e.g., on methods) was collected to validate data (e.g., density values).

For this purpose, we compiled population dynamics and ecological data using a narrative literature review. We followed the guidelines of systematic reviews (e.g., Pullin and Knight 2009). The protocol followed a strict method to guarantee transparency and to minimise sources of bias. We searched the Scopus and WOS databases by using a search string that combined different terms related to the WB population and ecological parameters of interests. The search was made in titles, abstracts and keywords in English-written articles published until June 2021 in the Scopus and WOS databases (see Table 1 for the full search string).

There may be a large amount of reviewable literature (including grey literature), as WB populations have grown markedly in recent years, and methods (e.g., telemetry) have greatly developed. Unpublished and grey literature was researched from other sources of internet (e.g., Google scholar) and through contact with researchers, administrations and wildlife managers collaborating with ENETWILD.

Table 1. List of keywords used in the systematic review.

Scopus + WOS	(TITLE-ABS-KEY ("wild boar") AND (TITLE-ABS-KEY (population) OR TITLE-ABS-KEY (dynamic)) OR (TITLE-ABS-KEY (movement) OR TITLE-ABS-KEY (gps) OR TITLE-ABS-KEY (telemetry))) AND (LIMIT-TO (DOCTYPE , "ar")) AND (EXCLUDE (SUBJAREA , "IMMU") OR EXCLUDE (SUBJAREA , "BIOC") OR EXCLUDE (SUBJAREA , "MEDI") OR EXCLUDE (SUBJAREA , "ARTS")) AND (LIMIT-TO (AFFILCOUNTRY , "Italy") OR LIMIT-TO (AFFILCOUNTRY , "Spain") OR LIMIT-TO (AFFILCOUNTRY , "Germany") OR LIMIT-TO (AFFILCOUNTRY , "France") OR LIMIT-TO (AFFILCOUNTRY , "Poland") OR LIMIT-TO (AFFILCOUNTRY , "United Kingdom") OR LIMIT-TO (AFFILCOUNTRY , "Portugal") OR LIMIT-TO (AFFILCOUNTRY , "Sweden") OR LIMIT-TO (AFFILCOUNTRY , "Russian Federation") OR LIMIT-TO (AFFILCOUNTRY , "Croatia") OR LIMIT-TO (AFFILCOUNTRY , "Czech Republic") OR LIMIT-TO (AFFILCOUNTRY , "Hungary") OR LIMIT-TO (AFFILCOUNTRY , "Switzerland") OR LIMIT-TO (AFFILCOUNTRY , "Austria") OR LIMIT-TO (AFFILCOUNTRY , "Netherlands") OR LIMIT-TO (AFFILCOUNTRY , "Belgium") OR LIMIT-TO (AFFILCOUNTRY , "Denmark") OR LIMIT-TO (AFFILCOUNTRY , "Slovenia") OR LIMIT-TO (AFFILCOUNTRY , "Lithuania") OR LIMIT-TO (AFFILCOUNTRY , "Norway") OR LIMIT-TO (AFFILCOUNTRY , "Greece") OR LIMIT-TO (AFFILCOUNTRY , "Bulgaria") OR LIMIT-TO (AFFILCOUNTRY , "Romania") OR LIMIT-TO (AFFILCOUNTRY , "Serbia"

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	) OR LIMIT-TO (AFFILCOUNTRY , "Slovakia") OR LIMIT-TO (AFFILCOUNTRY , "Estonia") OR LIMIT-TO (AFFILCOUNTRY , "Turkey") OR LIMIT-TO (AFFILCOUNTRY , "Finland") OR LIMIT-TO (AFFILCOUNTRY , "Latvia") OR LIMIT-TO (AFFILCOUNTRY , "Belarus") OR LIMIT-TO (AFFILCOUNTRY , "Ukraine") OR LIMIT-TO (AFFILCOUNTRY , "Ireland") OR LIMIT-TO (AFFILCOUNTRY , "Iceland") OR LIMIT-TO (AFFILCOUNTRY , "Armenia") OR LIMIT-TO (AFFILCOUNTRY , "Georgia") OR LIMIT-TO (AFFILCOUNTRY , "North Macedonia"))

From each publication we extracted available data on parameters describing the basic aspects of WB population dynamics relevant to understanding disease dynamics and improve science-based ASF management: (1) its general description (year of publication, journal, country); (2) general ecological factors (bioregion, predator presence, hunting pressure, supplementary feeding and ASF presence); (3) population characteristics (e.g. density, sex ratio, body size, group size, age structure by age…); (4) mortality (due to predation, diseases, by harvest, and others as road kills); (5) reproduction parameters (e.g. litter size, proportion of pregnant females); and (6) spatial behaviour (e.g. proportion of dispersants, dispersal period, distance travelled, home ranges) (see Tables 2 to 7, indicating response categories and units).

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Table 2. General characteristics of articles and drivers identified.

Location and period	Country Region Location Sampling year
Management, population, and environmental drivers	Bioregion Supplementary feeding (Y/N) Predator presence (Y/N) Predator spp ASF presence (Y/N) Epidemic/endemic (Y/N) Land use Main biome Climate Precipitation Population control (incl. hunting) Y/N? Population control method

Table 3. Density, population structure and aggregation data searched in articles.

Density, population structure and aggregation	Winter local density (ind/km^2)	
	Spring local density (ind/km^2)	
	Summer local density (ind/km^2)	
	Autumn local density (ind/km^2)	
	Local density (ind/km^2)	
	Abundance	
	Abundance method (Measure units)	
	Absolute abundance (individuals)	
	Carrying capacity (*K*, ind/km^2)	
	Sex ratio (males:females)	Foetus Juvenile Yearling Adult Population (Age not specified)
	Group size (number of individuals)	Male Female (maternal groups) Population (Spring) Population (Summer) Population (Autumn) Population (Winter) Population (year)

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<table>
<tr><td rowspan="3"></td><td>Age structure (% of classes)</td><td>Juvenile male
Yearling male
Adult male
Male (age not specified)
Juvenile Female
Yearling Female
Adult Female
Female (age not specified)
Juvenile (sex not specified)
Yearling (sex not specified)
Adults</td></tr>
<tr><td>Population growth rate (r)</td><td></td></tr>
<tr><td>Recruitment rate (young:adults)</td><td></td></tr>
</table>

Table 4. Average body size was reported in this review when it was described in articles, by sex an age group.

Body size	Juvenile male Yearling male Adult male Male (age not specified) Juvenile female Yearling female Adult female Female (age not specified) Juvenile (sex not specified) Yearling (sex not specified) Adults (sex not specified) Population

Table 5. Mortality (survival) data was searched in articles by sex and age group.

<table>
<tr><td rowspan="6">Mortality (survival)</td><td>Natural: by predator</td><td rowspan="6">Juvenile male
Yearling male
Adult male
Male (age not specified)
Juvenile female
Yearling female
Adult female
Female (age not specified)
Juvenile (age not specified)
Population (age and sex not specified)</td></tr>
<tr><td>Natural: by disease</td></tr>
<tr><td>Other: road kills</td></tr>
<tr><td>Natural mortality</td></tr>
<tr><td>By harvest</td></tr>
<tr><td>Mortality (natural + harvest)</td></tr>
</table>

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Table 6. Reproduction data searched in articles.

Reproduction y	Litter size	Juvenile Yearling Adult Female (age not specified) Foetus/female
	Pregnant female (proportion, %)	Juvenile Yearling Adult Female (age not specified)
	Seasonality of reproduction (% of pregnant females)	1 to 12

Table 7. Movement parameters searched in articles.

Movement	Juvenile dispersion: period (month/season)	Juvenile Male Yearling Male Juvenile Female Yearling Female Juvenile Yearling
	Dispersion: maximum distance (km)	Juvenile Male Yearling Male Adult Male Male (age not specified) Juvenile Female Yearling Female Adult Female Female (age not specified) Juvenile (sex not specified) Yearling (sex not specified) Adult (sex not specified) Family group Period Population
	Proportion of dispersants (%)	Male Female Population (sex not specified)
	Annual home range (50 & 95% K) based on X months (km^2)	Male (50%) Male (95%) Maternal group (50%) Maternal group (95%) Female (95%) Population (95%) Population (50%)

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	Annual home range (Convex polygon), MPC based on X months (km^2)	Juvenile male Yearling male Adult male Male (age not specified) Juvenile female Yearling female Adult female Female (age not specified) Juvenile (sex not specified) Population Family group Yearling

3. Results and discussion

We initially identified found 2391 articles of potential relevance, once duplicates were eliminated. We screened the articles to identify ecological and population dynamics parameters. After that, we removed those articles that did not present such parameters. The complete list of selected articles (n=424) is presented as an electronic appendix (https://doi.org/10.5281/zenodo.6327062).

3.1. General characteristics of articles and drivers identified

As for the general characteristics of articles and main drivers identified, reviewed articles established their study areas over 32 countries of the continental Europe, comprising published studies from 1977 until 2021 (June). Most data came from 1-year or less duration studies (69.8% of extracted parameters), but others (30.2%) were estimated for longer periods, which ranged up to fifty years.

According to European bioregions, East (27.7%), South (35.9%) and West (33.2%) collected most of the available WB population dynamic parameters, whereas the North bioregion showed lower data availability (3.2%).

In 47.4% of the WB studied populations, the existence of hunting pressure on the population was specified. However, in 1.9% of them hunting was not allowed, for instance, due to protection regimes of the study area. Moreover, in at least 28.1% of the analysed WB populations, the use of supplementary feeding was noticed, in most cases for hunting purposes or to mitigate crop damages. In other cases, these parameters were not indicated.

3.2. Density, population structure and aggregation parameters

In relation to WB density (N=299 density values collected from literature), the mean value was 4.8 (± 5.1) wild boars/km^2 at European level. However, this value fluctuated strongly among bioregions. Mean density for South (N=126) bioregion was 6.0 (±5.1) wild boars/km^2; whereas for West (N=73), mean density was 5.8 (± 5.7) wild boars/km^2. East (N=96) and North (N=2) bioregions showed the lowest mean density values, with 2.4 (± 3.7) and 1.0 wild boars/km^2 (standard deviation not available due to low sample size), respectively.

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In general, sex ratio (males:females; N=129) was 1.0 (±0.4), ranging from 0.4 to 3.4. By bioregions, sex ratio at East (N=7) was 1.0 (±0.4), at North (N=3) was 1.6 (SD not available), at South (N=51) was 1.0 (±0.6), and at West was (N=68) 1.0 (±0.2).

By age structure, WB juveniles (N=123) represented 35.5 (±17.5) % of the total population, 31.9 (±15.1) % yearlings (N=101), and 37.6 (±16.1) % adults (N=100). Generally, these parameters are extracted from harvested WBs, so these parameters values may be affected when hunting/culling activity were not randomly developed (e.g., hunters' preference, control strategy).

Aggregation data searched in articles showed mean group size (N=8) of 4.1 (±2.1) individuals but may vary among seasons. Female group (including offspring, N=5) averaged 2.9 (±3.9) WB.

Table 8 shows the average value, range, and standard error of each parameter.

Table 8. Density, population structure and aggregation average values (N is indicated within parenthesis). Average (range, SE).

Local density (ind/km^2) (299)	4.8 (0-32, 5.1)
Winter local density (ind/km^2) (16)	2.7 (0-11.2, 2.7)
Spring local density (ind/km^2) (20)	6.6 (0-21.4, 6.1)
Summer local density (ind/km^2) (20)	28.4 (0-72.9, 25.7)
Autumn local density (ind/km^2) (20)	20.1 (0-52.8, 20.7)
Carrying capacity (K, ind/km^2) (1)	19.6 (2)
Sex ratio (males:females)	Foetus (14) = 1.0 (0.6-1.5, 0.3) Juvenile (25) = 0.9 (0.4-1.3, 0.3) Yearling (25) = 1.3 (0.5-2.8, 0.5) Adult (38) = 1.4 (0.3-14.0, 2.4) Population (age not specified) (129) = 1.0 (0.4-3.7, 0.4)
Age structure	Juvenile male (43) = 20.4 (6.8-46.8, 9.4) Yearling male (52) = 16.7 (2.9-81.8, 12.4) Adult male (71) = 15.3 (1.1-44.4, 9.0) Male (age not specified) (27) = 44.8 (4.1-75.0, 17.9) Juvenile female (54) = 22.7 (4.6-53.2, 10.8) Yearling female (62) = 19.0 (3.8-68.4, 13.0) Adult female (88) = 19.7 (1.0-80.0, 12.5) Female (age not specified) (26) = 43.3 (2.7-68.0, 16.7) Juvenile (age not specified) (123) = 35.5 (0.0-88.2, 17.5) Yearling (age not specified) (101) = 31.9 (1.4-77.9, 15.1) Adult (age not specified) (100) = 37.6 (2.7-79.2, 16.1)
Group size (number of individuals)	Male (NA) Female (maternal groups) (5) = 3.0 (1.0-10.0,3.9) Population (spring) (7) = 4.8 (3.9-7.4, 1.6) Population (summer) (7) = 4.6 (3.4-6.8, 1.0) Population (Autumn) (8) = 4.1 (2.5-5.7, 0.9) Population (Winter) (7) = 3.4 (2.4-5.7, 1.1) Population (Year) (8) = 4.1 (1.6-8.7, 2.1)

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3.3. Average body weight by sex an age group

The average body weights by sex an age group are indicated in Table 11.

Table 11. Body weight average values (N is indicated within parenthesis). Average (range, SE).

Juvenile male (7) = 25.3 (8.7-30, 7.4) Yearling male (8) = 53.4 (29.0-86.8,17.6) Adult male (22) = 79.3 (39-133, 21.0) Male (age not specified) (8) = 55.4 (39.4-71.3, 12.3) Juvenile female (10) = 30.3 (8.9-40.9, 9.6) Yearling female (12) = 56.1 (28.0-69.4, 14.2) Adult female (28) = 67.6 (29-112.5, 19.0) Female (age not specified) (11) = 45.0 (32.0-64.2, 11.6) Juvenile (sex not specified) (20) = 34.4 (7.5-64.9, 15.9) Yearling (sex not specified) (18) = 41.2 (13.6-82.0, 19.7) Adults (sex not specified) (11) = 65.0 (17.9-114.5, 27.9) Population (22) = 47.5 (34.0-80.0, 10.5)

3.4. Mortality (survival) by sex and age group

The mortality (survival) parameters by sex and age group are shown in Table 12.

Table 12. Mortality (annual %, N is indicated within parenthesis). Average (range, SE).

Natural: by predator	Juvenile male (NA) Yearling male (NA) Adult male (NA) Male (age not specified) (NA) Juvenile female (NA) Yearling female (NA) Adult female (NA) Female (age not specified) (NA) Juvenile (sex not specified) (1) = 13.5 (NA) Population (age and sex not specified) (11) = 13.9 (2-63, 17.5)
Natural: by disease	Juvenile male (NA) Yearling male (NA) Adult male (NA) Male (age not specified) (NA) Juvenile female (NA) Yearling female (NA) Adult female (NA) Female (age not specified) (NA) Juvenile (age not specified) (NA) Population (age and sex not specified) (1) = 30.0 (NA)

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Other: road kills	Juvenile male (NA) Yearling male (NA) Adult male (NA) Male (age not specified) (NA) Juvenile female (NA) Yearling female (NA) Adult female (NA) Female (age not specified) (1) = 13.0 (NA) Juvenile (age not specified) (NA) Population (age and sex not specified) (6) = 11.1 (0.9-26.0, 10.0)
Natural mortality	Juvenile male (8) = 16.5 (6.0-35.2, 11.4) Yearling male (9) = 19.9 (5.4-39.1, 13.4) Adult male (6) = 13.7 (1.0-1.7, 15.0) Male (age not specified) (2) = 15.0 (NA) Juvenile female (8) = 29.6 (7.1-84.0, 26.0) Yearling female (7) = 24.9 (11.7-43.4, 11.4) Adult female (13) = 31.1 (1.6-90.0, 25.3) Female (age not specified) (1) = 13.0 (NA) Juvenile (age not specified) (8) = 40.4 (6.0-90.0, 25.3) Yearling (age not specified) (2) = 75.0 (NA) Population (age and sex not specified) (13) = 35.5 (1.7-100, 33.6)
By harvest	Juvenile male (20) = 24.6 (4.4-56.0, 13.0) Yearling male (22) = 35.5 (2.5-77.0, 30.2) Adult male (24) = 43.2 (10.5-76.0, 26.2) Male (age not specified) (3) = 45.5 (19.0-70.0, 25.6) Juvenile female (19) = 19.8 (2.0-44.0, 10.5) Yearling female (21) = 30.4 (1.0-70.0, 25.1) Adult female (21) = 38.5 (6.0-70.0, 21.1) Female (age not specified) (3) = 43.2 (39.0-50.7, 6.5) Juvenile (age not specified) (18) = 25.8 (0.0-60.0, 16.7) Yearling (age not specified) (18) = 43.7 (20.0-68.4, 13.0) Adult (age not specified) (19) = 43.2 (2.1-100.0, 28.7) Population (age and sex not specified) (64) = 56.0 (1.7-100, 26.0)
Mortality (natural + harvest)	Juvenile male (1) = 74.2 (NA) Yearling male (NA) Adult male (NA) Male (age not specified) (NA) Juvenile female (1) = 48.2 (NA) Yearling female (1) = 56.8 (NA) Adult female (NA) Female (age not specified) (NA) Juvenile (age not specified) (NA) Yearling (age not specified) (NA) Adult (age not specified) (NA) Population (age and sex not specified) (14) = 27.5 (9.4-64.0, 16.1)

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3.5. Reproduction

Reproduction parameters are summarized in Table 13.

Table 13. Reproduction and productivity (N is indicated within parenthesis). Average (range, SE).

Litter size	Juvenile (2) = 2.8 (1.6-4.0, 1.7) Yearling (5) = 3.6 (1.5-6.0, 1.8) Adult (4) = 5.5 (4.1-6.3, 1.0) Female (age not specified) (27) = 4.2 (0.4-7.0, 1.5) Foetus/juvenile female (14) = 3.5 (2.0-4.9, 0.8) Foetus/yearling female (30) = 5.0 (1.2-7.0, 1.1) Foetus/adult female (27) = 5.9 (3.3-9.0, 1.1) Foetus/female (7) = 4.6 (3.5-6.2, 0.9)
Pregnant female (proportion, %)	Juvenile (35) = 25.6 (0.0-73.0, 18.8) Yearling (33) = 42.7 (1.0-100, 23.6) Adult (36) = 49.8 (4.0-100, 33.2) Female (age not specified) (17) = 50.9 (17.7-86.0, 24.4)
Seasonality of reproduction (% of pregnant by month)	January (6) = 48.3 (2.5-80.0, 34.8) February (5) = 51.9 (16.5-80.0, 32.2) March (3) = 48.7 (35.0-65.0, 15.2) April (3) = 30.5 (16.5-55.0, 21.3) May (3) = 30.5 (0.0-55.0, 30.4) June (3) = 20.3 (3.0-55.0, 30.0) July (3) = 8.2 (2.0-18.0, 8.6) August (4) = 16.6 (2.5-43.0, 19.0) September (4) = 14.4 (3.5-31.0, 1.9) October (4) = 23.9 (0.0-70.0, 32.2) November (6) = 42.0 (0.0-80.0, 39.0) December (5) = 37.6 (2.0-80.0, 39.5)

3.6. Spatial dispersal parameters

Average values on spatial dispersal parameters are summarized in Table 14.

Table 14. Movement average values (N is indicated within parenthesis). Average (range, SE).

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Dispersion: maximum distance (km)	Juvenile Male (2) = 14.3 (NA) Yearling Male (5) = 54.0 (1.9-250; 109.6) Adult Male (1) = 24.2 (NA) Male (age not specified) (1) = 6.0 (NA) Juvenile Female (2) = 250.4 (NA) Yearling Female (2) = 11.5 (NA) Adult Female (2) = 3.1 (2.5-3.7, 0.9) Female (age not specified) (2) = 3.7 (2.5-4.9, 1.7) Juvenile (sex not specified) (1) = 60 (NA) Yearling (sex not specified) (3) = 2.3 (1.0-4.0, 1.5) Adult (sex not specified) (1) = 0.2 (NA) Population (12) = 12.0 (0.9-40.0, 11.9)
Proportion of dispersants (%)	Male (1) = 42.0 (NA) Female (1) = 16.0 (NA)
Home range (50 & 95% Kernel polygon, km^2)	Male (50%) (3) = 4.6 (1.4-11.1, 5.6) Male (95%) (1) = 8.7 (NA) Maternal group (50%) (3) = 0.2 (0.0-0.2, 0.1) Maternal group (95%) (8) = 3.3 (0.2-12.3, 4.0) Population (95%) (9) = 4.4 (2.0-14.1, 3.7) Population (50%) (1) = 0.8 (NA)
Home range (minimum convex polygon, km^2)	Juvenile male (NA) Yearling male (1) = 1.0 (NA) Adult male (4) = 4.5 (0.7-10.1, 4.5) Male (age not specified) (NA) Juvenile female (2) = 23.5 (NA) Yearling female (2) = 6.2 (NA) Adult female (4) = 2.9 (0.5-7.6, 3.3) Female (age not specified) (1) = 0.4 (NA) Juvenile (sex not specified) (1) = 0.5 (NA) Yearling (sex not specified) (1) = 23.5 (NA) Population (14) = 4.6 (0.5-12.6, 3.7)

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4. Conclusions and further steps

- Beyond the collection of current available data, we provided an open data model to allow academics and wildlife professionals to continuously update population parameters with new and/or hardly accessible data (i.e., grey literature which is not public or only available in local languages). This data model, understood as an open resource and collaborative approach, has been incorporated to the European Observatory of Wildlife (EOW) website (https://wildlifeobservatory.org/).
- To overcome the lack, or the availability of only unharmonized information, our data model includes several potential drivers and population parameters that should be specified in every study on WB (and wildlife in general) ecology and epidemiology at the proper spatio-temporal resolution.
- Even when we mostly focused on recent data (mainly from 2010 onwards), the temporal frame of available data does not always represent the current situation. WB populations have been increasing during the last decade in the absence of ASF, and in certain regions the direct impact of ASF and/or reactive and proactive policies have led to very different scenarios.
- The immediate potential impact of making available the information here reviewed on WB ecological and population dynamics parameters for ASF management in the EU are (i) better understanding the impact of ASF and ASF-management on WB populations and (ii) to identify gaps areas or management contexts to plan integrated and harmonized monitoring of WB population dynamics trends, so as the better strategy (e.g., EOW). In addition, (iii) reliable parameters are now available to feed population dynamics and epidemiological models.
- Next steps we identified are:
    - This harmonized approach of collection on WB population dynamics parameters should extend to other taxa as an essential tool to improve European capacities to monitor, to produce risk assessment and to manage wildlife under an international perspective. The EOW aims hosting a virtual space in the web and promote this activity among wildlife professionals and academics.
    - To promote the use of common standards to record and publish ecological and population dynamics parameters.
    - To continue data collection in the case of WB, also identifying sources from the grey literature.

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Annex A – Studies on basic aspects of wild boar population dynamics all over Europe

Table S1. Key review papers and reports describing the basic aspects of wild boar population dynamics all over Europe[(a)].

Type of parameter	Parameter	Spatial context	Observations	Ref
Population characteristic	Density (wb/km2)	West and Central Europe	Ranged from 1.2 to 90.9**[(b)]** based mostly on not reliable data.	Acevedo et al. 2007; Ruiz-Fons et al. 2008
Population characteristic	(Hunting) Growth rate	Europe	Growth rate varied from 0.9 to 1.46, based on hunting bag statistics	Massei et al. 2015
Population characteristic	(Hunting) Growth rate	West Europe (Spain)	Growth rate varied from 2.1 to 40.3, based on hunting bag statistics	Quirós-Fernández et al. 2017
Population characteristic	Growth rate	West and Central Europe, and Asia	Based on projection matrix models, growth rate varied from 0.85 to 1.63.	Bieber and Ruf, 2005
Mortality	By harvest	Central Europe	Based on hunted tracked WB, average mortality rate was 0.53.	Keuling et al. 2013
Mortality	By harvest and disease	West Europe (Spain)	Average mortality rate was 0.53 by harvest; and 0.30 by disease (tuberculosis).	Barasona et al. 2016
Reproductive	Litter size	Europe	Mean ranged from 3.58 to 6.5.	Bieber and Ruf, 2005
Reproductive	Litter size	West and Central Europe	Mean ranged from 2.2 to 4.	Rosell et al. 2001
Reproductive	Litter size	Europe	Mean ranged from 3.6 to 7.6	Fonseca et al. 2011
Reproductive	Litter size	West and Central Europe	Mean ranged from 3.1 to 6.9.	Bywater et al. 2010
Spatial behaviour	-	Global	Research tendencies and gaps, no values provided.	Morelle et al. 2014; Morelle and Lejeune, 2015

(a): Extensive literature is also available for feral pig population dynamics, especially in the USA, but of very low application to our cases.

(b): This value is reached under artificial conditions, such as fenced game estates with artificial feeding.

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Table S2. The main drivers identified on publications that could influence significantly on WB population dynamics.

Type of driver	Driver	Observations	Ref
Interspecific interactions	Predation	Lack of top-down control can favour population growth.	Bassi et al. 2020; Jędrzejewski et al. 1992; Segura et al. 2014
	Diseases & parasites	Effects on survival, reproductive or mortality rates.	Barasona et al. 2016; Ruiz-Fons et al. 2008
Landscape	Land use change	Easier food access or the increment of available and favourable habitat could contribute on WB population growth.	Acevedo et al. 2011; Hearn et al. 2014; Kodera et al. 2010
	Urban expansion		
	Rural abandonment		
Climatic	Global warming	Favourable climatic conditions increasing winter survival and food availability throughout the year.	Bieber and Ruf, 2005; Melis et al. 2006; Vetter et al. 2020; Vetter et al. 2015
	Drought episodes	Effect on reproductive performance.	Fernández-Llario and Carranza, 2000
Food availability	Productivity	Related with climatic conditions.	Barbosa et al. 2020; Frauendorf et al. 2016
	Supplementary feeding	Associated with higher recruitment rate and litter size.	Massei et al. 2015
Management	Hunting	Hunting induce mortality and affects WB dynamic. A decrease in the number of hunters, difficult population management.	Cromsigt et al. 2013; Holland et al. 2009; Merli et al. 2017
	Conservation or agroforestry policy	Differential effect on population dynamic among different applied policies.	Vicente et al. 2005

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Table S3. Parameters describing the basic aspects of WB population dynamics relevant to understanding disease dynamics and improve science-based ASF management. Colours of "trait" column indicate the priority of each parameter to be determined (orange: high; yellow: medium; green: low).

Population parameters	Trait	Sex by age class	Temporal	Spatial resolution	Units	Why is important?	Ref
Population characteristics	Local density		Optimally pre-harvest season (for standardization)	Management or ecological unit	ind/km^2 or social group/km^2	-Disease transmission is a density-dependent process. Population and individual traits are density dependent. Management is based on numbers (abundance indexes are not sufficient or comparable) -It could further elucidate complex species-habitat-management relationships in spatial distribution models	Kramer-Schadt et al. 2009
	Absolute abundance				Nº individuals		Yu et al. 2020
	Carrying capacity		Lowest over the year	Ecological unit	maximum population size or density (*K*)	-Variable due to habitat perturbations and environmental factors (e.g., resource availability and climate). Theoretically, maximum productivity (i.e., population growth rate) is achieved when the population is approx. 50% of the K (basic logistic growth models). Useful for modelling scenarios of potential population growth and consequences for disease spread, maintenance and control.	Groot Bruinderink et al. 1994
	Sex ratio	juvenile (< 1 y)	Optimally pre-harvest season (for standardization)	Management or ecological unit	ff:mm	-Essential to rebuild population structure and model population dynamics -Influence on the spatial behaviour and interactions among social units (groups) and modulate the spread of infectious diseases -Each sex by age class has distinct properties in terms of their demographic and infection dynamics -Key parameters to define population control strategy -These parameters are among those presenting larger variation over geographical distribution and management	Hema et al. 2020; Mortensen et al. 2016
		yearling (1-2 y)					
		adult (> 2 y)					
	Group size	male	average annual and by month or season		mean number of individuals, assumed 1		Loehle, 1995; Pepin et al. 2020; Podgórski et al. 2018
		maternal groups			mean number of individuals		
	Age structure	By sex	Pre-harvest season		%		Hoy et al. 2020

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	Population growth rate		yearly		% or increase rate (r)		Fonseca et al. 2011
	Recruitment rate				coefficient of young/adult		DeCesare et al. 2012
Population characteristics: mortality	Natural: predation/ disease	Sex by age. Especially on piglets (<3 months old)	yearly		% mortality (1/survival)		Bassi et al. 2020; Keuling et al. 2013; Lange et al. 2012; Merli et al. 2017; Tanner et al. 2019b
	By harvest						
	Other: e.g., road kills						
Reproduction (productivity)	Litter size	By age*	yearly		Number of offspring born by female age class		Fernández-Llario & Mateos-Quesada, 1998; Frauendorf et al. 2016
	Pregnant females		yearly and monthly		% of females becoming pregnant by age class		Fernández-Llario & Mateos-Quesada, 2005; Lombardini et al. 2014
Spatial behaviour	Proportion of dispersants	Sex by age	yearly		%	-Related with species geographical and disease dispersion. -Spatial behaviour determines interactions (within and among groups) -Spatial behaviour is relevant to implement effective management strategies. - Influenced by land uses and human activities among other factors, including population control and response to ASF	Casas-Díaz et al. 2013; Truvé & Lemel, 2003; Truvé et al. 2004
	Dispersal period	Sex by age			month/season		
	Dispersal distance				km		
	Home range (50 & 95%K)	Sex by age (males, maternal groups)	seasonal		km^2		Bisi et al. 2018; Keuling et al. 2008

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