



Review

Wild boar as a reservoir of antimicrobial resistance

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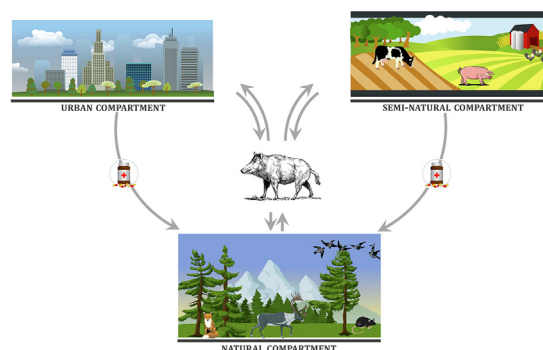
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HIGHLIGHTS

- Literature related to antimicrobial resistance of wild boar in Europe is reviewed.
- Growing interest in antimicrobial resistance in wild boar is highlighted.
- Wild boar are carriers of antimicrobial resistant bacteria.
- Research trends and future directions are discussed.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:

Received 1 August 2019

Received in revised form 19 September 2019

Accepted 14 October 2019

Available online 23 November 2019

Editor: Dr. Damia Barcelo

Keywords:

Wild boar
Antimicrobial resistance
Ungulates
Wildlife
One health

ABSTRACT

Antimicrobial resistance (AMR) has been recognized as an emerging and growing problem worldwide. Knowledge concerning AMR bacteria circulating in wildlife is currently limited, although it could provide important insights into AMR emergence and persistence. Across Europe, wild boar (*Sus scrofa*) populations have dramatically increased their distribution and number over the last decades. In the context of AMR dynamics, wild boar is a perfect model species to unveil the emergence, spread and persistence of AMR at the human-livestock-wildlife interface. Here, we summarize the current knowledge on the importance of wild boar as a reservoir of antimicrobial resistant bacteria, and its possible use as sentinel species for surveillance. Analyses of available data showed a rising interest on this topic in the last years, highlighting the growing concern on wild boar potential role as AMR facilitator and it is foreseen that the importance of antimicrobial resistance research in wild boar will continue to increase in years to come. Available studies have been focused on specific bacterial species, particularly *E. coli*, *Salmonella* spp. and *Enterococcus* spp., bioindicators of AMR, and have been mainly conducted in three countries: Spain, Portugal and Germany. Strikingly, AMR surveillance in wild boar is uneven and still poorly allocated as many wild boar high-density countries do not yet have publications on the topic. Overall, accumulated data showed that wild boar are carriers of antimicrobial resistant bacteria, with variation in the prevalence of bacterial species and the percentage of resistance to different antibiotics. The lack of harmonized sampling and testing protocols makes it difficult to compare AMR in wild boar. The need for the establishment of standardised protocols keen to provide quantitative comparable data is highlighted. We

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finally suggest the long-term monitoring of wild boar as a sentinel species for AMR surveillance in order to inform public policies on this topic.

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1. Introduction

Antimicrobials have revolutionised human healthcare practices worldwide (Spellberg et al., 2013). They have saved millions of lives. For example, penicillin lowered mortality associated with pneumococcal pneumonia from 20–40% to 5% (Laxminarayan et al., 2016). Nevertheless, shortly after the discovery of the “magic pill”, antimicrobial resistance (AMR) became a serious problem threatening the advances of the prior decades (Ventola, 2015). This resulted in a general reduction of the efficacy of antibiotics, leading the World Health Organization to identify AMR as a global, emerging, and unparalleled problem for public, animal and environment health (WHO, 2014). Although the development of natural resistance by some bacteria is an old and natural phenomenon (D’Costa et al., 2011), the acquired resistance is mostly due to the underuse, overuse, and misuse of antibiotics (Davies, 1996; Lammie & Hughes, 2016). In fact, antibiotic consumption is considered the primary driver of antibiotic resistance (Klein et al., 2018).

AMR is an urgent global problem, recently compared to the challenges of climate change since it is a global scale natural process that has been aggravated by human activity (Woolhouse et al., 2015). The loss of efficacy of antibiotics to common pathogens creates a huge clinical problem. Over 700,000 deaths worldwide are attributable to resistant bacterial pathogens each year (Laxminarayan et al., 2016). AMR is a complex, multi-layered problem, that does not recognize national borders, requiring an holistic framework to address it (Queenan et al., 2016; Walsh, 2018).

The AMR problem is not however confined to the human compartment, since part of the resistance burden in humans is attributable to antimicrobial use in livestock production, primarily for disease prevention and growth promotion (Marshall & Levy, 2011). For example, antimicrobials used in livestock are expected to account for circa 80% of the U.S.A. (Spellberg et al., 2016) and 84% of China’s annual antimicrobials consumption (Zhang et al., 2015). Impressive doses of antimicrobials are also used in agriculture, aquaculture and horticulture, to prevent infection, making resistance widespread in those settings as well (Hoyle et al., 2006; Laxminarayan et al., 2013). Several authors have advocated that the rising threat of AMR requires a holistic and multidisciplinary approach – a One Health perspective (Collignon et al., 2018; Puyvelde et al., 2018; Walsh, 2018) and that we have been

underestimating the tremendous importance of the animal compartment in contributing on AMR dissemination. The ‘One Health’ concept involves a focus on the multiple interfaces of AMR surveillance: human, animal (livestock and wildlife) and environmental. Given the complexity of the antimicrobial resistance challenge, it seems particularly important to emphasize the role of a One Health approach in addressing the problem, since it considers the underlying factors that influence AMR, including the socio-political, environmental, biological and economic factors (Kock, 2015; Lammie & Hughes, 2016). This is particularly true in the current scenario of antropogenic transformation of the landscapes, where natural habitats become increasingly fragmented, forcing wildlife into greater contact, both direct and indirectly, with humans and their livestock, ultimately increasing the opportunities for antimicrobial resistance transmission among populations (Jones et al., 2008). This inextricable connection between human populations, animals and the ecosystems further complicates the picture, strengthening the requirement for an integrated approach for human, animal and environmental health (Zinsstag et al., 2011).

Although AMR has already been reported in commensal bacteria of wildlife, which have the potential to act as reservoirs and dispersers of resistance genes (Arnold et al., 2016; Vittecoq et al., 2016), the knowledge concerning AMR bacteria circulating in wildlife is still limited. It is generally accepted that wildlife populations living in close proximity to humans exhibit higher levels of resistance: 95% of the bacterial isolates from rodents captured in rural England were resistant to antibiotics (Gilliver et al., 1999) while natural populations of moose, deer and voles in Finland had almost no resistance (Österblad et al., 2001). It is therefore hypothesised that contact with humanized environments can enhance wildlife contact with resistant bacteria as well as with selective agents and commensals from humans and other species, while vice-versa is also applicable (Vittecoq et al., 2016). Consequently, wildlife populations living in close contact to humans or agricultural areas have shown to exhibit higher levels of resistance (Gilliver et al., 1999; Allen et al., 2011; Bondo et al., 2016; Furness et al., 2017). Resistance however is not ubiquitous among wildlife species and different life-history traits may predispose some species as key actors in the cycle of AMR transmission. Wildlife species with a close association or tolerance for humans have been associated with the increase in AMR, with species foraging near human

settlements and farms reported as harbouring significant amounts of AMR bacteria (Rolland et al., 1985; Pesapane et al., 2013). It is obvious that wildlife can act as a potential, but still understudied, reservoir and disperser for AMR in the human-livestock-wildlife interface (Dhama et al., 2013), representing a major epidemiological link between natural and humanized environments, representing an additional challenge for human health, and hindering the management of wildlife species (Arnold et al., 2016; Vittecoq et al., 2016).

Wild boar (*Sus scrofa*) is considered one of the most extensively distributed mammals of the world, colonizing and occupying a variety of environments, from natural habitats to urban areas, exhibiting high tolerance to human disturbance, while also exploring anthropogenic food available in these environments. In the last decades, wild boar have experienced dramatically increases in number and distribution all over Europe and are now one of the most numerous and hunted ungulate species in Europe (Massei et al., 2015; Pittiglio et al., 2018). As a consequence of this expansion, new management challenges arise: its wide distribution and link between natural and humanized environments places this species in a central place as reservoir or carrier of several zoonotic pathogens, such as the agents of tuberculosis and brucellosis, or pathogens that can spill-over to domestic swine causing tremendous economic losses and embargo to animal trade, such as African swine fever virus (Fredriksson-Ahomaa, 2019). In the context of AMR dynamics, wild boar are perfect model species to unveil the emergence, spread and persistence of AMR in the wildlife-livestock interface. They are ubiquitous, have considerably large home ranges, are unlikely of being treated with antibiotics, at least in the wild setting, and overlap their habitat and distribution with livestock and humans, serving as a link between human-influenced settings and natural areas (Macdonald & Laurenson, 2006). Additionally, wild boar hunting and the manipulation of wild boar meat in various countries of the world are direct routes of transmission of resistant bacteria and associated genes between this species and humans. As the number of hunters across Europe appears to be either stabilizing or decreasing (Riley et al., 2003; Massei et al., 2015) and considering that hunting is the main source of wild boar population control, with urban wild boars nowadays a reality in several European countries (Castillo-Contreras et al., 2018), chances are that contact between wild boar and livestock and human will dramatically increase. These facts highlight the potential of wild boar as an important reservoir, and disperser of bacteria with antimicrobial resistance, posing additional concerns to public health.

However, despite its potential role in the AMR dynamics, which is of paramount importance to human health because of the increasing importance of zoonotic diseases, no attempt has been made to provide a comprehensive analysis of the knowledge accumulated to date regarding antimicrobial resistance in this species. Here, we systematically summarize the current understanding on the importance of wild boar as a reservoir of antibiotic resistant bacteria, and its possible use as sentinel species for surveillance, in Europe, where wild boar populations have greatly increased in the last decades, while discussing present knowledge gaps and future challenges.

2. Methodological approach

To gather the peer-reviewed database, literature searches were undertaken using major search engines and the resulting articles were manually reviewed. The literature search was conducted through the ISI's *Web of Science* online interface (<http://www.isi-knowledge.com>). Search results were delimited based on the following Boolean query executed within a single search. The

search strategy consisted of compiling search strings, one for each category (antimicrobial resistance and wild boar) and combining these by the Boolean operator "AND" to obtain only the intersection. Specifically, we used the following Boolean search statement: 'antimicrobial' OR 'antibiotic' AND 'resistant' OR 'resistance' AND 'wild boar' OR '*Sus scrofa*'. No time restrictions were placed on these searches, but locations were restricted to Europe, and only those published in English retrieved. The searches were last updated on 24th April 2019. Results for all articles were imported into a bibliographic referencing tool and assessed for relevance, removing articles that did not contain information relating to AMR in wild boar. All query results were verified manually before excluding duplicates. In addition, publications clearly indexed either as review, editorial, or errata were excluded. Bibliometrics, which is increasingly used to quantitatively assess scientific data and their trends over time, was used to evaluate and quantify the number and growth trend of the publications (Aria & Cuccurullo, 2017). The bibliometric analysis was performed on the full search results using the *bibliometrix* package in R (Aria & Cuccurullo, 2017).

3. Results and discussion

3.1. Temporal evolution of publications

Overall, a total of 88 documents were found in the ISI's *Web of Science*. From these, we selected those presenting novel data about antimicrobial resistance in free-ranging wild boar but excluded those living in captivity. In addition, publications clearly indexed either as review, editorial, or errata were excluded. In the end, only 40 peer-reviewed articles were included in the review. The full list of articles is presented in Appendix S1. Publications focusing on AMR in wild boar in Europe are relatively recent and date from 2007 to 2019 (Fig. 1). The number of documents on this topic has grown since 2007 until now, with some exceptions, particularly in years 2008, 2015 and 2016 (Fig. 1). The maximum number of documents on antimicrobial resistance in wild boar was published in the last two years of the period, in 2017 and 2018, with a total of 12 publications. It is important to stress that 2019 should follow the same trend as the database was last updated in April 2019. Overall, the temporal trend in publication on antimicrobial resistance in wild boar shows a growth in the number of documents published per year, with an annual percentage growth rate of 3.44% (Fig. 1). This trend evidences a growing awareness of the scientific community on the importance of wildlife, and in particular of wild boar, in the dynamic of antimicrobial resistance. Given this tendency, it is envisaged that the number of documents published on this topic will continue to rise in the upcoming years.

3.2. Distribution of bacterial species in the published studies

The vast majority of studies focusing on AMR in wild boar did not investigate antimicrobial susceptibility of the whole commensal bacteria community, but focus on specific isolated bacterial species (Fig. 2), particularly in *Escherichia coli*, *Salmonella* spp. and *Enterococcus* spp., as bioindicators for faecal contamination and AMR. Generally, the search is driven by human health and veterinary concerns associated with the focus bacteria (Vittecoq et al., 2016). *E. coli* is part of the normal gut microbiota of mammals in general, and humans in particular, and can easily be disseminated in different ecosystems, being used as an indicator species. *Salmonella* spp. is among the main causes of foodborne outbreaks and one of the most reported agents of zoonotic diseases in humans in Europe, with numbers of confirmed cases reaching over 90,000 in 2017 (EFSA and ECDC, 2018). This microorganism is con-

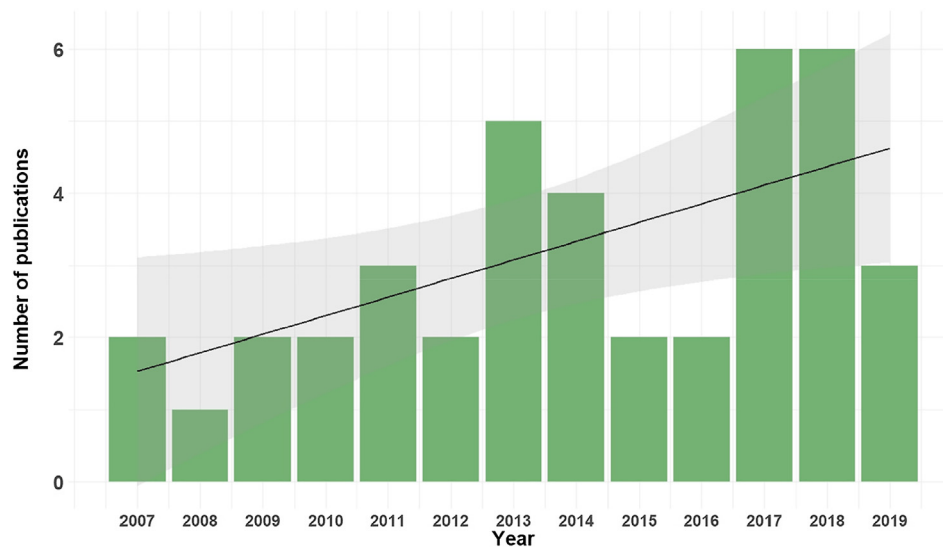


Fig. 1. Trends in number of publications on antimicrobial resistance in wild boar from 2007 to 2019.

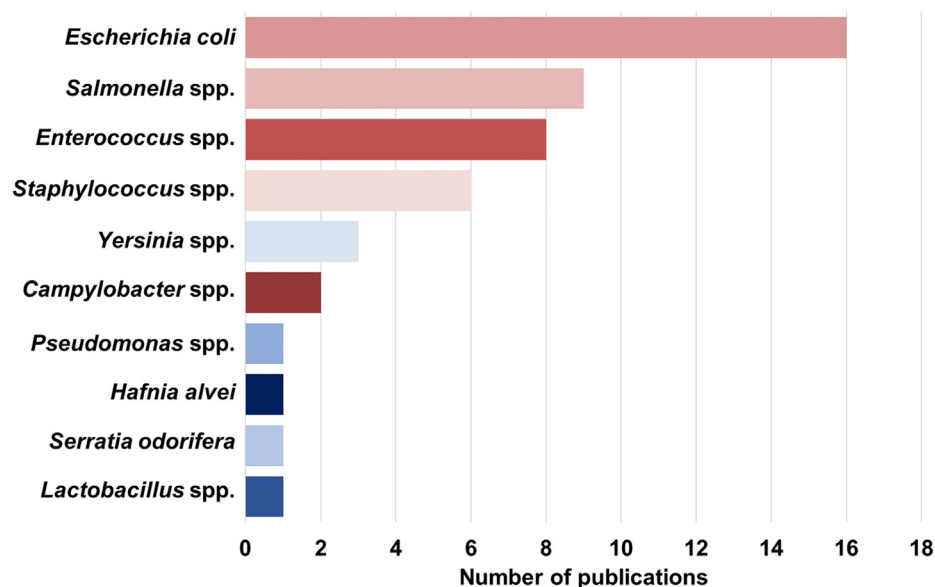


Fig. 2. Number of publications focusing on specific bacteria.

considered a multi-host pathogen with a long environmental persistence (Murray, 1991), being able to be transmitted among humans and other animal species, with reports of outbreaks tracked down to wildlife (Methner et al., 2018). Enterococci are part of the normal microbiota of healthy animals and humans but they can also act as pathogens that are able to cause different diseases of variable severity (Lozano et al., 2016). Furthermore, they have emerged as important causes of nosocomial and community acquired infections due to their ability to acquire virulence traits and increasing vancomycin resistance (Poeta et al., 2007a, 2008; Guerrero-Ramos et al., 2016).

Across Europe, studies reported a high variability in the prevalence of the three bacterial groups mentioned. *Escherichia coli* has been reported in wild boar populations with variable prevalence: higher prevalence was reported for several countries, with *E. coli* being found in 99% of wild boars in Czech Republic (Literak et al., 2010) and in up to 96% in central Portugal (Dias et al., 2015). It was also reported with a similar prevalence for Serbia (Velhner et al., 2018), while Navarro-Gonzalez et al. (2015) reported a lower

prevalence (about 3%) in northeast Spain. Similarly, *Salmonella* spp. occurred in populations of wild boar at different prevalence rates. In Germany, *Salmonella* spp. was isolated from 67% of wild boars (Methner et al., 2018) and, in Italy, the prevalence was similar, with about 66% of wild boars being *Salmonella* spp. carriers (Zottola et al., 2013). Both these report the highest prevalence of *Salmonella* spp.. In central Portugal, Dias et al. (2015) recorded a prevalence of 5% while Navarro-Gonzalez et al. (2013) reported similar prevalence in Barcelona (Spain). In northeast Spain, the prevalence of *Salmonella* spp. in cattle and cattle-free areas was compared and, interestingly, the occurrence of *Salmonella* spp. in wild boars from cattle areas was two times higher (35.67%) than in cattle-free areas (17.54%) (Navarro-Gonzalez et al., 2012). When we consider *Enterococcus* spp. in Portugal, reported prevalence can be up to 50% (Poeta et al., 2007a) with similar values reported in Spain (Navarro-Gonzalez et al., 2018), while lower prevalence rates (25.9%) were reported in Slovenia (Križman et al., 2017). Fewer studies focused on *Staphylococcus aureus* in wild boar populations and its lowest prevalence rate was reported for Germany at 4.8%

Table 1
Publication distribution by country.

Country	N° publications	%
Spain	12	33
Portugal	9	23
Germany	2	18
Austria	2	5
Italy	2	5
Poland	2	5
Switzerland	1	3
Czech Republic	1	3
Slovenia	1	3
Serbia	1	3

(Kraushaar & Fetsch, 2014), while its highest was reported in the same country with 36.9% of wild boar samples testing positive for this pathogen (Seinige et al., 2017).

3.3. Publication by country

Research has not been focused evenly on all European countries but is under particular focus in three of them: Spain (accounts for 33% of the publications), Portugal (23%) and Germany (18%) (Table 1). Altogether, these three countries have published 74% of the total number of papers dealing with antimicrobial resistance in wild boar. The low contribution of Switzerland, Czech Republic, Slovenia and Serbia is notable, with only one publication per country. Sample type and collection was also highly variable across studies with faecal samples representing nearly half the studies included (Appendix S1).

Wild boar distribution is generalized across Europe, with densities varying from 0.01 to 43 animals/km² (Pittiglio et al., 2018). Fig. 3 shows that the effort for AMR surveillance in wild boar is still poorly allocated, as there is a mismatch between areas or counties with some AMR monitoring and countries where densities are the highest. This highlights the critical need for wild boar monitoring in these high-density areas. Wild boar densities are expected to

continue to grow, as well as urban wild boar populations, therefore more work is needed to implement, and supplement, surveillance gaps.

3.4. Diversity of antimicrobial resistance patterns

When comparing studies across Europe, it is clear that the prevalence rates of bacterial species in wild boar are highly variable and so are their antimicrobial susceptibility profiles and resistance genes. Available studies tested the recovered bacteria against several antimicrobial agents and the percentage of resistance associated was demonstrated to be variable according to both geographical location and the examined strains. In addition, the susceptibility testing methods used also vary, making comparisons of antimicrobial susceptibility phenotypes of bacteria from wild boar sampled in different geographic origins difficult. Recently, studies have been interpreting bacterial susceptibility profiles based on their epidemiological cut-off values (ECOFFs) (e.g. Sousa et al., 2017; Methner et al., 2018; Navarro-Gonzalez et al., 2018; Dias et al., 2019), allowing to distinguish between wild type (WT) bacteria from bacteria with acquired resistance mechanisms (non-wild type – NWT), facilitating comparisons.

For *E. coli*, the prevalence of overall antimicrobial resistance varied between 0.9% in Italy (Bonardi et al., 2019) and 25% in Portugal (Dias et al., 2015). Regarding *Salmonella* spp., the prevalence of resistance was generally higher with all isolates being resistant to at least one antimicrobial in Germany (Methner et al., 2018) and up to 93% in Spain (Gil Molino et al., 2019). On the other hand, lower prevalence rates were reported for Spain (3%) (Navarro-Gonzalez et al., 2012). For the indicator bacteria *Enterococcus* spp., the prevalence of antimicrobial resistance varied between 4.9% (Lozano et al., 2016) and 95%, both rates reported for the same country, Spain (Navarro-Gonzalez et al., 2013). The highest percentages of resistance have been recorded for sulphonamides, tetracyclines and penicillins (Dias et al., 2015; Gil Molino et al., 2019; Leekitcharoenphon et al., 2019). This is not a surprising trend, since these antimicrobials were indicated as having the

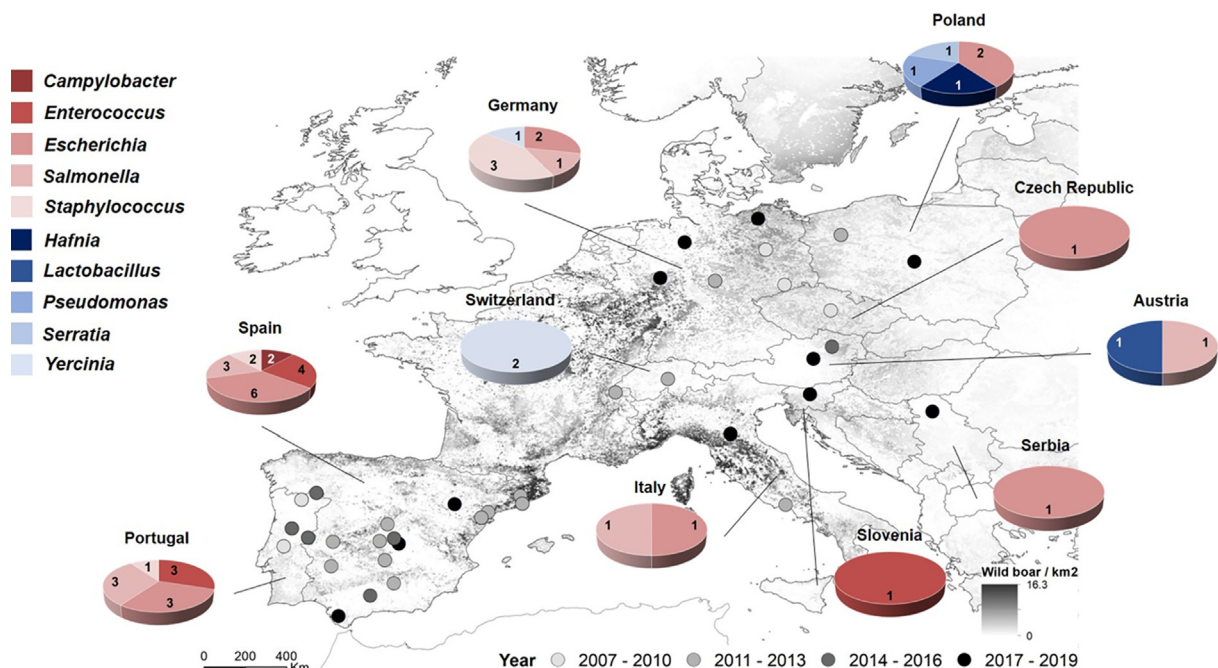


Fig. 3. Distribution of the publications by country and by bacterial genus with wild boar density illustrated. Each point corresponds to the study areas and can include more than one study and one bacteria (wild boar density map adapted, with permission, from Pittiglio et al. 2018 © Plos One).

highest sale rates for livestock in the last report of the European Surveillance of Veterinary Antimicrobial Consumption (ESVAC, 2018), accounting for 70% of the total sales in 2016. Sales of polymyxins also increased in 2016 by 69%, compared to 2010, and resistance to this antimicrobial has already been detected for wild boar (Reinhardt et al., 2018; Zottola et al., 2013). Resistance to cephalosporins (mostly cefotaxime), fluoroquinolones and linezolid has also been reported in Italy, Serbia, Czech Republic and Portugal (Literak et al., 2010; Sousa et al., 2017; Velhner et al., 2018; Bonardi et al., 2019). This is of special importance since these represent “critically important antimicrobials for human medicine” (WHO, 2019). These results highlight the possible direct and indirect routes of transmission of antibiotic-resistant bacteria in the human-livestock-wildlife interface.

The epidemiology of resistance genetic markers has also been investigated. Worryingly,

extended spectrum beta-lactamases (ESBL)-producing *E. coli* isolates have been isolated from samples of wild boar in Portugal (Poeta et al., 2009), Italy (Bonardi et al., 2019), Slovenia (Križman et al., 2017) and the Czech Republic (Literak et al., 2010). The class of beta-lactamases antibiotics (e.g. penicillin) is amongst the most important group of antimicrobial agents used in human and veterinary medicine. The detection of ESBL-producing *E. coli* in wildlife was firstly reported in 2006 (Costa et al., 2006) and since then it has been isolated from livestock, food and environmental samples, in different European countries (Poeta et al., 2009). In fact, ESBL-producing *E. coli* are now frequently found in wildlife (Guenther et al., 2011), particularly in birds and mammals (Silva et al., 2011; Gonçalves et al., 2012). For example, Simões et al. (2010) found that amongst the *E. coli* isolates from wild seagull faeces, 32% displayed an ESBL phenotype, which could be related to human waste. The variants of ESBLs already reported in wild boar include *bla*_{CTX-M-1}, *bla*_{TEM1-b} and *bla*_{TEM-52b} (Bonardi et al., 2019; Literak et al., 2010; Poeta et al., 2009). In fact, some of the above-mentioned studies reported a high number of ESBL isolates from wild boars contained the *bla*_{CTX-M-1} gene. CTX-M-1 gene is one of most prevalent ESBLs in Europe. It has been frequently detected in humans (Novais et al. 2007) as well as in food-producing animals (Meunier et al. 2006). ESBL-producing *E. coli* with *bla*_{CTX-M-1} has also been detected in wild birds (Poeta et al. 2008; Dolejska et al., 2009).

The reviewed studies showed that resistance to tetracyclines in *E. coli* is mainly encoded by *tetA*, *tetB* and *tetG* genes (Caleja et al., 2011; Literak et al., 2010) or by *tetM*, *tetS* and *tetK* in Gram-positive bacteria (Guerrero-Ramos et al., 2016; Poeta et al., 2007b). Resistance to tetracycline had also been recovered from *E. coli* isolates from small wild mammals in Poland (Swiecicka et al. 2003) and in Germany (Guenther et al. 2010). Interestingly, *mecA* resistance genes, which are commonly carried by methicillin-resistant *Staphylococcus aureus* (MRSA) were also found in some wild boar populations. MRSA is an important pathogen for humans, causing severe and hard to treat diseases in hospitals and in the community because of its ease dissemination and multiresistance against several antimicrobials, therefore is considered a public health concern due to the limited options for treatment. MRSA detection in wildlife (e.g., Eurasian griffon vulture, Iberian ibex, red deer, and wild boar) in Spain has revealed a very low prevalence but genotypes were related to livestock and humans (Porrero et al., 2014).

Some of the resistance genes described in this study, have been associated with mobile genetic elements such as conjugative plasmids, transposons or integrons. These elements play an important role in horizontal gene transfer, which has been responsible for the dissemination of antimicrobial resistance throughout diverse bacterial species (Barlow, 2009).

Overall, this review emphasizes that AMR is no longer an issue confined to the livestock and human settings in Europe, but is

instead a wider environmental issue of public health concern. Although previous studies have demonstrated the presence of AMR and resistance genes in wildlife (for review Arnold et al. 2016; Vittecoq et al., 2016), the current study examined the occurrence of AMR in one of the most fast expanding species, with increasing impacts and contact with humans, at a broader spatial scale, the European continent. Other studies have also showed the reliability of using other wildlife species as important sentinels for AMR [(for example, small mammals (Furness et al., 2017)] but wild boar close interaction with humans and livestock, their omnivorous behavior and large home ranges, and their consumption through hunting harvest, could favor dissemination of antimicrobial resistance to the wider environment. In fact, once wild boar is exposed, through various sources, to foreign commensal and antibiotic resistant microorganisms that have the potential to cross-talk with the microbiota of the species, creating a window of opportunity for cross selection and clonal spread of tolerant bacteria, it potentially becomes a significant carrier and disperser of AMR, originating the risk of ecological spread as it moves between the different compartments (urban – semi-natural – natural).

While the studies used in this review did not define exposure paths and transmission routes, most of them suggested that the level of resistant bacteria detected in wild boar seems to be related with the degree of association with human activity (Skurnik et al., 2006). Different studies showed that wildlife populations living in close proximity to humans or agricultural areas exhibit higher levels of resistance than those living in more remote or natural areas (Allen et al., 2010). For example, *E. coli* isolates from small mammals living on swine farms in Canada have higher rates of resistance than *E. coli* isolates from natural areas (Kozak et al., 2009) and African baboons in contact with humans harbour more antibiotic-resistant bacteria than those in remote areas (Rwego et al., 2008). Contrastingly, other studies showed the occurrence of multidrug-resistant bacteria in remote places therefore underlining the complexity of the spread of antimicrobial resistance in wild animals (Sjölund et al., 2008). Whereas this process is difficult to disclose mechanistically, advances in genetic and phylogenetic analyses, and also in whole-genome sequencing, have facilitated the detection of AMR genes, linking cases, defining exposure paths and transmission routes, enabling the deduction of clonal relationships and the unfolding of hypotheses concerning AMR amplification. For example, by performing phylogenetic analysis, Ward et al. (2014) showed that livestock was an important source of *Staphylococcus aureus* clonal complex 398 (CC398) in humans while Mather et al. (2011) reported that sympatric animals are improbable to be the main cause of *Salmonella* Typhimurium DT104 (DT104) in humans and that other sources of infections must be relevant.

4. Conclusions and future perspectives

Following this line, future steps should try to unveil the role of wild boar as reservoirs and amplifiers of AMR and the likely sources and mechanisms of persistence of AMR in this species. Thus, to fully understand the AMR pressures exerted on wild boar populations, it is important to continuously monitor resistance trends at sites that differ in exposure levels and to detect transfer of resistant bacteria or resistance genes from animals to humans and vice versa (Martel et al., 2001).

The studies analysed raise several concerns regarding the role of wild boars as carriers, reservoirs and dispersers of AMR and AMR strains into the environment, but they are mainly descriptive. Future studies must go beyond their descriptive nature and focus on understanding the role that anthropogenic activities may play on AMR in wild boar and wildlife in general. AMR research has been mainly focused on providing prevalence reference values

and identifying resistance patterns, even though the knowledge on how landscape drives AMR in wild and domestic hosts could further the understanding regarding AMR dissemination in the environment (Singer et al., 2006). With this in mind, we recommend the application of an ecological approach to AMR dynamics, with ecological tools contributing to the disclosure of the origins and transmission routes of AMR in the wildlife-livestock compartment with contrasting human influence in order to optimize the resources towards AMR management at a larger scale.

Whereas human health must remain a priority, it is timely to develop appropriate strategies under a complete agenda of the ecology of resistance in both human and animal populations (livestock and wildlife), as well as in the wider ecological network (Karesh et al., 2012; Torres et al. 2019). However, the lack of harmonized protocols, with a huge variation in the choice of bacterial species, sampling strategies, isolation procedures, susceptibility testing methods, panel of antimicrobials tested, data recording, computing and reporting, makes it difficult to compare prevalence of AMR bacteria in wild boar and this is an obvious setback. Mitigating resistance in wildlife will require the implementation of monitoring programs, based on harmonized protocols between different countries, otherwise we will miss valuable comparisons. The inherently sources of uncertainty in AMR research may be reduced by large and standardized collaborative studies. National governments require this data to develop, implement and monitor the magnitude of the problem and to establish baselines for taking action and mitigate the threaten of AMR. The study of AMR requires a holistic, harmonized perspective, as suggested by the One Health approach, in order to properly manage wild boar antimicrobial resistance occurrence and spread and contribute to AMR awareness and decision-making by public health officials, the scientific community and even society.

We restate that it is urgently needed that each country implements an harmonized network for surveillance of antimicrobial resistance directed to wild ungulates, particularly wild boar, which will enhance the ability to detect outbreaks, prevent ecological spread, and facilitate international collaboration and communication. Wild boar can be used as sentinel species for AMR spread and help characterize/understand the dynamics and mechanisms for resistance in the environment.

Conflict of interest statement

None of the authors has any financial or personal relationships that could inappropriately influence or bias the content of the paper.

Acknowledgments

We would like to thank J. D. Palmeira for his valuable insights on an early version of the manuscript. R. Torres is funded by national funds (OE), through FCT – Fundação para a Ciência e a Tecnologia, I.P., in the scope of the framework contract foreseen in the numbers 4, 5 and 6 of the article 23, of the Decree-Law 57/2016, of August 29, changed by Law 57/2017, of July 19. This work was supported by the project EcoARUn: POCI-01-0145-FEDER-030310-funded by FEDER, through COMPETE2020 - Programa Operacional Competitividade e Internacionalização (POCI), and by national funds (OE), through FCT/MCTES. Thanks are due to FCT/MCTES for the financial support to CESAM (UID/AMB/50017/2019), through national funds. J. Fernandes was supported by a grant (BI/CESAM/00056/POCI-01-0145-FEDER-030310) within the research project EcoARUn (POCI-01-0145-FEDER-030310). E. Serrano was funded by the Spanish Ministerio de Economía y Competitividad (MINECO) through a Ramon y Cajal agreement (RYC-2016-

2020). We would like to thank University of Aveiro (Department of Biology) and FCT/MEC for the financial support to CESAM RU (UID/AMB/50017) through national funds, co-financed by the FEDER, within the PT2020 Partnership Agreement.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2019.135001>.

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