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The Boar War: Five Hot Factors Unleashing Boar Expansion and Related Emergency

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Abstract: The recent and ever-growing problem of boar (*Sus scrofa* forms including wild boar, hybrid and feral pig) expansion is a very complex issue in wildlife management. The damages caused to biodiversity and the economies are addressed in different ways by the various countries, but research is needed to shed light on the causal factors of this emergency before defining a useful collaborative management policy. In this review, we screened more than 280 references published between 1975–2022, identifying and dealing with five hot factors (climate change, human induced habitat modifications, predator regulation on the prey, hybridization with domestic forms, and transfaunation) that could account for the boar expansion and its niche invasion. We also discuss some issues arising from this boar emergency, such as epizootic and zoonotic diseases or the depression of biodiversity. Finally, we provide new insights for the research and the development of management policies.

Keywords: wild boar; *Sus scrofa*; emergency; invasion; management; pest species; conservation; biodiversity

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1. Introduction

The wild boar (*Sus scrofa*) appeared in Western Eurasia about 1 million years ago after splitting from the Asian Suidae [1–4]. The early Palearctic domestication events of this species first occurred in the Near East between 8500 and 8000 y before the present, and then in many other geographical regions independently, originating from local populations [5–7]. These first domesticated animals were the ancestors of the European domestic pigs (*Sus scrofa domesticus*) [8], which soon after their arrival in northern Europe (~4500 BC), carried by Linearbandkeramik, were subject to continuous human-mediated selection, and were intentionally interbred with local wild forms [9–12]. These remarkable activities influenced the evolutionary trajectory of the pigs by promoting some desirable features, for example size, fatness, early sexual maturity and fertility [12–16]. Subsequently, due to different events accidentally or intentionally mediated by humans [17–19], many pig populations returned to the wild, becoming feral animals, sometimes even hybridising with wild boar [20–23]. This selective breeding and crossbreeding for specific traits resulted in a huge diversity of wild, domestic and feral forms, manifesting a variety of combinations of both naturally and artificially selected phenotypic patterns [24–28]. The relationship between these different *Sus scrofa* forms living sympatrically in several regions around the world is a tangled one, and many studies have explored the related evolutionary and management implications [29–35].

Nowadays, wild boar is one of the most widely distributed mammals throughout the Palearctic region, North Africa, and South-eastern Asia, and it is currently only absent from Antarctica [36–38]. It has been successfully introduced in many countries, becoming naturalised (named feral hog) in the New World and Australia [39–41]. Even today, the distribution of wild boar all over the world is affected by human activities such as hunting, the introduction of animals in areas desired by man, breeding of pigs in the wild and business involving swine (i.e., the marketing of animals used for the consumption of meat) [42–46]. These activities, by moving animals and promoting hybridization events, affect the natural potential of dispersion of the species, allowing the occupation even of the areas it probably could not have reached by Suidae.

In recent decades, wild boar has been experiencing a significant demographic increase [47–49] and has consequently invaded new ecological niches. Highly plastic ecological behaviour allows wild boar to inhabit a wide range of habitat types (e.g., Mediterranean scrubland, semi-desert and tropical rain forests, grasslands, and anthropogenic habitats) [50–53]. Furthermore, the species is a generalist omnivore, shaping its diet on the local availability of plants and animals, which it feeds on opportunistically [34,38,54,55]. Its invasiveness depends on the niche permissiveness in terms of limiting factors, such as the presence of road networks (linked to car collision events) or natural predators [56,57]. The natural predators that hunt wild boar depend on its geographical range: wolves (*Canis lupus*), bears (*Ursus* sp.), leopards (*Panthera pardus*), striped hyenas (*Hyaena hyaena*), Eurasian lynx (*Lynx lynx*), bobcat (*Lynx rufus*), mountain lion (*Felis concolor*), and eagles (mainly for piglets) [58–64].

This rapid and large-scale worldwide spread has made this species one of the top 100 worst invasive and pest animals in the world, even in its native distribution range [65,66], raising many conservation and management threats to agriculture, economy, human and animal health, biodiversity and human–wildlife conflicts [38,67–73].

Although several strategies have been employed to manage all these *Sus scrofa* forms [33,42,74–77], a scientifically calibrated approach must start from the investigation of the possible causes triggered by this phenomenon. All this is necessary to calibrate coherent management plans in order to mitigate the growing problem of the animal's expansion in terms of new geographical areas and ecological niches.

In this review, we explored the scientific contributions regarding the factors that could induce the boar emergency in order to summarize the main causes and highlight the relative importance of the different factors involved in boar expansion. We take stock of the situation here for the first time, and in the light of this investigation, we provide possible advice for management actions aimed at steaming the boar emergency, such as the impact on the ecosystem, on biodiversity and the conflict with human beings.

2. Methods

In this review, we use the term "boar emergency", "boar" meaning the main three different wild forms of *Sus scrofa* (wild boar, hybrid and feral pig), when these are not expressly indicated, and "emergency" meaning the circumstances arising from the boar expansion and niches invasion, with negative effects on biodiversity, health of the ecosystem and human culture (i.e., economy and social discontent).

Aiming at reviewing the existing studies addressing the issues (causal factors and their consequences) linked to the boar expansion worldwide, we performed searches of the scientific contributions in specialized databases (i.e., Google Scholar, ResearchGate and Scopus). We considered a variety of contributions, for instance: articles, reviews, commentaries, preprints, notes, book chapters, and also master's theses, doctoral dissertations and technical documents and reports, setting the searches in a 1975–2022 time interval. We used keywords such as: *Sus scrofa*, expansion, invasiveness, impact, damages, disturbances, plasticity, climate change, translocation, diet analysis, habitat use, African Swine Fever, mountain abandonment, hunting and management, considering investigations referring to the wild boar, hybrid and feral pig.

Furthermore, we created a Word Cloud graph with a free online word cloud generator (Wordclouds.com, accessed on 20 April 2022) to display how frequently typed keywords appeared in Google (https://www.google.it, accessed on 20 April 2022), the most-used search engine worldwide (Search Engine Market Share Worldwide, March 2022, https://gs.statcounter.com/, accessed on 20 April 2022), as a proxy of the perception of the boar emergency by community.

In particular, we used the value that indicates the approximate number of results returning from the Google search for 35 keywords. These were normalized in order to obtain figures that could be used for the construction of the Word Cloud graph, which requires the expression of values from 0 (lowest value) to 99 (highest value).

3. Results

Our searches on the databases returned over 350 contributions dealing differently with the topics linked to the keywords. From a detailed analysis of these references, we selected 283 contributions specifically focused on the boar emergency, all of which were mentioned below in the arguments dealt with. Based upon the most recurring topics existing in the literature, in addition to the most popular issues related to the boar emergency as perceived by public opinion (Figure 1), and to years of our expertise in research and management on the species, we selected and discussed five hot factors affecting the boar expansion, and their main consequences:

I. climate change;
II. human-induced habitat change;
III. predator regulation of the prey;
IV. hybridisation among boars;
V. transfaunation.

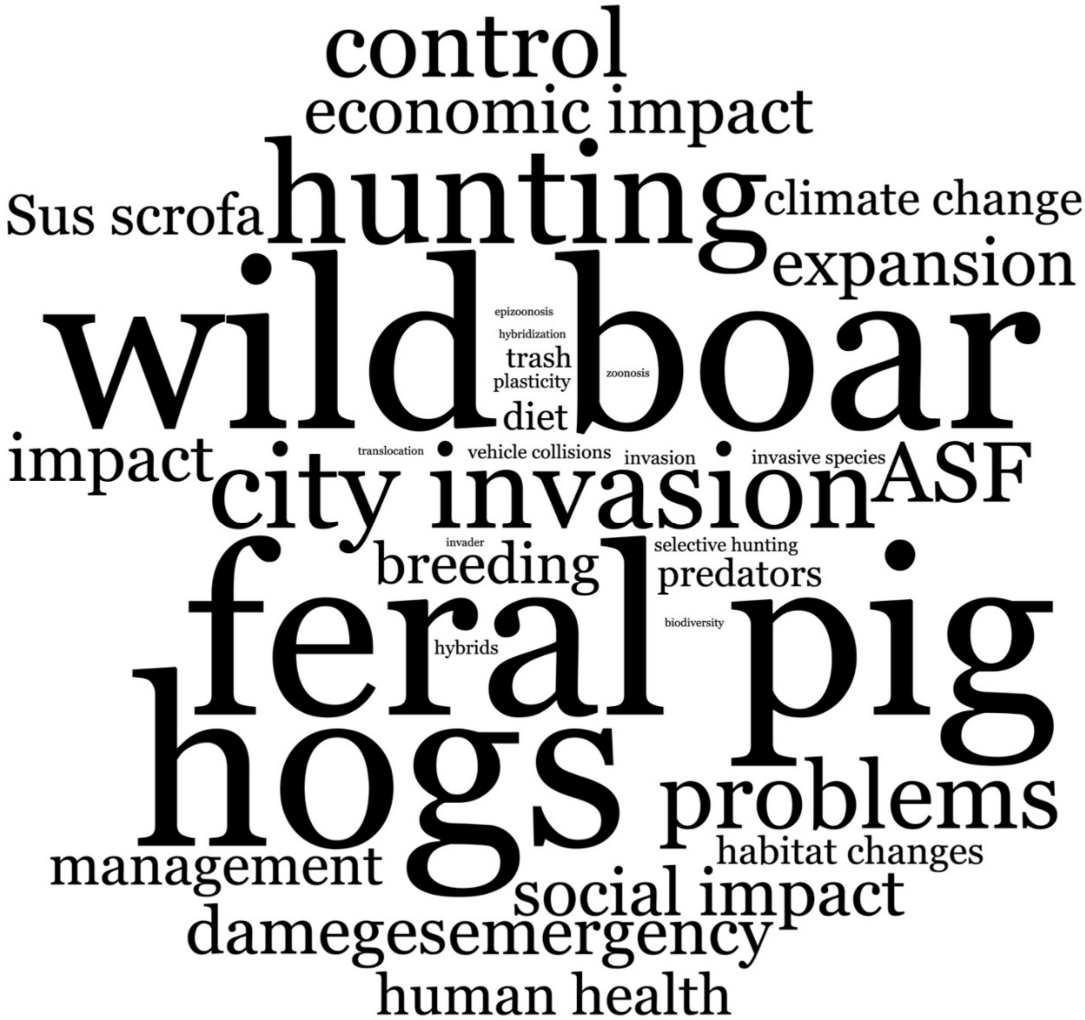

Figure 1. Word Cloud graph performed with a free online word cloud generator available at Wordclouds.com (accessed on 20 April 2022), using 35 keywords considering an investigation referring to the wild boar, hybrid and feral pig.

The boar has shown extraordinarily adaptive (and sometimes even pre-adaptive) behaviour, displaying a great capacity to disperse and invade new ecological niches, and an unexpected, bolder attitude. The latter phenomenon has just recently led to some emerging problems, such as incursions into urban areas [78–80], which are exacerbating the social intolerance of this ungulate.

3.1. Equipped to Cope with Climate Changes

Climate change has a significant impact on distribution, phenology, population structure, and demography in various species [81–87]. Some of these, in general specialists, cope poorly with the variation of climatic conditions, risking decline and extinction [88–91]. Other species, which are more flexible, pre-adapted and generalists, thrive, increasing their occurrence area or even their abundance [92], such as the wild boar [93–96].

A way by which climate change can impact the wild boar populations (i.e., in terms of presence range and demography) is the modification in both availability and amount of their trophic resources. For example, warmer temperatures can cause dry summers, milder winters or an upward shift in the snow line, leading some tree species to migrate upward, extend their range or become more rare, depending on latitudinal and longitudinal scales [97]. As a case in point, increased frequency of mast yields of beech (*Fagus sylvatica*) seedlings, a critical food for wild boar, has been reported in Sweden during the last two decades, probably as a consequence of climate and nitrogen deposition [98], influencing in turn wild boar spatial behaviour [99].

Greater food availability also induces females to reach sexual maturity earlier, already in their year of birth, the maximum lifespan increases, and piglets' mortality rate decreases [100,101]. However, the relationships between food availability and reproduction, more generally population growth, are still unclear and need further study [100,102].

Furthermore, some authors reported that when forage availability in natural habitats is low, wild boar could be induced to seek alternative food resources, such as agricultural crops [103], causing significant damage if population densities are high [104].

Climate change could also affect wild boar populations directly through changes in temperature and precipitation. Vetter and co-workers proposed a model according to which the improvement of favorable environmental conditions (i.e., increasing winter temperatures) affects the population structure, growth rate and phenotype [95], and leads to wild boar populations consisting of smaller individuals that give birth to fewer offspring, as recently observed in Mediterranean wild boar populations [94,105] and in other species [92,106].

Instead, according to some studies performed in Poland, the mortality of wild boar depends mainly on factors other than predation, such as the severity of winters. Indeed, because of deep snow, foraging by boar becomes difficult and energetically expensive, causing starvation and, possibly, the fast spread of diseases [107].

Nevertheless, the adaptability and plastic dietary habits of the wild boar contribute to its survival in a wide array of climatic conditions throughout the world, excluding only extreme winter polar climates and arid conditions in desert regions [96,108].

3.2. Living in a Changing Landscape

Abandonment of mountain pastures, agricultural land and traditional cultivation practices since the end of the World War II, the establishment of large European National Parks, and legislative exploitation activities, magnified by other factors, such as climate change, have had a significant impact on landscape texture [109–115] and, consequently, on the structure of animal communities [34,116–119]. In particular, the mosaic of the open areas and woodland patches has gradually been replaced by shrub and woodland encroachments due to a natural process of vegetation re-growth [120–124]. Looking at the woodland edge, a slight difference could be detected when comparing the pattern of the last decade [124]. This re-forestation has promoted, in many areas of the world, the recolonisation by large vertebrates, such as herbivorous and scavenging mammals, that preferentially use woodlands [125–130]. Indeed, because of relocation of anthropogenic activity flowing down to the valley and to the coast, a less disturbed environment has been welcomed by the boar populations, both in terms of suitable habitat for reproduction and availability of trophic resources.

The landscape changes induced by human actions, particularly in developed countries, consist also of the expansion of the road and railway networks, sometime even crossing the forests. This, together with increasing vehicle speeds and the high animal densities in the respective areas [131], has led to some traffic issues, such as wildlife–vehicle collision [57,132–136]. This phenomenon may also be due to an increased mobility as a consequence of human disturbance [137,138] or of biological factors (easier access ways to alternative food sources). Indeed, several authors showed a concurrence of wild pig–vehicle accidents and expansion of the populations observed throughout much of their non-native range [43,139,140].

The landscape structure can be modified also by the organization of the urban asset, in particular, by the management of the city limits, sometimes surrounded by discontinuous urban fabric, green areas and natural environment that could act as way for the wild boar to break into the city center. Some literatures reported how the poor management of urban greenery and waste could induce both the expansion and the invasion of boars [78,80,141–144]. In cities as Barcelona, Berlin, Houston, Hong Kong, and Rome, an 'urban adapter' and phenotypically plastic species [78,145–147], such as the wild boar, could benefit from natural and anthropogenic food, associated with low hunting and predation, reaching even higher population densities than the surrounding countryside [80,141]. Individuals of all ages have been found roaming around town at all hours [30,78–80], causing extensive damage to private gardens, public parks, sport grounds and cemeteries [142]. Not least, people occasionally leave food remains in natural and non-natural areas or provide food to wildlife, making the animals more confident around humans [148].

In our opinion, these events may be due to rapid adaptive capabilities of boars but also to recent and up-to-date exploitation of mountains by humans. Indeed, rural activities on the mountains give way to many professional and leisure exercises in the forests, such as logging, hunting, quad riding and walks with dogs, which could disturb wild fauna, with consequences for sociobiology and movements beyond the normal distribution range of boars [137,138,149–155]. There is also some evidence that human disturbance by hunting pressure increased in the last decades [48,52,156], which causes stress, the production of reproductive hormones [66,157] and earlier sexual maturity and reproduction activity in juvenile female wild boars [146,158]. This could induce a shortening in generation times, leading to higher population growth [158,159].

3.3. Prey-Predator Regulation

During the centuries in which agro-silvo-pastoral human activities were the rule [160], the intense pressure on wildlife had many ecological consequences [119,161,162]. Among these, the persecution of apex predators [163–166] resulted in the decimation of their populations [167–169], and consequently affected the structure of animal communities through the alteration of prey–predator interactions [170–174]. This could be one of the main conditions that favoured the increase in wild boar population density worldwide [126,128,175,176], especially where there was only one wild predator of this large ungulate [43,48,177]. For instance, during the 1970s, the Apennine wolf (*Canis lupus italicus*) experienced its historical minimum population size, fragmented in two areas in the Southern Apennines [167,178]. Since the late 1980s, thanks to increased efforts to protect large carnivores undertaken on most continents, including Italy [179–183], the wolf is gradually recolonising some territories of the Apennines [184–187]. In particular, in the Cilento, Vallo di Diano e Alburni National Park (Southern Italy), the widest protected area in Italy, the wolf population, estimated at four individuals in 1975 [178], is naturally expanding at a fast pace with a population currently estimated at many dozens of specimens [53]. This recovery in the wolf population has had important consequences on its role as a predator both in numerical terms (i.e., few wolves engaged in hunting activities) and on attack strategies (i.e., more packs) [62,188], influencing wild boar population dynamics via predator–prey cycles [189]. Unfortunately, this is still not enough to reduce the wild boar population density, which during this time has grown to exceed the carrying capacity of the environment [190].

3.4. The Hybridization among Boars

The *Sus scrofa* has both wild and domestic forms still present today that have the chance to hybridise [23,191] due to various occasional events or wilful human actions, such as free grazing practices and the escape of captive-bred individuals that return to the wild [18,19,192,193].

Hybridisation among wild boars and domestic forms is a complex issue in wildlife management because it could seriously compromise the genetic integrity of natural populations [194–197]. Indeed, genetic introgression from domestic to wild counterparts may disrupt some traits, such as behavior or reproduction rate, causing outbreeding depression and maladaptation to the environment in natural populations [198–202]. For example, no-camouflage spotted coat colour could make animals more visible to predators [203,204]. At the same time, introgressive hybridisation may sometimes result in mixed genotypes that are more adapted than their parental populations [21,205]. In [21], we demonstrated that the level of introgression from pig to wild boar is directly proportional to the increase in the litter size in the wild form. This leads to a clear consequence for the dynamics of population expansion and its invasive potential [206].

3.5. Moving the Animals Worldwide

The wild boar is a cosmopolitan species with morphology, reproductive potential and ecological requirement of populations varying throughout its global distribution range [35]. For example, the wild boars of the Mediterranean area frequent the scrub and holm oak wood whereas populations of the eastern Europe segregate in tall forests [48,207]. Furthermore, the wild boar reproductive potential seems to show a growing trend from southwest to northeast, going from about 4.5 cubs on average in the Iberian populations to over 6 cubs on average in northeast Europe populations [208].

Hybridisation events may involve different geographical populations (sometimes named as distinct subspecies), moved due to translocations and restocking [27,209]. For instance, restocking using exotic populations has resulted in genetic pollution of local stocks in several European regions, with relevant fitness consequences [208,210]. This is because the introduced populations could have a greater reproductive potential than the indigenous populations [208], influencing demography and expansion.

Moving the individuals into non-native range distributions, potentially alarming situations could arise for both the environment and the indigenous fauna and flora, where boar are invasive [17,43,67,211–216]. Indeed, allochthonous individuals more easily could invade ecological niches unattended by indigenous populations. This is probably because the indigenous populations have their habitat whereas the introduced individuals, having no such places, could be forced to exploit resources to survive in the new environment. Then, they could often also occupy niches or use food resources that are generally not used by the indigenous counterpart [43,217], with knock-out effects on the biodiversity [72,218,219]. This biodiversity-depressing effect is even more severe when wild boar is introduced to an area where it was previously absent [38].

The potential negative consequences of reckless introductions are also linked to the role of wild boar as a reservoir of epizootic and zoonotic diseases, such as bovine tuberculosis, trichinellosis or African Swine Fever (ASF), with the epidemiology depending on taxonomy, geographical location, and potential contact with domestic pigs [137,183,220–226]. As a case in point, [227] reported high density of yeasts in the faeces of a large population of wild boar that make this swine a spreader of pathogenic microorganisms in the environment. Not least, the role of wild boar in hosting ticks is reported from many parts of the world [228–231], with a link in the ecology of tick-borne pathogens [232].

4. Aptitude to the Niche Invasion

All the discussed arguments must be interpreted taking into account not only the reciprocal synergistic effects, but also the extremely adaptable nature of the wild boar [233]. In fact, optimisation of biological traits and niche conservatism are arguably [51,234–237] among the main factors allowing a species to invade different areas across the globe [238,239].

The wild boar shows adaptive abilities that make it prone to the environment it is about to invade, suggesting a sort of pre-adaptation, meaning advance knowledge of niches before they are explored. As a case in point, the sense of smell, linked to many vital activities such as food search and intraspecific communication [240–243], if early developed in the prenatal stage, could be interpreted as a kind of prenatal learning [29,34]. In [29], we showed that the sense of smell in the wild boar is already developed at about 44% of the gestation period, an early stage compared to the rat (93% of the gestation period) [244] or humans (77% of the gestation period) [245,246].

The chemical molecules passing through the amniotic fluid [247,248] represent previous knowledge acquired before birth [249] that give to young animals an advantageous knowledge of the environment and capacity for enhanced fitness [250,251]. In fact, the aptitude of piglets to readily accept foods containing flavors already perceived via the maternal diet, before and after birth, confers to the wild boar the ability to rapidly expand into different new environments, within a few generations [252–254]. Further investigation of these dynamics, to understand if they can also apply to other traits, could add new insights to the understanding of the speed of the adaptation. This peculiarity, combined with the k reproductive strategy, is the basis of the extraordinary adaptability to new colonising environments [29,34,254].

5. Management Implications

The extensive analysis of the available literature revealed that the boar emergency depends on a combination of causal factors that can act simultaneously with varying influence and can affect each other. Some of these can be present at different levels (i.e., local and global), and the results can be expected within a reasonable timeframe; other factors, for instance global climate changes, require major efforts, both in terms of resources and actors involved.

Here, we discuss five factors that emerged as among the hottest in determining the critical issues connected to the expansion of the boars, in terms of number of individuals and invaded niche. Although several other factors are in play, we believe that framing firstly the most important ones and their correlated aspects is a primary concern in order to calibrate pervasive strategies aimed at stemming the boar emergency. We also believe that political intervention can help by, for instance, establishing well-defined goals that can be effective in the short, medium and long term. For example, better management actions aimed at the protection of the predator could help restore its natural role for control of the wild boar populations. For instance, in the case of the wolf in Italy, protection actions have already been adopted, but further efforts should be made to counter the persecution due to poaching or to conflicts with human–livestock activities. The wolf, in fact, must be considered an important natural resource to regulate wild boar populations both in terms of number and social structure. Some studies highlighted the selective predation behavior of the wolf directed mainly on vulnerable segments of the population, such as weaker or younger individuals [255].

Also, tangible results could be obtained by acting against transfaunations and the containment of wild–domestic hybridisation. These actions, particularly in recent years, have also become extremely necessary to avert the danger linked to the spread of diseases such as ASF [256], mainly due to serious economic repercussions for the pig industry worldwide. More resources need to be invested in implementing rigorous virus-spread prevention procedures in intensive and sub-intensive pig farms and in providing support to pig farmers to invest in improving biosecurity, mainly where non-commercial pig production is essential for survival.

Greater attention must also be paid to prevent the uncontrolled illegal trade in pork products. Indeed, although the virus is not dangerous for human health, it remains in feces and urine or in blood and tissues of swine for prolonged periods (days or weeks), even in carcasses or processed pork meat products, with a very high potential for contamination [257,258].

A further strategy to deal with the boar emergency could carry out greater control over the health and genetic characteristics of wild boars used for restocking practices by the local government and hunting associations. Furthermore, an effort should be made to educate hunters (which in some regions have illegally or legally managed wild boar populations) to optimize hunting [259–263], through 'good rules' in handling practices. For example, it is important to state that it is necessary to properly dispose of the offal and scraps of the culled animals, avoiding burying or dispersing them improperly in the environment, and to report any case of the wild boar carcasses on which health services can carry out the appropriate investigations. This is a citizen science strategy that could provide a valuable contribution to significantly reduce the uncontrolled spread of boars and their negative consequences, for instance, the early identification of any hotspot of infection dangerous for humans and other animals, allowing rapid and incisive interventions.

In addition, and maybe above all, the training of specialised personnel in selective boar hunting is a successful weapon in the wild boar war. These selection hunters should be trained to selectively target animals suggested by experts who, on the basis of field studies and scientific research, will indicate the number, sex and age class of the animals to be killed, depending on the structure [264], local densities, and impact of the targeted population in a given region.

The use of chemical sterilisation, repellents and capture cages are additional methods to address the problem, especially in areas where selective hunting becomes problematic to manage, for example in cities and residential centers. However, these solutions, not being selectively directed to wild boar, introduce significant logistical requirements, such as the need to protect non-target wildlife or the setup of procedures that foresee the fate of the captured animals (i.e., killing and disposal of carcasses, meat controls and commercialisation, sterilisation and release, translocation to teaching farms, state-owned forests or elsewhere).

Although selective hunting remains the preferred solution, electric fences have also been used successfully in the fight against the wild boar's damage to crops (less time consuming than training hunters), but it would be necessary to provide funding to purchase these structures, and technical support for their correct installation, especially to small business owners or local farmers.

Concerning the collisions with vehicles, different possible solutions could be used [265], such as wildlife fencing along roads, overpasses/underpasses, wildlife crossing signs, and sonic deterrents [266–268], whose selection depends on ecological and socio-economic context [57]. For example, wildlife fencing could represent a no-crossing barrier [267,269,270] or could be useless when animals move around the fence ends, through fence gaps and climb or jump over it [271,272]. Also, although physical structures are often effective, the installation is expensive and sometimes impossible [273]. Contrarily, the use of signposts is less expensive but rarely effective when they are not precisely designed and located [274,275]. Cserkèsz and co-workers in 2012 reported that of many kinds of repellents tested, only one was effective in the short term [276]. Thus, the identification of the hot spots of wildlife–vehicle collision risk and the drivers of this phenomenon, such as the habitat characteristics, is crucial to the selection of mitigating strategies [274,277,278].

Efforts could also be directed at sensitising local communities to the importance of wild boar as a part of biodiversity which, if properly managed, can represent an ecological and economic resource (i.e., [215,277,279–281]); indeed, one of the main problems we have observed in our working areas is the misperception of the wild boar emergency, with consequent discomfort. This triggers a very strong frustration in human populations, which can also make the emergency more complex than it really is. This is also intensified by the increased frequency of individuals with bolder personalities in animal populations invading urban and peri-urban areas [78,80,282,283].

From our analysis, the boar system seems to be a typical example of a complex social-ecological system. These latter are often associated with environmental and health problems that need to be addressed from a trans-disciplinary framework in which different sectors collaborate. As such, government agencies, NGOs, academia and local inhabitants should collaborate towards describing the complexity of the problem at the local scale, and maybe at larger scales, and ultimately to develop viable solutions for such complex problems. Considering the exceptional intricacy of the situation, this contribution, rather than claiming a keystone to solving the problem, aims at suggesting a *modus operandi* whose sharing could lead to positive effects. In some cases, the best solution may be a diversified strategy acting on multiple fronts. Tackling the boar emergency is a challenge to identify practical, sustainable and situation-specific solutions and must be addressed using integrated strategies that require the concerted action of different entities (i.e., territorial management institutions, municipalities, researchers, farmers, breeders, etc.). This choice depends on the environmental, political and social context and on economic resources, and often involves the need for continuous calibration.

Protected areas (National Parks), hunting territories and urban and agricultural areas compose a mosaic on which the application of a divergent and non-concerted management is unthinkable. Our contribution provided management suggestions to better contain both expansion and niche invasion of boar and their consequences, outlining some hypotheses of works worthy of being addressed in order to better investigate this complex topic.

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