



# Factors affecting the crop damage by wild boar (*Sus scrofa*) and effects of population control in the Ticino and Lake Maggiore Park (North-western Italy)

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## Abstract

Wild boar foraging impacts the crops, pastures, and meadows causing remarkable losses to agricultural income. Protected areas located in plains, such as the Ticino Valley Natural Park, are characterized by the coexistence of important natural habitats and intensive agricultural areas. In the Park, from 2010 to 2017, 49% of the complaints report an event of damage to maize and 43% to meadows. The total expense for reimbursements of the maize amounted to € 439,341.52, with damages concentrated in May, after sowing period and between August and September, during the milky stage of maize. For meadows reimbursements amounted to € 324,768.66, with damage events concentrated in February and March. To reduce damage to crops, the Park administration carried out lethal control of the wild boar population. From 2006 to 2017, the most used control method was culling from hunting hides. In our analysis, we did not find significant relationships between the number of shot boars and the damage amount. The factors that determine the decrease of damage probability to crops are mainly related to human disturbance and the characteristics of the fields. The predictive model of damage risk built comparing damaged and undamaged fields showed a good predictive ability. The population viability analyses showed that it is impossible to obtain a drastic reduction of population with the current harvest rate. By tripling it and focusing on the females and sub-adult a numerical reduction of 50% of the population would be achievable in 7 years and the probability of population survival would be halved in 3 years.

**Keywords** Crop damages · Invasive species · Human–wildlife conflict · Risk prediction model · Selective culling

## Introduction

The range expansion and the growing number of ungulate populations in Europe are showing increasing problems of coexistence with man. The problems are complex and

vary according to species involved and the human activities. Among those species, the wild boar has shown a progressive growth of populations in Europe and worldwide. In many countries, starting from the sixties of last century, the species has re-colonized its historical range, expanding even towards many peri-urban areas (Apollonio et al. 2010; Massei et al. 2015; Stillfried et al. 2017; Castillo-Contreras et al. 2018; Gonzalez-Crespo et al. 2018; Amendolia et al. 2019). Forest expansion is one of the most important factors that favoured the expansion of the wild boar populations (Keuling et al. 2009; Servanty et al. 2011). Moreover, the releases carried out for hunting purposes emphasised the expansion of the species, thanks also to its high reproductive potential, the limited presence of natural predators in a considerable portion of its range, and its high ability to adapt to very different habitats (Brangi and Meriggi 2003; Bieber and Ruf 2005; Sales et al. 2017; Johann et al. 2020) where the species, when overabundant, could have different negative impacts.

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Many studies shows that wild boar can have a strong influence on biodiversity. Negative impacts are generally related to trampling and feeding activities together with predation upon invertebrates, small vertebrates, and eggs of ground-nesting birds (Baubet et al. 2003; Amori et al. 2016; Senserini and Santilli 2016; Oja et al. 2017; Mori et al. 2020). Moreover, depending on the intensity of rooting, wild boar can alter soil properties (Bueno et al. 2013; Palacio et al. 2013) and damage plant communities (Brunet et al. 2016; Sondej and Kwiatkowska-Falińska 2017).

In Italy, the Po Valley is generally an area where both protected natural environments and fragmented habitats are part of a human-dominated landscape, strongly used for agricultural production, and the conflicts related to the presence of the wild boar are expressed at different levels.

Wild boar can be a problem for the preservation of health of reared pigs, since the species may transmit some pathogens such as the virus of the swine fever diseases, causing huge economic losses (FAO et al. 2019). Moreover, the wild boar may be a vehicle of zoonoses, representing a serious threat to human health too (Bueno et al. 2009; Meng et al. 2009; Schley et al. 2008; Pisanu et al. 2012). Furthermore, road accidents are also a growing concern for human safety (Thurfjell et al. 2015). Nevertheless, the currently most common, widespread and increasing problems arise from the damage to agricultural productions. In France, for examples, compensation for crop damage caused by wild boars increased from 2.5 million Euros in 1973 to 21 million Euros in 2005 and 32.5 million Euros in 2008 (Guibert 2008; Mailard et al. 2010). A similar trend, with a doubling of the amount of damage every 10 years, has been observed in several other European countries (Schley et al. 2008; Slovenia Forest Service 2014). At present, an annual cost of 80,000,000 Euros is estimated for the whole Europe (Apolonio 2010; Linnell et al. 2020).

In general, the extent of crop damages depends on the population density, the population structure, the food availability in forest areas, the development of margins between forest and cultivated areas, the distance from human settlements, and on the stage of crop maturation (Schley et al. 2008; Novosel et al. 2012; Frackowiak et al. 2013; Laznik and Trdan 2014).

Despite the strong impact of wild boar on farming, attempts to model and predict the occurrence of damage and its intensity have so far been limited. The feeding activity of wild boar in cultivated fields can be analyzed from the perspective of the general predictions of the optimal foraging theory, trying to identify which factors related to energy intake, energy expenditure and animal safety contribute to the choice of fields in to go to for food (Stephen and Krebs 1986; Krebs and Kalcenik 1991; Begon et al. 2006; Rubenstein and Alcock 2018). Through the analysis of the factors that influence the occurrence of

damage, it is possible to formulate predictive risk models that allow to identify the most threatened areas and to act before the damage occurs with prevention tools (Ficetola et al. 2014; Lombardini et al. 2017; Cappa et al. 2019).

Moreover, numerical control is often assumed be effective for damage reduction but there is little evidence of this, and lethal control is ethically questionable and controversial (Meriggi et al. 2016; Linnell et al. 2020; Vajas et al. 2020). In particular, the effectiveness of numerical control should be measured in terms of substantial damage and population reduction but often it is measured in the number of animals removed. In doing so, the true objective of numerical control is lost sight of (Sinclair et al. 2006) especially when numerical control is carried out in wooded protected areas where wild boar is an important element of the ecosystem that should be preserved.

The main aims of our study were to identify the factors affecting the crop damage and to assess the effectiveness of lethal control to reduce it. The study was carried out in the Regional Park of the Ticino Valley (Piedmont region, North-western Italy), which together with the adjoining Lombard Park of the Ticino Valley, represents the largest protected area in Europe located in lowland environment. The research started from the observation that, despite the efforts made by the administration of the protected area to contain wild boar population and reduce damage to agriculture, the trend of damages is still increasing. Damages in the Park area from 2010 to 2017 were analysed to highlight their trend, distribution and the most affected crops. Furthermore, the trend of wild boar killing was analysed to verify any relationship with the extent of damages. A predictive model of the risk of damage was then formulated by comparing the characteristics of the damaged fields with those of the undamaged ones. Finally, simulations of the population viability (PVA) were carried out under different culling rate scenarios.

To achieve our aims, we tried to answer the following questions: (a) are there crop types selected by the wild boar?, (b) does the current wild boar culling rate affect the overall amount of damages?, (c) is it possible to foresee the risk of damage based on the characteristics of the fields?, (d) does the current rate of culling affect the dynamics of the wild boar population?, and (e) does an increasing of culling on a particular age class and sex produce a significant reduction in the population?

Considering the dramatic increase in wild boar populations and their range in Europe, this study could find wide application in similar environmental contexts, because the problems facing large parks to reduce the damage caused by wildlife to crops are similar throughout Europe (Apolonio 2010; Morelle and Lejeune 2015; Gren et al. 2020; Johann et al. 2020; Linnell et al. 2020).

## Materials and methods

### Study area

Our study area corresponds to the Ticino Valley Natural Park (66.5 km<sup>2</sup>; 45° 34' 1.2" N, 8° 40' 58.8" E; located in the Novara Province (Piedmont Region, North-western Italy), South of Lake Maggiore and ranging from 96 to 290 m a.s.l. (Fig. 1). The Park is characterized by a mixed natural and agricultural landscape. The climate is temperate, with cold winters and hot and sultry summers. The average yearly temperature was 11.8 °C (the monthly average of minimum temperature of the coldest month, January, was - 2.9 °C and the monthly average of maximum temperature of the hottest month, July, was 28.3 °C). The average rainfall was 1000 mm, with two peaks in spring (April–May) and autumn (November) (SMAM 2008). Woods, with prevailing broad-leaved trees such as oak *Quercus robur*, hornbeam *Carpinus betulus*, elm *Ulmus minor* and locust-tree *Robinia pseudoacacia* cover 60% of the protected area surface. Agricultural areas cover 23 km<sup>2</sup>, of which 65% are meadows, 26% maize, 4% rice fields, and 5% winter cereals and soybean. Agriculture characterises the floodplain which develops longitudinally and it is bordered on one side by the wooded areas along the river bank and on the opposite side by the woods that extends on the escarpment of the river terrace going to define a cultivation corridor interrupted transversally by human infrastructures (railway, highway, main roads) (Fig. 1). These characteristics allow the wild boars to invade the crops being always close to refuge areas. A network of secondary roads for agricultural use, cycle paths and trekking paths spread through cultivated areas and wooded areas. Moreover, the presence of settlements is scarce and represented mainly by farmsteads scattered in the Park.

### Data collection

We used the official data of damage claims from 2010 to 2017 from the Wildlife Service of the Novara Province. The data included the following information: (a) date; (b) private data of the owner; (c) type of crop affected by the damage; (d) type of damage (trampling, rooting and feeding, wallowing); (e) amount of damage in Euros; (f) damaged surface (ha). We also collected the data on the numerical control on the population, for the period 2006–2017. All data were geo-referenced with QGIS software 3.4.5.

## Damage analyses

We calculated the occurrence of damage claims considered as damage events and the compensation paid for each event, year, month and crop type. First, we compared the observed damage occurrence per crop type with the expected ones on the basis of the proportion of crop types, by the  $\chi^2$  Goodness-of-Fit test and Bonferroni's Confidence Interval Analysis (Manly et al. 2002); for this, we considered the occurrence of damages in the whole study period (2010–2017) and the average availability proportions of the different crop types in the same period (Agricultural Service, Province of Novara) assuming quite constant percentages of crop types in the years. Then, we analysed the damage trend (event number and compensation paid) by linear regression and curve fit analyses with the year as time variable, testing the fit of linear, quadratic, and cubic models by the determination coefficient ( $R^2$ ) and the Analysis of Variance (ANOVA). Moreover, we tested for the difference between the observed monthly distribution of damages and the expected one based on a hypothesis of evenness by the  $\chi^2$  Goodness-of-Fit test.

### The predictive model of damage risk

To formulate the predictive model of damage risk, we compared the characteristics of the damaged fields with those of undamaged ones following an use vs. unused design (Cumming 2000; Boyce et al. 2002). We calculated for each field 12 variables of which two (area and perimeter) related to the size of feeding patches and, consequently, to the amount of food, two other concerning the energy expenditure required to go to feeding patches from shelter areas (distance from the woods and from water bodies), five variables related to the anthropogenic disturbance (distances from buildings, railroads, main and secondary roads and cycle paths), one variable related to the position of the fields in respect to the flood plain (inside or outside the flood plain), and, finally, two variable descriptive of the field complexity (shape index and fractal dimension) (see Table 1). The distances from the woods were coded in three levels: adjacent to the woods (1), within 100 m from the woods (2) and over 100 m from woods (3). We calculated the distances using the "NNjoin" plugin, implemented in the QGIS 3.4.5 software. We calculated the area ( $A$ ) and the perimeter ( $P$ ) of the fields with QGIS, respectively, with the functions "area" and "length", while the fractal dimension ( $2 \times (\ln(P)/(\ln A))$ ) and the shape index ( $P/(2\sqrt{\pi A})$ ) of the fields have been calculated with Microsoft Office Excel. Moreover, we calculated the average number of culled wild boar from 2013 to 2017 in each municipality of the Park and used it as predictor in the risk model.

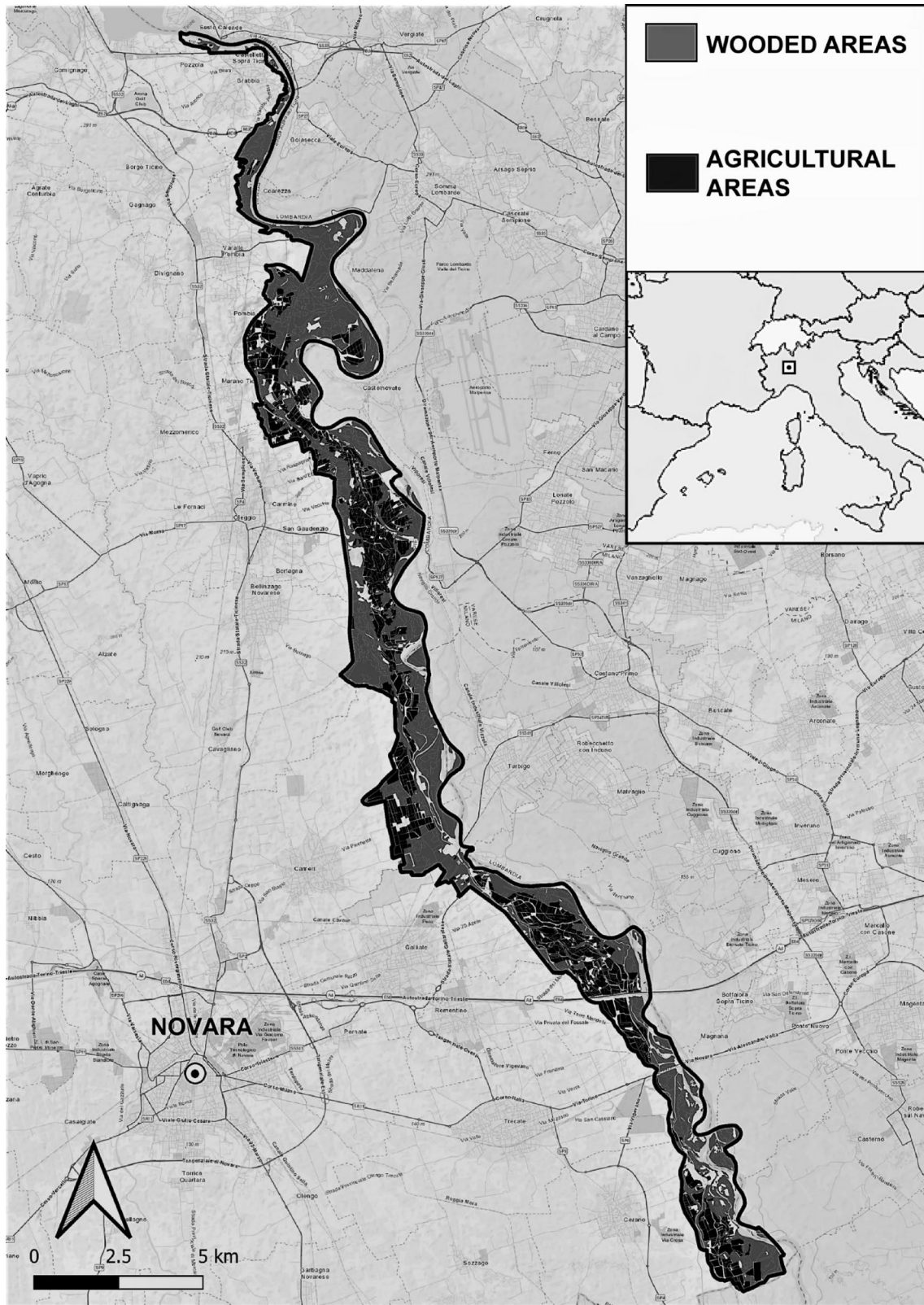


Fig. 1 Study area with detail of forest (grey) and agricultural areas (black)



**Table 1** Results of Logistic Regression Analysis of damaged ( $n = 1026$ ) vs. undamaged ( $n = 560$ ) fields

| Field variables               | <i>B</i> | SE   | <i>Z</i> | <i>P</i> | Exp ( <i>B</i> ) | VIF  |
|-------------------------------|----------|------|----------|----------|------------------|------|
| Position out of flood plain   | - 0.6    | 0.13 | - 4.86   | < 0.0001 | 0.528            | 1.12 |
| Shape index                   | 0.5      | 0.06 | 8.31     | < 0.0001 | 1.661            | 1.08 |
| Distance from railways        | 0.3      | 0.08 | 4.07     | < 0.0001 | 1.373            | 1.08 |
| Distance from main roads      | 0.2      | 0.04 | 4.39     | < 0.0001 | 1.184            | 1.14 |
| Distance from woods (2)       | 0.4      | 0.14 | 2.98     | 0.003    | 1.516            | 1.09 |
| Distance from woods (3)       | 0.6      | 0.17 | 3.59     | 0.0003   | 1.845            |      |
| Distance from buildings       | 0.1      | 0.04 | 3.54     | 0.0004   | 1.147            | 1.03 |
| Distance from secondary roads | - 0.1    | 0.03 | - 2.15   | 0.032    | 0.938            | 1.06 |
| Intercept                     | - 8.7    | 0.99 | - 8.79   | < 0.0001 | 0.0002           |      |

We tested each variable by the Mann–Whitney *U* test to identify the field variables with significant differences between damaged and undamaged fields. Then, we used those significantly different as predictors to perform a Binary Logistic Regression Analysis (BLRA) with the response variable 0 (undamaged fields) and 1 (damaged fields) and to assess the damage probability in relation to the values of field variables (Saino and Meriggi 1990; Treves et al. 2004; Dondina et al. 2015). Variables that showed significant deviation from normality were transformed; in particular we used the  $\log(x + 1)$  transformation for the variables heavily skewed (Legendre and Legendre 1998). We used the stepwise forward procedure and the Akaike Information Criterion to select the best model (Akaike 1973; Anderson et al. 2001; Burnham and Anderson 2002; Symonds and Mousalli 2011). The importance of predictor variables was measured by the significance of the regression coefficients and by the Exp (*B*). We verified the collinearity among variables by the Variance Inflation Factor (VIF), retaining VIF = 3 as a threshold value (Zuur et al. 2010). We evaluated the model performance subdividing the total cases in two randomly selected subsets of equal size. Each subset was then used to formulate a logistic model and to predict the probability of damage occurrence for the other subset. We then used the  $\chi^2$  test to verify for significant differences from random classifications and Spearman rank correlations between predicted probability classes ( $n = 10$ ) and the frequency of true positive cases to evaluate the model performance (Boyce et al. 2002). We performed all statistical analyses with the software R (R Core Team 2017); a value of  $P = 0.05$  was used as significance threshold.

### Effects of population control on damages

We calculated the total number of wild boars removed by the operators in the study area, their distribution for each control technique (shooting from hides, drive hunting, captures with live traps), and their yearly distribution from 2006 to 2017 from records by Park administration. Moreover, shot wild boars were classified by sex and age using the fur colour,

body weight, and tooth eruption and erosion. We analysed the trend of wild boar culled for numerical control by linear regression with curve estimation, setting the number of individuals as the dependent variable and the time (year) as independent one. Moreover, we carried out correlation analyses (Pearson's correlation coefficient) between the number of removed wild boars and the number of damages (event number and refunds) of the same and of the following year to highlight a possible delayed effect of culling on the damage.

### Population viability analysis

We carried out population viability analyses (PVA) to evidence the effect of present culling rate on the size and survival probability of the wild boar population and to test the effectiveness of additional culling to reduce the population size in the Park (Galimberti et al. 2001; Chilvers 2012; Carroll et al. 2014; Meriggi et al. 2016). For PVA, we used the control data provided by the Park administration from 2006 to 2016, assuming that control was not selective on sexes and age classes (Meriggi et al. 2016). In particular, we estimated the average values ( $\pm$ SD) of the following demographic parameters of the wild boar population: (a) age of first reproduction of females (the youngest female with foetuses in the study period), (b) maximum reproduction age of female (the oldest female with foetuses in the study period), (c) maximum litter size (maximum number of foetuses over the study period), (d) litter size distribution (considering all females with foetuses over the study period), (e) breeding success (% of females with foetuses in each year), (f) first-year mortality (%), (g) second-year mortality (%), (h) mortality after second year (%). Mortality was calculated for males and for females in each year by Life Table method. The absence of a monitoring plan of the wild boar in the study area determined the lack of data on the size and density of the population. Thus, we defined the starting population considering the number of animal shot in 2018 (410 animals, latest data available) and accounting for two different scenarios: S1) the shot wild boars were 30% of the total population present in the Park and S2) the wild

boar population size was at the carrying capacity level. The carrying capacity was estimated from bibliographic data on post-birth densities in three different wooded areas in Italy: 12 individuals per km<sup>2</sup> (Massolo and Mazzoni Della Stella 2006), 11.6 individuals per km<sup>2</sup> (Cutini et al. 2013), and 23.9 individuals per km<sup>2</sup> (Maselli et al. 2014). The average density obtained was therefore 15.8 individuals per km<sup>2</sup> (SD = 6.93). Considering the number of animal shot during the study period, the carrying capacity obtained was too low to be realistic, therefore, we decided to double it. The carrying capacity was, therefore, 2101 wild boars (SD = 426.26). Additional scenarios were then simulated for each population level, doubling (S1a, S2a) and tripling (S1b, S2b) the harvest rate and concentrating it on the sub-adults and adult females. For each scenario, 100 iterations were carried out and the predictions of the population trend and its survival probability were made over 30 years. PVA was carried out with the software VORTEX 10.3.6.0 (Lacy et al. 2000).

## Results

### General description of crop damage

From 2010 to 2017, 560 damage events occurred in the study area. The most affected crops were meadows and maize (50 and 43% of events, respectively). The differences between observed and expected occurrence of events was globally significant ( $\chi^2 = 87.23$ ,  $gl = 3$ ,  $P < 0.0001$ ); in particular, the observed proportions (OP) were significantly ( $P < 0.05$ ) lower than the availability ones (AP) for meadows (OP = 0.50; SE = 0.021; AP = 0.65) and for rice fields (OP = 0.02; SE = 0.006; AP = 0.04), and greater for maize (OP = 0.43; SE = 0.021; AP = 0.26), winter cereals and soybean were used in proportion to the availability (OP = 0.05; SE = 0.009; AP = 0.05). The total refunds in the study period amounted to € 928,858 (35% for meadows and 47.3% for maize). The damages occurred mainly between February and March, in May, and between August and September ( $\chi^2 = 122.88$ ,  $gl = 11$ ,  $P < 0.001$ ). The damage to maize was concentrated in May and between August and September ( $\chi^2 = 203.05$ ,  $gl = 11$ ,  $P < 0.001$ ), while the damage to the meadows occurred mainly between February and March ( $\chi^2 = 127.85$ ,  $gl = 11$ ,  $P < 0.001$ ).

During the study period, there was no significant trend either for damage events ( $R^2 = 0.141$ ; SEE = 15.64; Beta = - 0.375;  $P = 0.360$ ) or refunds ( $R^2 = 0.003$ ; SEE = 39,677.48; Beta = - 0.05;  $P = 0.902$ ).

### The predictive model of damage risk

Out of 1586 fields present in the study area, 1026 were damaged by wild boars during the study period

(2010–2017). All the measured field variables with exception of the distance from cycle paths and of the average number of shot wild boars showed significant differences between damaged and undamaged fields (Mann–Whitney  $U$  test,  $P \leq 0.001$  in all cases). Consequently, we used 11 predictors for risk modelling.

Out of the 11 predictors, seven were included in the predictive model of damage risk (Table 1). The shape index and the distances from railways, main roads and buildings had positive effects on the risk probability, while the distance from secondary roads had a negative one. Moreover, the risk probability decreased for fields out of the flooded plain and increased for those at distances greater than 100 m from woods. The model correctly classified 71.6% of the original cases, 32.5% of the undamaged fields and 92.9% of damaged ones. Classifications obtained with the models formulated with the two random subsets resulted significantly other than randomness (Subset 1:  $\chi^2 = 69.62$ ,  $df = 1$ ,  $P < 0.0001$ ; Subset 2:  $\chi^2 = 55.80$ ,  $df = 1$ ,  $P < 0.0001$ ). The frequency of damaged fields resulted highly correlated with the predicted probability classes (Rho = 0.960,  $P < 0.0001$ ) showing a good performance of the risk model.

### Numerical control and relationships with the damages

The wild boars culled between 2006 and 2017 amounted to 2423. The years with the highest number of removed animals were 2013 and 2017 (450 and 472, respectively). The most used control method was shooting from hides, with 1990 individuals culled over the study period, while 122 wild boars were shot by drive hunting, and 220 were trapped. The number of removed wild boars showed a positive and significant trend ( $\beta \pm SE = 26.199 \pm 7.69$ ;  $P = 0.007$ ) according to a linear model which explained 53.7% of the variance ( $R^2 = 0.537$ ; SEE = 92.04). No significant correlations resulted between the number of removed wild boars and the number of damage events or refunds in the study period (Table 2).

**Table 2** Results of the correlation analysis between the number of wild boars removed each year and damage events and reimbursement amount

| Damage variables                    | <i>r</i> | <i>P</i> |
|-------------------------------------|----------|----------|
| Damage events in the same year      | 0.446    | 0.192    |
| Damage events in the following year | 0.099    | 0.785    |
| Refunds in the same year            | 0.481    | 0.227    |
| Refunds in the following year       | - 0.590  | 0.123    |

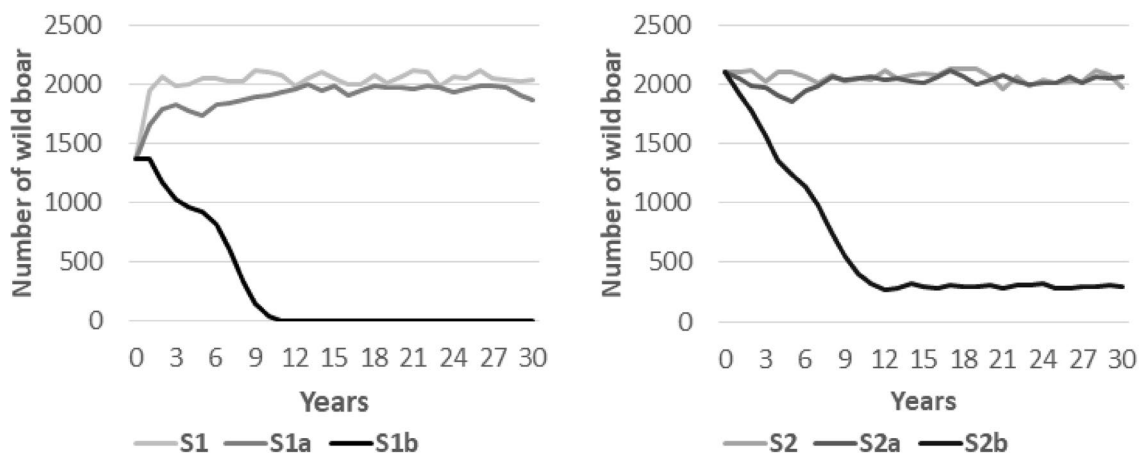
**Table 3** Demographic input values used for the population viability analyses

| Variables                                     | Scenario 1                                | Scenario 2 |
|---|---|------------|
| Extinction                                    | Only one sex remaining                    |            |
| Lethal equivalent                             | 6.29                                      |            |
| Proportion of lethal genetic load             | 50%                                       |            |
| Mating system                                 | Polygynous                                |            |
| Age of the first reproduction (females)       | 1 year                                    |            |
| Age of the first reproduction (males)         | 2 years                                   |            |
| Maximum reproduction age (years)              | F 6 years–M 8 years                       |            |
| Sex ratio at birth                            | 1:1                                       |            |
| Maximum litter size                           | 8   |            |
| Mean litter size ( $\pm$ SD)                  | 4.7 ( $\pm$ 1.3)                          |            |
| Reproductive success % ( $\pm$ SD)            | 29 ( $\pm$ 13)                            |            |
| Mortality before year 1 ( $\pm$ SD) (age 0)   | F 0.34 ( $\pm$ 0.32)–M 0.3 ( $\pm$ 0.42)  |            |
| Mortality year 1 to year 2( $\pm$ SD) (age 1) | F 0.56 ( $\pm$ 0.25)–M 0.39 ( $\pm$ 0.25) |            |
| Mortality year 2 to year 3( $\pm$ SD) (age 2) | M 0.58 ( $\pm$ 0.39)                      |            |
| Males in a breeding pool                      | 100%                                      |            |
| Starting population                           | 1367                                      | 2101       |
| Males and females of age 1                    | 318–308                                   | 489–474    |
| Carrying capacity ( $\pm$ SD)                 | 2101 ( $\pm$ 426.26)                      |            |

**Population viability analysis**

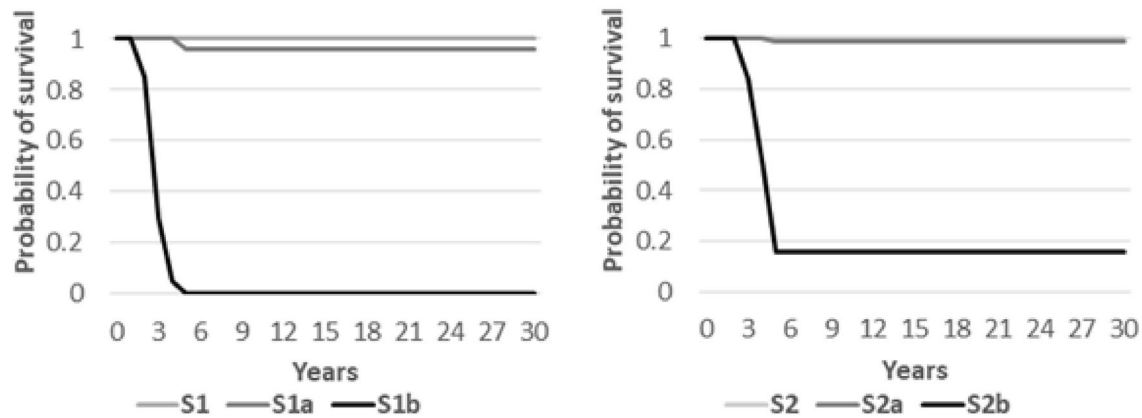
The simulation S1 showed that a population decrease, and a survival probability reduction are not achievable with the current removal rate. A slight difference resulted doubling the removal rate and concentrating it on the sub-adults and

females (S1a simulation). The same result occurred for the simulation S2 and S2a. By tripling the removal rate on the same sex and age classes, a drastic reduction in the population (50% in 7 years) and a halving of survival probability in 3 (S1b) and 4 years (S2b) was obtained (Table 3) (Figs. 2 and 3).



**Fig. 2** Population size of Ticino Valley Natural Park wild boar population based on Population Viability Analysis (PVA) simulations. On the left, the first simulation of the current harvesting rate on the population assuming that shot wild boars were 30% of the total population present in the Park (S1) ( $r=0.473$ ,  $SD=0.187$ ,  $PEE=0$ ) in light grey, simulation of the doubled harvesting rate (S1a) ( $r=0.414$ ,  $SD=0.212$ ,  $PEE=0.04$ ) on sub-adults and females in grey and simulation of the triplicate harvesting rate (S1b) ( $r=-0.039$ ,  $SD=0.244$ ,

$PEE=1$ ) on sub-adults and females in black. On the right, the second simulation of the current harvesting rate assuming that the population size is at the carrying capacity (S2) ( $r=0.471$ ,  $SD=0.188$ ,  $PEE=0$ ) in light grey, simulation of the doubled harvesting rate (S2a) ( $r=0.433$ ,  $SD=0.198$ ,  $PEE=0.01$ ) on sub-adults and females in grey and simulation of the triplicate harvesting rate (S2b) ( $r=0.236$ ,  $SD=0.310$ ,  $PEE=0.84$ ) on sub-adults and females in black



**Fig. 3** Survival probability of the Ticino Valley Natural Park wild boar theoretical population based on Population Viability Analysis (PVA) simulations. On the left, simulation (S1) that represents the 30% of the population in light grey, simulation of the doubled harvesting rate (S1a) on sub-adults and females in grey and simulation of the triplicate harvesting rate (S1b) on sub-adults and females in black.

## Discussion

Our results confirm that the wild boar selects specific types of crops. The maize is one of the most damaged crop by wild boar in many areas (e.g. Spain, Nores et al. 1999; Herrero et al. 2006; China, Cai et al. 2008; Luxembourg, Schley et al. 2008; Italy, Serrani 2012). Several studies indicate a wild boar preference for maize respect to winter cereals (Briedermann 1976; Herrero et al. 2006). The damage to maize fields, as confirmed by our results, is typically concentrated in the periods of sowing and milky ripening of the cob (Vasudeva et al. 2017; Boyce et al. 2020) that occurs between July and September. In this period, usually characterized by the absence of natural caloric food such as acorns, the cobs are odorous and juicy and, therefore, very attractive for wild boar and easier to digest (Schley and Roper 2003; Calenge et al. 2004; Cai et al. 2008). In addition, maize crops provide good coverage from early summer to autumn compared to other crops (Geisser 2000). The meadows are the second most important type of cultivation damaged in our study area, even if we have found a significant underutilization probably due in part to their great availability. The use of grassland by wild boar as a foraging habitat is common in several countries (Schley and Roper 2003; Schley et al. 2008; Thurfjell et al. 2009; Frackowiak et al. 2013; Lombardini et al. 2017). The damages can be linked both to rooting and trampling activities (Barrios-Garcia and Ballari 2012; Bueno et al. 2013), and our results confirm that the meadows are particularly affected by wild boar in late winter and early spring (Brangi and Meriggi 2003; Schley et al. 2008; Amici et al. 2012) because in this period, the earthworms and many insect larvae inhabit the upper layers of

On the right, simulation of the current harvesting rate (S2) assuming that the population size is at the carrying capacity in light grey, simulation of the doubled harvesting rate (S2a) on sub-adults and females in grey and simulation of the triplicate harvesting rate (S2b) on sub-adults and females in black

the soil, making them more accessible (Baubet et al. 2004; Frackowiak et al. 2013). The diet of the wild boar, with a high presence of corn and acorns, is rich in carbohydrates. Therefore, the proteins offered by invertebrates, mainly earthworm (Baubet et al. 2003, 2004; Bueno and Jiménez 2014), inhabiting the meadows are important supplementary food sources (Massei et al. 1996; Schley and Roper 2003; Ballari and Barrios-García 2014).

The predictive model of damage risk showed how anthropic disturbance, the location of the field and its characteristics affect the probability of damage. In particular, the risk of damage decreases in the fields near the main roads, the rail network and buildings. This condition is mainly due to the disturbance caused both by the vehicular traffic and by the tourist use of the park, because, despite the wild boar is able to colonize peri-urban environments (Cahill et al. 2012), wooded habitats are preferred by the species (Merli and Meriggi 2006; Hebeisen et al. 2008; Amendolia et al. 2019). Fields with complex shape, located within the floodplain are at greater risk of damage. In the floodplain, there are more natural habitats such as woods, reeds and marshes, which represent the shelter places of the wild boar in our study area. Consequently, the fields placed in this environment represent easier to reach and safer feeding places (Lima and Dill 1990; Tolon et al. 2009; Thurfjell et al. 2013; Morelle and Lejeune 2015). Surprisingly, the fields adjacent to the woods have a lower probability of risk than those further away. This could be caused by the control activity from hides which are mainly placed at the edge of the woods. In accord with the Optimal Foraging theory in our study area, wild boar seems to select the most profitable crops in the periods when they can offer high-quality food and in conditions that can guarantee greater safety (Begon et al. 2006).



To reduce long-term impacts of wild boar, one of the most used methods is the lethal control of populations, which has proven to be an effective method in different countries (Geisser and Reyer 2004; ELO 2012; Mazzoni della Stella et al. 2014; Giménez-Anaya et al. 2016). In the Ticino and Lake Maggiore Park, from 2006 to 2017, the control was not selective, the ratio between males and females removed was one. Moreover, the most used control method was shooting from hides. The correlation between the number of removed boar and the number of damages that occurred the following year was close to the significance threshold. This result suggests a possible delayed effect of lethal population control, which should be considered in planning long-term population control but, in general, the ineffectiveness of culling carried out in the study area is demonstrated by the absence of a damage reduction during the study period.

The present control seems not to be effective for wild boar, because unable to mitigate the population increase, even in situations of strong hunting pressure (Servanty et al. 2011; Massei et al. 2015). The hunting acts differently from the natural mortality that tends to concentrate on individuals under 1 year old (Servanty et al. 2011; Keuling et al. 2013; Bassi et al. in press). Furthermore, it alters the spatial behaviour of individuals, causing an increase in the size of the home range (Scillitani et al. 2010), and a greater use of "secondary" habitats, including cultivated ones (Stankowich 2008; Thurfjell et al. 2013). Furthermore, the effectiveness of the culling plan may have been affected by the availability of natural food, in particular acorns for which no data are available. This parameter can have an important influence on the selection of secondary habitats, such as crops, by wild boar for feeding.

The absence of a population-monitoring plan in the study area led to the absence of information such as population density, which is essential for planning a numerical control strategy for wild boar. Furthermore, data regarding the mast production are lacking. Considering this background, the numerical control methods could be useless, if not self-defeating, when not scientifically supported. For this purpose, population viability analyses could be effectively used (Meriggi et al. 2016; Gürtler et al. 2017; Gonzalez-Crespo et al. 2018). Our PVA simulations showed that to obtain a drastic reduction in the size of the population, it would be necessary to carry on a massive culling plan focused on reproductive females and sub-adults. In this way, the reproductive potential of the population can be reduced year by year without triggering a density-dependent compensation.

Several studies have shown that, in open populations, a high harvest rate could be useful to obtain a fast decrease in population size (Keuling et al. 2013; Bengsen et al. 2014; González-Crespo et al. 2018) and, in specific, applying a removal of 30–40% of post-birth population can be possible to stop population growth (Croft et al. 2020; Vetter

et al. 2020), but applying massive culling could be costly and unrealistic in the long run. A recent study, which concerned the wild boar populations of the Castelporziano State Reserve (Croft et al. 2020) in Italy also showed that in a closed population, it is necessary to have a high harvest rate, similar to what emerged from our simulations, to obtain a marked reduction of the population in a reasonable time. The authors also evaluated the effects of the simultaneous application of culling and fertility control methods which showed how integrating a realistic culling rate with fertility reduction allows to obtain significant results in a short time. Although fertility control alone was not sufficient to achieve the desired results, the application of a control strategy based on a balanced mix of culling and sterilization seems to be an important opportunity to reduce wild boar populations. In this way, it is possible to shorten the time needed to reduce the population to a sustainable level, limiting in the same time the stress caused to other species. This should be a priority when control activities are carried out in protected areas or where high levels of culling may not be socially acceptable. Unfortunately, these evidences are based on the study of a closed population, a condition that is certainly difficult to find in the usual territorial realities such as our study area where the population is open to immigration and emigration. Furthermore, an effective fertility control campaign would require intensive trapping, marking and manipulation of individuals, which can result in an increase in the management costs of the species that could be not economically advantageous or sustainable.

## Conclusions

Although it is an autochthonous species of a large part of the European continent, wild boar can have characteristics of invasive species because of several factors attributable to man. The abandonment of marginal agricultural areas, changes in agricultural practices, releases for hunting or reduction in harvesting pressure, lack of predators, and climatic changes (Genov 1981; Sáez-Royuela and Telleriá 1986) have led to a significant increase in its populations which, in turn, have produced and they still produce ecological as well as economic damages (Massei and Genov 2004). Consequently, a management plan for wild boar is now necessary in all those situations where the species reaches population densities that are not compatible with the ecological but also the economic context. To properly plan the management, the biological traits that make wild boar a potentially invasive species must be considered, with particular reference to population growth rates and opportunistic characteristics of foraging behaviour (Pastick 2012; Sales et al. 2017).

In landscapes where farming is particularly developed, also thanks to high-quality crops, an effective management plan for the wild boar aimed to reduce the conflicts between the species and humans becomes an increasingly priority need. The basic knowledge for the plan comes from a monitoring program of wild boar populations and from an updated inventory of economic damages caused by the species.

Prevention methods (electric fences, sound and olfactory bollards and dissuasive foraging) are commonly used to mitigate the impact of the wild boar on agriculture but they can be very expensive if adopted indiscriminately over large areas (Santilli and Stella 2006; Schlageter and Haag-Wackernagel 2012). To allow the implementation of targeted and effective prevention measures, it is desirable to formulate predictive models of risk that allow the identification of the fields most exposed to damages (Saito et al. 2012; Ficetola et al. 2014; Meriggi et al. 2016). In most cases, the prevention methods, where and when adopted, are applied after the damages have already occurred, and without a cost–benefit analysis (Massei et al. 2011; Meriggi et al. 2016). The formulation of risk prediction models allows acting in advance by assigning a risk class to each field and therefore to identify the fields most at risk (Cappa et al. 2019), where it is possible to provide deterrent systems such as electrified fences or acoustic deterrents. This would improve the effectiveness of these tools and could partially reduce their economic impact on single farms.

The control activities aiming to produce a significant reduction in population size by means of culling should be concentrated on females older than or equal to 1 year, piglet and sub-adults (Bieber and Ruf 2005; Servanty et al. 2011; Gamelon et al. 2012; Meriggi et al. 2016). The culling of sub-adults is necessary, because they more easily use secondary habitats such as cultivated areas, and because they will enter in the reproductive pool in the following year (Keuling et al. 2008). Concerning the wild boar culling methods, those that ensure greater precision in the selection of individuals to be removed would be preferred. Although in some cases, collective culling methods have proven effective in reducing damage (Giménez-Anaya et al. 2016), we believe that collective hunting methods, although they may have good results, are not the correct way to manage the problem of damage within protected areas, because of the possible disturbance caused to other species, such as *Capreolus capreolus*.

The adoption of preventive methods aimed at the crops mostly at risk together with the targeted numerical control can be the solution that allows to reduce damage, while maintaining the presence of the wild boar.

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**Data availability** Datasets as well as analytical information used for the current study are available from the corresponding author on reasonable request.

## Declarations

**Conflict of interest** On behalf of all authors, the corresponding author states that there is no conflict of interest.

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## References

- Akaike H (1973) Information theory as an extension of the maximum likelihood principle. In: Petrov BN, Csaki F (eds) 2nd international symposium on information theory. Akademiai Kiado, Budapest, pp 267–281
- Amendolia S, Lombardini M, Pierucci P, Meriggi A (2019) Seasonal spatial ecology of the wild boar in a peri-urban area. *Mammal Res* 64:387–396
- Amici A, Serrani F, Rossi CM, Primi R (2012) Increase in crop damage caused by wild boar (*Sus scrofa* L.): the “refuge effect.” *Agron Sustain Dev* 32:683–692. <https://doi.org/10.1007/s13593-011-0057-6>
- Amori G, Luiselli L, Milana G, Casula P (2016) Negative effect of the wild boar (*Sus scrofa*) on the population size of the wood mouse (*Apodemus sylvaticus*) in forest habitats of Sardinia. *Mammalia* 80(4):463–467
- Anderson DR, Link WA, Johnson DH, Burnham KP (2001) Suggestions for presenting the results of data analyses. *J Wildl Manag* 65:373–378
- Apollonio M, Andersen R, Putman R (eds) (2010) European ungulates and their management in the 21st century. Cambridge University Press, Cambridge, UK, New York
- Ballari SA, Barrios-García MN (2014) A review of wild boar *Sus scrofa* diet and factors affecting food selection in native and introduced ranges: a review of wild boar *Sus scrofa* diet. *Mammal Rev* 44:124–134. <https://doi.org/10.1111/mam.12015>

- Barrios-García MN, Ballari SA (2012) Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review. *Biol Invasions* 14:2283–2300. <https://doi.org/10.1007/s10530-012-0229-6>
- Baubet E, Ropert-Coudert Y, Brandt S (2003) Seasonal and annual variations in earthworm consumption by wild boar (*Sus scrofa* L.). *Wildl Res* 30:179–186
- Baubet E, Bonenfant C, and Brandt S (2004) Diet of the wild boar in the French Alps. *Galemys* (16):99–111
- Begon M, Harper JL, Townsend CR (2006) *Ecology: from individuals to ecosystems*, 4th edn. Blackwell, Oxford, United Kingdom
- Bengsen AJ, Gentle MN, Mitchell JL, Pearson HE, Saunders GR (2014) Impacts and management of wild pigs *Sus scrofa* in Australia. *Mammal Rev* 44(2):135–147
- Bieber C, Ruf T (2005) Population dynamics in wild boar *Sus scrofa*: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers: population dynamics in wild boar. *J Appl Ecol* 42:1203–1213. <https://doi.org/10.1111/j.1365-2664.2005.01094.x>
- Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FKA (2002) Evaluating resource selection functions. *Ecol Model* 157:281–300. [https://doi.org/10.1016/S0304-3800\(02\)00200-4](https://doi.org/10.1016/S0304-3800(02)00200-4)
- Boyce CM, VerCauteren KC, Beasley JC (2020) Timing and extent of crop damage by wild pigs (*Sus scrofa* Linnaeus) to corn and peanut fields. *Crop Protection* 133105131. <https://doi.org/10.1016/j.cropro.2020.105131>
- Brangi A, Meriggi A (2003) Espansione del cinghiale (*Sus scrofa*) e danni alle coltivazioni in un'area delle prealpi occidentali. *Hystrix Ital J Mammal* 14:95–105
- Briedermann L (1976) Ergebnisse einer Inhaltsanalyse von 665 Wildschweinemagen. *Zoologischer Garten, Neue Folge, Jena*, 46:157–185
- Brunet J, Hedwall PO, Holmström E, Wahlgren E (2016) Disturbance of the herbaceous layer after invasion of an eutrophic temperate forest by wild boar. *Nord J Bot* 34(1):120–128
- Bueno CG, Jiménez JJ (2014) Livestock grazing activities and wild boar rooting affect alpine earthworm communities in the Central Pyrenees (Spain). *Appl Soil Ecol* 83:71–78
- Bueno CG, Alados CL, Gómez-García D, Barrio IC, García-González R (2009) Understanding the main factors in the extent and distribution of wild boar rooting on alpine grasslands. *J Zool* 279:195–202. <https://doi.org/10.1111/j.1469-7998.2009.00607.x>
- Bueno CG, Azorín J, Gómez-García D, Alados CL, Badía D (2013) Occurrence and intensity of wild boar disturbances, effects on the physical and chemical soil properties of alpine grasslands. *Plant Soil* 373:243–256
- Burnham KP, Anderson DR (2002) *A practical information-theoretic approach*. Model selection and multimodel inference, 2nd edn. Springer, New York
- Cahill S, Llimona F, Cabañeros L, Calomardo F (2012) Characteristics of wild boar (*Sus scrofa*) habituation to urban areas in the Collserola Natural Park (Barcelona) and comparison with other locations. *Anim Biodivers Conserv* 35:221–233
- Cai J, Jiang Z, Zeng Y, Li C, Bravery BD (2008) Factors affecting crop damage by wild boar and methods of mitigation in a giant panda reserve. *Eur J Wildl Res* 54:723–728. <https://doi.org/10.1007/s10344-008-0203-x>
- Calenge C, Maillard D, Fournier P, Fouque C (2004) Efficiency of spreading maize in the garrigues to reduce wild boar (*Sus scrofa*) damage to Mediterranean vineyards. *Eur J Wildl Res*. <https://doi.org/10.1007/s10344-004-0047-y>
- Cappa F, Lombardini M, Meriggi A (2019) Influence of seasonality, environmental and anthropic factors on crop damage by wild boar *Sus scrofa*. *Folia Zool* 68:47–54
- Carroll C, Fredrickson RJ, Lacy RC (2014) Developing metapopulation connectivity criteria from genetic and habitat data to recover the endangered Mexican wolf. *Conserv Biol* 28:76–86
- Castillo-Contreras R, Carvalho J, Serrano E, Mentaberre G, Fernández-Aguilar X, Colom A, López-Olvera JR (2018) Urban wild boars prefer fragmented areas with food resources near natural corridors. *Sci Total Environ* 615:282–288
- Chilvers BL (2012) Population viability analysis of New Zealand sea lions, Auckland Islands, New Zealand's sub-Antarctics: assessing relative impacts and uncertainty. *Polar Biol* 35:1607–1615
- Croft S, Franzetti B, Gill R, Massei G (2020) Too many wild boar? Modelling fertility control and culling to reduce wild boar numbers in isolated populations. *PLoS ONE* 15(9):e0238429
- Cumming GS (2000) Using between-model comparisons to fine-tune linear models of species ranges. *J Biogeogr* 27:441–455. <https://doi.org/10.1046/j.1365-2699.2000.00408.x>
- Cutini A, Chianucci F, Chirichella R, Donaggio E, Mattioli L, Apollonio M (2013) Mast seeding in deciduous forests of the northern Apennines (Italy) and its influence on wild boar population dynamics. *Ann For Sci* 70:493–502. <https://doi.org/10.1007/s13595-013-0282-z>
- Dondina O, Meriggi A, Dagradi V, Perversi M, Milanese P (2015) Wolf predation on livestock in an area of northern Italy and prediction of damage risk. *Ethol Ecol Evol* 27(2):200–219
- ELO (European Landowners' Organization) (2012) . L'Explosion démographique du sanglier en Europe. Enjeux et défis. Rapport à l'Intergruppe Chasse durable, Biodiversité, Activités rurales et Forêt. Bruxelles: Parlement Européen. p 72
- FAO, OIE EC (2019) African swine fever in wild boar ecology and biosecurity. *FAO Animal Production and Health Manual* No. 22. Rome. <https://doi.org/10.4060/CA5987EN>
- Ficetola GF, Bonardi A, Mairota P, Leronni V, Padoa-Schioppa E (2014) Predicting wild boar damages to croplands in a mosaic of agricultural and natural areas. *Curr Zool* 60:170–179. <https://doi.org/10.1093/czoolo/60.2.170>
- Frackowiak W, Gorczyca S, Merta D, Wojciuch-Ploskonka M (2013) Factors affecting the level of damage by wild boar in farmland in north-eastern Poland: factors affecting damage by wild boar in Poland. *Pest Manag Sci* 69:362–366. <https://doi.org/10.1002/ps.3368>
- Galimberti F, Sanvito S, Boitani L, Fabiani A (2001) Viability of the southern elephant seal population of the Falkland Islands. *Animal conservation forum*. Cambridge University Press, pp 81–88
- Gamelon M, Gaillard J-M, Servanty S, Gimenez O, Toïgo C, Baubet E, Klein F, Lebreton J-D (2012) Making use of harvest information to examine alternative management scenarios: a body weight-structured model for wild boar: Population management based on incomplete data. *J Appl Ecol* 49:833–841. <https://doi.org/10.1111/j.1365-2664.2012.02160.x>
- Geisser H, Reyer H-U (2004) Efficacy of hunting, feeding and fencing to reduce crop damage by wild boars. *J Wildl Manag* 68:939–946. [https://doi.org/10.2193/0022-541X\(2004\)068\[0939:EOHFAF\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2004)068[0939:EOHFAF]2.0.CO;2)
- Genov P (1981) Food composition of wild boar in north-eastern and western Poland. *Acta Theriol (Warsz)* 26:185–205
- Giménez-Anaya A, Herrero J, García-Serrano A, García-González R, Prada C (2016) Wild boar battues reduce crop damages in a protected area. *J Vertebr Biol* 65:214–220. <https://doi.org/10.25225/fozo.v65.i3.a6.2016>
- Gren IM, Andersson H, Mensah J, Pettersson T (2020) Cost of wild boar to farmers in Sweden. *Eur Rev Agric Econ* 47(1):226–246. <https://doi.org/10.1093/erae/jbz016>
- González-Crespo C, Serrano Seán E, Raquel C, Castillo-Contreras L, José María C, López-Martín J, Roldán S, Jorge Ramón L, López-Olvera E, Cameron Z (2018) Stochastic assessment of



- management strategies for a Mediterranean peri-urban wild boar population. *PLOS ONE* 13(8):e0202289. <https://doi.org/10.1371/journal.pone.0202289>
- Guberti V, Khomenko S, Masiulis M, Kerba S, Food and Agriculture Organization of the United Nations, International Office of Epizootics, European Commission, 2019. African swine fever in wild boar ecology and biosecurity.
- Guibert B (2008) Bilan national de l'indemnisation des dégâts agricoles de sangliers. Modalités de gestion du sanglier, Actes du colloque tenu à Reims (Marne) les 1 et 2 mars 2007. In: Klein F, Guibert B, Baubet E (eds) Paris, France, pp. 73–78. F.N.C.–O.N.C.F.S
- Gürtler RE, Izquierdo VM, Gil G, Cavicchia M, Maranta A (2017) Coping with wild boar in a conservation area: impacts of a 10-year management control program in north-eastern Argentina. *Biol Invasions* 19:11–24
- Hebeisen C, Fattebert J, Baubet E, Fischer C (2008) Estimating wild boar (*Sus scrofa*) abundance and density using capture–resights in Canton of Geneva, Switzerland. *Eur J Wildlife Res* 54:391–401
- Herrero J, García-Serrano A, Couto S, Ortuño VM, García-González R (2006) Diet of wild boar *Sus scrofa* L. and crop damage in an intensive agroecosystem. *Eur J Wildl Res* 52:245–250. <https://doi.org/10.1007/s10344-006-0045-3>
- Johann F, Handschuh M, Linderoth P et al (2020) Adaptation of wild boar (*Sus scrofa*) activity in a human-dominated landscape. *BMC Ecol* 20:4. <https://doi.org/10.1186/s12898-019-0271-7>
- Keuling O, Stier N, Roth M (2008) Annual and seasonal space use of different age classes of female wild boar *Sus scrofa* L. *Eur J Wildl Res* 54:403–412. <https://doi.org/10.1007/s10344-007-0157-4>
- Keuling O, Stier N, Roth M (2009) Commuting, shifting or remaining? *Mamm Biol* 74:145–152. <https://doi.org/10.1016/j.mambio.2008.05.007>
- Keuling O, Baubet E, Duscher A, Ebert C, Fischer C, Monaco A, Podgórski T, Prevot C, Ronnenberg K, Sodeikat G, Stier N, Thurjfell H (2013) Mortality rates of wild boar *Sus scrofa* L. in central Europe. *Eur J Wildl Res* 59:805–814. <https://doi.org/10.1007/s10344-013-0733-8>
- Krebs JR, Kacelnik A (1991) Decision making. In: Krebs JR, Davies N (eds) *Behavioural Ecology: An Evolutionary Approach*. Blackwell Scientific Publishers, Oxford, pp 105–137
- Lacy RC (2000) Structure of the VORTEX simulation model for population viability analysis. *Ecological Bulletins*, pp 191–203
- Laznik Ž, Trdan S (2014) Evaluation of different soil parameters and Wild Boar (*Sus Scrofa* [L.]) grassland damage. *Ital J Anim Sci* 13:3434. <https://doi.org/10.4081/ijas.2014.3434>
- Legendre L, Legendre P (1998) *Numerical ecology*. Second English edition. Elsevier Science BV, Amsterdam, The Netherlands
- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool* 68:619–640
- Linnell JD, Cretois B, Nilsen EB, Rolandsen CM, Solberg EJ, Veiberg V, Kaltenborn B (2020) The challenges and opportunities of coexisting with wild ungulates in the human-dominated landscapes of Europe's Anthropocene. *Biol Cons* 244:108500
- Lombardini M, Meriggi A, Fozzi A (2017) Factors influencing wild boar damage to agricultural crops in Sardinia (Italy). *Curr Zool* 63:507–514
- Maillard D, Gaillard JM, Hewison M, Ballon P, Duncan P, Loison A, Saint-Andrieux C (2010) Ungulates and their management in France. *European ungulates and their management in the 21st century*, pp 44–474
- Manly BFL, McDonald L, Thomas DL, McDonald TL, Erickson WP (2007) *Resource selection by animals: statistical design and analysis for field studies*. Springer Science & BusinessMedia
- Maselli V, Ripa D, Russo G, Ligrone R, Soppelsa O, D'Aniello B, Raia P, Fulgione D (2014) Wild boars' social structure in the Mediterranean habitat. *Ital J Zool* 81:610–617
- Massei G, Genov PV (2004) The environmental impact of wild boar. *Galemys* (16):135–145
- Massei G, Genov PV, Staines BW (1996) Diet, food availability and reproduction of wild boar in a Mediterranean coastal area. *Acta Theriol (Warsz)* 41:307–320. <https://doi.org/10.4098/AT.arch.96-29>
- Massei G, Roy S, Bunting R (2011) Too many hogs? A review of methods to mitigate impact by wild boar and feral hogs. *Hum-Wildl Interact* 5:79–99
- Massei G, Kindberg J, Licoppe A, Gačić D, Šprem N, Kamler J, Baubet E, Hohmann U, Monaco A, Ozoliņš J, Cellina S, Podgórski T, Fonseca C, Markov N, Pokorny B, Rosell C, Náhlik A (2015) Wild boar populations up, numbers of hunters down? A review of trends and implications for Europe: wild boar and hunter trends in Europe. *Pest Manag Sci* 71:492–500. <https://doi.org/10.1002/ps.3965>
- Massolo A, Della Stella RM (2006) Population structure variations of wild boar *Sus scrofa* in central Italy. *Ital J Zool* 73:137–144
- Mazzoni della Stella R, Calovi F, Burrini L (2014) The Wild boar management in a province of the Central Italy. *J Mt Ecol* 3:213–216
- Meng XJ, Lindsay DS, Sriranganathan N (2009) Wild boars as sources for infectious diseases in livestock and humans. *Philos Trans R Soc B Biol Sci* 364:2697–2707. <https://doi.org/10.1098/rstb.2009.0086>
- Meriggi A, Lombardini M, Milanese P, Brangi A, Lamberti P, Giannini F (2016) Management of wild boar in protected areas: the case of Elba Island. *Problematic wildlife*. Springer, pp 229–251
- Merli E, Meriggi A (2006) Using harvest data to predict habitat-population relationship of the wild boar *Sus scrofa* in Northern Italy. *Acta Theriologica* 51(4):383–394. <https://doi.org/10.1007/BF03195185>
- Morelle K, Lejeune P (2015) Seasonal variations of wild boar *Sus scrofa* distribution in agricultural landscapes: a species distribution modelling approach. *Eur J Wildl Res* 61:45–56
- Mori Francesco E, Alessandro F, Leonardo L, La Greca E, Fattorini SN (2020) Impact of wild boar rooting on small forest-dwelling rodents. *Ecological Research* 35(4):675–681. <https://doi.org/10.1111/1440-1703.12113>
- Nores C, Fernández A, García E (1999) Wild boar damage selection in the Cantabrian Mountains, Spain. *Pirineos* vol 153–154 p 194
- Novosel H, Piria M, Safner R, Kutnjak H, Šprem N (2012) The game damages on agricultural crops in Croatia. *J Cent Eur Agric* 13:631–642. <https://doi.org/10.5513/JCEA01/13.4.1102>
- Oja R, Soe E, Valdmann H, Saarma U (2017) Non-invasive genetics outperforms morphological methods in faecal dietary analysis, revealing wild boar as a considerable conservation concern for ground-nesting birds. *PLoS ONE* 12(6):e0179463
- Palacio S, Bueno CG, Azorín J, Maestro M, Gómez-García D (2013) Wild-boar disturbance increases nutrient and C stores of geophytes in subalpine grasslands. *Am J Bot* 100(9):1790–1799
- Pastick J (2012) The biology of native and invasive Wild Boar (*Sus scrofa*) and the effect it is having in its invasive range. *Eukaryon* 8:60–63
- Pisanu S, Farris E, Filigheddu R, García MB (2012) Demographic effects of large, introduced herbivores on a long-lived endemic plant. *Plant Ecol* 213:1543–1553. <https://doi.org/10.1007/s11258-012-0110-9>
- R Core Team (2017) R: a language and environment for statistical computing. <https://www.R-project.org/>
- Rubenstein D, Alcock J (2018) *Animal behavior*. Sinauer Associates, Oxford
- Sáez-Royuela C, Tellería JL (1986) The increased population of the wild boar (*Sus scrofa* L.) in Europe. *Mammal Rev* 16:97–101

- Saino N, Meriggi A (1990) Habitat occupancy and breeding densities of coexisting Hooded Crows and Magpies: a multivariate approach. *Ethol Ecol Evol* 2(2):205–214
- Saito M, Momose H, Mihira T, Uematsu S (2012) Predicting the risk of wild boar damage to rice paddies using presence-only data in Chiba Prefecture. *Japan Int J Pest Manag* 58:65–71
- Sales LP, Ribeiro BR, Hayward MW, Paglia A, Passamani M, Loyola R (2017) Niche conservatism and the invasive potential of the wild boar. *J Anim Ecol* 86:1214–1223
- Santilli F, Stella RMD (2006) Electrical fencing of large farmland area to reduce crops damages by wild boars *Sus scrofa*. *Agric Mediterr* 136:79
- Schlageter A, Haag-Wackernagel D (2012) Evaluation of an odor repellent for protecting crops from wild boar damage. *J Pest Sci* 85:209–215. <https://doi.org/10.1007/s10340-012-0415-4>
- Schley L, Roper TJ (2003) Diet of wild boar *Sus scrofa* in Western Europe, with particular reference to consumption of agricultural crops. *Mammal Rev* 33:43–56
- Schley L, Dufrene M, Krier A, Frantz AC (2008) Patterns of crop damage by wild boar (*Sus scrofa*) in Luxembourg over a 10-year period. *Eur J Wildl Res* 54:589–599. <https://doi.org/10.1007/s10344-008-0183-x>
- Scillitani L, Monaco A, Toso S (2010) Do intensive drive hunts affect wild boar (*Sus scrofa*) spatial behaviour in Italy? Some evidences and management implications. *Eur J Wildl Res* 56:307–318. <https://doi.org/10.1007/s10344-009-0314-z>
- Senserini D, Santilli F (2016) Potential impact of wild boar (*Sus scrofa*) on pheasant (*Phasianus colchicus*) nesting success. *Wildl Biol Pract* 12:15–20
- Serrani F (2012) Interazione tra il cinghiale (*Sus scrofa*) e le attività antropiche con particolare riferimento al sistema agro-silvo-pastorale. PhD Thesis
- Servanty S, Gaillard J-M, Ronchi F, Focardi S, Baubet É, Gimenez O (2011) Influence of harvesting pressure on demographic tactics: implications for wildlife management: harvesting & demographic tactics. *J Appl Ecol* 48:835–843. <https://doi.org/10.1111/j.1365-2664.2011.02017.x>
- Sinclair ARE, Fryxell JM, Caughley G (2006) *Wildlife ecology conservation and management*, 2nd edn. Blackwell Science, Oxford
- Slovenia Forest Service (2014) *Yearly hunting management plans for all Slovene hunting management districts for 2014* (in Slovene). Slovenian Forest Service, Ljubljana, Slovenia
- SMAM (2008) Servizio Meteorologico dell'Aeronautica Militare, Atlante climatico d'Italia. VV. 3
- Sondej I, Kwiatkowska-Falińska AJ (2017) Effects of wild boar (*Sus scrofa* L.) rooting on seedling emergence in Białowieża Forest. *Polish J Ecol* 65(4):380–389
- Stankowich T (2008) Ungulate flight responses to human disturbance: a review and meta-analysis. *Biol Conserv* 141:2159–2173
- Stephens DW, Krebs JR (1986) *Foraging theory*, vol 1. Princeton University Press
- Stillfried M, Fickel J, Börner K, Wittstatt U, Heddergott M, Ortman S, Frantz AC (2017) Do cities represent sources, sinks or isolated islands for urban wild boar population structure? *J Appl Ecol* 54(1):272–281
- Symonds MRE, Moussalli A (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behav Ecol Sociobiol* 65:13–21. <https://doi.org/10.1007/s00265-010-1037-6>
- Thurfjell H, Ball JP, Åhlén P-A, Kornacher P, Dettki H, Sjöberg K (2009) Habitat use and spatial patterns of wild boar *Sus scrofa* (L.): agricultural fields and edges. *Eur J Wildl Res* 55:517–523. <https://doi.org/10.1007/s10344-009-0268-1>
- Thurfjell H, Spong G, Ericsson G (2013) Effects of hunting on wild boar *Sus scrofa* behaviour. *Wildl Biol* 19:87–93. <https://doi.org/10.2981/12-027>
- Thurfjell H, Spong G, Olsson M, Ericsson G (2015) Avoidance of high traffic levels results in lower risk of wild boar-vehicle accidents. *Landsc Urban Plan* 133:98–104
- Tolon V, Day S, Loison A, Zeileis A, Fischer C et al (2009) Responding to spatial and temporal variation in predation risk: space use of a game species in a changing landscape of fear. *Can J Zool* 87:1129–1137
- Treves A, Naughton-Treves LISA, Harper EK, Mladenoff DJ, Rose RA, Sickley TA, Wydeven AP (2004) Predicting human-carnivore conflict: a spatial model derived from 25 years of data on wolf predation on livestock. *Conserv Biol* 18(1):114–125
- Vajas P, Calenge C, Richard E, Fattebert J, Rousset C, Saïd S, Baubet E (2020) Many, large and early: hunting pressure on wild boar relates to simple metrics of hunting effort. *Sci Total Environ* 698:134251
- Vasudeva Rao V, Naresh B, Tripathi RS, Sudhakar C, Ravinder Reddy V (2017) Reduction of wild boar (*Sus scrofa* L.) damage in maize (*Zea mays* L.) by using castor (*Ricinus communis* L.) as barrier. *J Entomol Zool Stud* 5:426–428
- Vetter SG, Puskas Z, Bieber C et al (2020) How climate change and wildlife management affect population structure in wild boars. *Sci Rep* 10:7298. <https://doi.org/10.1038/s41598-020-64216-9>
- Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. *Methods Ecol Evol* 1:3–14

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