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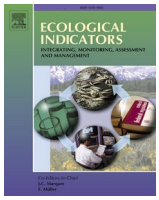

Original Articles

Rooting as indicator of wild boar density: environmental drivers and spatial variation across protected areas

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ABSTRACT

Wild ungulates play crucial roles in food webs and their impacts can propagate across trophic levels. The recent spread of wild boar *Sus scrofa* is generating concerns worldwide for its potential negative impacts on biodiversity and human activities. Under particular conditions, its foraging activity through digging the topsoil (i.e., rooting) may affect endangered plant/animal species or agriculture. Identifying environmental drivers of rooting is crucial to address spatially-explicit measures to reduce negative impacts, as well as to clarify the often unclear link between rooting and wild boar density. We performed six-year intensive spring-summer surveys (763 sampling plots; 3343 surveys between 2019–2024) in 9 protected areas of central Italy encompassing heterogeneous habitats and a gradient in wild boar densities, to investigate spatial variations in wild boar rooting and relevant drivers. Strong support was obtained for a positive relationship between rooting, at both large (i.e., study area) and fine (i.e., sampling plot) scales, and wild boar density in the area. Results supported lower rooting with increasing landscape diversity. Rooting was affected by topography, being reduced by rock cover and terrain steepness, and increased with distance from the nearest road/railway. Models of fine-scale rooting variation were elaborated to develop high-resolution (10 × 10 m) predictive maps of rooting impact, providing a tool scalable to ecologically comparable areas. Findings support the control of wild boar population density and maintenance of high landscape diversity as measures to reduce wild boar impacts. Finally, the present study also supports that rooting can serve as an effective indicator of within- and between-area variations in wild boar density.

1. Introduction

Wild ungulates have a central role in ecosystem dynamics. They can act as bottom-up restrainers of carnivore abundance as well as top-down regulators of vegetation structure (Hobbs, 1996; Hebblewhite et al., 2005; Ripple et al., 2015; Kaštovská et al., 2024). Their presence may also help to preserve habitat patchwork, e.g., by regulating forest expansion and seed dispersal (Hobbs, 1996; Bueno et al., 2011; Albert et al., 2015; Kaštovská et al., 2024). Nevertheless, under some conditions and especially at high population densities, their activities may become detrimental for the conservation status of particular species, e.g., altering habitat structure and threatening endangered plant and animal *taxa* (Côté et al., 2004; Barrios-Garcia and Ballari, 2012; Foster et al., 2014; Barasona et al., 2021). The recent increase in abundance and distribution of wild ungulates across temperate ecosystems has expectedly led to increased interactions with other organisms and human activities. In turn, there is an increasing necessity to identify key indicators that would be able to detect the most at-risk situations and to drive actions for reducing impacts (Caplenor et al., 2017; Pascual-Rico et al., 2021; Carpio et al., 2021).

The wild boar *Sus scrofa* is the most widespread wild ungulate in the world (Barrios-Garcia and Ballari, 2012; Massei et al., 2015). It is characterized by wide plasticity in habitat and food requirements, adapting its diet and space use to local resources and conditions (Herrero et al., 2006; Ballari and Barrios-Garcia 2014; Laguna et al., 2021). This suid is also considered an ecosystem engineer as it can

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modify habitats and biotic communities through its feeding activities (Massei and Genov, 2004; Bueno et al., 2009; Wirthner et al., 2011). The main foraging activity of wild boar is known as "rooting" and consists of using the final part of the snout to dig the soil searching for food (mainly bulbs, rhizomes, and other hypogeous storage organs of plants, but also invertebrates such as insect larvae). Rooting can reach depths of 5–15 cm and can perform superficial tillage over wide areas (Massei and Genov, 2004; Bueno et al., 2009; Barrios-Garcia and Ballari, 2012; Bueno and Jiménez, 2014; Horčičková et al., 2019). The rooting activity may modify soil structure and moisture (Mohr et al., 2005; Tierney and Cushman, 2006; Bueno et al., 2013), altering nutrient cycles and seed-bank richness (Bueno et al., 2011; Bueno et al., 2013; Palacio et al., 2013), potentially affecting plant and animal species (Barrios-Garcia and Ballari, 2012; Mori et al., 2020; Barasona et al., 2021; Labadessa and Ancillotto, 2023). In ecosystems where the wild boar is native, the activity of this suid should not be considered detrimental *per se* (Sondej and Kwiatkowska-Falinska, 2017; Labadessa and Ancillotto, 2023; Scherer et al., 2025). The negative magnitude of its impact should be scaled considering local characteristics, e.g., the presence of rare/endangered plant and animal species or agricultural activities, and environmental/anthropogenic drivers that could boost rooting. For example, the intensity of rooting may vary according to resource availability, soil conditions, and other environmental characteristics (Welander, 2000; Sütő et al., 2020; Ferretti et al., 2021; Calosi et al., 2024). The occurrence and quality of food resources from the surface to the first soil layers, as well as the proximity of alternative resources such as crops or grasslands, may either attract or divert wild boar attention, locally intensifying or reducing rooting (Welander, 2000; Herrero et al., 2006; Ballari and Barrios-García, 2014; Laguna et al., 2021). Rainfall could boost vegetation growth and create damp soil, which would be richer in undersoil fauna and easier to dig compared to a dry one (Hone 1995; Welander, 2000; Sandom et al., 2013a), generating conditions that favour wild boar sense of smell (Brivio et al., 2017), thus prompting rooting activity (Sandom et al., 2013a; Calosi et al., 2024).

Most importantly, wild boar rooting impact may be exacerbated by population densities (Hone, 2002; Sandom et al., 2013a; Calosi et al., 2024). The relationship between wild boar population density and rooting activity is contradictory, with some studies showing a positive association (Hone, 2002; Sandom et al., 2013a; Calosi et al., 2024) and others failing to support it (Massei et al., 2018; Adams et al., 2019; Ferretti et al., 2021). Disentangling this matter is crucial, considering the recent sharp increase in wild boar densities and distribution, mostly primed by anthropogenic factors (e.g., deliberate local releases and favourable hunting management, anthropogenic foraging opportunities in rural/periurban areas, Massei et al., 2015). The spread of wild boar has been also favoured by the recent climatic trends towards milder winters, and was facilitated by key biological traits such as adaptability and high reproductive potential (Massei et al., 2015; Vetter et al., 2015; Markov et al., 2022). Unravelling the relative role of possible determinants of rooting is a key step forward to address the spatial variation of impacts. Spatially explicit predictions of wild boar impact would be important to identify the appropriate spatial ranges over which management actions should be targeted to mitigate it. Moreover, identifying whether rooting estimates may act as indicators of temporal and/or spatial variations in wild boar population density would be important to support management strategies involving population control to reduce impacts.

Here, we evaluated the effects of wild boar population density, accumulated rainfall, and various environmental factors related to habitat characteristics, on wild boar rooting intensity at two different spatial scales. The ultimate goal was to develop a set of variables suitable to identify the major environmental drivers of rooting at a fine scale, and then to use them to build predictive maps. By conducting six year-intensive surveys in nine protected areas of central Italy, we achieved both fine-scale and large-scale estimates of wild boar rooting impact. Surveys were conducted in early summers, i.e., at the end of the vegetative season in our areas, to assess and model the environmental drivers of wild boar impact on habitats. Model outputs were used to produce high-resolution predictive maps of wild boar rooting impact to provide novel tools to identify the most at-risk situations and to assist actions aimed at mitigating wild boar impacts.

We expect that (1) rooting intensity, both at the large and fine scales, would be positively related to wild boar density in the area (Calosi et al., 2024). Then, we expect that local environmental features would also shape spatial dynamics of rooting independently from population densities (Bueno et al., 2009; Ferretti et al., 2021). In particular, rooting impact would be boosted by: (2a) milder soil and terrain conditions, i.e., rooting would decrease with increasing rock cover and terrain steepness; (2b) greater amount of accumulated rainfall, as affecting vegetation growth and soil moisture; (2c) habitat homogeneity, because a greater landscape diversity would be expectedly able to provide a wider range of alternative food resources and cover sites, thus reducing the rooting activities; (2d) proximity to persistent wet assets. Finally, we expect that (3) human presence would not reduce wild boar rooting activity, as surveys were conducted in low-populated protected areas, as well as because behavioural flexibility may lead wild boar to shift its temporal activity rather than moving to avoid human interactions (Ohashi et al., 2013; Podgórski et al., 2013; Johann et al., 2020).

2. Materials and methods

2.1. Study areas

The study was performed for six years (2019–2024), from late spring (mid-June) to early summer (July), in nine protected areas of central Italy with extents ranging from 10.5 to 90 km^2 and an elevation range of 0–1,453 m above sea level (Acquerino-Cantagallo Nature Reserve – ACNR; Alpe della Luna Nature Reserve – ALNR; Alto Merse Nature Reserve – AMNR; Basso Merse Nature Reserve – BMNR; Foresta di Berignone Nature Reserve – FBNR; Foresta di Monterufoli e Caselli Nature Reserve – FMCNR; Maremma Regional Park – MRP; Monte Penna Nature Reserve – MPNR; Sasso di Simone Nature Reserve – SSNR; Fig. 1). Main geographic and environmental features of study areas are summarized in Table 1. All the study areas are located in the Mediterranean bioregion, with generally dry summers and mild winters. Their distribution covers longitudinal and elevational climatic gradients, with the Mediterranean climate gradually acquiring from sub-Mediterranean/temperate traits to continental ones with increasing elevation and distance from the coastline, as approaching the Apennine chain (Pesaresi et al., 2014).

The study areas are mainly covered by broadleaved woodlands (67.8 %, on average), followed by agricultural lands (10.9 %), conifers (5.1 %), shrublands (4.3 %), mixed woodlands (3.7 %), and grasslands (3.5 %) (Fig. 1). Artificial surfaces, bare and rocky substrate, and water bodies cover an average of 3.7 % of the land. Wetlands cover the 0.04 % on average and are present only in MRP. Other ungulates inhabiting the study areas are the roe deer *Capreolus capreolus*, occurring in all study areas, the fallow deer *Dama dama*, in all areas except ACNR and MPNR, and the red deer *Cervus elaphus*, only in ACNR, AMNR, FMCNR, MPNR, and ALNR. Livestock is present locally (cattle: MRP, SSNR; horses: MRP, MPNR, ALNR, AMNR; donkeys: MPNR, ALNR; goats: ALNR; sheep: MPNR, MRP). The wolf *Canis lupus* occurs in all areas and the wild boar has been shown as its major prey (Mori et al., 2016, for a review in Italy; Capitani et al., 2004; Mattioli et al., 2004; Lovari and Sangiuliano, 2006; Ferretti et al., 2019; Lazzeri et al., 2024, for wolf diet in our study region). Recreational hunting is not allowed in any study area, although wild boar may be harvested for population control in some areas (selective culling: FMCNR, FBNR, MRP, SSNR; trapping: MRP) depending on local population density.

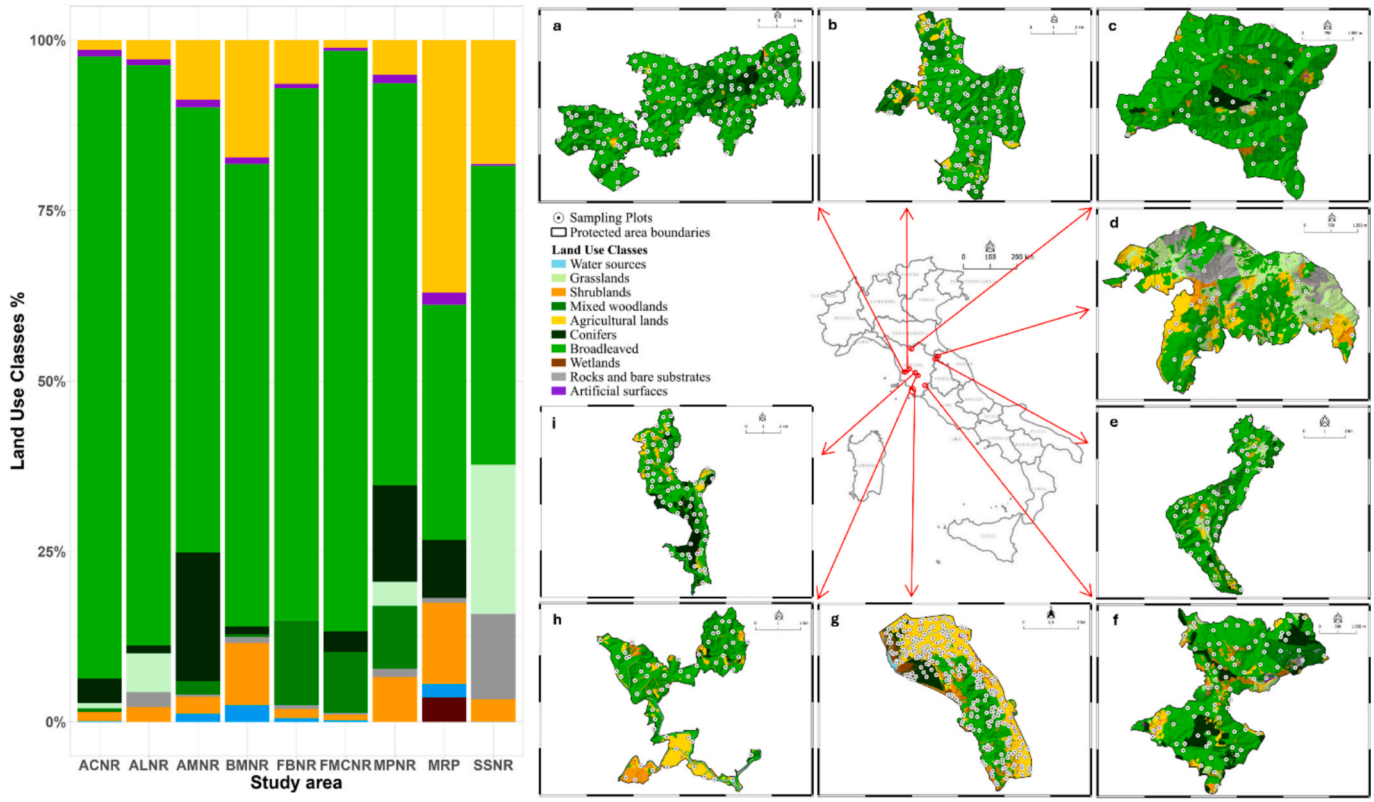

Fig. 1. Study area — Left panel: Composition of Land Use (% classes) in each study area; **right panel**: Location of sampling plots for rooting estimates and land use in each study area: a) Foresta di Monterufoli e Caselli Nature Reserve – FMCNR; b) Foresta di Berignone Nature Reserve – FBNR; c) Acquerino-Cantagallo Nature Reserve – ACNR; d) Sasso di Simone Nature Reserve – SSNR; e) Alpe della Luna Nature Reserve – ALNR; f) Monte Penna Nature Reserve – MPNR; g) Maremma Regional Park – MRP; h) Basso Merse Nature Reserve – BMNR; i) Alto Merse Nature Reserve – AMNR.

Table 1
Summary of geographic and environmental features derived at the study area-scale. Location is given for the centroid of each study area (WGS84). The number of plots includes the number of sampling plots used either for density (all the plots) or rooting (plots in natural/seminatural habitats) estimation. Study areas: Acquerino-Cantagallo Nature Reserve – ACNR; Alpe della Luna Nature Reserve – ALNR; Alto Merse Nature Reserve – AMNR; Basso Merse Nature Reserve – BMNR; Foresta di Berignone Nature Reserve – FBNR; Foresta di Monterufoli e Caselli Nature Reserve – FMCNR; Maremma Regional Park – MRP; Monte Penna Nature Reserve – MPNR; Sasso di Simone Nature Reserve – SSNR.

Study area	Centroid coordinates	Elevation range of the study area (m a.s.l.)	Mean slope (%)	Extent (km^2)	No. plots (Density – Rooting)
ACNR	44.006895°N; 11.054998°E	367–1219	25.4	18.6	60 – 60
ALNR	43.650348°N; 12.166402°E	549–1452	47.0	15.4	48 – 48
AMNR	43.196382°N; 11.202669°E	190–488	14.7	19	65 – 65
BMNR	43.115059°N; 11.333300°E	103–416	11.1	16.4	55 – 50
FBNR	43.331584°N; 10.950866°E	92–554	26.4	22	100 – 100
FMCNR	43.255552°N; 10.783597°E	72–597	30.3	48.3	139 – 136
MRP	42.644144°N; 11.094017°E	0–414	15.2	89	271 – 171
MPNR	42.775285°N; 11.690544°E	484–1104	33.5	10.5	75 – 75
SSNR	43.759573°N; 12.290271°E	692–1207	23.0	16.4	50 – 45

2.2. Rooting and density estimates

Wild boar rooting and population densities were estimated through a design-based, stratified sampling strategy repeatedly described in previous works conducted in the same areas (see Fattorini et al., 2011; Ferretti et al., 2016; Fattorini and Ferretti, 2020; Ferretti et al., 2021; Ferretti et al., 2023, for more details). Sampling plots were circular areas with a 5 m radius, distributed with an effort of ~ 1 plot/0.3 km^2 in each study area (863 plots, overall). Simulations to assess how the uncertainty of ungulate density estimates varied with the number of sampling plots were previously conducted in our largest study area, supporting the effectiveness of this sampling effort in achieving adequate precision (Fattorini et al., 2011). The density estimation was conducted through faeces counts, using the faecal accumulation rate technique (Mayle et al., 1999). This technique requires visiting each sampling plot twice: a first survey is required for the clearance of previously deposited wild boar faeces; a second survey is conducted after ~ 35–40 days (Ferretti et al., 2016; Fattorini and Ferretti, 2020; Ferretti et al., 2021) to count all wild boar faeces accumulated in plots since the clearance day. An unbiased estimator of faeces abundance and a conservative estimator of its standard error (Fattorini et al., 2011; Fattorini and Ferretti, 2020) were used to estimate the density of wild boar faeces. Wild boar densities were derived by using the wild boar daily defecation rate estimated in summer on a semi-captive Mediterranean wild boar herd localized ~ 40–110 km away from our study areas (6.7 faeces/individual/day; Fattorini and Ferretti, 2020). Although an area-specific defecation rate of wild boar populations would have improved our investigation, the value we used is the only estimate available for Mediterranean populations, in summer, and the one based on the highest number of individuals sampled (Table S4, Supplementary Material).

Rooting intensity was estimated during the clearance surveys,

between mid-June and July, in the same sampling plots used for density estimation. The percentage of plot covered by rooting signs attributable to wild boar was visually estimated and used as an index of rooting intensity (e.g., uprooting of soil and plants and lack of vegetation cover, together with hoofprints and other signs of presence; Adams et al., 2019). Rooting signs may persist for weeks or even months, but we performed rooting estimation after the end of the rainy season, under relatively stable weather at the peak of vegetative growth (late spring-early summer), ensuring that most visible signs reflected relatively recent activity. Visual estimates of impact indices are common in assessments of ungulate impacts (e.g., Felton et al., 2022; Treichler et al., 2023). The same 2–5 trained operators conducted the surveys across study areas and years. At the beginning of each field season, all operators performed joint calibration surveys to harmonize estimation criteria and minimize inter-observer bias. In addition, the operators were supported by preprinted reference images of circular plots covered by simulated percentages of rooted ground, and by reference paper sheets measuring 0.785 m^2 in size, thus able to quantify 1 % rooting extent in plots (sampling plot size: ~ 78.5 m^2). Nonetheless, incorporating formal metrics of inter-observer agreement in future studies could help rule out potential estimation bias. The percentage of rooted area within the circular plots was estimated in classes: 0 %; above 0 % but less than 1 %; then considering integer values: 1–5 %; 6–10 %, 11–15 %; and so on, with a range of 5 % up to the 96–100 % class (Fattorini and Ferretti, 2020; Ferretti et al., 2021). For the statistical analyses, each rooting class was represented by its midpoint value (e.g., 0 % for the 0 % class, 0.5 % for > 0–1 % class, 3 % for 1–5 % class, 8 % for 6–10 % class, 13 % for 11–15 % class, as per the above-defined rooting classes). These midpoint values were used as continuous variables in the models to approximate rooting intensity (e.g., Fattorini and Ferretti, 2020; Ferretti et al., 2021). We considered only those plots located in natural or seminatural habitats (763 plots) to avoid including potential ground alterations by human agricultural activities.

Rooting was estimated on the clearance surveys because our major interest was monitoring this impact during the critical phase of plant growth. In Mediterranean biomes, the peak of plant growth is followed by a season with low rainfall and high temperatures. Disturbances during this time can hinder plant cover recovery, potentially causing long-lasting damage to ecosystems and habitat loss (Belnap, 1995). Although rooting estimates and faeces counts were recorded at different times, the temporal gap between the two surveys was relatively short and constant across years (35–40 days), suggesting relative demographic stability in wild boar populations (i.e., after the birth season, which occurs in spring; Scandura et al., 2022). Considering the short time window, both density and rooting estimates likely refer to the same population and can be meaningfully compared.

2.3. Environmental predictors

For analyses of environmental covariates of wild boar rooting at the fine-scale, rock cover percentage was visually estimated in each plot following the same evaluation criteria used for rooting estimates. Elevation (metres a.s.l.) and terrain slope (%) of sampling plots were obtained from a high-resolution digital elevation model provided by SITA-Regione Toscana (https://geoblog.regione.toscana.it/-/open-geodata; resolution: 10 × 10 m), using Qgis 3.38.

For land use classes, the CORINE land cover (CLC) classification was considered by integrating local refinements and fine-scale improvements within the Tuscany region boundaries made by SITA-Regione Toscana (land use and cover – UCS vector: https://dati.toscana.it/dataset/ucs; reference year: 2019, after implementing the CLC version 2018). For areas close to the Tuscany region boundaries, the UCS layer was extended for 5 km outside regional limits, merging the UCS with the CLC vector provided by the Copernicus Land Monitoring service (https://land.copernicus.eu/en/products/corine-land-cover/clc2018; reference year: 2018). The CLC land use categories were re-classified into 10 broader land-cover classes to enhance ecological interpretability and reduce model complexity, following a hierarchical logic based on the official CLC nomenclature. Specifically, the following classes were considered at the third level of the CLC nomenclature: *i*) grasslands and meadows, i.e., natural/semi-natural meadows with no scattered trees or bushes; *ii*) shrublands, i.e., transitional habitats between woodland and open areas such as meadows with scattered trees and/or bushes, or abandoned olive groves; *iii*) mixed woodlands; *iv*) woodlands dominated by conifers; *v*) woodlands dominated by broadleaves. The following classes were grouped according to the first CLC level: *vi*) agricultural lands, such as cereal crops, vineyards, arable lands, and set-asides; *vii*) wetlands; *viii*) water bodies; *ix*) rock and bare soil; *x*) artificial surfaces. For the correspondence of the broader classes to the original CLC classes, see Table S2 (Supplementary Material). The ten classes were used to calculate the Shannon diversity index adopted as a proxy of heterogeneity in landscape composition potentially affecting wild boar rooting behaviour. Conversely, only the first seven classes were used to assess the percentage of the area covered by each land use class around the sampling plots, as proxies for the cover of natural/seminatural habitats available to wild boar. Both landscape diversity and cover were calculated in circular buffers of 1100 m radius around the central point of each plot. The buffer size was determined by following Calosi et al. (2024), as the mean of the annual home ranges (weighted by number of individuals sampled) obtained in our largest study area (Massei et al., 1997) and in an area geographically close and ecologically comparable to the study areas (Boitani et al., 1994). As discriminating sex and age class of the individual wild boar that performed rooting is not possible, the smaller home range, i.e., the female one (3.9 km^2– radius: 1100 m; males: 7.1 km^2 radius: 1500 m), was considered as representative for the maximal area likely used by the majority of wild boar (Calosi et al., 2024). This approach included both the focal plot and the surrounding habitats likely influencing the behaviour of the wild boar responsible for the observed rooting.

In line with this, distances from the central point of each plot to the edges of key landscape features were calculated to account for the potential influence of these elements on rooting behaviour. Distances (m) from the central point of each plot to the nearest road/railway, as a proximity index to human disturbance, and the nearest persistent wet asset, as a proxy for water availability, were calculated using the shortest path (point to layer) feature in Qgis 3.38. The former was based on the road and rail network layer and the latter on a new layer created by merging the hydrographic network layer, the water infrastructure layer and inland waters of the above-mentioned UCS layer, each provided by SITA-Regione Toscana and spanning the Tuscany region (road/rail: http://dati.toscana.it/dataset/grafo-civici; water sources: https://www.regione.toscana.it/-/reticolo-idrografico-e-di-gestione). For areas close to the Tuscany region boundaries, the layers were extended for 5 km beyond Tuscany region boundaries. The road/rail layer was extended by merging the DBPrior10K vector provided by CISIS (Centro Interregionale per I Sistemi Informatici Geografici e Statistici; http://www.centrointerregionale-gis.it/DBPrior/Dati/DBPriorItalia.zip), and the water source layer was extended by merging the water infrastructure vector provided by the Italian national geoportal (https://geodati.gov.it/geoportale/; Table S3, Supplementary Material). Water sources are an important limiting factor for wild boar (Massei et al., 1997). Ephemeral water bodies such as small ponds and ditches were not georeferenced, possibly leading to underestimating water availability. Nevertheless, the surveys were performed in summer, a season characterized by high aridity in our study region. These conditions do not favour the creation of puddles. Consequently, persistent water resources (e.g., ponds, rivers, and lakes) likely represent the main wet asset available to wild boar during the survey period.

Rainfall has a central role in wild boar ecology (Thurfjell et al., 2014; Brivio et al., 2017), especially by influencing environmental parameters such as soil moisture and vegetation growth, which in turn may affect wild boar rooting behaviour (Welander, 2000; Calosi et al., 2024). Thus,

cumulative amounts of rainfall (millimetres) were evaluated at three different temporal scales to investigate either the direct effect on rooting impact by moisturizing the soil (7 days) or the indirect effect on rooting through enhanced vegetation growth (15–30 days). The maximum temporal window was selected based on a global analysis of the effects of accumulated rainfall on vegetation growth, while considering the vegetation types present in the study areas (~30 days; Ding et al., 2020). Rainfall data were gathered by the professional weather stations (ARPAE Emilia Romagna, for ALNR: https://simc.arpae.it/dext3r; Servizio Idrologico Regione Toscana, for all the others: https://www.sir.toscana.it) closest to the centroid of each study area (Table S1, Supplementary Material). Rainfall data were downloaded and elaborated, obtaining 7, 15, and 30 days-cumulative rainfall before the survey date (rooting estimation) of each sampling plot.

Together with the distance from the nearest road/railway, the human population density was also considered as a proxy for the degree of human presence. The Global Human Settlement raster provided by the Copernicus Emergency Management Service, indicating the number of residential people per raster cell (Schiavina et al., 2023; resolution: 100 × 100 m) was used to obtain the average number of people living in the 1100 m radius circular buffer around each plot.

2.4. Statistical analyses

Statistical analyses were performed through generalized linear mixed models (GLMMs; Zuur et al., 2009). Separate analyses were performed for rooting estimates at the (*a*) large- (study area) and (*b*) fine- (sampling plot) scales.

(a) At the study area-scale, the response variable was the probabilistic rooting estimate for each study area and year resulting from the plot-level estimates. This value was then converted into a proportion and was modelled against the estimate of wild boar population density in the same area (fixed effect; continuous, as number of individuals/km^2). Rooting intensity was modelled through beta errors (link function: logit), as recommended for continuous proportions bounded through the 0–1 range (ordered beta parametrization: Kubinec, 2023). Since the response variable represents an estimate with associated uncertainty, it was weighed by the inverse of the standard error of the rooting proportion estimate, in turn accounting for the precision of rooting estimates. As the number of data-points is given by 39 rooting estimates, the model would not allow the inclusion of further predictors. Considering that the surveys were repeated within the same study years and areas, the variables 'Year' and 'Study area' were included as random intercepts. This model specification, where the study area is treated as a random intercept, accounts for both the within- and between-area effects. Thus, such model would provide the effect of wild boar population density on rooting independently of the study area, meaning that, if a positive density effect on rooting is found, density can predict rooting both within a study area (i.e., between-years in the same area) and between different study areas (i.e., on an 'average' year). To further assess this possibility, the model was re-fitted through a mathematical specification able to distinguish within- versus between-area effects ('within-group centring'; Van de Pol and Wright, 2009). Thus, wild boar population density was centred on its study area-mean and used as a predictor, and the mean population density in each study area was also added as a further predictor. The other model components were kept identical.

(b) At the sampling plot-scale, three global models were run separately, one for each period over which cumulative rainfall was considered (7, 15, and 30 days-cumulative rainfall). This approach allowed testing direct and indirect effects of rainfall on rooting intensity, which could not be handled together in the same model due to high collinearity (7 days *vs* 15 days: $r = 0.85$; 7 days *vs* 30 days: $r = 0.73$; 15 days *vs* 30 days: $r = 0.77$). Rooting intensity estimated in each sampling plot (response variable) was converted into a proportion and modelled through beta errors. The ultimate goals were to identify the major environmental drivers of rooting at a fine scale, and then to use this set of drivers to build predictive impact maps. Thus, collinearity among variables was checked to avoid potentially strong correlations among local environmental characteristics. Only variables showing a correlation of $|r|<0.4$ with others were retained as fixed effects (Fig. S1, Supplementary Material). As a result, shrubland cover was excluded due to collinearity with landscape diversity and distance from persistent wet assets; elevation was excluded due to collinearity with grasslands cover; broadleaves woodland cover was excluded as it represented the most common habitat type among the study areas and showed collinearity with agricultural lands, conifer woodland cover and landscape diversity (Fig. S1, Supplementary Material). Additionally, wetland cover was excluded as present only in MRP. Therefore, the fixed effects included in the global models were: (1) wild boar population density (continuous, as number of individuals/km^2); (2) 7, 15 or 30 days-cumulative rainfall before the survey date (continuous, in millimetres); (3) rock cover (continuous, as % in each plot); (4) distance from the nearest persistent wet asset (continuous, in metres); (5) distance from the nearest road/railway (continuous, in metres); (6) slope (continuous, as %); cover of: (7) mixed woodlands, (8) grasslands and meadows, (9) agricultural lands, and (10) conifers within the buffer (predictors 7 to 10: continuous, as % land class cover in 1100 m circular buffers); (11) landscape diversity within the buffer (continuous, as Shannon index in 1100 m circular buffers); (12) human population density within the buffer (continuous, as average number of people living in each buffer). To account for repeated rooting estimates obtained within the same study year, study area, and sampling plot, 'Year', 'Study area', and 'ID plot' were included as random intercepts. In each global model, there was no multicollinearity among explanatory variables (all VIFs ≤ 1.8) and covariates were scaled to increase coefficients' interpretability and model convergence, as well as to compare effect sizes of different predictors.

For each global model in both (*a*) and (*b*), an all-subset model selection was performed, as each combination of predictors could represent a different *a priori* hypothesis that could not be discarded in advance (Harrison et al., 2018). Thus, all possible combinations among predictors, as well as the null model (i.e., the model with only the random intercepts), were ranked and weighted from each global model (in *a*, only the null model was the possible competing model). Ranking was based on the AICc value of each model and the relevant ΔAICc, i.e. its difference with the model with the lowest AICc value. Models were selected if they showed ΔAICc < 2 and, following the "nesting rule" (Harrison et al., 2018), when they were not more complex than any simpler alternative with a lower AICc value. Thus, either a single top-ranked model (Table S5, Supplementary Material) or a set of top-ranked competing models (Table S6, Supplementary Material) was obtained from the model selection procedure, depending on the analysis. Model weight was standardised within the subset of selected models. Coefficients of predictors and 95 % confidence intervals were estimated from the best model. The effects of predictors were assessed by checking whether 95 % confidence intervals of coefficients overlapped '0'. Best models were validated by visually checking residual patterns (Zuur et al., 2009). GLMMs and model selection were run respectively through the packages *glmmTMB* (Brooks et al., 2017) and *MuMIn* (Bartoń, 2023), using the R software version 4.4.0 (R Core Team, 2023).

2.5. Predictive maps of wild boar rooting

The second aim of this study was to map the wild boar rooting impact continuously across space in the study areas, to identify the most-at-risk sites. A model-assisted approach based on predictive variables available for any location of the study areas was adopted. The only predictive variable visually estimated *in situ,* and as such not available wall-to-wall, was the rock cover. Therefore, all the global models and model selections adopted in the study for assessing drivers of rooting (see *section 2.4*) were re-fitted without considering rock cover among predictors. Although rock cover was a driver of rooting intensity (see *section 3.2*), its exclusion did not affect model selection, which supported the same best model, only differing for the lack of rock cover (cf. Table S6-S7, Supplementary Material). Moreover, the best models fitted with and without rock cover provided identical predictive capacity (Pearson correlation between observed and predicted values, for both models: $r = 0.64$; $R^2 = 0.42$), and predicted values from the two models were almost perfectly positively correlated ($r = 0.99$; $R^2 = 0.98$). Thus, excluding rock cover from predictors did not qualitatively affect the predictive capacity of the maps. Maps were built at the finest possible resolution considering constraints in computational effort, but attempting to achieve the closest possible resolution to the original data extent. Thus, raster cell (i.e., pixel) resolution was set at 10 × 10 m, i.e., 100 m^2. To the best of our knowledge, there is no map concerning wild boar impact available at such a fine resolution. The rooting impact was predicted for each study area and year separately. Because the use of the plot identity as a random intercept would have precluded the interpolation in raster cells outside the sampling plots, predictor coefficients were estimated from the best model without including this random intercept (mapping model, Table S8, Supplementary Material).

At each raster cell, the area-specific raster layers of predictor variables in the mapping model were used, exploiting its mathematical equation (Equation 1, Supplementary Material). The model intercept was adjusted for each area and year by considering the random intercept values estimated by the mapping model in the same study area (Equation 1, Supplementary Material), as well as by holding the area-specific value of wild boar population density at its mean value, calculated across the study years (Fig. S2, Supplementary Material).

Once predictions at each raster cell were achieved for each study area and year by exploiting the mapping model, the residuals were calculated for each sampled location (i.e., sampling plot), where both predicted and observed values were available. We followed the novel approach by Fattorini et al. (2024) to spatially interpolate the residuals at non-sampled locations by the inverse distance weighting interpolation, with the smoothing parameter selected from sample data by a leave-one-out technique. Finally, the interpolated residuals were added to the model predictions to achieve the mapped values. Contrary to geostatistical techniques that necessitate several more or less realistic assumptions, this mapping strategy is design-based, avoiding any reliance on model assumptions. Also, the statistical properties of the maps are objective, as they stem from the sampling scheme actually adopted in the field. In particular, under tessellation stratified sampling, the resulting maps have been proven consistent, i.e., they converge to the true maps as the number of sampling locations increases (Fattorini et al., 2024).

After obtaining area- and year-specific maps, since rooting was estimated on natural/seminatural habitats, portions of the study areas covered by water bodies, anthropic surfaces, and agricultural lands were cut out.

3. Results

3.1. The relationship between rooting and density across protected areas

Estimates of wild boar population density (39 estimates) varied from 1.7 to 22.4 individuals/km^2, and those of rooting impact at the study area scale from 0.6 % to 12.9 % of rooted area (for study year and study area-specific estimates, see Fig. S2, Supplementary Material). The model including the wild boar population density as predictor was selected over the null model (Table S5, Supplementary Material), supporting a positive relationship between wild boar density and rooting, and showing more than a two-fold increase of rooting impact when wild boar population density increased from 1.7 to 22.2 individuals/km^2 (Fig. 2a; Table 2a). The same model re-fitted to distinguish within- (i.e., centred density) versus between-area (i.e., average density) effects provided identical results, confirming that the positive effect of wild boar population density on rooting occurred both within the same area (thus, between years) and between different study areas, with the former effect being stronger (Table S9, Supplementary Material).

3.2. Environmental drivers of fine-scale rooting estimates

At the plot sampling-scale, the percentage of ground with rooting varied from 0 to 93 % (3343 plot-surveys), with 36.0 % of the estimates yielding no rooting impact, 50 % of the estimates showing rooting intensities above 0 % but less than 10 %, and 14 % of the estimates showing rooting impact above 10 %. Two top-ranked models were selected to explain factors influencing wild boar rooting at the plot-scale for each cumulative rainfall temporal window (Table S6). The best model was the same for all the three analyses, supporting the effects of (1) wild boar population density, (2) rock cover, (3) distance from the nearest persistent wet asset, (4) distance from the nearest road/railway, (5) slope, (6) the % of mixed woodlands, (7) the % of agricultural lands, and (8) landscape diversity. Rooting increased with increasing wild boar population density, which had the strongest effect among predictors, indicating more than a twofold increase when density increased from 1.7 to 22.4 individuals/km^2 (Fig. 2b; Table 2b). In addition, rooting impact decreased with increasing rock cover within the plot (Table 2b; Fig. 3a), terrain steepness within the plot (Table 2b; Fig. 3b), landscape diversity within the buffer (Table 2b; Fig. 3c), and distance from the nearest road/railway (Table 2b; Fig. 3d), although the latter showed a weak effect size. The percentage of mixed forests and that of agricultural lands within the buffer, as well as the distance from the nearest persistent wet asset, were selected in the best model, but confidence intervals overlapped "0″, indicating them as uninformative predictors (Table 2b).

3.3. Map of spatial variations in rooting activity

Area-specific, spatially-explicit maps of wild boar rooting impact were obtained by averaging year-specific maps for each study area (Fig. 4). Year-specific spatially-explicit maps are depicted in Supplementary Material (Fig. S3 and S4).

4. Discussion

The recent and ongoing spread of wild boar across temperate ecosystems is raising concerns on the potential negative impacts of this suid on natural habitats as well as human activities (Massei and Genov, 2004; Barrios-Garcia and Ballari, 2012). Identifying determinants of wild boar impact on habitats is crucial to define adequate mitigation measures. Our results provided strong support for the roles of wild boar population density, landscape heterogeneity, and topography in influencing rooting activity. These findings can be used to obtain site-specific information driving spatially-explicit management actions.

4.1. Wild boar population density: a critical driver of rooting pressure

The results supported a positive relationship between wild boar population density and rooting, both at the study area and sampling plot scales (prediction 1). Data were based on six-year intensive sampling, during which rooting and density estimates were collected within the same sampling plots. This methodological consistency likely

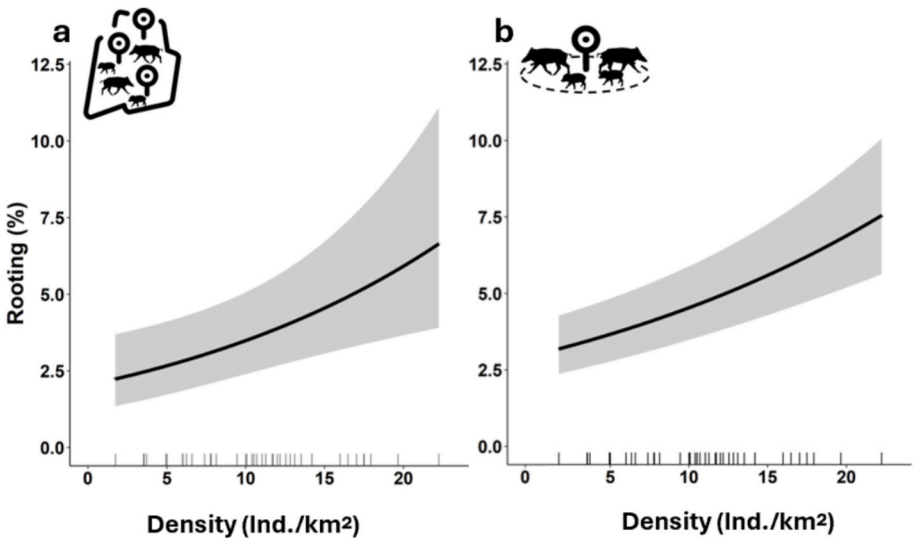

Fig. 2. Wild boar population density effect — Relationships between rooting (a) at the study area-scale and (b) at the sampling plot-scale and wild boar population density in the area, as estimated by GLMMs. Marks along the x-axis show the distribution of observed values for each covariate. Lines: predicted values. Bands: 95% confidence intervals.

Table 2
Parameters estimated from top-ranked GLMMs predicting wild boar rooting (a) at the study area-scale and (b) at the sampling plot-scale: coefficients (β) and 95% confidence intervals (95% CIs). An asterisk marks the coefficients whose 95% CIs do not include 0. Variance of random intercepts in the model (σ^2) is also shown.

Response variable	*Predictors*	*β*	*95 % CIs*
(a) Proportion of rooting at area-scale	(Intercept)	−3.392	−3.806, −2.978*
$\sigma^2_{Area} = 0.574$	Wild boar population density	0.261	0.246, 0.275*
$\sigma^2_{Year} = 0.220$			
(b) Proportion of rooting at plot-scale	(Intercept)	−2.999	−3.273, −2.724*
$\sigma^2_{Area} = 0.348$	% Mixed woodlands	0.061	−0.003, 0.125
$\sigma^2_{Year} = 0.154$	% Agricultural lands	0.056	−0.016, 0.128
$\sigma^2_{ID\ Plot} = 0.554$	Wild boar population density	0.190	0.130, 0.250*
	Nearest wet asset distance	−0.056	−0.130, 0.018
	Nearest road/railways distance	−0.099	−0.175, −0.022*
	Landscape diversity	−0.181	−0.282, −0.080*
	Slope	−0.125	−0.192, −0.059*
	Rock cover	−0.226	−0.304, −0.148*

strengthened the observed relationship, which otherwise might have appeared weaker using shorter time series or smaller samples of study areas (Nakagawa and Cutchill, 2007; e.g., Massei et al., 2018; Adams et al., 2019; Ferretti et al., 2021). The wild boar is a gregarious species and higher population densities often lead to larger aggregations of individuals (Massei et al., 1997; Barrios-Garcia and Ballari, 2012). Local clustering of individuals can amplify the effects of behaviours such as rooting and trampling, intensifying impacts on soil and vegetation (Massei et al., 1997; Hone et al., 2002; Barrios-Garcia and Ballari, 2012). The magnitude of these impacts, as well as thresholds of population density beyond which impacts may become threatening for ecosystems, would be expected to depend on local environmental carrying capacity, which may vary across seasons and years (Massei et al., 1997; Barrios-Garcia and Ballari, 2012). Based on our results, moderate-to-high wild boar population densities (~15–20 ind./km^2 in summer, i.e., after births) were associated with significant rooting activity (~5–8 % of rooted area), which may pose a threat to vulnerable habitats. The occurrence of detrimental effects should depend on the local ecological context, as well as on the local abundance and distribution of focal *taxa* affected by rooting (e.g., orchids or other vulnerable plants; threatened birds, smaller vertebrates or invertebrates). The effect of population density could be exacerbated by environmental factors that favour rooting, such as abundant food resources underground or specific habitat characteristics (Baubet et al., 2004; Bueno et al., 2009; Lombardini et al., 2017). Nevertheless, density-independent negative effects of rooting should not be ruled out. For instance, even a small number of individuals may exert negative impacts on rare and localized *taxa* (e.g., orchid species) and their habitats. In addition, unmeasured variables such as predator pressure and population structure may mediate the observed relationship between density and rooting. These factors could influence wild boar population dynamics and behaviour (Lingle, 2001; Scandura et al., 2022), locally altering the rooting intensity. For example, predation pressure may exert a top-down control on prey density, while increased predation risk may lead to larger group sizes in ungulates (Lingle, 2001), thus modifying the spatiotemporal distribution and magnitude of their impacts. Individual traits such as sex, age, and physiological stage may also affect foraging behaviour. Males typically live solitary or in small groups whereas sows tend to aggregate in larger family groups, particularly while weaning their offspring (Scandura et al., 2022). Also, time spent foraging differs with age: piglets may allocate about twice the time to foraging activities more than adults (Spitz and Janeau, 1995). Consequently, females with piglets may exert a cumulatively greater rooting impact than males, due to both greater time spent foraging and larger group size typical of maternal groups (Spitz and Janeau, 1995; Scandura et al., 2022). Future studies should investigate whether such unaccounted demographic and behavioural factors mediate the observed density-effect on rooting impact. Furthermore, an increased sampling effort in areas with low wild boar density and rooting pressure, where the number of '0 counts' increases, thus inflating the variance of estimates (Fattorini and Ferretti, 2020), may improve the investigation of the relationship between density and rooting. Eventually, we acknowledge that our density estimates

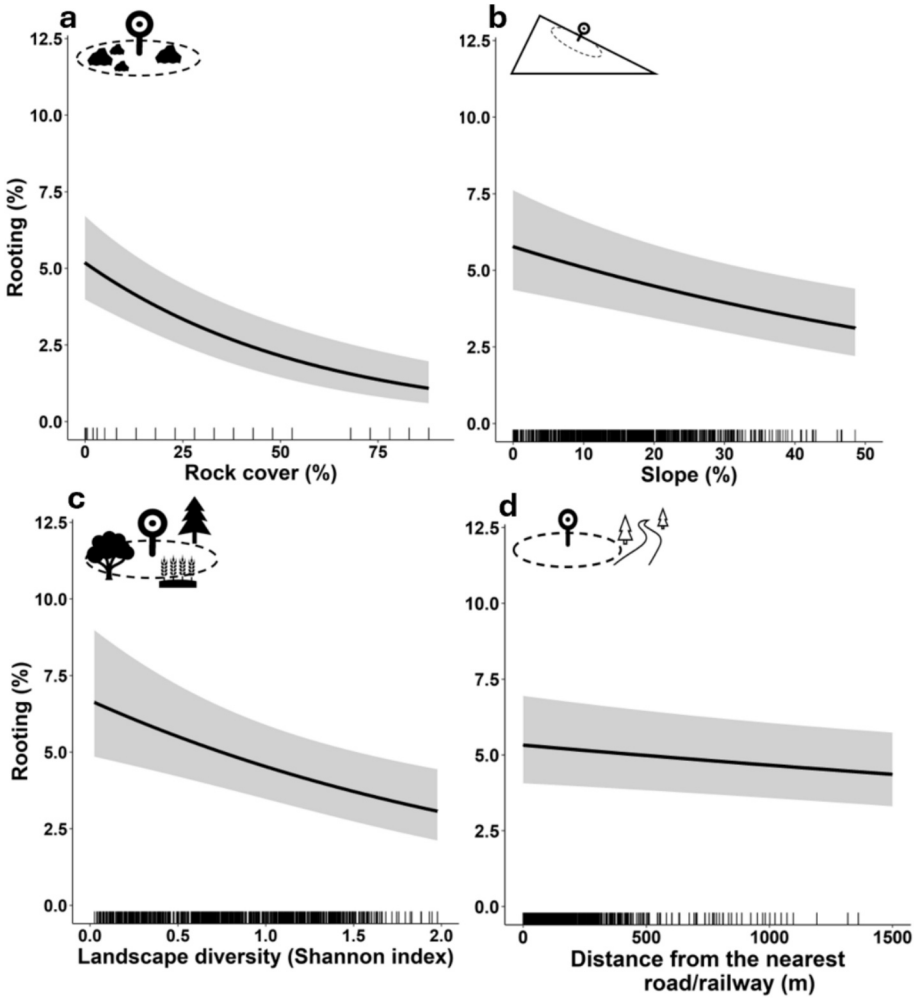

Fig. 3. Environmental predictors effects — Relationships between rooting at the sampling plot-scale and (a) rock cover, (b) terrain steepness, (c) landscape diversity, and (d) distance from the nearest road/railway, as estimated by GLMMs. Marks along the x-axis show the distribution of observed values for each covariate. Lines: predicted values. Bands: 95% confidence intervals. Confidence intervals for all the above predictors do not overlap zero.

rely on defecation rates derived from a semi-captive population (Fattorini and Ferretti, 2020), which might not fully reflect those in wild populations. Although the use of defecation rates estimated under captive or semi-captive conditions is a common approach to monitor ungulate density through faeces counts (Adams et al., 2019; Plhal et al., 2014), future studies could enhance the accuracy of our density estimates by directly obtaining defecation rates from wild individuals (e.g., through field tracking or isotopic labelling), thereby strengthening the observed rooting-density relationship.

4.2. *Environmental drivers of rooting pressure*

Rooting decreased with increasing rock cover and terrain steepness, confirming prediction (2a) (Ferretti et al., 2021; Calosi et al., 2024). Rocky terrains and steep slopes can enhance water percolation, which in turn reduces soil moisture (Penna et al., 2009; Lange et al., 2010). This may harden the first layers of soil, locally hampering wild boar digging activity (Sandom et al., 2013a).

Accumulated rainfall was not selected in the best model, not supporting an effect of rainfall on rooting activity, contrary to prediction (2b). Rainfall can affect wild boar ecology (e.g., Fernandez-Llario and Mateos-Quesada, 2005; Thurfjell et al., 2014; Colomer et al., 2024). Previous analyses conducted on a single habitat type and throughout the year, thus covering a gradient from rainy to drier periods, showed that rooting activity was favoured by precipitation (Calosi et al., 2024). The weather homogeneity within a single, relatively dry season, such as late spring-early summer, may have limited the potential of detecting the effects of rainfall on rooting activity. At the multi-habitat scale of our investigation, wild boar dependence on rain-mediated food resources could be buffered by the presence of habitats rich in food resources year-round (e.g., woodland for undersoil resources or agricultural land for herbaceous supply) which could be selected in arid periods, mitigating the effect of rainfall (Herrero et al., 2006; Keuling et al., 2009; Ruf et al., 2023). Future analyses incorporating rainfall and soil moisture data at a finer spatial scale could help reveal relevant effects that may have been underestimated at the broader scale of our investigation.

Results showed weak (i.e., confidence intervals overlapping ‘0′) support for the effects of specific land use classes on rooting, such as percentages of agricultural land and woodland within wild boar home range. They supported higher rooting activity in areas with lower landscape diversity. Those results partially confirmed prediction (2c), suggesting that the wild boar is not strictly tied to specific land uses but rather responds to overall landscape composition and specific local conditions (Briedermann, 1990; Morelle et al., 2016; Fettebert et al., 2017; Yang et al., 2024). Habitat composition shapes wild boar ranging patterns (Keuling et al., 2009; Fettebert et al., 2017; Yang et al., 2024). Ecological plasticity enables wild boar to adjust their movements by selecting cost-effective food resources and suitable resting sites (Keuling et al., 2009; Morelle et al., 2016; Fettebert et al., 2017; Scandura et al., 2022). Heterogeneous landscapes are expected to provide abundant and

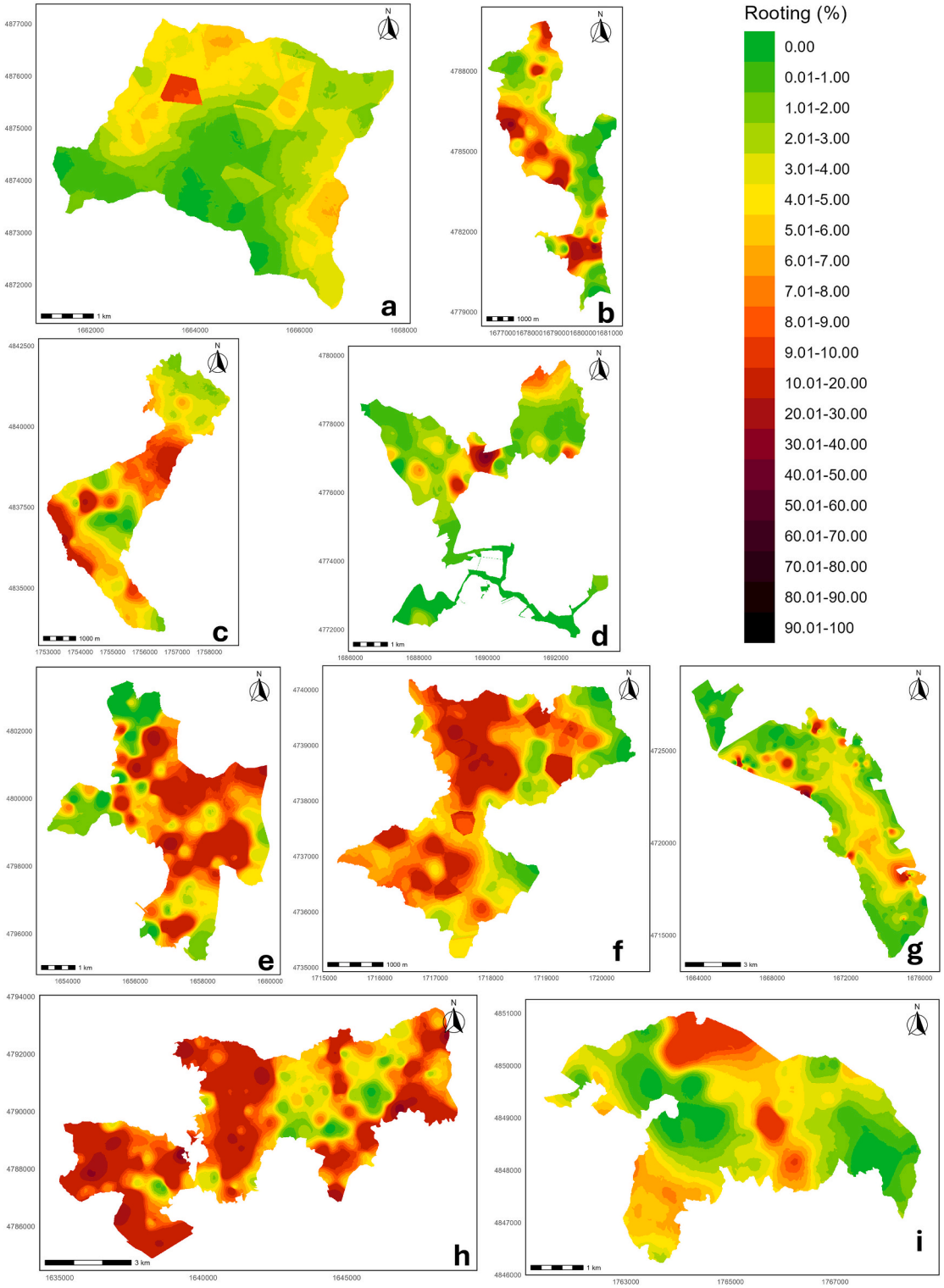

Fig. 4. Predictive maps of impact – Predictive maps of wild boar rooting obtained by averaging year-specific maps within each study area. Rooting estimates (%) are displayed in 1 % classes up to > 10 % for a more immediate interpretation. **Study areas:** NR – Nature Reserve; RP – Regional Park; a) Acquerino-Cantagallo NR; b) Alto Merse NR; c) Alpe della Luna NR; d) Basso Merse NR; e) Foresta di Berignone NR; f) Maremma RP; g) Monte Penna NR; h) Foresta di Monterufoli e Caselli NR; i) Sasso di Simone NR.

diverse food resources to wild animals, thereby influencing both spatial behaviour and foraging strategies. For example, the availability of heterogeneous resources at close range may reduce the need for animals to range over large areas (Ward and Saltz, 1994; Mangipanea et al. 2018). The role of greater landscape heterogeneity and presence of ecotones in reducing individual movements (e.g., Lucherini and Lovari, 1996; Saïd and Servanty, 2005; Lovari et al., 2013) and in promoting dietary diversity (Minder, 2011; Mangipanea et al., 2018) has been reported for several mammalian species. In wild boar, these patterns may reflect two complementary mechanisms: (1) movement constraints, whereby

increased local resource availability may reduce the need for extensive ranging and intensive rooting to meet nutritional demands; and (2) dietary shifts, as individuals may rely on a broader range of easily accessible food resources, thus reducing the reliance in underground items obtained through rooting (Massei et al., 1997; Schley and Roper, 2003; Scandura et al., 2022). These findings emphasize the importance of accounting for habitat heterogeneity when evaluating rooting dynamics, as local environmental conditions can significantly influence the extent of rooting behaviour. Additionally, seasonal patterns may alter the observed relationships. Previous research has reported different rooting intensity driven by seasonal shifts in food availability and soil conditions (e.g., Massei et al., 1997; Welander, 2000; Calosi et al., 2024). For instance, high mast availability in autumn may mitigate rooting activity, thereby reducing the impact on ground vegetation independently of the surrounding landscape mosaic. Conversely, increased precipitation during the same season may promote rooting by enhancing wild boar olfactory capabilities and making the soil easier to dig (Welander, 2000; Sandom et al., 2013a). Future research comparing seasonal patterns of rooting activity across climatic gradients could help disentangle the relative contributions of local and seasonal effects.

Contrary to prediction (2d), water availability appeared to constrain rooting activity weakly, as the confidence intervals of the estimates overlapped zero. Wild boar select habitats along water edges throughout the year for wallowing in mud and resting (Thurfjell et al., 2009). These habitats are particularly crucial in summer, as mud-bathing helps with thermoregulation (Bracke, 2011; Olczak et al., 2015; Ruf et al., 2023). The results suggest that wild boar may fulfil its foraging needs independently of water availability, possibly by accessing wet areas separately from feeding activities. Notably, the model excluding rock cover (i.e., the one used for producing the impact maps), supported increased rooting in woodland-dominated landscapes and approaching the closest persistent wet assets. These results suggest that rock cover interacts with other variables, potentially masking their effects, and support a role of woodland and water availability in shaping rooting behaviour in rock-free terrains.

4.3. Human activities and rooting pressure

Results supported that rooting activity was not influenced by human population density within the wild boar home range, and rooting activity increased closer to the nearest road or railway – albeit with a relatively weak effect size. This confirms prediction (3), suggesting that wild boar may take advantage of human-made features such as forest roads for cost-effective, easier, and faster movements between resting and foraging sites (Thurfjell et al., 2015). The study areas are all protected, with very low human population density (~0.1–3.8 inhabitants/km^2; data from Schiavina et al., 2023), while roads predominantly follow forest tracks, and mostly have restricted vehicle access. As a result, vehicle traffic is minimal, and roads could be perceived as safe corridors that facilitate movement, particularly during nighttime when people are absent (Keuling et al., 2009; Thurfjell et al., 2015; Podgórski et al., 2013). Previous studies showed that human activities such as intensive agricultural and recreational practices (e.g., hiking or hunting) can alter wild boar behaviour and habitat use (Podgórski et al., 2013; Brivio et al., 2017; Brogi et al., 2020). However, wild boar behavioural flexibility could allow this suid to shift its temporal activity patterns in response to human pressures (Keuling et al., 2009; Podgórski et al., 2013; Gordigiani et al., 2022), for example by foraging closely to roads during the night. Future research should investigate wild boar activity patterns in relation to proximity to human settlements to shed light on this possibility.

4.4. Assessing and mapping rooting pressure on habitats

Results suggest that the distribution and intensity of rooting activity were context-dependent and influenced by multiple factors across protected areas. Rooting activity should not be interpreted as a stand-alone negative indicator of habitat alteration. Moderate levels of rooting may generate positive effects such as soil aeration, control of the spread of pioneer species, and maintenance of open habitats (Groot Bruinderink and Hazebroek, 1996; Barrios-Garcia and Ballari, 2012; Barrios-Garcia et al., 2023). Rather, negative impacts may arise when rooting is both intense and frequent, particularly in combination with specific environmental conditions (Burrascano et al., 2015). In the short term, it may cause a decline in focal plant species of the impacted habitat, facilitating the establishment of ruderal or nitrophilous species. When the alteration persists over time, it could lead to shifts in plant species composition (Burrascano et al., 2015), to the extinction of habitat-specific focal species (Sandom et al., 2013b; Burrascano et al., 2015), ultimately resulting in a reduction of the habitat surface (e.g., Bratton, 1974; Barrios-Garcia and Ballari, 2012). A reduction or alteration of 1 % of surface in rare or declining habitats has been considered as a threshold for identifying significant pressures for conservation, deserving appropriate mitigation measures (Case C-258/11, European Union Court of Justice, 2013). For example, repeated rooting by high wild boar densities may threaten habitats such as some grassland types, particularly during the growing season, potentially leading to a significant reduction in ground vegetation cover (Calosi et al., 2024, for EU priority grasslands, codes '6210′ and '6220′). If these changes affect characteristic species, the local conservation status of that habitat might be at risk, potentially leading to its extinction when already rare or fragmented. Suggestively, preliminary surveys conducted in priority-protected grasslands of one of our study areas (MPNR), showed that vegetation cover was much lower in rooted compared to unrooted patches, and species composition in rooted patches shifted toward ruderal, low-quality *taxa*, not typical of the same grassland habitat (our unpublished data). In the long-term, such a shift in plant species composition may trigger cascading effects on animal communities, particularly those species that depend on specific host plants for reproduction and survival (e.g., insects; Howe et al., 1981; Singer et al., 1984; Scandurra et al., 2016). In this context, monitoring vegetation shifts in response to rooting is crucial to better understand these potential effects and inform conservation strategies.

To the best of our knowledge, this is the first study producing spatially-explicit maps of wild boar rooting impact on natural and seminatural habitats in protected areas (see e.g. Yang et al., 2024, for risk maps of wild boar crop damage). This approach can be calibrated over other protected areas with comparable land use composition and climatic conditions, in combination with local wild boar population density estimates, to identify the most endangered sites within areas. Maps can be generated using widely available land cover data (e.g. CLC; Copernicus, 2023), digital elevation models, and by exploiting the model proposed in this study at least for ecologically comparable areas (Table S8, Supplementary Material) or by adapting it to local environmental conditions (i.e., integrating relevant site-specific predictors). Our approach could be further improved by validating the maps through independent rooting surveys, which were not available in our study. Such limitation could be addressed in future research by combining complementary methodologies, such as drone-based aerial surveys or systematic ground measurements, enhancing the accuracy of our mapping approach.

Maps would provide conservationists, practitioners, and stakeholders with a tool to identify spatial variations in rooting pressure, helping prioritize conservation efforts in sites that host threatened plant or animal species or that are particularly sensitive to damage (Yang et al., 2024). In turn, evidence-based management and conservation strategies would be supported to mitigating wild boar negative impacts on ecosystems. Nonetheless, we recommend caution in generalising the transferability of our specific findings, which were obtained in protected areas, i.e., areas sparsely populated by humans, encompassing a mosaic of natural and semi-natural habitats dominated by woodland, within the Mediterranean bioregion along an elevation-dependent climate

gradient. Consistency with other ecological contexts, such as human-dominated areas and different bioregions or seasons, remains to be evaluated.

4.5. Conclusions and implications

Our study provides insights into the environmental drivers of wild boar rooting during late spring and early summer in Mediterranean protected areas. First, our findings support that rooting at both local and broader spatial scales can be used as an effective indicator of changes in wild boar density. This result suggests that estimates of rooting impact can serve as a reliable and cost-effective proxy for evaluating the within-area, between-years variation in wild boar densities, if standardised and conducted in the same season. This finding also supports management strategies aimed at controlling population densities to mitigate wild boar impacts on habitats. Yet, the observed density–impact relationship was conditional on the two spatial scales of rooting evaluated (Table 2), calling for future investigations conducted along a scale gradient. Second, results emphasise the role of landscape diversity as a potential buffer against wild boar impact through rooting. Consequently, strategies that promote or restore ecosystem diversity could serve as an indirect approach to reducing wild boar pressure on habitats. Third, we provide a framework to produce predictive maps potentially helpful to identify the most at-risk locations in natural/semi-natural habitats. In turn, targeted management actions could be planned. These may involve site-specific control of wild boar density, preventive measures based on small fences to prevent wild boar rooting around focal plants or plant groups where feasible, or through specific dissuasive actions in sites and periods of higher threat to particular habitats.

Fundings

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CRediT authorship contribution statement

Martina Calosi: Writing – review & editing, Writing – original draft, Investigation, Data curation, Formal analysis, Conceptualization. **Niccolò Fattorini:** Writing – review & editing, Formal analysis, Data curation, Conceptualization, Investigation. **Rosa Maria Di Biase:** Writing – review & editing, Software, Formal analysis. **Agnese Marcelli:** Writing – review & editing, Software, Formal analysis. **Caterina Pisani:** Software, Writing – review & editing, Formal analysis. **Chiara Gabbrielli:** Investigation. **Sonia Aleotti:** Investigation. **Mattia Galdangelo:** Investigation. **Francesco Ferretti:** Supervision, Data curation, Writing – review & editing, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.113806.

Data availability

Data are available from the authors upon reasonable request

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