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RESEARCH

Factors influencing wild boar rooting in a forest environment

Jakub Drimaj[1] · Jakub Špoula[1,2] · Jiří Kamler[1] · Ondřej Mikulka[1] · Marie Balková[3] · Radim Plhal[1] · Miloslav Homolka[1,4]

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Abstract

The wild boar population has been steadily increasing worldwide over the last few decades, causing increasing damage to forests and crops. In the south-eastern Czech Republic in 2022 and 2023, 3,899 rooted areas recorded in sample lines were assessed for a range of properties and analyzed. The rooted areas were assessed for their size, the proportion of rooting in organic and mineral layers, the depth of rooting in organic and mineral layers, and the proportion of bare soil, grasses and dicots. Our objectives were to describe which environmental factors affect wild boar rooting in ecologically valuable and protected Pannonian thermophilic sandy oak forests which are extremely threatened by desiccation and disturbance. These forests support large numbers of wild boar throughout the year due to their rich food supply. 10.93% of the forest area was disturbed by wild boars in the first year and 7.95% in the second year. We found that tree species, stand age, stocking density and height of the main tree species all had a significant effect on the size of the rooted area. The distance from streams and feeding sites had a significant effect on rooted area size, with larger rooted areas closer to streams and feeding sites. Vegetation cover (grasses and dicots) was also positively correlated with the size of rooted areas. Our results show that rooting depth in either the organic or mineral horizons is not affected by total rooted area.

Keywords Soil disturbance · *Sus scrofa* · Rooting distribution · Habitat selection · Anthropogenic impact

Introduction

The wild boar (*Sus scrofa*) is a mammal native to Eurasia and is now widely distributed on all continents except Antarctica (Lewis et al. 2017). Populations of wild boar have significantly increased worldwide in recent decades (Massei et al. 2015tő et al. 2020; Lee and Park 2022). Outside Eurasia wild boar is often considered an invasive pest species. In Europe, wild boar is primarily discussed in a negative light, as an agricultural pest, a vector for the transmission of various diseases affecting humans and livestock (Barrios-Garcia and Ballari 2012), and the cause of traffic accidents. Furthermore, in areas of Central Europe with high densities of wild boar, the previously overlooked impacts of their feeding behaviour on forest regeneration and the diversity and stability of ecosystems are also gaining importance (e.g., Kamler et al. 2016).

Wild boar significantly limit regeneration of forest stands by consuming large quantities of tree seeds and removing seedlings, both newly reforested and young trees from natural regeneration (Skoták et al. 2021). They also cause damage to tree trunks by rubbing. However, the most disturbing behaviour of wild boar is rooting and digging (Mitchell et al. 2008; Cuevas et al. 2012). Rooting disturbs the grass sod, which hinders the attachment and germination of tree seeds and can greatly impede the natural regeneration of desirable woody species such as oak (Kamler et al. 2016). Additionally, it can alter soil characteristics by increasing nutrient cycling, decomposition rates, and nutrient loss through leaching and by reducing hill slope hydrological connectivity and sediment transport (Bueno et al. 2013; Hancock et al. 2016; Pitta-Osses et al. 2022). Repeated rooting enhances

✉ Jakub Drimaj
jakub.drimaj@mendelu.cz

1 Faculty of Forestry and Wood Technology, Department of Forest Protection and Wildlife Management, Mendel University in Brno, Zemědělská 1, Brno 613 00, Czech Republic

2 Forestry & Game Management Research Institute, Strnady 136, Jíloviště 252 02, Czech Republic

3 Faculty of Forestry and Wood Technology, Department of Geology and Soil Science, Mendel University in Brno, Zemědělská 1, Brno 613 00, Czech Republic

4 Institute of Vertebrate Biology, Czech Academy of Sciences, Květná 8, Brno 603 65, Czech Republic

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all these effects. It can also damage plant assembles (Brunet et al. 2016), and affect vertebrates and invertebrates through predation (Jolley et al. 2010; Mori et al. 2020). The extent of damage depends on a wide array of factors including wild boar population density, population structure, food availability in forests, the development of edges between forests and cultivated areas, distance from human settlements and the stage of crop maturity (Frackowiak et al. 2013; Boyce et al. 2020; Cappa et al. 2021; Calosi et al. 2024). In addition, in areas with supplementary feeding, factors such as the location, nutritional composition and management of artificial feeding sites may also play a role, potentially influencing rooting behavior or acting as diversionary feeding points (Oja et al. 2015; Engvall 2022).

The intensity of wild boar rooting activity is primarily contingent on population density, the availability and quality of food resources and by the extent of disturbances (hunting, public roads, hiking trails, etc. (e.g., Sütő et al. 2020; Drimaj et al. 2021; Miettinen et al. 2023). The distribution of wild boar in the forest environment outside the growing season is not uniform (Fonseca 2008), but is influenced by a number of variables that are also reflected in the distribution of rooting activity. Wild boar spends most of the day in young forest stands where they have plenty of cover and quiet, well away from human disturbance (Orłowska and Nasiadka 2022). At night, however, it emerges from the thickets and its activity is dominated by foraging (Miettinen et al. 2023). Artificial feeding sites are commonly used in the study area and provide a significant supplement to natural food resources. These sites are typically located near hunting facilities, where hunters wait for wild boar at night using night vision and thermal imaging equipment. However, hunters do not wait there all the time and wild boar visit the feeding sites intensively even at the risk of being killed (Vajas et al. 2020). Moreover, wild boar can distinguish between hunting grounds and places with intense and extensive hunting pressure (Miettinen et al. 2023). Less attractive, but still attractive, are water sources that provide water in winter, allow wild boar to bathe, and offer them water-dependent food (Calosi et al. 2024). In terms of forest structure, wild boar prefer mature stands of mast trees that offer plant and animal food resources. How this distribution of occurrence translates into the distribution of the rooting has not yet been determined.

Wild boar prefers energy-rich food with low fiber content. In forests, tree seeds, such as acorns and beech nuts, are the main natural source of food for wild boar. Their availability depends on whether it is a seed year for these fruit-bearing trees (Sütő et al. 2020). As a result of fallout, the seeds are available on the ground under the tree canopy, concentrated in terrain irregularities and at the base of tree trunks, but also at a range of depths below the surface where they have been buried by animals [e.g. rodents (Focardi et al. 2000; Amori et al. 2015), jays (Pérez-Camacho et al. 2023)]. Fungal fruiting bodies also develop underground, and a wide range of invertebrates prefer the damp conditions and mild, constant temperatures underground (Labadessa and Ancillotto 2023). All these are attractive food sources for wild boar, leading to their disturbance of topsoil, including vegetation, and thereby habitat modification (Massei and Genov 2004; Wirthner et al. 2012).

From an ecosystem perspective, rooting is a disturbance to the ecosystem represented by a change in the availability of resources or the physical environment (as discussed by Pickett et al. 1985). Thus, by rooting, wild boar act as agents of natural disturbance, creating microhabitats at early successional stages with considerable potential to influence forest regeneration (Kamler et al. 2016), vegetation dynamics (Cuevas et al. 2012; Barrios-Garcia and Ballari 2012), soil biota (Mohr et al. 2005), and soil composition and sedimentation processes (Pitta-Osses et al. 2022). The disturbed vegetation cover and the exposed mineral soil layer create favorable conditions for the germination of woody species and competitively weaker plants, potentially enhancing plant diversity and supporting early successional processes (Barrios-Garcia and Ballari 2012; Sandom et al. 2013a, b). In some cases, such habitat modification presents ideal conditions for the spread of unwanted invasive plant species, threatening the natural ecosystem (Brunet et al. 2016; Barrios-Garcia et al. 2022). From the point of view of forest regeneration, rooting has generally positive effects on the species diversity and dynamics of native forest communities (Sandom et al. 2013a, b), but also negative (e.g. Cuevas et al. 2012). From the point of view of herbaceous communities, rooting often has deleterious effects. While the ecological impacts of rooting have been discussed extensively, there remains limited understanding of the spatial patterns and environmental drivers of rooting behavior. In particular, comprehensive studies focusing on rooting activity in forest stands with varying characteristics, distances from streams and anthropogenic features under conditions of Pannonian thermophilic sand oak forests are still lacking. These forests are particularly vulnerable to drought and to various forms of disturbance, including rooting, which may pose a risk to unique localities with numerous protected or endangered species (e.g. Kasper 2022). Although this study does not directly assess the ecological impact of rooting on these species or habitats, the sensitivity of the area - protected as both a Natura 2000 site and a national nature reserve (Roleček et al. 2017) - highlights the importance of understanding rooting patterns in such ecosystems.

The aim of this research was to investigate the share of total rooted area by wild boar in relation to: (i) forest stand characteristics (age, tree species, stocking density and height); (ii) distance from streams, roads and feeding sites; and (iii) vegetation cover and depth of rooting. Defining the key factors influencing the rooting activity of wild boar is crucial to ensure the protection of the natural regeneration of forest trees (through the consumption of seeds and fruits), as well as ecologically valuable habitats (threatened by water or wind erosion, endangered plant and animal populations). This study may thus become a pilot study on which to base management measures to guide the occurrence of wild boar in the forest environment, taking into account the potential risks associated with its rooting activity. Ultimately, it will be possible to classify the forest environment in terms of the intensity of the threat posed by its disturbance activities.

Materials and methods

Study area

The study area was located in the south-eastern Czech Republic, in close proximity to the town of Hodonín, and covered an area of 976 ha (Figs. 1 and 48.8727 N, 17.0890E). The altitude ranged from 164 to 210 m a.s.l. The bedrock was composed of nutrient-poor Pleistocene eolian sands overlying Tertiary impermeable nutrient-rich sediments (Roleček et al. 2017). Low and medium organic matter and nutrient supplied soils without groundwater influence predominate (>50% of the area). Sites with impervious subsoil and periodic precipitation influence occur on 33% of the area. The average density of streams was 855 m/km^2.

The area was predominantly covered by deciduous forest with an average age of 67 years, but it also included overgrown and mostly oak coppices (dominated by *Quercus robur*). The principal part of the forest complex consisted of economic forest stands with oak (*Quercus* sp.) (20%), Scot's pine (*Pinus sylvestris*) (17%), linden (*Tilia cordata*) (14%), birch (*Betula pendula*) (13%) and alder tree (*Alnus glutinosa*) (10%). Marginally represented (26%) were black locust (*Robinia pseudoacacia*), hornbeam (*Carpinus betulus*) and larch (*Larix decidua*). In young and middle-aged forest stands there was usually a very sparse grass-herb vegetation, whose species diversity and biomass increased in mature forest stands due to thinning. The study site, which includes a unique area of Pannonian thermophilic sand oak forests, fell within a protected area as a Site of Community Importance (CZ0624070 – Hodonínská Dúbrava) and as a National Nature Monument (NPP Hodonínská Dúbrava).

The study area was occupied by wild boar, roe deer (*Capreolus capreolus*) and brown hare (*Lepus europaeus*). The most important species was wild boar. Its population density in the study area, assessed via hunting evidence (via method: drive counts, Borkowski et al. 2011), was 60 ind/km^2 in 2022 and 35 ind/km^2 in 2023. The wild boar population was relatively stable throughout the year within the area and its migration was quite sporadic. The abundance of wild boar was influenced by reproduction, hunting, and occasionally road mortality. The wild boar's diet primarily consisted of natural food sources, including fallen seeds and fruit from trees, as well as food obtained by rooting. Supplementary food was supplied by hunters to feeding sites (2 sites/km^2). Feeding sites can be defined as places where hunters present attractive food items in order to attract wild boar to hunt them. Supplementary feeding consisted of corn, cereals and legumes (10–15 kg/day per feeding site), and was regularly conducted during the non-vegetation period, from October to April. Within 40 m of these feeding sites, hunting facilities have been placed where hunters wait for animals (at night). These facilities were operated in the same way within the study area and the feeding was presented in the same way in terms of quantity and quality. Hunting of wild boar was allowed throughout the entire year, and hunting pressure remained relatively uniform across seasons. The average density of roads in the study area was 3.7 km/km^2 for tracks and 1.25 km/km^2 for tourist and bike paths.

Data collection

Monitoring of rooting was carried out in 2022 and 2023 in March/April. The study area was overlaid with 51 randomly generated sampling lines in 75 m apart. The lines were generated using QGIS Desktop 3.16.10 in a north-south direction. The total length of the sample lines was 129.8 km and the average length of a line was 2.545 km (SD = 0.99 km). The length of each line varied depending on the boundary line (see Fig. 1). A GPX layer containing predefined sampling transects was uploaded to Garmin Oregon 600 GPS units. Observers followed these transects on food and visually inspected a 6 m wide strip (3 m on each side of the transect line) for signs of wild boar rooting. Upon detection of rooting, a 6 × 6 m (36 m^2) square study plot was established. The plot centre was located 3 m from the start of the rooting zone in the direction of the transect and georeferenced using the GPS unit. Within each plot, the following parameters were recorded:

- rooted area (m²), visually estimated as the surface area disturbed by wild boars;
- rooting depth (cm) in the organic and mineral soil layers, measured as the mean of ten randomly selected points per layer using a ruler and a measuring rod. The organic (topsoil) layer was defined as the biologically active upper soil horizon rich in organic matter and fine roots, typically corresponding to the litter layer or upper part of horizon A. The mineral soil layer referred to the underlying mineral substrate with low organic content;

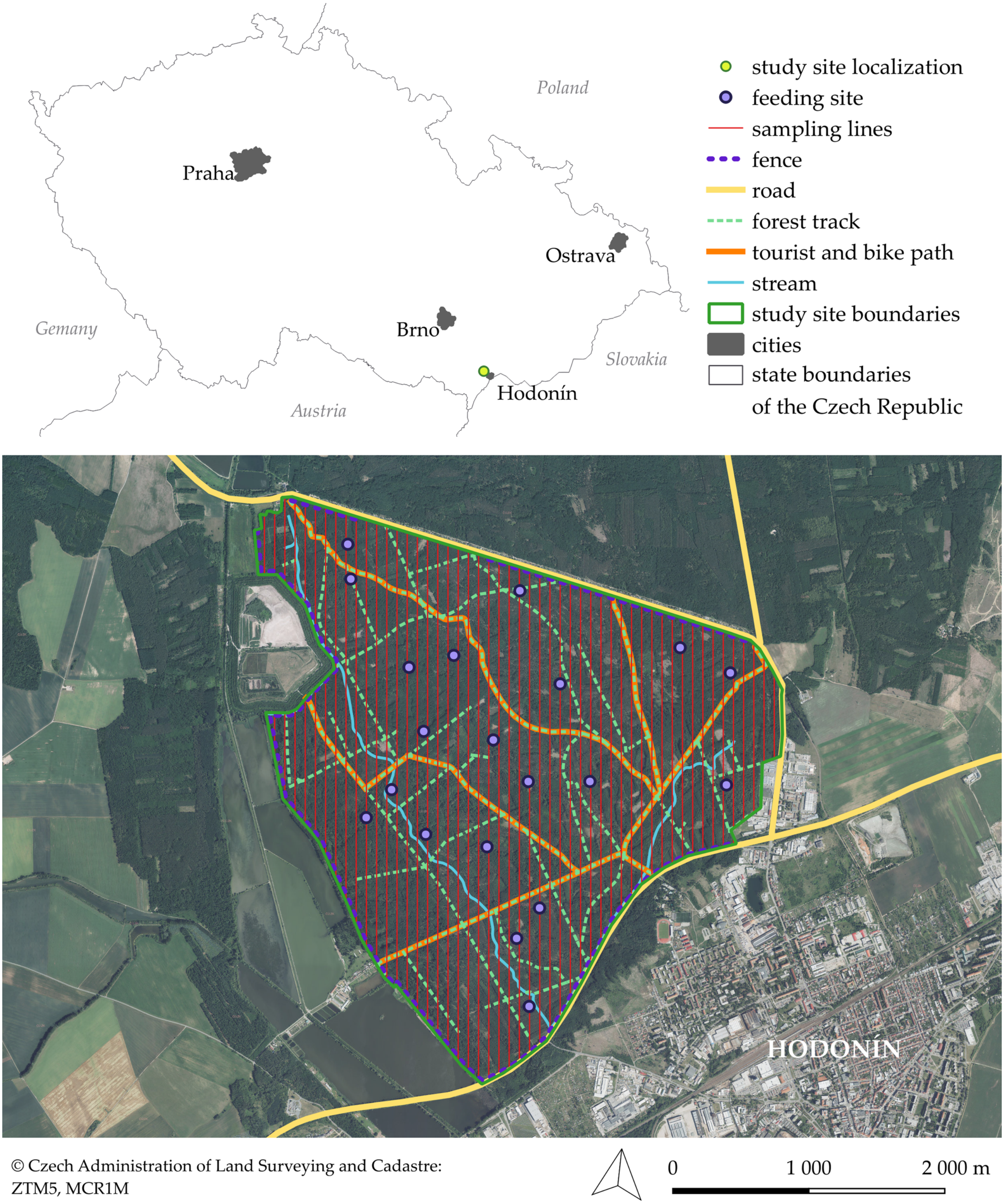

Fig. 1 Location of the study area in the Czech Republic with sampling lines. The centre of the area is located here: 48.8727 N, 17.0890E

- proportion of rooted area within the organic and mineral layers;
- vegetation cover (%; i.e. percentage cover of grasses, dicots plants and bare soil) was visually estimated by trained observers at the end of winter, when most herbaceous plants were dormant. Despite the absence of actively growing vegetation, dry stems, basal rosettes, and other structural remnants of the previous year's vegetation were still clearly visible and identifiable. Based on these remains, observers visually estimated the percentage cover of each vegetation component using 5% cover classes (0–100%) based on vertical projection across the entire 6 × 6 m plot. Although cover estimates made outside the peak growing season may be less precise, similar approaches have been shown to provide sufficiently robust data for evaluating disturbance effects on vegetation structure (Milchunas and Lauenroth 1993; Kent 2012).

Only fresh rooting from the non-vegetation period (autumn and winter) was recorded, identified in the field based on visual indicators such as loose soil, sharply defined edges, and absence of vegetation regrowth.

Data analysis – GIS

After data collection in the field, waypoints were downloaded from all GPS devices and merged into a single shapefile layer. Based on actual GPS tracks, corrected transect lines were generated to minimize spatial inaccuracy caused by walking in uneven terrain. The exact lengths of these corrected lines (after deducting fenced areas inaccessible to large ungulates and correcting for the actual sample line walked) were then calculated (124.118 km in 2022 and 123.626 km in 2023). Along these lines, a new set of spatially distributed points was generated at regular 6 m intervals to represent non-rooted sampling locations between rooted areas. These "additional points" served as reference points for estimating the total proportion of rooted versus unrooted area along the transects. In total, 18,495 and 19,038 such points were generated in 2022 and 2023, respectively.

Terrain data about rooting and its characteristics as well as the information about vegetation cover were added to the layer with rooted areas. Subsequently, metadata were added to the attribute tables of both point layers (rooted areas and additional points) to fully describe the natural and anthropogenic characteristics of the surroundings. These characteristics were:

a) forest stand data: stand code, the age, stocking density, tree species composition, the main species, heights and share tree species from the Forest Management Plan,
b) distances to linears and points: the shortest distances from the points to the nearest forest track, road, bike path, stream (linear) and feeding sites (point) (ZABAGED®: Planimetric Components) were calculated (using module GRASS in QGIS).

Data analysis - Statistics

To evaluate the effects of stand age, stocking density, and height of main tree species on rooting of wild boar, a generalized linear mixed model (GLMM) with log link function and Gamma distribution was made using the glmer function from package *lme4* (Bates et al. 2015). The total rooted area was treated as a continuous response variable and fixed factors (stand age, stocking density and height of the main tree species) were treated as continuous variables. The conifer/deciduous main tree species of the stand was treated as a categorical variable.

A generalized linear model (GLM) with Poisson distribution was made using the function glm from the *stats* package to assess the effects of different tree species on rooting. The total rooted area was treated as a continuous response variable and tree species were treated as categorical factors. A pairwise post hoc test using functions aov and TukeyHSD from the package *stats* were used to evaluate differences.

To evaluate the effects of distances from anthropogenic features and streams on rooting, a GLMM with log link function and Gamma distribution was made using the glmer function in package *lme4*. The total rooted area was treated as a continuous response variable and the distances from forest tracks, roads, bike paths, feeding sites, and streams were treated as continuous fixed effects.

To evaluate the effects of grasses and dicots on rooting, a GLMM with log link function and Gamma distribution was made using the glmer function from package *lme4*. The total rooted area was treated as a continuous response variable and the share of grasses, dicots and bare soil were treated as continuous fixed effects.

To evaluate the effects of depths of rooting in the organic layer and mineral topsoil, the function glmmTMB with nbinom2 distribution and a log link function from package *glmmTMB* was used (Brooks et al. 2017). Depths of rooting in the organic layer and mineral topsoil were used as continuous response variables. Total rooted area, rooted area in organic layer, and rooted area in mineral topsoil were treated as continuous fixed factors.

In every GLMM, the ID of the rooted area sample was treated as a random effect. The overdispersion of the models with Poisson distribution was tested using the function dispersiontest from the *AER* package (Kleiber and Zeileis 2008) and overdispersion of models with a nbinom2 distribution was tested via the check_overdispersion function from package *performance* (Lüdecke et al. 2021). The overdispersion of models with Gamma distribution was not tested. The marginal and conditional R^2 were computed using the function r2_nakagawa from package *performance* (Nakagawa et al. 2017) and function r.squaredGLMM from package *MuMIn* (Nakagawa and Schielzeth 2013). Multicollinearity between fixed factors was assessed using the variance inflation factor function (VIF) from the package *regclass* to ensure model accuracy. The GLMMs were tested for overfitting of the data using the *caret* package (Kuhn 2007). The goodness of fit of models was assessed using the null model through the function lr_test from package *lmtest* (Zeileis and Hothorn 2002). All analyses were performed at the confidence interval of $\alpha = 0.05$ and conducted in RStudio (version 2023.12.0+369).

Results

Observers checked a total area of 74.5 ha and 74.2 ha in 2022 and 2023, respectively. Within this area 2,261 study plots (81,396 m^2) were marked out in 2022 and 1,638 (58,968 m^2) in 2023. The average size of a rooted area was 12.3 ± 10 m^2. Of the total study area assessed, 10.93% and 7.95% of the soil surface was disturbed by wild boar rooting in 2022 and 2023, respectively.

Forest stand characteristics

The rooted areas were recorded at various forest stands containing 14 different tree species. The GLMM ($R^2 = 0.22$, $p < 0.001$) indicated that all fixed effects had a significant effect on rooted area. The extent of rooted area increased with the height of the main tree species, but it decreased with the stand age and stocking density of the main tree species (Table 1). The rooted area was also larger in coniferous stands compared to deciduous-dominated stands.

The GLM ($\chi^2(12) = 555.55$, $p = 0.001$, $R^2 = 0.13$) confirmed the results of the previous GLMM that rooted area occurred in areas regardless of whether the stand was deciduous or coniferous, although 73.2% of the rooted areas occurred in deciduous dominated forest stands. More than half of the rooted areas (55.7%) occurred in *Quercus* dominated stands. The GLM indicates that coniferous tree species had positive effects on the size of rooted areas and the effects of deciduous species were diverse (Table 2). The GLM confirmed significant differences in rooted area among dominant tree species. Rooted area was more frequent in stands dominated by some deciduous trees (*Acer*, *Tilia*, *Alnus*, *Populus*) and certain conifers (*Larix*, *Picea*), while it was lower in stands with *Fraxinus*, *Juglans* and *Betula*. No significant effect was found for *Quercus*, *Prunus* or *Pseudotsuga*. Detailed estimates and statistical values are provided in Table 2. Significant differences in rooted area between tree species were found (Fig. 2).

Table 1 Results of the GLMM model describing the relationship between the size of rooted area and fixed effect factors

Fixed Effects	Estimate	Std. Error	t	*p*
Intercept	2.345	0.080	29.181	<0.001
Stand age	−0.002	0.001	−3.674	<0.001
Primarily conifer or deciduous forest	0.150	0.037	4.078	0.01
Stocking density of main tree species	−0.002	0.001	−3.039	<0.001
Height of main tree species	0.015	0.003	4.294	<0.001

Distance from streams, paths and feeding sites

The average distance (±SD) of rooted areas from forest tracks was 67.9 ± 69.5 m, from roads 786.9 ± 535.8 m, from bike paths 240.4 ± 163.8 m, from feeding site 318.9 ± 161.5 m and from streams 448.2 ± 358.3 m. The size of rooted areas was significantly affected by the distance from streams and feeding sites. Specifically, rooted area size decreased with increasing distance from streams (GLMM; $R^2 = 0.223$, $p < 0.001$; Table 3; Fig. 3) and also with increasing distance from feeding sites ($p = 0.008$). In contrast, distance from forest tracks, roads, and bike paths had no significant effect on rooted area (Table 3). The strong negative effect of stream distance is illustrated by the dense concentration of larger rooted area near watercourses and a gradual decline in rooted area beyond 1000 m from the stream (Fig. 3).

Table 2 Results of the GLM describing the relationship between size of rooted area and tree species

Effects	Coniferous/deciduous	Estimate	Std. Error	z	*p*
Intercept		2.47	0.1	273.27	**<0.001**
Acer	deciduous	0.68	0.04	18.24	**<0.001**
Alnus	deciduous	0.14	0.02	8.04	**<0.001**
Betula	deciduous	−0.1	0.03	−3.93	**<0.001**
Fraxinus	deciduous	−1.28	0.28	−4.35	**<0.001**
Juglans	deciduous	−0.62	0.14	−4.43	**<0.001**
Larix	coniferous	0.57	0.15	3.69	**<0.001**
Picea	coniferous	0.37	0.11	3.42	**<0.001**
Populus	deciduous	0.2	0.09	2.24	**0.025**
Prunus	deciduous	0.3	0.25	1.19	0.233
Pseudotsuga	coniferous	−0.22	0.023	−0.97	0.331
Quercus	deciduous	0.01	0.1	1.29	0.198
Tilia	deciduous	0.25	0.02	11.02	**<0.001**

Category Pinus was omitted from results because it was used as the reference level in the aov test.

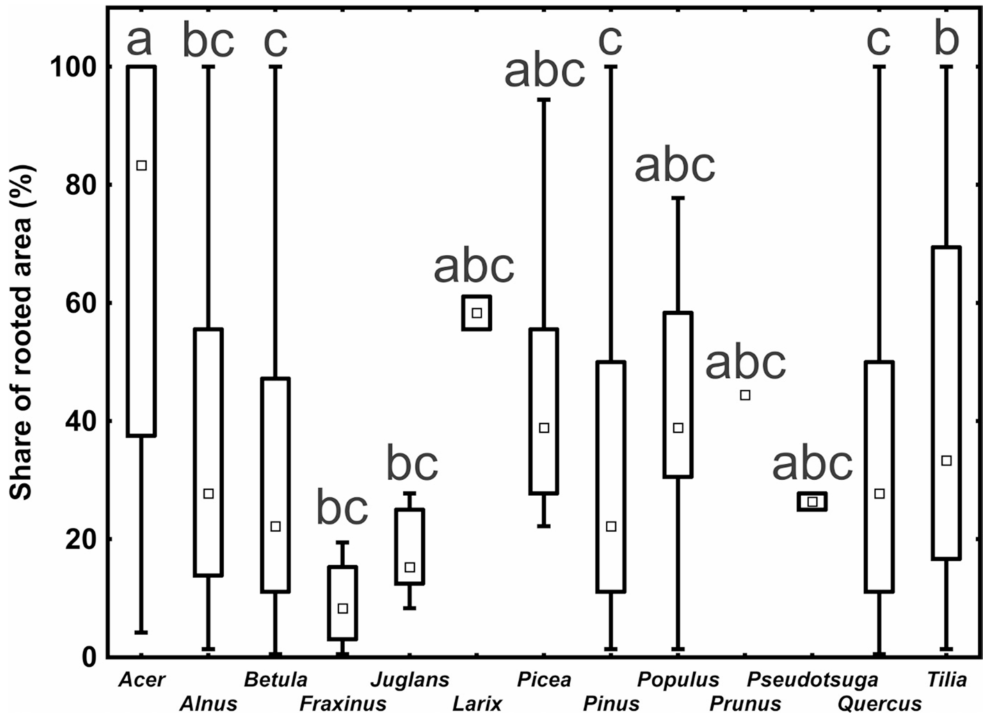

Fig. 2 Highly significant differences ($p < 0.001$) in rooted area among different tree species are labelled with letters. Categories labelled with the same letter do not differ significantly. Squares indicate medians, rectangles interquartile range, whiskers minimum and maximum values

Table 3 Results of the GLMM describing the relationship between size of rooted area and the effects of distances

Fixed Effects	Estimate	Std. Error	t	*p*
Intercept	2.59	0.0010	2046.9	< 0.001
Distance from forest track	0.0003	0.0002	1.25	0.212
Distance from road	0.0001	0.0001	1.63	0.103
Distance from bike path	0.0001	0.0001	0.26	0.791
Distance from feeding site	−0.0001	0.0001	−2.65	0.008
Distance from stream	−0.0004	0.0001	−13.45	< 0.001

Vegetation cover and depth of rooting in soil

The average share of bare soil was 55.1 ± 36.32, grasses 37.4 ± 35.45 and dicots 6.59 ± 11.24%. A significant relationship between the size of rooted areas and all the fixed effects was found by the GLMM ($R^2 = 0.206$, $p < 0.001$). All the effects had a positive effect on size of rooted area. The vegetation cover of the soil did not influence rooting, as the

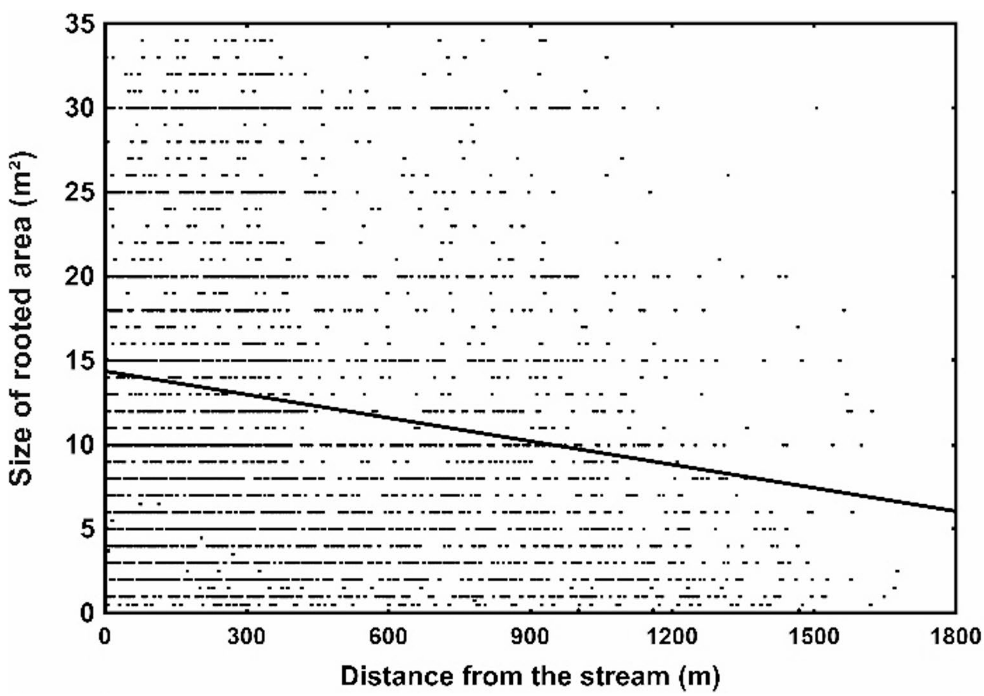

Fig. 3 Scatter plot showing the relationship between size of rooted area and distance from streams. The solid line is the regression line

proportion between rooted bare and grassed soil was balanced (Table 4).

The average rooting depth in the organic layer was 2.96 ± 3.83 cm and that in mineral topsoil 3.92 ± 5.88 cm. Both GLMMs indicated that the depths of rooting in the organic layer and mineral topsoil are not positively influenced by the total size of the rooted area, but by the share of areas of rooted into organic layer and mineral topsoil. Unlike the rooting depth in mineral topsoil, the rooting depth in organic layer was positively influenced ($R^2 = 0.467$, $p < 0.001$) by the share of rooted area in organic layer (Table 5), but the depth of rooting in mineral topsoil was positively correlated (Table 6) with both the proportion of rooted area in organic layer and mineral topsoil ($R^2 = 0.17$, $p < 0.001$).

Discussion

In the study area, both the wild boar population and the total rooted area were smaller in the second year of the study (2023) compared to the first year (2022). However, when accounting for the population size, the extant of disturbance, and the size of the area of interest, the average wild boar caused a complete disturbance of 1.78 hectares of land (2022) and 2.21 hectares in 2023. Although we were not able to analyse the effect of population density quantitatively due to the lack of reliable and spatially detailed data, we acknowledge that it may have contributed to the observed interannual variation. It is likely, however, that the primary driver of the increased disturbance per individual in 2023 was the sharp decline in acorn availability, which reduced an important food source during the autumn and winter (Kamler et al. 2016; Mikulka et al. 2018). The decrease in the number of acorns in 2023 was because 2022 was the mast year of *Quercus*. The absence of this abundant energy-rich foodstuff causes feral hogs to orientate themselves towards less nutritious food sources in the form of energy-poor vegetation, grain residues in hunting blinds, or food in the soil (Zeman et al. 2018). The soil in the study area, in particular, offers locally large quantities of tubers, bulbs and succulent roots of plants that are preparing for the growing season in the pre-spring period and can be decimated by wild boar (Genov et al. 2017).

Furthermore, the mild, snow- and frost-poor winters of recent decades may have resulted in the incomplete suppression of zooedaphone activity and fungal communities in the topsoil (Tauber and Tauber 1981), which wild boar preferentially seek out (Carpio et al. 2022). In addition to these food sources, wild boar also concentrate on small rodent food reserves, which are often associated with the bases of logs and decaying stumps (Focardi et al. 2000). This was confirmed during the field survey. The reduction in the variety of food items presented at feeding sites may also have contributed to the increase in rooting activity in the second year (Zeman et al. 2018). This situation compelled the wild boar to rely more on natural, nutritionally poorer food sources.

Table 4 Results of a GLMM describing the relationship between size of rooted area and the effects of vegetation

Fixed Effects	Estimate	Std. Error	t	*p*
Intercept	1.6855	0.1583	10.648	< 0.001
Bare soil	0.0084	0.0016	5.337	< 0.001
Share of grasses	0.004	0.0016	2.532	0.0113
Share of dicots	0.0135	0.0020	6.688	< 0.001

Table 5 Results of the GLMM describing the relationship between depth of rooting in organic layer and share of rooted area

Fixed Effects	Estimate	Std. Error	z	*p*
Intercept	0.4047	0.0447	9.059	< 0.001
Total rooted area	−0.0258	0.0036	−7.135	< 0.001
Rooted area in organic layer	0.1824	0.0074	24.807	< 0.001
Rooted area in mineral topsoil	−0.0019	0.0045	−0.412	0.68

Table 6 Results of the GLMM describing the relationship between depth of rooting in mineral topsoil and share of rooted area

Fixed Effects	Estimate	Std. Error	z	*p*
Intercept	1.1882	1.1882	23.46	< 0.001
Total rooted area	−0.0518	0.0047	−11.09	< 0.001
Rooted area in organic layer	0.1116	0.0087	12.82	< 0.001
Rooted area in mineral topsoil	0.0760	0.0067	11.29	< 0.001

Forest stand characteristics

It has been established that wild boar play a significant role in the disruption of forest soil surfaces (Barrios-Garcia and Ballari 2012; Genov et al. 2017). Although the study area represents a unique locality where wild boar are present throughout the year, the association of wild boar with the forest environment during the non-growing season is typical of all areas where wild boar occur (Orłowska and Nasiadka 2022). The present study did not consider soil disturbance that occurred during the growing season; instead, it focused on the extend of rooting activity during autumn and winter. The damage to the soil surface was not uniform, it was determined by the structure of the surrounding forest environment. A clear preference was observed for mature stands, irrespective of the dominance of deciduous or coniferous trees. This may be attributed to the availability of food, cover and environmental conditions. Mature stands produce larger quantities of tree fruits and seeds, which are collected by wild boar in autumn and winter after they fall or are buried in the ground and under leaves. The stocking density and height of the main tree species had a significant effect on the size of the rooted areas. This finding aligns with those of other studies, which indicate that wild boar tend to root in areas with more secure shelter due to denser vegetation cover (e.g., high stocking density and greater height of trees) (Massei and Genov 2004; Barrios-Garcia and Ballari 2012).

Stand age also had a significant effect on the size of rooted areas. The soil in mature forest stands is often well developed, comprising a thick layer of forest litter, which is rich and soft. This makes it easier to root and turn than soil in young and middle-aged stands. In mature forest stands, the accumulation of living and decomposing organic matter gives rise to a multitude of microhabitats characterised by specific conditions that support the life and growth of fungi and animals (e.g. invertebrates, small mammals). In mature forest stands that are not densely vegetated, stable communities of grasses, herbs, mosses and regenerating forest trees emerge, facilitated by the availability of light, and thus creates a favourable environment for wild boar. It is the mature stands with sunlit grasslands that female wild boar prefer for nesting and rearing piglets (Keuling et al. 2017). The grass is used for nest construction, the sunlight improves thermal comfort in the nest, and the piglets explore the surrounding environment, gather food and root (Špinka 2009).

Acer stands contained the highest proportion of rooted areas. No studies about the relationship between wild boar and *Acer* stands have yet been published, so our results cannot be compared with other studies. However, these results can be at least partially explained by the fact that wild boar generally tend to root in stands dominated by broadleaved tree species, due to the higher availability of food (Schley and Roper 2003) and vegetation cover (Massei and Genov 2004). With regard to tree species preference (frequency of rooting), wild boar demonstrated a strong affinity for oak stands, which were the most pervasive in the region. However, the impact of *Quercus* stands on the size of the rooted area was not statistically significant. This can be explained by the fact that wild boar are the primary consumers of acorns, and the production of these nuts affects wild boar population fluctuations (Touzot et al. 2023). Wild boar are concentrated in oak forests, particularly during mast years, when the number of acorns is high (Kamler et al. 2016). During autumn and winter, the main activity of wild boar is feeding on acorns, a nutrient-rich and energy-dense food source.(Kamler et al. 2016). Acorns fall from August to November and serve as a popular food source for various animals, including wild boar, other large ungulates, small mammals, and birds (Kamler et al. 2016). Acorns are consumed throughout the non-growing season until they germinate (Zeman et al. 2016). It should be noted that acorns are not only collected directly under the tree after falling, they are also actively sought in vegetation, under foliage, in terrain irregularities, and in small mammal reservoirs, all of which contribute to rooting activity (Focardi et al. 2000). Furthermore, soils in oak stands are often rich in organic material that supports a high diversity and biomass of fungi and invertebrates. All of this represents an attractive food source for the wild boar as an omnivore.

The smallest proportion of rooted area was found in *Juglans* and *Fraxinus* dominated forests. Black walnut contains juglone, a toxic isomer of lawsone and a plant growth inhibitor (Chudhary et al. 2020). Juglone may, therefore, decrease food availability in black walnut dominated stands, helping to explain the low levels of rooting in *Juglans* dominated stands. In the case of *Fraxinus* stands, ash trees produce less litter, which decomposes more rapidly than the litter of other broadleaved species (Dahlsjö et al. 2024). Consequently, the soil under ash trees has a lower organic matter richness, which may explain the reduced attractiveness to wild boar. Wild boars were also observed to be engaged in intensive excavation activities within pine stands. As (Haaverstad et al. 2014) have observed, the preference for pine soils is primarily attributable to the fact that the soil is characterised by a high degree of looseness, which is a consequence of the substantial quantity of slowly decomposing needles. Additionally, specific fungal fruiting bodies (e.g., *Elaphomyces* spp., Ławrynowicz et al. 2006) may serve as a significant source of attraction in *Pinus* stands.

Distance from streams, and paths and feeding sites

The presence of water in forest habitats provides wild boar with a softer and more accessible substrate for rooting (Calosi et al. 2024), more consistent food and water sources, and potentially more favourable conditions for survival. Such habitats are conducive to the survival of wild boar during the winter and early spring months (Schley and Roper 2003; Massei and Genov 2004), when vegetation flourishes and small animals emerge. These factors likely contribute to the observed preference for rooting in water-influenced forest stands. Similarly, our results showed that rooted area was significantly higher in the vicinity of feeding sites, which corresponds with previous studies demonstrating that artificial feeding can strongly influence wild boar behaviour and space use. Feeding sites attract animals by providing concentrated and predictable food sources, especially during the non-vegetation period, leading to increased local densities and prolonged activity, including soil disturbance in the surrounding area (Massei et al. 2015). Moreover, artificial feeding does not eliminate rooting; on the contrary, it may stimulate foraging activity in the vicinity, as wild boars also search for belowground resources such as invertebrates and plant storage organs (Schley and Roper 2003; Baubet et al. 2004; Fagiani et al. 2014). Therefore, feeding sites likely act as focal points of disturbance and should be considered in wildlife management planning.

Human disturbance is typically concentrated during daylight hours; however, nocturnal presence of wild boar on and around roads is much riskier (Lima et al. 2015). Since 2018, hunters in the Czech Republic have been permitted to utilise thermal imaging equipment for the purposes of monitoring and hunting wild boar, a practice which is actively employed (Kamler and Drimaj 2021). In practice, it appears that hunters traverse public and forest roads in vehicles, monitor the presence of wild boars in the area, and pursue them when they approach a suitable distance. Hunters employ this method of hunting due to the proximity of the road, which allows for the relatively easy transportation of hunted animals from the terrain. Additionally, the dense network of forest roads optimises the spatial distribution of hunting within the forest unit (Gaynor et al. 2021, 2024). However, in our study, distances from roads and paths had no significant effect on rooting.

Vegetation cover and depth of rooting in soil

Previous studies have shown that the level of ecosystem disturbance caused by rooting may strongly depend on the population density of wild boar (Ferretti et al. 2021). In our study, although we did not analyse this relationship directly, we observed that changes in rooted area between years coincided with changes in estimated population size and hunting pressure, suggesting that wildlife management interventions may play an important role in regulating disturbance. While population density was not influenced by migration in this study, the regulatory pressure from hunters may have played a critical role. Besides direct population control, increased hunting pressure can also elevate stress levels in wild boars, potentially increasing food intake and foraging activity, including rooting (e.g. Fernández-Llario and Carranza 2000). Even short-term inadequate control of animal abundance can cause irreversible and far-reaching changes to ecosystems, where it can have a detrimental impact on the environment, accelerating erosion by exposing forest soils (e.g., Hancock et al. 2016tő et al. 2020). In certain terrains, wild boars contribute to the slowing of runoff and the increasing infiltration or sedimentation of various materials (Pitta-Osses et al. 2022). It is therefore evident that this has an impact on the dynamics of forest ecosystems and the plant and animal communities therein (e.g. Calosi et al. 2024; Špoula et al. 2024). Wild boar rooting changes both the biotic and abiotic properties of the soil, thereby impacting decomposition rates (Barrios-Garcia et al. 2022). Rooting was more frequent in deciduous forests (Bruinderink and Hazebroek 1996). Our results show that rooting depth in either the organic or mineral horizons is not affected by total rooted area suggesting that wild boar respond to olfactory cues at a specific location rather than rooting across a wide area. However, based on field observations, it is evident that flat thermophilous oak woodlands on sand are significantly threatened by the disruption of the thin organic layer, leading to the formation of sterile areas with exposed mineral soil and a lack of growing vegetation.

The consequences of disturbance activities

The study area is part of valuable ecosystems with a special management regime, which is fully subordinated to the preservation of the stability of forest communities. Conventional forestry and accompanying activities (harvesting, timber transport, planting, etc.; Prescott et al. 2019) can disturb the thin organic layer of the soil and locally sterilise the habitat by leaching organic material, thus exposing the infertile mineral layer. Human activity is therefore subordinate to nature conservation and nature's interests. However, these restrictions do not apply to wildlife, which can cause even more serious damage than humans. According to our study, wild boar disturbs the soil in about 1/10 of the area, making it a non-negligible environmental factor that needs to be actively managed for nature conservation. By disturbing the soil, rooting may initiate processes of water and wind erosion, particularly in vulnerable habitats (Pitta-Osses et al. 2022). Although we did not record repeated rooting events at the same locations, it is plausible that such recurrence could act as a catalyst for degradation in certain ecosystems. This hypothesis may be relevant not only for dry habitats, but also for forests under standard management (e.g., forest stands on slopes, or with soils over rocky subsoils). Further research could be directed in this field.

By consuming the seeds and fruits, wild boar removes the reproductive material of trees, thus limiting the natural regeneration of forests (Kamler et al. 2016). In the case of higher densities in the area, or the presence of other omnivores and herbivores (e.g., roe deer, red deer, fallow deer, but also hares, which are common in the Czech Republic), or outside the seed years, the complete seed crop (most often acorns) can be completely destroyed during autumn and winter (Kamler et al. 2016). On the other hand, disturbance of the soil surface can facilitate the germination of seeds of vascular plants and thus have a positive impact on biodiversity. The creation of initiation habitats creates opportunities for the establishment and growth of invasive plant species (e.g., *Reynoutria* sp. (Negrea et al. 2022) or

Impatiens glandulifera, typical for the Czech Republic), which can cause further habitat degradation in ecologically valuable habitats. As the rooting activity of wild boar is caused mainly by foraging for food of various origins, the destruction of endangered plants and animals may again have fatal consequences for nature conservation. The wild boar's preference for aquatic environments, with loose and moist soil, can also interfere with the stability of the shoreline and the composition of the communities there, as well as causing soil pollution of water bodies, affecting sediment transport, etc. Rooting in the vicinity of feeding sites should be considered when siting them, as e.g. in forest stands with a need for natural regeneration of trees, much more damage could occur than in the rest of the forest units.

In short, wild boar possesses highly destructive behaviors that cause cascading trophic effects with broad impacts on ecosystems (Barrios-Garcia and Ballari 2012). In sites such as this study area, the destructive effects caused by wild boar should be assessed and a proactive approach taken to control their numbers or to exclude their presence by mechanical means and in valuable sites (e.g., mechanical fencing, electric fencing). Before irreversible damage occurs.

Our findings are linked to the specific environment where wild boars occur throughout the year and where forest habitats are very sensitive to any disturbance. However, they may also be valid to some extent in other types of forest environments, where other circumstances will always need to be taken into account. For example, in an environment with high foraging competition or the presence of large carnivores, wild boar behaviour will be somewhat different due to different distribution and spatial use. Although the GLMMs revealed statistically significant relationships (which were probably facilitated by the large sample size), the conditional R^2 values ranged from 0.13 to 0.47. These relatively low to moderate values suggest that, although the detected effects are statistically significant, they may have limited biological relevance or explanatory power" into discussion.

Further research could be directed towards verifying soil degradation and habitat change due to wild boar rooting.

Conclusions

The findings of this study confirm that wild boar is an important disturbance agent in forest ecosystems. Their rooting activity in the forest environment is unevenly distributed and is influenced by certain stand characteristics. Wild boar also prefers to rooting water-influenced habitats. These findings can be used in ecologically valuable areas where they should be reflected in active hunting management or habitat protection by other measures.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

Ethical approval No approval of research ethics committees was required to accomplish the goals of this study because the work did not involve capture, handling or experimentation on any animal.

References

Amori G, Luiselli L, Milana G, Casula P (2015) Negative effect of the wild Boar (Sus scrofa) on the population size of the wood mouse (Apodemus sylvaticus) in forest habitats of Sardinia. https://doi.org/10.1515/mammalia-2015-0023. Mammalia 80

Barrios-Garcia 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

Barrios-Garcia MN, Gonzalez Polo M, Simberloff D, Classen A (2022) Wild Boar rooting impacts soil function differently in different plant community types. Biol Invasions 25:1–10. https://doi.org/10.1007/s10530-022-02936-x

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48. https://doi.org/10.18637/jss.v067.i01

Baubet E, Bonenfant C, Brandt S (2004) Diet of the wild boar in the French Alps. Galemys 16:101–113. https://doi.org/10.7325/Galemys.2004.NE.A8

Borkowski J, Palmer SCF, Borowski Z (2011) Drive counts as a method of estimating ungulate density in forests: mission impossible? Acta Theriol (Warsz) 56:239–253. https://doi.org/10.1007/s13364-010-0023-8

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 Prot 133:105131. https://doi.org/10.1016/j.cropro.2020.105131

Brooks M, Kristensen K, van Benthem K et al (2017) Glmmtmb balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J 9:378–400. https://doi.org/10.32614/RJ-2017-066

Bruinderink GWTAG, Hazebroek E (1996) Wild Boar (*Sus scrofa scrofa* L.) rooting and forest regeneration on podzolic soils in the Netherlands. For Ecol Manag 88:71–80. https://doi.org/10.1016/S0378-1127(96)03811-X

Brunet J, Hedwall P-O, Holmström E, Wahlgren E (2016) Disturbance of the herbaceous layer after invasion of an eutrophic temperate forest by wild boar. Nord J Bot 34:120–128. https://doi.org/10.1111/njb.01010

Bueno G, Azorín J, García D et al (2013) Occurrence and intensity of wild Boar disturbances, effects on the physical and chemical soil properties of alpine grasslands. Plant Soil 373:1–14. https://doi.org/10.1007/s11104-013-1784-z

Calosi M, Gabbrielli C, Lazzeri L et al (2024) Seasonal and ecological determinants of wild boar rooting on priority protected grasslands. Environ Manage 74:268–281. https://doi.org/10.1007/s00267-024-01952-y

Cappa F, Bani L, Meriggi A (2021) 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). Mamm Biol 101:451–463. https://doi.org/10.1007/s42991-021-00125-2

Carpio AJ, García M, Hillström L et al (2022) Wild boar effects on fungal abundance and guilds from sporocarp sampling in a boreal forest ecosystem. Animals 12:2521. https://doi.org/10.3390/ani12192521

Chudhary Z, Khera RA, Hanif MA et al (2020) Chap. 49 - Walnut. In: Hanif MA, Nawaz H, Khan MM, Byrne HJ (eds) Medicinal plants of South Asia. Elsevier, pp 671–684

Cuevas MF, Mastrantonio L, Ojeda R, Jaksic F (2012) Effects of wild boar disturbance on vegetation and soil properties in the Monte desert, Argentina. Mamm Biol 77:299–306. https://doi.org/10.1016/j.mambio.2012.02.003

Dahlsjö CAL, Atkins T, Malhi Y (2024) Large invertebrate decomposers contribute to faster leaf litter decomposition in *Fraxinus excelsior*-dominated habitats: implications of ash dieback. Heliyon 10:e27228. https://doi.org/10.1016/j.heliyon.2024.e27228

Drimaj J, Kamler J, Plhal R et al (2021) Intensive hunting pressure changes local distribution of wild Boar. Hum-Wildl Interact 15:9. https://doi.org/10.26077/b792-8211

Engvall E (2022) Wild boar feeding site effects on targeted and non-targeted species. Master's thesis. Swedish University of Agricultural Sciences, Grimsö, Swedish kingdom

Fagiani S, Fipaldini D, Santarelli L et al (2014) Monitoring protocols for the evaluation of the impact of wild boar (*Sus scrofa*) rooting on plants and animals in forest ecosystems. Hystrix Ital J Mammal 25(1):31–38. https://doi.org/10.4404/hystrix-25.1-9314

Fernández-Llario P, Carranza J (2000) Reproductive performance of the wild boar in a mediterranean ecosystem under drought conditions. Ethol Ecol Evol 12(4):335–343. https://doi.org/10.1080/08927014.2000.9522791

Ferretti F, Lazzeri L, Mori E et al (2021) Habitat correlates of wild boar density and rooting along an environmental gradient. J Mammal 102:1536–1547. https://doi.org/10.1093/jmammal/gyab095

Focardi S, Capizzi D, Monetti D (2000) Competition for acorns among wild boar (*Sus scrofa*) and small mammals in a mediterranean woodland. J Zool 250:329–334. https://doi.org/10.1111/j.1469-7998.2000.tb00777.x

Fonseca C (2008) Winter habitat selection by wild boar *Sus scrofa* in southeastern Poland. Eur J Wildl Res 54:361–366. https://doi.org/10.1007/s10344-007-0144-9

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. Pest Manag Sci. https://doi.org/10.1002/ps.3368

Gaynor K, Mcinturff A, Brashares J (2021) Contrasting patterns of risk from human and non-human predators shape Temporal activity of prey. J Anim Ecol 91:13621. https://doi.org/10.1111/1365-2656

Gaynor K, Mcinturff A, Abrahms B et al (2024) Hunting mode and habitat selection mediate the success of human hunters. Mov Ecol. https://doi.org/10.1186/s40462-024-00471-z

Genov P, Focardi S, Morimando F et al (2017) Ecological impact of wild boar in natural ecosystems. In: Ecology, Conservation and Management of Wild Pigs and Peccaries. pp 404–419

Haaverstad O, Hjeljord O, Wam HK (2014) Wild boar rooting in a Northern coniferous forest – minor silviculture impact. Scandinavian J Res 29:90–95. https://doi.org/10.1080/02827581.2013.865781

Hancock G, Lowry J, Dever C (2016) Surface disturbance and erosion by pigs - A medium term assessment for the monsoonal tropics: surface disturbance and erosion by pigs. Land Degrad Dev 28. https://doi.org/10.1002/ldr.2636

Jolley D, Ditchkoff S, Sparklin B et al (2010) Estimate of herpetofauna depredation by a population of wild pigs. J Mammal 91:519–524. https://doi.org/10.1644/09-MAMM-A-129.1

Kamler J, Drimaj J (2021) Stabilization of wild Boar populations: reproduction potential of current Boars vs. hunting potential of current hunters – review. ZLV 66:95–103

Kamler J, Dobrovolný L, Drimaj J et al (2016) The impact of seed predation and browsing on natural sessile oak regeneration under different light conditions in an over-aged coppice stand. iForest 9:569–576. https://doi.org/10.3832/ifor1835-009

Kasper A (2022) Nemoral European Beech and Oak Forests under Climate Change. Dissertation thesis. Georg-August-Universität Göttingen, Göttingen, Germany

Kent M (2012) Vegetation description and data analysis: a practical approach. Wiley-Blackwell, Chichester, UK

Keuling O, Podgórski T, Monaco A et al (2017) Eurasian Wild Boar *Sus scrofa* (Linnaeus, 1758). In: Ecology, Conservation and Management of Wild Pigs and Peccaries. pp 202–233

Kleiber C, Zeileis A (2008) Applied econometrics with R. Springer, New York, NY

Kuhn M (2007) caret: Classification and Regression Training. 6.0–94

Labadessa R, Ancillotto L (2023) Small but irreplaceable: the conservation value of landscape remnants for urban plant diversity. J Environ Manag 339:117907. https://doi.org/10.1016/j.jenvman.2023.117907

Ławrynowicz M, Faliński JB, Bober J (2006) Interactions among hypogeous fungi and wild boars in the Subcontinental pine forest. Biodiv Res Conserv 2006:102–106

Lee S-H, Park C-M (2022) The effect of hunter-wild boar interactions and landscape heterogeneity on wild boar population size: a simulation study. Ecol Model 464:109847. https://doi.org/10.1016/j.ecolmodel.2021.109847

Lewis J, Farnsworth M, Burdett C et al (2017) Biotic and abiotic factors predicting the global distribution and population density of an invasive large mammal. Sci Rep. https://doi.org/10.1038/srep44152

Lima SL, Blackwell BF, DeVault TL, Fernández-Juricic E (2015) Animal reactions to oncoming vehicles: a conceptual review. Biol Rev 90:60–76. https://doi.org/10.1111/brv.12093

Lüdecke D, Ben-Shachar MS, Patil I et al (2021) Performance: an R package for assessment, comparison and testing of statistical

models. J Open Source Softw 6(60):3139. https://doi.org/10.21105/joss.03139
Massei G, Genov P (2004) The environmental impact of wild boar. Galemys 16:135–145
Massei G, Kindberg J, Licoppe A et al (2015) Wild boar populations up, numbers of hunters down? A review of trends and implications for Europe. Pest Manag Sci 71:492–500. https://doi.org/10.1002/ps.3965
Miettinen E, Melin M, Holmala K et al (2023) Home ranges and movement patterns of wild boars (*Sus scrofa*) at the Northern edge of the species' distribution range. Mamm Res 68:611–623. https://doi.org/10.1007/s13364-023-00710-5
Mikulka O, Zeman J, Drimaj J et al (2018) The importance of natural food in wild boar (*Sus scrofa*) diet during autumn and winter. Folia Zool 67(3–4):165–172. https://doi.org/10.25225/fozo.v67.i3-4.a3.2018
Milchunas DG, Lauenroth WK (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecol Monogr 63:327–366. https://doi.org/10.2307/2937150
Mitchell J, Dorney W, Mayer R, McIlroy J (2008) Ecological impacts of feral pig diggings in North Queensland rainforests. Wildl Res 34:603–608. https://doi.org/10.1071/WR06065
Mohr D, Cohnstaedt L, Topp W (2005) Wild boar and red deer affect soil nutrients and soil biota in steep oak stands of the Eifel. Soil Biol Biochem 37:693–700. https://doi.org/10.1016/j.soilbio.2004.10.002
Mori E, Ferretti F, Lagrotteria A et al (2020) Impact of wild boar rooting on small forest-dwelling rodents. Ecol Res 35:675–681. https://doi.org/10.1111/1440-1703.12113
Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol Evol 4:133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x
Nakagawa S, Johnson PCD, Schielzeth H (2017) The coefficient of determination R2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. J R Soc Interface 14:20170213. https://doi.org/10.1098/rsif.2017.0213
Negrea B-M, Stoilov-Linu V, Pop C-E et al (2022) Expansion of the invasive plant species *reynoutria japonica* Houtt in the upper Bistrița mountain river basin with a calculus on the productive potential of a mountain meadow. Sustainability 14:5737. https://doi.org/10.3390/su14095737
Oja R, Zilmer K, Valdmann H (2015) Winter supplemental feeding of wild Boar (Sus scrofa) in Estonia is driven by habit and convenience rather than science. PLoS ONE 10(8):e0135254. https://doi.org/10.1371/journal.pone.0135254
Orłowska L, Nasiadka P (2022) The winter preferences for different forest habitats by wild Boar Sus scrofa estimated using the track counting method. Sylwan 166:500–511. https://doi.org/10.26202/sylwan.2022048
Pérez-Camacho L, Villar-Salvador P, Cuevas JA et al (2023) Spatial decision-making in acorn dispersal by Eurasian Jays around the forest edge: insights into oak forest regeneration mechanisms. For Ecol Manage 545:121291. https://doi.org/10.1016/j.foreco.2023.121291
Pickett STA, Pickett ST, White PS (1985) The ecology of natural disturbance and patch dynamics. Academic
Pitta-Osses N, Centeri C, Fehér Á, Katona K (2022) Effect of wild boar (*Sus scrofa*) rooting on soil characteristics in a deciduous forest affected by sedimentation. Forests 13:1234. https://doi.org/10.3390/f13081234
Prescott CE, Frouz J, Grayston SJ et al (2019) Chap. 13 - Rehabilitating forest soils after disturbance. In: Busse M, Giardina CP, Morris DM, Page-Dumroese DS (eds) Developments in soil science. Elsevier, pp 309–343
Roleček J, Vild O, Sladký J, Řepka R (2017) Habitat requirements of endangered species in a former coppice of high conservation value. Folia Geobot 52:59–69. https://doi.org/10.1007/s12224-016-9276-6
Sandom CJ, Hughes J, Macdonald DW (2013a) Rooting for rewilding: quantifying wild boar's *Sus scrofa* rooting rate in the Scottish highlands. Restor Ecol 21:329–335. https://doi.org/10.1111/j.1526-100X.2012.00904.x
Sandom CJ, Hughes J, Macdonald DW (2013b) Rewilding the Scottish highlands: do wild boar, *Sus scrofa*, use a suitable foraging strategy to be effective ecosystem engineers?? Restor Ecol 21:336–343. https://doi.org/10.1111/j.1526-100X.2012.00903.x
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. https://doi.org/10.1046/j.1365-2907.2003.00010.x
Skoták V, Drimaj J, Kamler J (2021) Evaluation of damage to forest tree plantations by wild Boar in the Czech Republic. Human-Wildl Interact 15:13. https://doi.org/10.26077/109A-E424
Špinka M (2009) Behaviour of pigs. Ethol Domest animals: introductory text modular texts 177–191. https://doi.org/10.1079/9781845935368.0177
Špoula J, Stočes D, Drimaj J, Mikulka O (2024) The effects of wild boar rooting on epigeic arthropods in oak forests. Forests 15:1169. https://doi.org/10.3390/f15071169
Sütő D, Farkas J, Siffer S et al (2020) Spatiotemporal pattern of wild boar rooting in a central European dry oak forest. Eur J Forest Res 139:407–418. https://doi.org/10.1007/s10342-019-01248-5
Tauber CA, Tauber MJ (1981) Insect seasonal cycles: genetics and evolution. Ann Rev Ecol Evol Syst 12:281–308. https://doi.org/10.1146/annurev.es.12.110181.001433
Touzot L, Venner S, Baubet E et al (2023) Amplified cyclicality in mast seeding dynamics positively influences the dynamics of a seed consumer species. Am Nat 201:38–51. https://doi.org/10.1086/721905
Vajas P, Calenge C, Richard E et al (2020) Many, large and early: hunting pressure on wild boar relates to simple metrics of hunting effort. Sci Total Environ 698:134251. https://doi.org/10.1016/j.scitotenv.2019.134251
Wirthner S, Schuetz M, Page-Dumroese D et al (2012) Do changes in soil properties after rooting by wild boars (Sus scrofa) affect understory vegetation in Swiss hardwood forests? Can J Res 42:585–592. https://doi.org/10.1139/X2012-013
Zeileis A, Hothorn T (2002) Diagnostic Checking in Regression Relationships. R Journal 2
Zeman J, Hrbek J, Drimaj J et al (2016) Wild boar impact to the natural regeneration of oak and acorn importance in its diet. Acta Univ Agric Silvic Mendelianae Brun 64:579–585. https://doi.org/10.11118/actaun201664020579
Zeman J, Hrbek J, Drimaj J et al (2018) Habitat and management influence on a seasonal diet composition of wild boar. Biologia. https://doi.org/10.2478/s11756-018-0027-4

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