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Wild boar rooting: influence from environmental variables and effect on ground-dwelling rodents in a Mediterranean oak forest

Giorgia Bertagni [1,*], Paola Bartolommei [1], Stefania Gasperini [1], Giuseppe Puddu [2], Sara Savazza [1,3], Andrea Bonacchi [1], Emiliano Manzo [1] & Roberto Cozzolino [1]

[1] Fondazione Ethoikos, Convento dell'Osservanza snc, 53030 Radicondoli, Siena, Italy.
[2] Regione Lazio – Riserva Naturale Lago di Vico, S.R. Cimina km 12, 01032 Caprarola, Viterbo, Italy.
[3] Department of Life Sciences, University of Trieste, Via Licio Giorgieri 10, 34127 Trieste, Italy.

[*] Corresponding author: giorgia.bertagni12@gmail.com

Abstract. Wild boar rooting behaviour can be shaped by several environmental variables (e.g., food availability and habitat features) and can directly or indirectly influence various habitats, ecological processes and taxa. One of these, ground-dwelling rodents, are known to be affected by wild boar foraging activity due to food competition and direct disturbance. In the current study, the following questions were investigated: do vegetation composition, structural components of forest habitats (at ground, shrub, and tree levels) and acorn availability influence rooting activity of wild boars and consequently, also the abundance of *Apodemus flavicollis* and *A. sylvaticus* in the same area. This research was carried out in a Mediterranean deciduous oak forest across 12 sampling sites. The results showed that, among the habitat variables considered, only shrub cover at 1 m height had a significant association with the extent of wild boar rooting. Contrary to expectations, acorn availability did not significantly influence rooting activity, suggesting either a more complex relationship between food availability and rooting behaviour or the influence of other local factors. Likewise, the number of *Apodemus* spp. individuals captured was not significantly related to rooting activity, indicating no detectable effects of wild boar rooting on rodents in the study area. This study contributes to our understanding of the factors driving this foraging behaviour and its ecological and socioeconomic implications.

Keywords. *Sus scrofa*, *Apodemus*, food availability, foraging behaviour, vegetation features, acorn.

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Introduction

The wild boar *Sus scrofa* has been reported to directly or indirectly impact a wide array of taxa, habitats and ecological processes through its rooting behaviour (see Fagiani *et al.* 2014; Drimaj *et al.* 2025). Rooting consists of dislodging soil, leaves and twigs to obtain food, such as invertebrates, small vertebrates, roots, bulbs and seeds (Welander 2000; Massei & Genov 2004; Ballari & Barrios-Garcia

2014). In recent decades, the consequences of rooting activity on habitats and biotic communities have been the subject of several studies (e.g., Massei & Genov 2004; Barrios-Garcia & Ballari 2012; Bongi *et al*. 2017). Ground-dwelling rodents, which are part of the biotic community impacted by rooting activity in forest ecosystems, have recently received attention due their pivotal role as seed dispersers and as key prey species for most predators in these ecosystems (Bertolino *et al.* 2015; Mori *et al.* 2020). Wild boar rooting activity may negatively affect ground-dwelling rodents by altering the shrub layer of the vegetation that rodents use as shelters from predators and as food sources. In addition, wild boars can disrupt underground rodent burrows and consume seeds that rodents hoard, thus acting as potential interspecific competitors for seeds. In Mediterranean forests, wild boar may also exert direct competitive pressure on *Apodemus* spp. through its ability to locate and consume acorn caches stored in the ground by these rodents (Focardi *et al.* 2000). Although evidence suggests that rooting may affect *Apodemus* spp., the magnitude and direction of this effect remain uncertain due to contrasting findings among different studies (Focardi *et al*. 2000; Muñoz *et al.* 2009; Fagiani *et al*. 2014; Amori *et al*. 2016; Mori *et al*. 2020). Acorns represent an important food resource for both wild boars and rodents, driving the foraging and spatial behaviour, individual survival and population density of these species (Cutini *et al*. 2013; Gasperini *et al*. 2016; Sunyer *et al*. 2016; Bisi *et al*. 2018; Sütő *et al*. 2020). Acorn availability usually changes across seasons and years, possibly driving variations in rooting activity (Focardi *et al*. 2000; Bisi *et al*. 2018; Sütő *et al*. 2020). Although the occurrence and extent of wild boar rooting are driven primarily by food resources, this activity can also be influenced by environmental variables, such as soil layer characteristics, vegetation composition and habitat type (Welander 2000; Bueno *et al*. 2009; Calosi *et al.* 2025; Drimaj *et al.* 2025). Among habitat types, forests are known to sustain high wild boar densities and, depending on local environmental conditions, may be characterized by intense rooting activity (Welander 2000; Sütő *et al.* 2020; Ferretti *et al.* 2021). However, the effects of forest composition and structure on rooting extent and occurrence have rarely been examined (e.g., Drimaj *et al.* 2025), with most studies focusing instead on soil characteristics and grass composition (e.g., Bueno *et al*. 2009; Macci *et al*. 2012; Burrascano *et al*. 2015).

The aims of the current study, conducted in a deciduous oak forest, were threefold: (i) to investigate whether habitat features at the ground, shrub, and tree levels are associated with wild boar rooting activity; (ii) to evaluate whether seasonal and interannual variation in acorn availability influences rooting activity; and (iii) to assess whether rooting activity is associated with the number of *Apodemus* spp. individuals captured in the study area. We considered the two *Apodemus* species occurring in the study area (*A. flavicollis* and *A. sylvaticus*) jointly at the genus level, as both are ground-dwelling, granivorous rodents that consume and cache acorns and therefore have similar ecological roles in this context (Gasperini *et al.* 2026). Given the limited information available on how composition and structure shape wild boar rooting, the first objective was exploratory. In contrast, because acorns are a key food resource for wild boar, we predicted that rooting activity would be significantly influenced by acorn availability. Finally, we hypothesised that, if wild boar rooting represents a source of disturbance or food competition, the number of *Apodemus* spp. individuals captured would decline with increasing rooting activity.

Material and methods

This study was conducted in the La Selva Forest (43°13′ N, 11°4′ E), a Mediterranean deciduous oak forest in central Italy, approximately 45 km west of Siena. The study area with a size of 900-hectares lies between 350 and 700 m a.s.l. The climate is Mediterranean, characterized by warm, dry summers (mean monthly temperature ≈ 23°C) and cool, wet winters (mean monthly temperature ≈ 4°C), with an average annual precipitation of 750–1600 mm (D.R.E.Am. s.c 1993). Historically, the forest was managed by cutting back smaller trees while leaving select large trees to mature (coppicing), with individual stands harvested at different times. The forest is mainly dominated by *Quercus cerris*, accompanied by *Q. pubescens* and other deciduous tree species, including *Sorbus domestica*, *S. torminalis*, *Acer campestre*, *Ulmus minor*, and *Ostrya carpinifolia*.

Wild boars are common throughout the study area, although data on the species' population density are unavailable. We selected 12 sampling sites, which encompass a wide forest heterogeneity gradient deriving from the combined effect of different types of interventions (coppicing, conversion to high forest, thinning). At each site, we established a trapping grid (60 × 60 m) for *Apodemus* spp. captures, and nested inside this grid, we identified a sampling area (20 × 40 m) where we collected data on rooting activity, vegetation composition, structural components of the forest habitat and acorn production. The sampling area was subdivided into eight 10 × 10 m quadrats to record accurate measurements of these variables. Wild boar rooting activity was visually estimated as the percentage of ground cover showing signs of rooting. After measuring the area affected by rooting activity, rooting marks were manually erased to ensure that only newly created rooting signs would be recorded in the subsequent sampling session. For assessing vegetation composition and structural components, we considered the following variables: the cover of grass, litter, bare soil and twigs, the cover of shrubs at 0.5 m and 1 m height, the number of stems per m^2, and the species richness of all plants with a Diameter at Breast Height (DBH) ≥ 1 cm. Each cover variable was quantified as a percentage of the sampling area. To estimate the total acorn biomass at each sampling site, we counted and weighed all fallen acorns that settled on the ground within two circular plots (0.5 m radius) around each productive oak (DBH > 20 cm). To investigate the relationship between rooting activity and relatively stable habitat characteristics, we assessed rooting occurrence, vegetation composition and structural component once a year, in May (coinciding with vegetation regrowth), from 2012 to 2014 and from 2017 to 2018, thereby minimizing seasonal variation in environmental conditions. To examine the influence of seasonal resource availability (i.e., acorns) on wild boar rooting and its relationship with *Apodemus* spp., a more intensive sampling scheme was implemented in 2017 and 2018. Rooting was recorded four times during each year (February, May, July, and November) to account for seasonal variation in foraging activity. Because acorn production is highly seasonal and varies markedly among years, fallen acorns were sampled each November in 2016, 2017 and 2018 immediately after seed fall. During the same period, eight mouse trapping sessions were conducted (in February, May, July, and November of 2017 and 2018, respectively) following a capture–mark–recapture protocol. In each session, we placed 49 Heslinga live traps spaced 10 m apart, left them open for three consecutive days and checked for captures daily in the morning.

Captured individuals were identified at the genus level because the aim of this study was to assess the overall response of the *Apodemus* community to wild boar rooting rather than species-specific patterns. Individuals were marked without anesthesia with a subcutaneous passive integrated transponder tag (1.25 × 8.5 mm Therapet/Bioforlife) upon first capture. Recaptured individuals were identified by checking with a handheld reader for the presence of previously implanted tags. Animals were released at the point of capture.

First, to investigate the influence of habitat characteristics on wild boar rooting activity, rooting extent recorded in May was analysed using zero-inflated beta generalised linear mixed models (GLMMs; R package *glmmTMB*) with a logit link function to account for the excess of zero values. The extent of rooting was related to vegetation composition and forest structural components. Second, to investigate the influence of acorn availability on wild boar rooting activity, we analysed the more extensive dataset collected during 2017–2018. We used zero-inflated beta GLMMs to evaluate spatial and temporal variation in rooting extent among sampling grids, sampling sessions and years. Variation in acorn production among sampling grids and years was then analysed using GLMMs. Acorn production recorded in November 2016 was excluded from these analyses because it was consistently close to zero across all sampling grids, providing insufficient variation for meaningful statistical analyses. Rooting activity was subsequently modelled in relation to acorn biomass using zero-inflated beta GLMMs. Acorn biomass was set to zero in May and July to reflect the very low to negligible availability of acorns outside the main autumn–winter fruiting period in Mediterranean oak ecosystems, where most acorns are either consumed, dispersed or germinate shortly after seed fall (Gómez-Casero *et al*. 2007; Leiva & Perelló-Rodríguez 2024). Finally, Poisson GLMMs (R package *glmmTMB*) were used to relate the number of *Apodemus* spp. individuals captured per trapping session to the rooting activity recorded in the same session.

TABLE 1

Results of the zero-inflated beta generalised linear mixed models with a logit link function (including a null model), which related the extent of rooting recorded in May to the vegetation composition and structural components of the sampling sites. The models were ranked by AICc (Akaike's information criterion). For each model, the table reports the AICc, **Δ**AICc, parameter estimates, standard errors (SE), test statistics (*z-values*), and corresponding *p*-values to show the magnitude, direction, and significance of each predictor. The asterisks indicate statistical significance.

Model rank		AICc	ΔAICc	Estimate	SE	z-value	p-value
1	Shrub cover (1 m)	32.79	0.00	-4.07	1.27	-3.21	0.001*
2	Species richness	36.55	3.76	0.19	0.07	2.62	0.009*
3	Null model	39.99	7.21	-1.15	0.43	-2.66	0.007
4	Grass cover	40.45	7.67	-0.36	0.25	-1.47	0.14
5	Shrub cover (0.5 m)	41.64	8.86	-3.89	4.08	-0.95	0.34
6	Twigs	42.06	9.27	-0.28	0.36	-0.78	0.44
7	Bare ground cover	42.58	9.79	0.19	0.65	0.30	0.76
8	Litter cover	42.66	9.87	0.006	0.06	0.09	0.93
9	Stems × m^2	43.43	10.65	0.22	0.23	0.94	0.35

We included only the data from the May, July, and November 2018 rooting recording and rodent (181 *Apodemus* spp. individuals) trapping sessions in this analysis. Trapping data collected between 2017 and February 2018 were excluded from the analysis because *Apodemus* capture rates remained close to zero throughout this period, and including these data could have confounded the relationship between rooting activity and *Apodemus* captures. In fact, this period coincided with a population crash, corresponding to the low point of the cyclical fluctuations in rodent abundance observed in our study area (unpublished data).

For all GLMM analyses, we included the sampling grid and session as random effects to account for the nonindependence of the data and constructed a set of univariate models (individually testing all the variables) for model selection, including a null model. We performed model selection using Akaike's information criterion corrected for finite samples (AICc) and considered models with ΔAICc <2 as having substantial empirical support (Anderson 2008). All analyses were performed using R Statistical Software (R Core Team 2023).

Results

We observed high variation in the rooting extent recorded in May among grids and years, ranging from 0 to 99% (mean±SD: 13.47±23.90%). Among all variables recorded at ground, shrub and tree levels, only shrub cover at 1 m height showed a clear effect, being the only model receiving substantial empirical support, and exhibiting a strong negative relationship with rooting extent ($\beta=-4.07\pm1.27$, $z=-3.21$, $p=0.001$, Table 1). Although species richness showed a significant effect, it did not fall within the top-performing models (ΔAICc ≤ 2, Table 1).

Acorn biomass varied markedly between years (mean annual acorn production was 4.76 g/m² in 2017 and 31.27 g/m² in 2018, respectively) but showed no consistent differences among sampling grids. The model including only the sampling year received overwhelming support (Appendix: Table S1), whereas models including grid effects or the null model received little support. Despite this temporal variation in resource availability, rooting activity showed marked temporal variation among sampling sessions, but no clear interannual or spatial variation. The model including only sampling session received the strongest support as compared to models including year, sampling grid or the null model (Appendix: Table S1).

TABLE 2

Results of the zero-inflated beta generalised linear mixed models with a logit link function and Poisson generalised linear mixed models (including the null models), which related rooting extent to acorn production and *Apodemus* spp. individuals to rooting extent. The models were ranked by AICc (Akaike's information criterion). For each model, the table reports the AICc, **Δ**AICc, parameter estimates, standard errors (SE), test statistics (*z-values***)**, and corresponding *p*-values to show the magnitude, direction, and significance of each predictor.

Model rank		**Model family**	**AICc**	**ΔAICc**	**Estimate**	**SE**	***z-value***	***p-value***
Rooting extent								
1	Null model	Beta(logit)	-39.19	0.00	-2.90	0.23	-12.52	<0.001
2	Acorn	Beta(logit)	-38.56	0.63	-0.005	0.004	-1.22	0.22
Apodemus spp. individuals								
1	Null model	Poisson	187.73	0.00	1.19	0.43	-2.11	0.006
2	Rooting extent	Poisson	190.14	2.41	-0.86	2.36	2.93	0.72

Results of the GLMMs relating rooting extent to acorn biomass indicated that the null model had the strongest support (Table 2). Although the model including acorn biomass fell within 2ΔAICc (Table 2), acorns did not significantly influence rooting extent ($\beta = -0.005 \pm 0.004$, $z = -1.22$, $p = 0.22$).

Similarly, the analysis relating *Apodemus* spp. captures to wild boar rooting activity identified the null model as the best-supported model (Table 2), indicating that rooting activity was not a significant predictor of the number of captured individuals.

Discussion

The variability in rooting extent observed in our study is consistent with findings from other deciduous woodland systems (e.g., Mori *et al*. 2020; Calosi *et al.* 2025; Drimaj *et al.* 2025). Among the forest composition and structure variables we considered, shrub cover at 1 m height emerged as the best-supported predictor, showing a strong negative relationship with rooting extent. This result suggests that understory cover may limit rooting activity by reducing access to the soil surface and increasing the costs of foraging, in accordance with Barrios-García & Ballari (2012) who highlighted the importance of vegetation structure in shaping wild boar foraging behaviour. Likewise, Massei & Genov (2004) noted that although dense shrub layers provide shelter for wild boar, they may also hinder rooting by creating physical barriers at ground level. Although Drimaj *et al.* (2025) reported effects of environmental variables on the size of rooted areas, our results indicated that most of the habitat structural features we considered may not directly influence rooting behaviour in our study area. Several researchers have investigated how environmental variables can influence wild boar population parameters, which could affect rooting activity. For instance, wild boar density has been reported to positively affect rooting, although this positive relationship is still debated (e.g., Massei *et al.* 2018; Calosi *et al*. 2025). Consequently, we cannot exclude the possibility that the variables we considered might influence wild boars' foraging behaviour indirectly.

Food availability is considered to be the main driving force behind wild boar population parameters (e.g., density) and rooting activity (Sütő *et al*. 2020; Ferretti *et al*. 2021; Colomer *et al*. 2024; Drimaj *et al.* 2025). Although the wild boar is an opportunistic omnivore, it primarily feeds on plant matter with high-calorie seeds such as acorns serving as a major food source from autumn to spring in oak forests (Massei & Genov 2004; Ballari & Barrios-García 2014; Bongi *et al.* 2017; Sütő *et al*. 2023). Based on the ecological importance of acorns for wild boar, we predicted that rooting activity would increase with acorn availability. However, this prediction was not supported, as seasonal and interannual variation

in acorn production did not significantly influence rooting activity in our study area. This may indicate a more complex relationship between acorn availability and rooting, as also suggested by Sütő *et al*. (2023), who did not find a direct fine-scale association between rooting intensity and acorn density. In addition to seeds, wild boars exploit a wide variety of trophic resources obtained through rooting, including fruits, bulbs and roots (Welander 2000; Ballari & Barrios-Garcia 2014; Sütő *et al*. 2020). Such dietary flexibility may explain the absence of a clear relationship between seasonal acorn availability and rooting activity observed in our study. Nevertheless, we cannot exclude the possibility that the limited temporal coverage of acorn availability data reduced our ability to detect such a relationship.

Despite the lack of a detectable relationship between acorn availability and rooting activity, the importance of acorns for wild boar is well documented; the species often digs into rodent tunnels to steal hoarded acorns, potentially impacting rodents at both the individual and population levels (Focardi *et al*. 2000; Mori *et al.* 2020). Several authors reported a clear decrease in the presence of *Apodemus* spp. in evergreen oak forests with intense rooting activity, attributed to food competition and direct disturbance (Focardi *et al*. 2000; Muñoz *et al*. 2009; Amori *et al*. 2016). Accordingly, we hypothesised that, if wild boar rooting represented a source of disturbance or food competition in our study system, the number of *Apodemus* spp. individuals captured would decrease with increasing rooting activity. However, this prediction was not supported, as rodent captures were not significantly related to rooting activity. Instead, our results align with those of Fagiani *et al*. (2014) and Mori *et al*. (2020), who reported negligible effects of wild boar activity on *Apodemus* spp. population abundance in deciduous oak forests. According to these authors, relatively low levels of competition for acorns between wild boars and rodents may explain why rooting activity was not associated with the number of *Apodemus* spp. individuals captured in our study. The absence of this relationship may also indicate that the direct effects of wild boar rooting on rodents are generally weak in this system. Nevertheless, the limited number of rodent trapping sessions might have reduced our ability to detect subtle effects. In addition, the number of individuals captured may not reflect behavioural responses to rooting, such as local avoidance or shifts in space use, which could occur without changes in capture numbers. Although we found no evidence that rooting activity affected *Apodemus* captures, wild boar rooting may still influence rodents through behavioural or other ecological mechanisms that were not assessed in this study.

We acknowledge that our results might differ when compared to longer time series of data. Furthermore, fine-scale variations in other local factors (e.g., habitat use, and the availability of other trophic resources) could also have influenced the rooting patterns we recorded. The lack of information on local wild boar abundance also represents a limitation of the current study and may partly account for the unexplained variation in rooting activity. Nonetheless, our study contributes valuable insights into the foraging activity of wild boar, which is known to have relevant ecological and socioeconomic impacts (Bongi *et al.* 2017).

Ethics approval

All procedures regarding animal capture and manipulation took place in compliance with the European Council Directive 92/43EEC (Italian law DPR 357/1997 and DPR 102/2019), Italian law D.Lgs 157/92 and LR 3/1994, were approved by Regione Toscana, with the supervision of the committee of the Italian Institute for Environmental Protection and Research (ISPRA) (Regione Toscana, DR 5941/2015, DR 455/2018), and were in compliance with the European Union Directive 2010/63/EU (Italian law D.Lgs 2014/26).

Availability of data and material

The survey data that support the findings of this study are available from the corresponding author upon reasonable request.

Competing interests

On behalf of all authors, the corresponding author states that there are no conflicts of interest.

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Authors' contributions

Conceptualization, P.B., S.G., and R.C.; methodology, P.B., S.G., G.P., A.B. and E.M.; formal analysis, G.B., S.S.; investigation, P.B., S.G., G.P., A.B., E.M.; data curation, P.B., S.G., G.P., A.B. and E.M.; writing—original draft preparation, G.B., P.B. and S.G.; writing—review and editing, G.B., P.B., S.G., G.P., S.S., A.B., E.M. and R.C.; supervision, P.B., S.G. and R.C. All authors have read and agreed to the published version of the manuscript.

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Appendix

Table S1. Results of GLMMs and the zero-inflated beta GLMMs (including the null models), which related the acorn production to years and grids and the rooting activity to years, grids and sessions. The models were ranked by AICc (Akaike's information criterion). For each candidate model, the table reports the AICc, **Δ**AICc, and the Akaike weight (W_i).

Model rank		**AICc**	**ΔAICc**	**W_i**
Acorn				
1	Year	227.68	0.00	1
2	Null Model	241.56	13.89	0
3	Grid	74.05	46.37	0
Rooting activity				
1	Session	-43.51	0.00	0.84
2	Null Model	-39.44	4.07	0.11
3	Year	-38.00	5.51	0.05
4	Grid	-28.11	15.40	0.00