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High acorn predation limits assisted regeneration in Mediterranean oak woodlands

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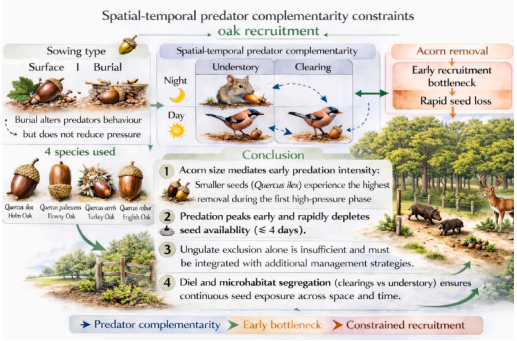
HIGHLIGHTS

- Wood mice and jays drove acorn loss within 4 days in Mediterranean oak woodlands.
- *Q. ilex* showed highest removal, *Q. robur* lowest, along a seed-size gradient.
- Buried acorns shifted foraging behaviour, but did not consistently reduce loss.
- Predators segregated wood mice nocturnal understory jay diurnal across habitats.
- Ungulate fencing alone failed; regeneration needs integrated strategies.

GRAPHICAL ABSTRACT



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ABSTRACT

Regeneration in Mediterranean oak woodlands is increasingly constrained by intense post-dispersal seed predation. Inside an ungulate-exclosure fence in the Castelporziano Presidential Estate (Central Italy), we conducted a factorial field experiment by sowing 1728 acorns of four native oaks (*Quercus cerris, Q. pubescens*, *Q. ilex*, *Q. robur*) under two seed-placement treatments (surface vs. buried) across paired microhabitats (clearing vs. understory), while monitoring predators with infrared camera traps. Acorn loss was rapid, with most removal occurring within four days. At the plot level, acorn loss differed among species (Kruskal-Wallis, $p = 0.009$); *Q. ilex* showed the highest mean removal, and the only Bonferroni-supported contrast was *Q. ilex* > *Q. robur* ($p = 0.010$). These two species represent the extremes of the seed-size spectrum, with *Q. ilex* producing smaller and lighter acorns and *Q. robur* larger and heavier ones (diameter, length, and mass; ANOVA, all $p < 0.0001$), suggesting a contribution of acorn morphology to interspecific removal differences. Removal tended to be higher

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in the understory than in clearings and higher for surface than buried acorns, but plot-paired tests did not support these patterns ($n = 4$ plot pairs). Camera trapping revealed strong habitat-diel segregation: wood mice (*Apodemus* spp.) were recorded only at night and exclusively in understory plots, whereas Eurasian jays (*Garrulus glandarius*) were strictly diurnal and used both habitats. Behavioural responses shifted with seed placement, with burial increasing exploration and digging and surface acorns eliciting more removal/consumption. Overall, early acorn fate was shaped primarily by predator identity and context-dependent activity, while seed placement modulated accessibility and behaviour rather than consistently reducing losses.

These findings indicate that, although ungulate exclosures are essential for preventing browsing and supporting regeneration, they may not be sufficient to reduce early-stage seed predation. Assisted regeneration strategies should therefore combine microhabitat diversification with targeted seed protection during the critical post-dispersal early stages.

1. Introduction

Mediterranean forests, despite being globally recognized biodiversity hotspots (Médail and Myers, 2004; Mittermeier et al., 2011), are increasingly threatened by both anthropogenic and climate-driven pressures. Major drivers of degradation include land-use change (Kumar et al., 2024), wildfires, invasive species, and prolonged drought events (Bussotti and Pollastrini, 2020; Cawson et al., 2018; Underwood et al., 2018).

Oaks (*Quercus* spp.) play a key ecological role in Mediterranean ecosystems. However, their natural regeneration is constrained by multiple ecological and environmental factors, as observed in the Castelporziano Presidential Estate, our research site, a peri-urban forest located in the coastal area of Rome, central Italy. This protected site hosts a rare example of lowland Mediterranean oak woodlands, currently undergoing senescence (Romagnoli et al., 2018) and experiencing regeneration failure (Antoniella et al., 2025). Its long-term conservation history makes it an ideal setting for ecological experiments under semi-controlled conditions and for testing management-oriented restoration strategies. In Mediterranean oak woodlands, acorn predation strongly limits natural regeneration due to the high nutritional value and palatability of acorns, which are consumed by numerous vertebrates. Post-dispersal predation is considered a key bottleneck for oak recruitment (Santos and Tellería, 1997; Gómez et al., 2003).

Although oaks primarily rely on gravity for seed dispersal, several animals also contribute, often influencing where acorns germinate and seedlings establish. Key dispersers and predators include wild ungulates, rodents, birds, and insects. In forest ecosystems, rodents significantly influence regeneration dynamics through their dual role as seed consumers and dispersers (Mason et al., 2022; Zeng et al., 2022). This role is further supported by Lianos-Guerrero et al. (2024), who showed rapid demographic responses of small mammals to variations in acorn availability in Mediterranean forests. Moreover, large herbivores can indirectly influence rodent-mediated seed predation by altering vegetation structure and ground cover through browsing and trampling. Reduced protective vegetation cover may increase perceived predation risk for rodents, limiting their foraging activity in open areas and thereby affecting acorn removal and survival patterns (Morán-López et al., 2022). Several studies have tested how microhabitat type, seed burial, and oak species influence post-dispersal acorn predation. Pons and Pausas (2007a), working in the eastern Iberian Peninsula, investigated acorn preferences in *Q. ilex*, *Q. suber*, and *Q. coccifera* across different vegetation types, finding that rodents, primarily wood mice, strongly preferred *Q. ilex* acorns, with removal rates influenced by shrub cover and habitat type. Pérez-Ramos and Marañón (2008) quantified seed predation in *Q. suber* and *Q. canariensis* in a Mediterranean oak woodland in southwestern Andalusia, and found higher predation rates for surface-exposed acorns, in densely vegetated microhabitats, and particularly for *Q. suber*; fencing did not reduce predation, implicating rodents as the main consumers. González-Rodríguez and Villar (2012) studied seed removal in *Q. ilex*, *Q. suber*, *Q. faginea*, and *Q. pyrenaica* in a Mediterranean forest of southern Spain, showing that removal was faster in plots without herbivore exclusion, where approximately 85% of seeds disappeared within nine days, and that species and microhabitat specific preferences varied with herbivore presence. Despite this growing body of literature, few studies have simultaneously quantified early-stage acorn predation, predator identity, and behavioural responses under controlled yet realistic field conditions, particularly in Mediterranean oak woodlands.

Building on these insights, this study was directly motivated by field observations from a previous (unpublished) restoration attempt conducted within the same fenced area. In that trial, hundreds of oak seedlings from the same native species were planted with controlled water (irrigated vs non-irrigated) and light (full sun vs. understory) as part of an assisted regeneration effort. However, nearly all seedlings were removed within a few days, especially in shaded plots, due to intense post-dispersal predation. Although no animals were directly observed, feeding signs and acorn remains suggested substantial seed predation, including the removal of acorns still attached at the base of the seedlings placed in the soil. This indicates that acorns remain a key nutritional resource even after germination, due to the reserves contained in the cotyledons. These unexpected losses, despite fencing against large vertebrates, highlighted the need to clarify how microhabitat conditions and seed handling affect acorn fate, particularly under rodent and bird predation, thereby motivating the experimental approach adopted in this study. All trials were conducted within a fenced area to exclude wild ungulates, whose intense browsing and seed predation pressure severely limit natural regeneration. In Mediterranean oak systems, wild boar can strongly reduce acorn availability through direct consumption, as their diet is largely based on fruits (up to 57% of the annual diet), particularly acorns, which alone can account for up to 47% (Fournier-Chambrillon et al., 1995). Rodents and birds, however, interact with acorns differently, contributing to both seed predation and dispersal through scatter-hoarding behaviour, whereas wild boar primarily act as seed consumers, directly reducing acorn availability (Sunyer et al., 2015). In the study area, long-term monitoring (1989–2025) indicates that wild boar density fluctuated widely over time, with observed minimum values of approximately 20 individuals/km^2 and maximum values exceeding 60 individuals/km^2 (Franzetti et al., in press), suggesting a potentially strong pressure on acorn availability. Conducting the experiment within an ungulate exclosure therefore allowed us to isolate the role of smaller seed consumers and to assess acorn fate under conditions where the strong effect of large omnivores was removed. Outside fenced areas, the understory of oak forests is almost entirely absent due to chronic overbrowsing, resulting in negligible tree regeneration (Antoniella et al., 2025). Within the fenced area, some understory vegetation and regenerating shrubs are present; however, oak regeneration remains extremely limited (Piccinno, 2021).

The main objective of this study was therefore to quantify early-stage acorn predation under controlled field conditions by disentangling the relative effects of oak species identity, seed placement (surface vs buried), microhabitat characteristics (clearing vs. understory), and predator activity on seed fate, while providing management-relevant insights for assisted regeneration based on artificial sowing. In parallel, camera trapping was used to identify predator taxa and characterize

their diel and habitat-specific activity patterns. A total of 1728 acorns were deployed across treatments and microhabitats, ensuring sufficient replication for robust ecological inference. Based on previous field observations, we tested the hypothesis that acorn removal would be lower in open microhabitats, likely due to higher perceived predation risk for small mammals, and that buried acorns would experience slower removal than surface-sown acorns. No strong a priori hypotheses were formulated regarding species-specific preferences or predator identity, as these were expected to depend on local ecological conditions and had not been previously investigated at the study site. However, based on previous studies in Mediterranean oak systems (Pons and Pausas, 2007a, 2007b; Pérez-Ramos and Marañón, 2008; González-Rodríguez and Villar, 2012), some degree of species-specific selectivity was expected, although potentially varying with local predator assemblages and environmental context. This investigation advances a mechanistic understanding of acorn fate under realistic ecological constraints by integrating experimental and observational approaches, while providing management-relevant insights for assisted regeneration in Mediterranean oak woodlands, where protection from large herbivores alone is insufficient to ensure early seedling establishment.

2. Materials and methods

2.1. Study area

The experimental site, known as Campo di Rota (41°43′35.30″N, 12°23′31.06″E), is located within the Castelporziano Presidential Estate, a 6000-ha protected area forming part of the Natura 2000 network. Located near Rome and the Tyrrhenian coast of Central Italy, this peri-urban forest is subject to both ecological and human pressures and provides key ecosystem services. The site is characterized by a typical Mediterranean climate, with a mean annual temperature of 16 °C and mean annual precipitation of 743 mm, concentrated in spring and autumn. These values are based on in situ monthly average data collected at Castelporziano over the period 1995–2022 (Fig. 1). In line with climate change signals, recent analyses report a clear warming trend in the study area, with annual maximum temperature (Tmax) increasing by ~1.5 °C over 1995–2023 and the strongest seasonal increases occurring in summer and autumn; similar warming is also observed in surrounding urbanized regions (Di Giuseppe et al., 2026).

The forest canopy is dominated by native deciduous and evergreen oak species, mainly *Quercus cerris*, *Q. ilex*, *Q. frainetto*, *Q. robur*, and *Q. suber*. The understory, typical of Mediterranean maquis, includes sclerophyllous and shrub species such as *Phillyrea latifolia*, *Myrtus communis*, *Arbutus unedo*, and *Erica arborea*, contributing to a complex vegetation structure. The fence is a non-electric physical barrier, approximately 2 m high and buried about 0.5 m underground. It consists of a 10 × 10 cm welded wire mesh below ground and a 5 × 4 cm hexagonal double-twist mesh above ground, allowing the passage of small rodents while effectively excluding larger herbivorous mammals.

2.2. Microhabitat selection and plot design

Mature acorns were collected in October and November 2024 directly beneath mother trees of four native oak species, *Q. cerris*, *Q. pubescens*, *Q. ilex* and *Q. robur*. Acorns were manually selected for integrity and stored under controlled conditions (2–3 °C, 60–70% RH, dark), following guidelines for short- to medium-term storage of recalcitrant oak seeds (Forest Service, 2008). Non-viable acorns (e.g., empty or insect-infested) were removed via water flotation (Bonfil, 1998). The experimental design comprised eight main plots, each covering an area of 16 m^2. To characterize canopy structure and support microhabitat classification, high-resolution LiDAR (Light Detection and Ranging) data were used to derive three-dimensional canopy metrics. LiDAR-based

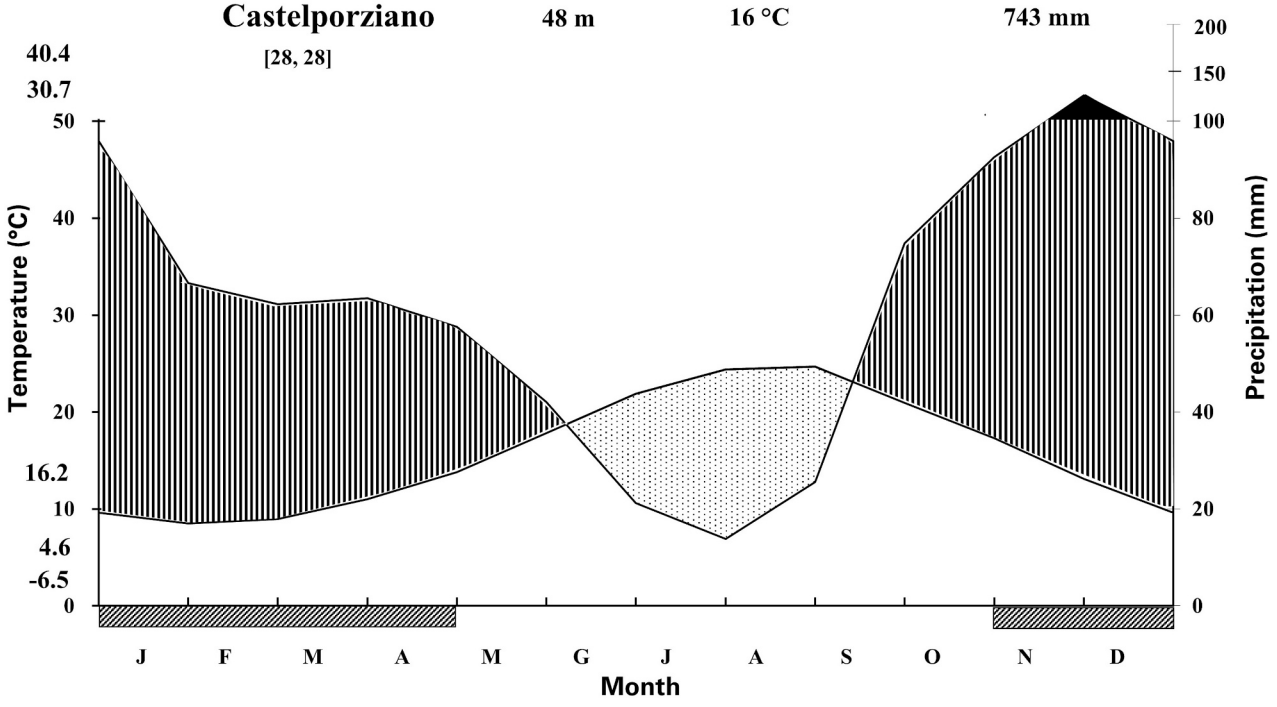

Fig. 1. Walter-Lieth climate diagram based upon monthly averages for temperature and precipitation for the Castelporziano site (period 1995–2022). Vertical black shading where the precipitation curve supersedes the temperature curve indicates a moist period. The top black area indicates monthly precipitation exceeding 100 mm, reported on a logarithmic scale. Bold numbers close to the left axis correspond to (from top to bottom): (1) annual absolute maximum temperature, (2) average daily maximum temperature of the warmest month, (3) annual thermal excursion, (4) average daily minimum temperature of the coldest month, (5) annual absolute minimum temperature. Dashed bars below the horizontal line indicate the possibility of frost with average daily minimum temperature above 0 °C, while a black bar below the horizontal line indicates average daily minimum temperature below 0 °C. [28] is the number of years; 48 m is the elevation a.s.l.; 16 °C is the mean annual temperature; 743 mm is the mean annual precipitation.

maps allowed the identification of forest patches spanning a gradient of canopy density, which were subsequently validated in the field using hemispherical photography. Based on this classification, four plots were randomly located within relatively open canopy gaps and four within closed-canopy understory areas, spatially paired to minimize environmental heterogeneity. Plot pairs were separated from each other by a distance ranging from 15 to 20 m, ensuring spatial independence while maintaining comparable environmental conditions. Canopy closure values were consistently higher in understory plots (> 98%) and lower, though more variable, in clearing plots (~ 60–91%), reflecting the intended canopy-openness between paired microhabitats. Microhabitats were defined on a relative basis within each plot pair, such that plots classified as clearings always exhibited lower canopy cover than their paired understory plots. Accordingly, canopy cover was analysed as a relative, paired contrast, where each clearing plot exhibited lower canopy cover than its corresponding understory plot, regardless of absolute values. Furthermore, these differences were associated with strong and consistent contrasts in plant area index (PAI), with understory plots showing approximately 1.7 to 3.6-fold higher PAI values than paired clearings, based on hemispherical photographs (Fig. S.2; Supplementary Material). Canopy closure, derived from hemispherical images as the proportion of sky obscured by vegetation differs conceptually from PAI, which integrates the cumulative plant area along the profile. Consequently, small differences in canopy closure, especially under high-closure conditions (>90%), can correspond to substantial differences in PAI. This distinction is particularly relevant in structurally complex Mediterranean forests.

Each main plot contained 12 subplots, corresponding to three replicates per oak species (*Q. cerris*, *Q. pubescens*, *Q. ilex*, *Q. robur*). In each subplot, nine acorns were arranged in a 3 × 3 grid over a 0.3 × 0.3 m area using a standardized planting template. This resulted in 108 acorns per main plot (9 acorns × 3 replicates × 4 species), and 864 acorns per sowing treatment. In total, 1728 acorns were sown across both treatments, with equal representation of species and sowing depth. Species assignment to subplots followed a randomized split-plot design to prevent spatial bias (Fig. 2). Additional details on plot selection are provided in the Supplementary Material (Section S1: Plot layout and subplot structure).

2.3. Sowing treatments

The experiment was carried out through two consecutive sowing campaigns, ensuring an identical spatial layout and plot structure. The second campaign was conducted two weeks after the first, under comparable soil moisture and climatic conditions, confirming environmental consistency between surface and buried sowing treatments. The first campaign involved surface sowing, in which acorns were placed directly on the ground and left uncovered to simulate passive gravity dispersal. The second campaign involved buried sowing, performed shortly thereafter, where acorns were sown at 2–3 cm depth to mimic endozoochorous or scatter-hoarding dispersal (Xiao et al., 2006; Bossema, 1979).

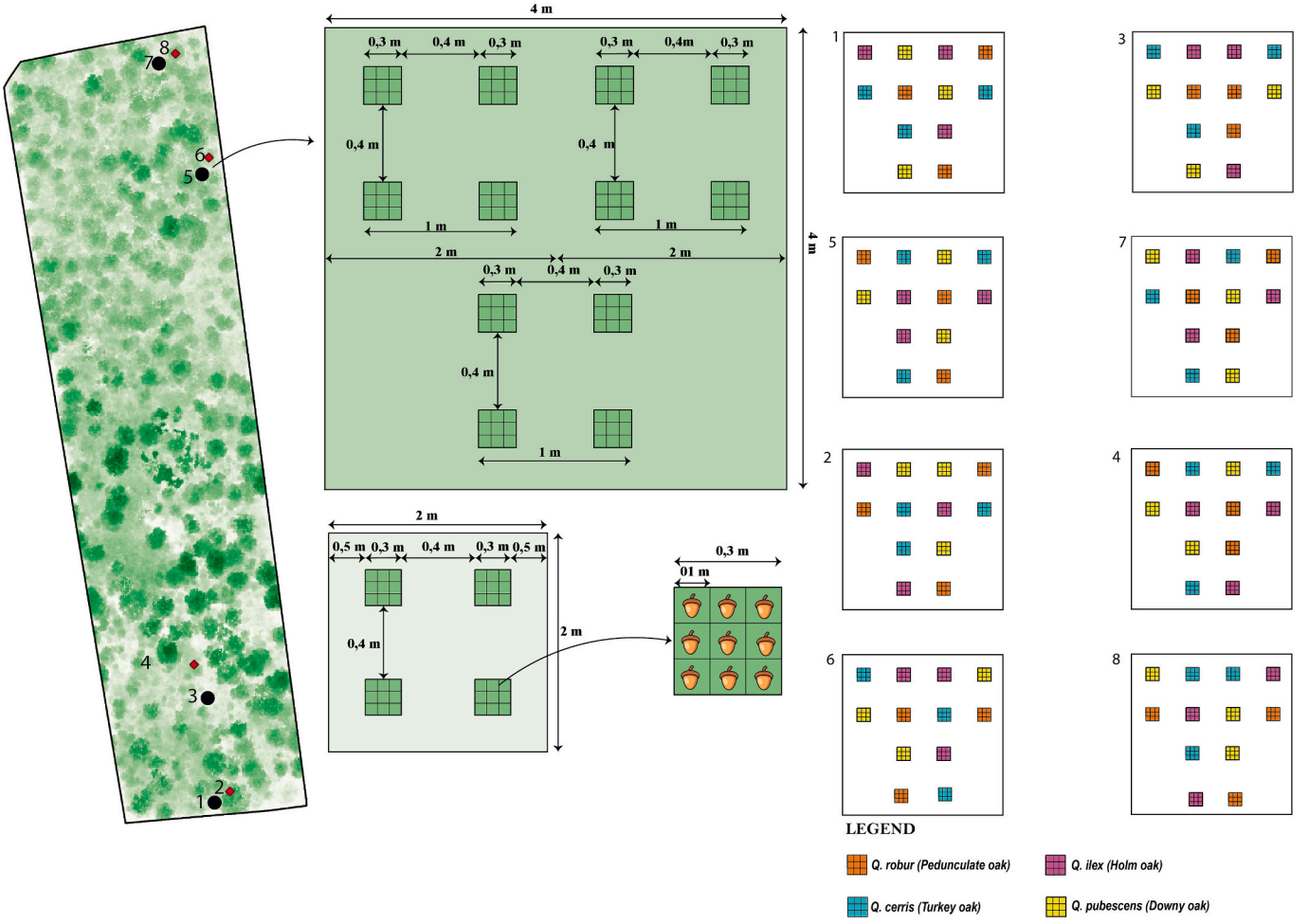

Fig. 2. Plot selection and within-plot layout. (left) LiDAR-derived canopy map of the Campo di Rota sector showing the eight experimental plots (clearing = black bullets; understory = red rhombuses). (right) Schematic of the replicated within-plot layout used in each plot, showing the experimental layout and factorial design (seed placement × species); 12 subplots per plot (3 replicates × 4 species), each with a 3 × 3 acorn grid.

2.4. Monitoring protocol and camera trapping

Acorn fate was assessed at 4-day intervals. In parallel, infrared motion-triggered camera traps were deployed in each main plot to identify the consumers responsible for acorn losses and to quantify context-dependent activity. Cameras were positioned to maximize coverage of the sowing grids while minimizing disturbance and were checked during each monitoring visit; video files were downloaded and archived systematically. Each independent video record was annotated for taxon identity, microhabitat (Clearing vs Understory), and diel period (day and night). The diel period was assigned by matching the timestamp of each record to local sunrise and sunset times. Behaviour was classified into six mutually exclusive categories: (i) removal, (ii) on-site consumption, (iii) exploration of the sowing area, (iv) digging, (v) passage without manipulation, and (vi) territorial marking. For downstream analyses, behaviors were also pooled into manipulative (removal, consumption, digging) and non-manipulative (exploration, passage, marking) classes to separate direct seed-handling events from background activity.

2.5. Statistical analysis

2.5.1. Acorn morphology

Morphological traits of acorns (diameter, length, and weight) were analysed to assess interspecific differences prior to burial. For each trait, one-way analyses of variance (ANOVA) were performed with species as the grouping factor. Assumptions of normality (Shapiro-Wilk test) and homogeneity of variances (Levene's test) were evaluated; although minor deviations were detected for some variables, sample sizes were balanced and no influential outliers were observed, supporting the use of ANOVA. Pairwise differences among species were assessed using Tukey's HSD post-hoc tests. In addition, a multivariate analysis of variance (MANOVA) was conducted to test for overall species differences across all morphological traits jointly.

2.5.2. Seed predation rates

Normality of acorn loss data was rejected across groups (Shapiro-Wilk tests, all $p < 0.001$); thus, non-parametric tests were used where appropriate for univariate comparisons. Analyses were performed separately for each sampling interval. Habitat effects (understory vs. clearing) were evaluated at the plot-pair level using paired Wilcoxon signed-rank tests, stratified by burial treatment. To provide an integrative assessment, linear mixed-effects models were fitted with burial treatment, light environment, and their interaction as fixed effects. Random intercepts for plot pairs and for plots nested within pairs were included to reflect the paired design and repeated observations within plots. Model inference used Satterthwaite's approximation for degrees of freedom, and post-hoc contrasts were computed using estimated marginal means with Bonferroni correction. For species-level comparisons, replicate observations within plots were averaged to avoid pseudoreplication, species effects were then tested using Kruskal-Wallis tests followed by Bonferroni-adjusted pairwise Wilcoxon tests. All analyses were conducted in R (version 4.4.3) with $\alpha = 0.05$.

2.5.3. Camera trap data and predator activity

Camera trap data were used to characterize predator assemblages, diel activity patterns, and habitat-associated behaviors in relation to experimental acorn plots. Each video record was classified by species identity, behaviour type, habitat (clearing vs. understory), and diel period (day vs. night). Behaviors were further grouped into manipulative (acorn removal, digging, or on-site consumption) and non-manipulative categories. However, it was not possible to determine which acorn species was handled by each animal, as behaviour could not be directly linked to seed identity due to limitations in camera framing and field of view.

An initial multivariate overview of predator-context associations was obtained using correspondence analysis (CA), applied to a contingency table of species occurrences across combined habitat × diel categories (clearing-day, clearing-night, understory-day, understory-night). The CA was used as an exploratory tool to visualize dominant ecological gradients structuring predator activity, rather than as a paired inferential test. Subsequently, habitat-related differences in predator activity were examined using paired comparisons. For each plot pair, relative frequencies of species occurrence and manipulative behaviors were calculated separately for clearing and understory plots, and differences were evaluated using paired Wilcoxon signed-rank tests. In addition, activity percentiles (25_{th}, 50_{th}, and 75_{th}) were calculated for the main seed consumers to provide a general description of activity timing across sowing treatments. Differences in activity timing between groups were assessed using Wilcoxon rank-sum tests.

3. Results

Acorn removal differed significantly among intervals (Kruskal-Wallis on plot means, $p = 0.00036$): Interval 1 losses were higher than Intervals 2 and 3 (both $p = 0.003$), while Interval 2 and 3 did not differ ($p = 0.95$). This pattern reflects a rapid depletion of available acorns early in the experiment; consequently, subsequent analyses focus on the first interval, when predation pressure was highest and biologically most informative.

3.1. Morphological differences among oak species

Mean acorn diameter, length, and weight differed significantly among species (Table 1; one-way ANOVA, all $p < 0.0001$). Across species, acorn size varied markedly, with *Q. ilex* showing the smallest and *Q. robur* the largest acorns across traits (diameter 14.63–19.07 mm, length 28.44–33.57 mm, weight 3.71–7.18 g; Table 1). Pairwise differences among species for each trait were assessed using Tukey's HSD (Table 1).

These differences were consistent across traits, as confirmed by multivariate analysis of variance (MANOVA) with an overall species effect when considering all traits jointly (Pillai's trace = 0.58, $F_{9,636} = 17.10$, $p < 0.001$).

3.2. Factors affecting seed predation rates

At the site level, mean acorn loss showed clear contrast between clearing and understory microsites across paired plots (Fig. 3). In three out of four plot pairs, acorn removal was higher under understory conditions, where mean loss ranged from 91.7% to 100%, compared with 64.8% to 86.1% in clearings. In contrast, one plot pair exhibited an opposite pattern, with higher removal in clearing microsites (e.g. 82.4% vs 64.8% for buried acorns). Consistent with this site-level heterogeneity, paired comparisons between habitats did not detect statistically significant differences within plot pairs for either burial treatment (all $p > 0.18$). However, this may reflect the limited statistical power of paired tests based on a small number of site-level replicates ($n = 4$).

Table 1
Mean values (±SD) of acorn morphological traits for four Quercus species ($n = 54$ acorns per species). Superscript letters indicate Tukey's HSD post-hoc significance groups ($\alpha = 0.05$) within each trait: means sharing at least one letter are not significantly different, whereas means with no letters in common differ significantly (Tukey-adjusted $P \leq 0.05$). Asterisks indicate significance for one-way ANOVAs ($p < 0.0001$) for each trait.

Species	Diameter*** (mm)	Length*** (mm)	Weight*** (g)
Q. ilex	14.63 ± 2.44^{a}	28.44 ± 1.62^{a}	3.71 ± 1.24^{a}
Q. pubescens	15.98 ± 1.36^{b}	29.89 ± 7.48^{ab}	4.61 ± 1.18^{b}
Q. cerris	15.89 ± 1.56^{b}	31.89 ± 2.72^{bc}	5.43 ± 1.36^{c}
Q. robur	19.07 ± 2.51^{c}	33.57 ± 3.81^{c}	7.18 ± 1.75^{d}

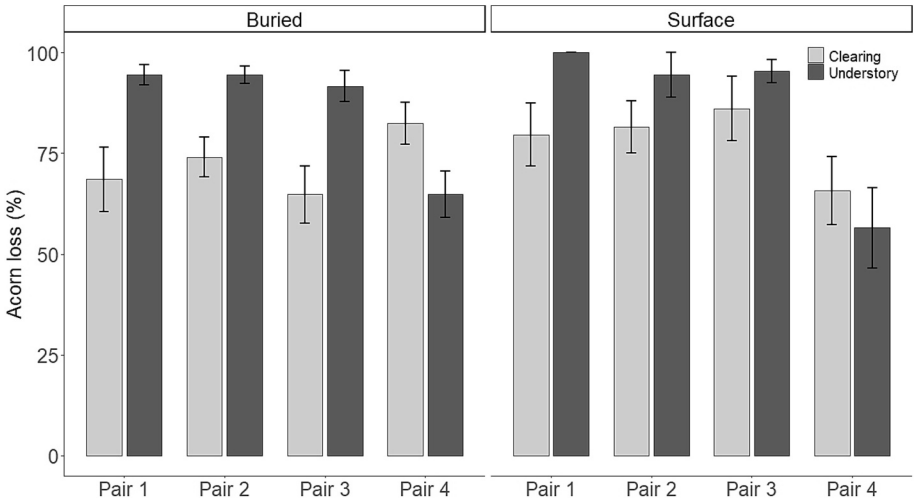

Fig. 3. Mean percentage of acorn loss (± SE) for buried and surface acorns during the first sampling interval, shown separately for each paired plot. Panels represent plot pairs (Pair 1 = plots 1–2; Pair 2 = plots 3–4; Pair 3 = plots 5–6; Pair 4 = plots 7–8), illustrating site-level variability in habitat responses.

The linear mixed-effects model did not detect a significant effect of light environment in the first interval (estimate = 13.9%, $p = 0.19$), and no treatment × habitat contrasts were significant after multiple-comparison correction. These results indicate that while local variability exists and mean removal tended to be higher in shaded microsites, support for a consistent habitat effect was limited once non-independence within plots was explicitly accounted for.

3.3. Species-specific acorn removal

Paired Wilcoxon tests comparing understory vs clearing within plot pairs showed no significant habitat differences for any species or burial treatment (all $p \geq 0.18$). When analysed across habitats and treatments, acorn loss differed among species (Kruskal-Wallis test, $p = 0.009$). Bonferroni-corrected pairwise comparisons indicated higher removal in *Q. ilex* than in *Q. robur* ($p = 0.010$), whereas all other species contrasts were not significant after correction (all $p \geq 0.167$).

Despite limited power ($n = 4$), mean values consistently suggested high susceptibility of *Q. ilex* (Fig. 4), particularly in the understory (buried mean: 91.7%, range: 77.8–100%; surface mean: 99.1%, range: 96.3–100%). In contrast, the other species showed lower and often more variable removal under the same conditions (e.g., *Q. robur* buried mean: 80.6%, range: 51.9–92.6%; surface mean: 79.6%, range: 40.7–100%). In the clearing, surface acorns showed especially strong divergence between species, with *Q. ilex* at 98.1% (range: 92.6–100%) and *Q. robur* at 48.1% (range: 40.7–51.9%), indicating high removal of *Q. ilex* and consistently low removal of *Q. robur*. In contrast, mean acorn loss for buried acorns overlapped more among species (e.g., *Q. pubescens*: mean 82.4%, range 77.8–88.9%; *Q. ilex*: mean 75.0%, range 51.9–96.3%), reflecting greater between-plot heterogeneity.

When species were analysed separately within each habitat, no differences emerged in the understory (all adjusted $p \geq 0.50$). In the clearing, the only significant contrast after correction was higher removal of Q. pubescens than *Q. robur* ($p = 0.037$), while *Q. ilex* also tended to exceed *Q. robur* ($p = 0.068$). Finally, surface acorns showed higher mean loss than buried acorns in 5 of 8 species-habitat combinations (62.5%), suggesting a modest protective effect of burial; however, no within-species contrast remained significant after Bonferroni correction (all adjusted $p \geq 0.229$).

These patterns indicate consistently higher removal rates for *Q. ilex*

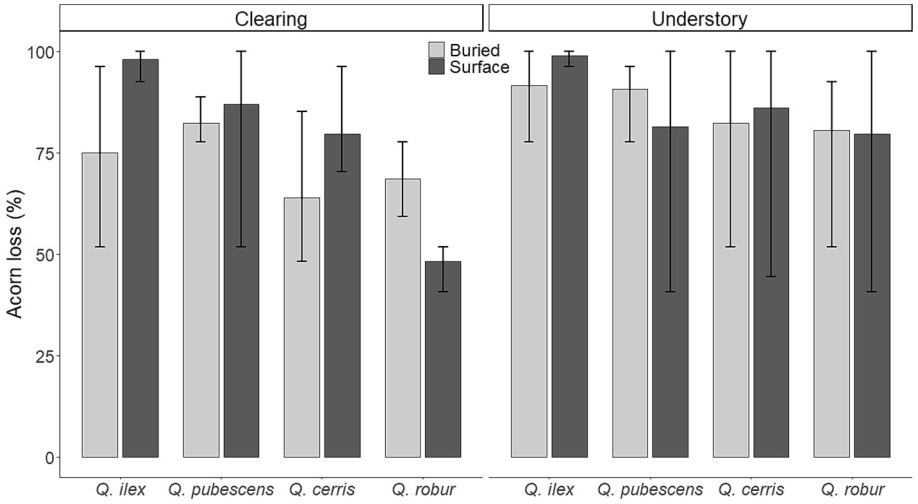

Fig. 4. Mean species percentage of acorn loss by burial treatment and habitat during the first sampling interval. Oak species are shown on the x-axis in decreasing order of overall removal, while the y-axis represents the percentage of predated acorns. Bars represent mean plot-level values (n = 4 independent plots per species × habitat × treatment), and error bars indicate the observed range across plots. Bars are coloured according to burial treatment, with buried and surface acorns shown in light blue and light green, respectively. Panels represent plots located clearing (left) and understory (right) habitats.

compared to *Q. robur*. However, camera trapping did not allow direct attribution of seed selection to specific animal taxa, and thus the inference remains indirect. The temporal and spatial segregation of wood mice and Eurasian jay, together with the repeated pattern of higher *Q. ilex* removal across habitats, suggests that both taxa may contribute to this species-specific pattern.

3.4. Overall animal assemblage and behavioural patterns

Ten animal taxa were recorded interacting with experimental acorns. Although the study area was enclosed by a fence designed to exclude large ungulates, some medium-sized mammals (e.g., foxes) were occasionally recorded, likely entering through small ground-level openings, while larger herbivores were effectively excluded.

The most frequently observed species were the wood mice *Apodemus* spp. (given the morphological similarity between *A. sylvaticus* and *A. flavicollis* in camera trap recordings, captures were pooled at the genus level), accounting for 42.9% of all recorded events ($n = 555$), followed by the Eurasian jay (*Garrulus glandarius*; 23.0%, $n = 297$) and the red fox (*Vulpes vulpes*; 17.9%, $n = 231$). All remaining species individually accounted for less than 5% of observations, including badger (*Meles meles*; 3.9%), blackbird (*Turdus merula*; 3.1%), pine marten (*Martes martes*; 2.2%), and crested porcupine (*Hystrix cristata*; 1.6%), while black rat (*Rattus rattus*) and hooded crow (*Corvus cornix*) were recorded only sporadically.

Across species and treatments, exploratory behaviour was by far the most frequently recorded activity, representing 48.2% of all events ($n = 624$), followed by simple passage without manipulation (24.5%, $n = 317$). Behaviors directly involving acorn manipulation, such as removal (7.4%, $n = 96$), digging (5.9%, $n = 77$), and on-site consumption (4.0%, $n = 52$), were comparatively less frequent. All remaining behaviors, including territorial marking, accounted for only a small proportion of the dataset. Selected video recordings illustrating acorn handling by the main seed consumers (*Apodemus* spp. and *Garrulus glandarius*) are provided as Supplementary material (Videos S1–S2) to support the behavioural observations reported in the text.

3.4.1. Associations between species, diel period and environmental contexts

Species occurrence was significantly associated with habitat type and diel period ($\chi^2 = 598.5$, $p < 0.001$). Standardized residuals (stdr) showed clear patterns: wood mice were strongly over-represented in understory at night (stdr = +18.43) and under-represented during the day (clearing-day: −12.38; understory-day: −8.62), whereas Eurasian jay was strongly associated with daytime contexts (Understory-Day: +10.88; Clearing-Day: +7.67) and strongly under-represented in understory at night (−13.95) (Fig. 5).

Dim_1, representing a diel activity gradient, accounted for 62.6% of the total inertia (i.e., 62.6% of the departure from independence between species and habitat-diel contexts), primarily contrasting nocturnal understory activity with daytime contexts and separating wood mice from Eurasian jay. Dim2, reflecting a habitat-use gradient, explained a further 29.6% of the total inertia and was dominated by the "clearing at night" context, largely driven by badger occurrence. Together, the first two dimensions captured 92.2% of total inertia, indicating that these two gradients summarize most of the association structure in the analysis. Larger mammals showed intermediate or distinct positions in the ordination space. Badgers were closely associated with night-time activity in clearings, while red foxes occupied a more central position, indicating flexible use of both habitats and diel periods. Overall, the ordination highlights a clear partitioning of predator activity along diel and habitat gradients during the period of highest acorn removal.

When classifying behaviors into functional categories, manipulation (acorn removal, on-site consumption, and digging), exploration, transit, and marking, we observed that manipulation behaviors, including acorn removal, digging, and consumption, were strongly concentrated in just two taxa: the wood mouse and the Eurasian jay. Specifically, wood mice accounted for 105 manipulation events, and jays for 91, with minimal contributions from other species (e.g., 10 for badgers, 15 for red foxes, and none for carrion crows), indicating that these two taxa accounted for most direct interactions determining acorn fate.

Exploration accounted for 54% of Eurasian jay observations and 67% of wood mouse observations, highlighting how acorn predation was embedded in broader exploratory strategies.

Given their dominance in acorn manipulation, subsequent analyses will focus specifically on these two species. We examine how their foraging behaviors vary across experimental treatments (burial, microhabitat, time), providing deeper insight into context-dependent

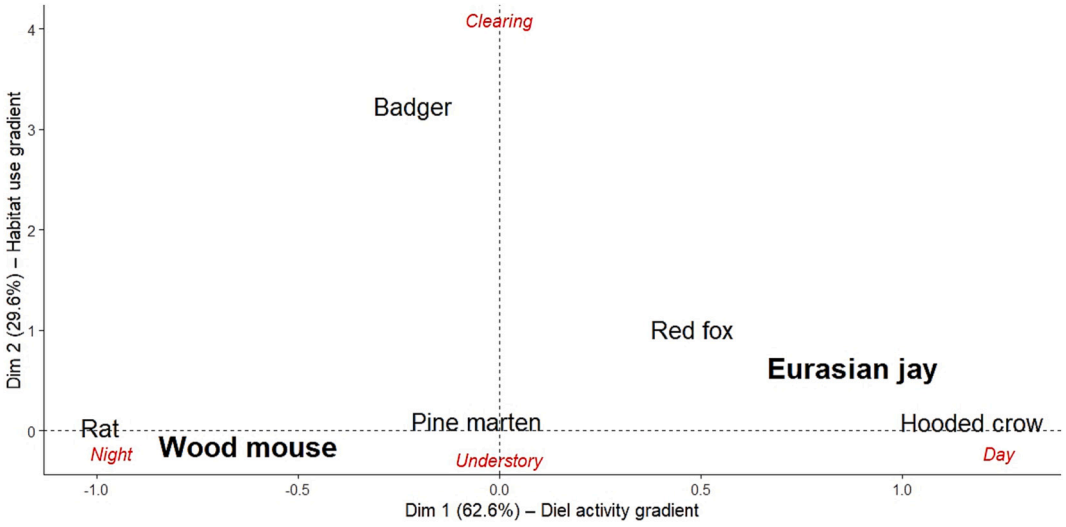

Fig. 5. Correspondence analysis (CA) of animal species in relation to habitat type and diel period during the first sampling interval (Interval 1). The biplot displays associations between recorded animal species (black labels) and habitat-period combinations (red coloured labels: night, day, understory and clearing). The first dimension (Dim 1; 62.6% of inertia) represents a diel activity gradient, separating predominantly nocturnal taxa (negative scores) from diurnal species (positive scores). The second dimension (Dim 2; 29.6% of inertia) reflects a habitat-use gradient, contrasting understory- and clearing-associated activity. Proximity between species and habitat-period categories indicates stronger associations. Dashed lines mark the origin of the ordination space. Only data from the first sampling interval (surface and buried acorns) are included.

predation patterns.

3.4.2. Context-dependent behaviour and treatment responses

The wood mouse (*Apodemus* spp.) was never recorded in clearing plots and was therefore excluded a priori from paired habitat comparisons. Paired Wilcoxon signed-rank tests comparing species occurrence between clearing and understory plots among the remaining species revealed no statistically significant differences (all $p > 0.10$). Eurasian jay showed a consistent, though non-significant, tendency toward higher relative manipulation rates in the understory (36% vs. 29%).

Wood mice showed predominantly exploratory behaviour (67%), followed by manipulation events (19%), whereas Eurasian jays exhibited a more balanced behavioural profile, with slightly higher manipulation rates in the understory.

Behavioural responses to seed burial treatments differed between the two main seed consumers (Fig. 6).

For the Eurasian jay, buried acorns were predominantly explored (84%), whereas surface acorns elicited a broader behavioural repertoire, including increased removal or consumption (27.8%) and passage events. Digging behaviour was rare across treatments (Eurasian jay: $n = 10$; wood mouse: $n = 5$), preventing robust inference regarding treatment effects. Under buried conditions, seed retrieval may occur without digging being recorded as a distinct event, for example when acorns are shallowly buried and removed with little or no visible soil disturbance, or when the digging action is not fully captured in the video recording. Wood mice showed predominantly exploratory behaviour, particularly for buried acorns, whereas removal/consumption was more frequent for surface seeds (35.7% vs. 19.7%).

Activity timing remained broadly consistent between sowing treatments for both main seed consumers. Eurasian jay showed a diurnal activity window in both treatments, with the central 50% of detections occurring between 10:00 and 18:00 in Surface and between 12:00 and 18:00 in Buried treatments (median = 15:30 and 14:00, respectively). Wood mouse remained strongly nocturnal under both treatments, with activity concentrated between 22:00 and 00:00 in Surface and between 22:00 and 01:00 in buried treatments (median = 23:00 and 00:00, respectively). For Eurasian jay, activity timing did not differ significantly between microhabitats (Wilcoxon rank-sum test, $p = 0.395$).

4. Discussion

4.1. Drivers of acorn predation: the interplay between seed traits and habitat structure

Our study indicates that habitat structure and seed traits jointly shape post-dispersal acorn predation. At the plot level, acorn loss differed among oak species (Kruskal-Wallis, $p = 0.009$), and Bonferroni-corrected comparisons showed higher removal for *Q. ilex* than *Q. robur* ($p = 0.010$), while other contrasts did not remain significant after correction. These species represent the extremes of the measured seed-size range (smallest and lightest in *Q. ilex* vs. largest and heaviest in *Q. robur*), which is consistent with a role of acorn morphology in shaping detectability and handling costs.

The higher removal of *Q. ilex*, when compared with the other species, may be driven by different animals according to the habitats. In the understory, where *Apodemus* spp. were almost exclusively active, removal may reflect small-mammal preferences for compact, easily handled seeds. This is consistent with Muñoz et al. (2012), who found that smaller and more compact acorns were preferentially removed by scatter-hoarding rodents in Mediterranean environments. In contrast, in clearing plots, where *Garrulus glandarius* predominated, the same pattern of high *Q. ilex* removal may instead result from foraging by jays, potentially guided by visual cues or differences in palatability. In particular, surface-placed acorns may be more easily detected in open habitats, although intrinsic seed traits likely also influence selection by avian consumers. Jays are known to prefer *Q. ilex* acorns over other Mediterranean oaks, and to select intact, uninfested acorns of intermediate-to-large size (Pons and Pausas, 2007b; Wróbel et al., 2025). In central European contexts, smaller acorns may be favored, indicating that both habitat structure and intrinsic acorn traits shape jay foraging behaviour (Mitrus and Szabó, 2020).

These findings align with earlier work reporting predator preferences for smaller or more palatable acorns in Mediterranean systems (Bonacchi et al., 2015). However, contrasting results have been observed in other ecological contexts. For instance, Cheng et al. (2024) found that rodents in a temperate deciduous forest in northern China preferred larger acorns of *Q. liaotungensis*, whereas Chen et al. (2022), using a dataset of 41 species in a subtropical evergreen broad-leaved forest in southwestern China, reported that seed size effects varied within species, but followed a hump-shaped pattern across species, with intermediate-sized seeds showing the highest removal rates. These contrasting results highlight the context-dependence of trait-mediated

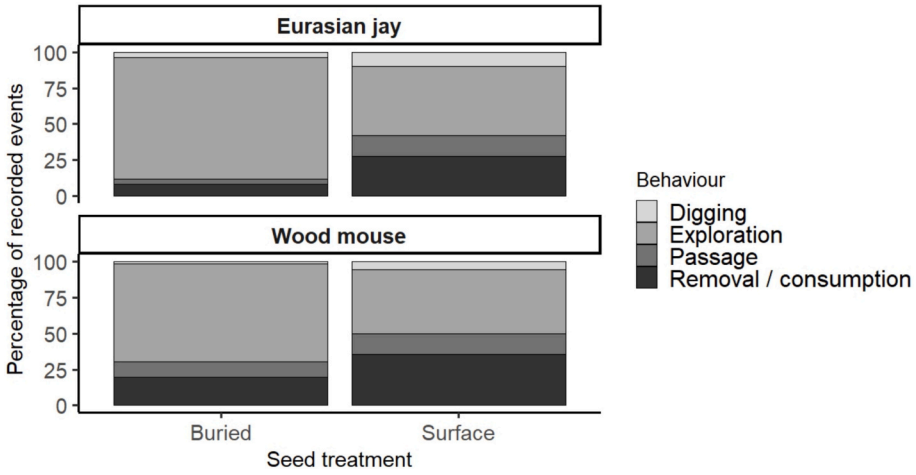

Fig. 6. Behavioural responses of key seed consumers across seed burial treatments. Proportional distribution of behavioural events recorded for the two main seed consumers, the wood mouse (*Apodemus* spp.) and the Eurasian jay (*Garrulus glandarius*), under two seed placement treatments (Buried and Surface) during the first sampling interval. Bars represent the percentage of events assigned to four functional behaviour categories: exploration, removal/consumption, passage, and digging. Digging refers to substrate disturbance only and does not imply seed consumption.

predation and emphasize the need for site-specific data to inform oak regeneration strategies. Although we did not measure chemical traits such as tannin content, it is plausible that seed composition contributed to the observed interspecific differences. For example, Zhang et al. (2018) showed that tannin levels influence rodent foraging and population dynamics. Our data suggest that habitat openness interacts with seed traits: under dense understory cover, high predation pressure may mask fine-scale differences among species, whereas in clearings, greater exposure and detection constraints may enhance selective removal of easily handled acorns (Perea et al., 2011a; García-Hernández et al., 2016), or reflect preferences linked to acorn palatability (Pons and Pausas, 2007a, 2007b) although this could not be directly assessed in our study. While our study included multiple oak species, it reinforces the broader notion that morphological traits like seed size play a central role in shaping foraging decisions. In addition, mean acorn removal tended to be higher in the understory than in clearings and higher for surface than buried acorns, indicating context-dependent trends consistent with reduced detectability and accessibility under burial. However, these effects were not statistically supported in our plot-paired analyses and should be interpreted as directional patterns rather than confirmed differences.

4.2. High predation rate and the role of exclosures

Overall acorn removal was rapid and substantial, confirming that post-dispersal seed predation represents a critical bottleneck for oak recruitment in Mediterranean oak woodlands. The majority of acorns were removed within the first four days, indicating intense and immediate foraging activity. Importantly, high removal rates were observed even inside the fenced area, suggesting that the exclusion of ungulates does not necessarily translate into low seed predation rates. Rodents, however, may play a dual role as both seed predators and dispersers. Indeed, small mammal density is negatively correlated with ungulate density (Afonso et al., 2024), suggesting that the exclusion of ungulates may indirectly increase rodent abundance and thus seed predation pressure. Similar findings were reported by Pérez-Ramos and Marañón (2008), who observed higher acorn predation within exclosures, and by González-Rodríguez and Villar (2012) and Morán-López et al. (2022), who emphasized the indirect role of large herbivores and predators in modulating rodent foraging behaviour.

Comparable rapid acorn depletion has been documented in other Mediterranean systems. For example, Perea et al. (2011b) observed complete acorn removal within a few days, reinforcing the idea that shelter availability and microhabitat structure strongly shape rodent foraging behaviour. In contrast, Pons and Pausas (2007a) reported slower removal dynamics over 68 days, with more gradual emergence of species-specific preferences. Our findings, therefore, are consistent with the fast-paced dynamics typical of Mediterranean oak woodlands, while also highlighting that removal rates and patterns vary with local context, including predator assemblages, habitat heterogeneity, and the potential role of avian consumers such as the Eurasian jay (*Garrulus glandarius*). Overall, even in the absence of wild ungulates, acorn fate remains strongly biotically controlled, although seed removal does not necessarily imply direct seed loss.

4.3. Species-specific foraging strategies

Camera trap data showed that post-dispersal acorn fate was primarily determined by two taxa: wood mice and Eurasian jay, which together accounted for over 90% of all interaction events. This dominance is consistent with patterns observed in Mediterranean oak systems, where a few vertebrate taxa drive most seed fate outcomes (Gómez et al., 2003; Perea et al., 2011a, 2011b). Eurasian jays were recorded more frequently at surface-placed acorns, whereas wood mice were frequently recorded also under buried placement, indicating taxon-specific differences in detectability and search behaviour. Indeed, jays, relying on visual cues, were less frequently recorded at buried seeds, though they remained the main removers in open habitats. In contrast, wood mice interacted both surface and buried acorns, likely using olfactory cues, a behaviour supported by experimental evidence (Vander Wall, 2003). However, mice allocated more time to exploratory behaviour when seeds were buried, reflecting the increased search effort required to locate them. The two species also showed diel and spatial segregation: jays were diurnal and active in clearings, while mice operated nocturnally in the understory. The activity timing percentile-based analysis further indicates that these temporal patterns were stable across sowing treatments, despite the two campaigns being conducted at different times. This supports the interpretation that diel activity was primarily species-specific rather than treatment-dependent, reflecting adaptive responses to variation in predation risk across the diel cycle (Lima and Dill, 1990; Kronfeld-Schor and Dayan, 2003). This led to continuous foraging pressure across microhabitats and time periods. Similar dynamics have been associated with recruitment bottlenecks in oak systems, where rodent foraging aligns with high seed availability (Sunyer et al., 2015). These findings underscore that while burial can delay predation, seed fate reflects the interaction between consumer behaviour and seed traits, with both factors jointly shaping post-dispersal outcomes (Yi et al., 2015).

4.4. Management implications for oak regeneration

This study provides practical insights for the ecological management of Castelporziano Presidential Estate and similar Mediterranean oak woodlands. In particular, it highlights how microhabitat conditions, seed handling strategies, and consumer behaviour interact to shape early regeneration outcomes, with direct implications for designing more effective assisted regeneration interventions.

Maintaining a heterogeneous canopy may help buffer seed predation risk across microhabitats, potentially promoting a more balanced regeneration of different oak species. More open microsites may reduce removal pressure, especially when seeds are moderately buried (2–3 cm), a depth that may delay detection by jays and reduce access by rodents, offering partial protection for vulnerable species such as *Q. ilex*. However, open conditions may also increase water stress and seedling mortality, highlighting stage-dependent trade-offs during regeneration.

Fencing design is another critical factor. While exclosures are necessary to prevent herbivory by large ungulates, large continuous fenced areas may inadvertently create safe foraging zones for small granivores like wood mice. In contrast, smaller or fragmented fenced patches, integrated within the broader forest matrix, could reduce this effect by exposing rodents to higher predation risk. However, the feasibility of implementing fine-scale seed protection strategies at operational scales remains a key challenge. Pilot experiments and adaptive management approaches will be crucial for testing scalable interventions across different forest contexts.

Given the rapid and intense acorn removal observed within just a few days, management actions should prioritize seed protection during the critical early post-sowing period. Alongside burial strategies, temporary physical protection (e.g. camouflage, light covers) or placing seeds in more open microsites with lower predator activity may reduce encounter rates. Additionally, “distraction seeding” techniques, placing decoy seeds in peripheral or predator-frequented zones, could help deflect foraging pressure away from target regeneration sites, although this approach requires further testing and may be strongly context-dependent.

Ultimately, restoration strategies should not rely solely on the exclusion of ungulates, but also address the behaviour and foraging patterns of dominant seed consumers. We recommend that managers integrate seed protection measures, such as moderate burial, temporary covers, or spatial diversification of sowing sites, into restoration protocols, especially in contexts with high small-mammal activity. Tailoring interventions to local predator assemblages, seed traits, and

microhabitat structure is essential to overcoming key ecological bottlenecks in oak regeneration. Finally, we also emphasize the importance of post-intervention monitoring to assess the effectiveness of sowing and protection strategies under real-world conditions, and to refine protocols based on observed seedling emergence and survival.

CRediT authorship contribution statement

Gabriele Antoniella: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Dario Capizzi:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Investigation, Conceptualization. **Annagrazia Calò:** Software, Methodology, Conceptualization. **Roberto Corsanici:** Writing – review & editing, Methodology, Conceptualization. **Dora Cimini:** Writing – review & editing, Methodology, Conceptualization. **Riccardo Salvati:** Methodology, Conceptualization. **Marzio Zapparoli:** Writing – review & editing, Methodology, Conceptualization. **Giuseppe Scarascia Mugnozza:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition. **Dario Papale:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition. **Tommaso Chiti:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition. **Maurizio Sabatti:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

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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.scitotenv.2026.181834.

Data availability

Data will be made available on request.

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