

Original article

Wild ungulates and carbon dynamics in Mediterranean peri-urban forests: Evaluating their impact on soil and biomass carbon storage

Gabriele Antoniella^{a,*}, Abhay Kumar^a, Federico Valerio Moresi^a, Annagrazia Calò^a, Giuseppe Scarascia Mugnozza^{a,b}, Maurizio Sabatti^a, Tommaso Chiti^a

^a Department for Innovation in Biological, Agro-food and Forest systems (DIBAF), University of Tuscia, Viterbo, Italy

^b European Forest Institute (EFI), Biocities Facility, Rome, Italy



ARTICLE INFO

Keywords:

Ungulate exclusion
Peri-urban forest
Carbon sequestration
Soil organic carbon
Long-term monitoring

ABSTRACT

This study investigates the impact of wild ungulates on carbon (C) storage in a Mediterranean oak forest within Castelporziano Presidential Estate (Rome-Italy). Using a paired-site approach, we aimed to compare a fenced (FE) area, undisturbed from ungulates for 11 years, with an adjacent unfenced (UN) area exposed to continuous wild ungulate activities. Our findings reveal that ungulates increased soil organic carbon (SOC) in deeper layers (30–60 cm) by 87.2 %, likely driven by trampling-induced organic matter redistribution, while no significant changes were occurred in upper soil layers (0–10 and 10–30 cm). Aboveground living biomass C stocks were overall similar between treatments, however, shrub biomass was markedly lower by 78 % in the UN area, reflecting the effects of strong browsing pressure. Although total ecosystem C stocks were 26.3 % higher in the UN area, this difference was not statistically significant due to high spatial variability among plots. Overall, ungulates had a positive effect on SOC stocks but negatively affected understory vegetation. Their net impact on total ecosystem C sequestration remains unclear, possibly due to the short exclusion period and the prevailing dominance of pre-existing mature trees. Moreover, the observed vegetation shift, characterized by a transition from oak-dominated high-forest to mixed stands increasingly dominated by *Carpinus spp.*, suggesting complex interactions between herbivory, browsing pressure, historical management, and climate change. These findings highlight the need for long-term monitoring to understand these effects and define effective forest conservation strategies.

1. Introduction

In the last decades, the pressure caused by invasive wild ungulates on Mediterranean ecosystems has increased significantly (Carpio et al., 2017), especially in areas where they are non-native (Caughley, 1970). The most immediate consequences of this growing pressure are evident in agricultural landscapes, where crop damage and yield losses are directly observable. However, the impact goes beyond farmland, also affecting infrastructure and contributing to traffic accidents (Colomer et al., 2024). Less visible but ecologically relevant effects include changes to soil organic carbon (SOC), which vary by land use: studies show ungulates may increase SOC in grasslands but reduce it in forests (Marks et al., 2024). Given these complexities, this study focuses on Mediterranean forests, which are recognized as global biodiversity hotspots (Médail and Myers, 2004; Mittermeier et al., 2011), to better understand how large herbivores influence SOC, vegetation, and

ecosystem functions.

Despite their high ecological value and tree species richness (Médail, 2008), Mediterranean forests are facing severe degradation driven by land use change (Kumar et al., 2024), wildfires, biological invasive species, and prolonged drought periods (Bussotti and Pollastrini, 2020; Cawson et al., 2018; Underwood et al., 2018). The degradation is especially pronounced near the Castelporziano Presidential Estate, in Rome, Italy, the site of our study, where urban sprawl has contributed to environmental decline (Trotta et al., 2015). This peri-urban deciduous oak forests represents one of the most vulnerable Mediterranean ecosystems, particularly those located in coastal areas (Recanatesi et al., 2020). From a biological perspective, invasive species are contributing to forest decline within the Castelporziano estate, where the combined impact of the alien insect *Toumeyella parvicornis* and the native *Tomicus destruens* caused the loss of over 250 ha of *Pinus pinea* L. in just six years (Guidolotti et al., 2025). Additionally, in this region, the wild boar (*Sus*

* Corresponding author.

E-mail addresses: antoniellagab@unitus.it, gabri.antoniella@hotmail.it (G. Antoniella).

<https://doi.org/10.1016/j.ufug.2025.128967>

Received 1 April 2025; Received in revised form 15 July 2025; Accepted 16 July 2025

Available online 17 July 2025

1618-8667/© 2025 The Author(s). Published by Elsevier GmbH. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

scrofa L.), originally native to Eurasia, has become one of the most widespread large mammals (Long, 2003; Barrios-Garcia and Ballari, 2012).

Although numerous studies have explored the effects of wild ungulates on Mediterranean grasslands (Bueno et al., 2013; Martínez-Estévez, et al., 2013; Yu et al., 2017), a growing body of research has also addressed their impact on forest ecosystems. Nevertheless, transferring findings across ecosystems remains challenging, and the impact of wild ungulates on soil carbon (C) dynamics remains inconclusive (Marks et al., 2024; Don, 2022). In forest ecosystems, wild ungulates, can influence SOC dynamics, plant biomass, and species composition (Pastor et al., 1993). In some cases, their presence has been associated with increased soil organic matter mainly due to fecal inputs and nutrient enrichment (Peco et al., 2006; Pulido et al., 2018). Their ecological impacts are mediated through multiple pathways, including browsing, trampling, and rooting activities that reduce shrub cover, litter accumulation, and aboveground C stocks (Lecomte et al., 2019). A meta-analysis by Tanentzap & Coomes (2012), based on studies from temperate, tropical, and arctic ecosystems, found that herbivore effects on C stocks can diminish over time. This trend is likely due to gradual ecosystem adaptation to grazing pressure. However, the same study highlighted a major knowledge gap concerning below-ground biomass and soil C, especially in areas with high herbivore densities. Conversely, some reports suggest that ungulates can degrade soil structure and C dynamics through compacting soil, disturbing litter layers, and suppressing vegetation (Gizicki et al., 2018; Napoletano et al., 2025). These contrasting finding reflects the complexity and context-dependence of herbivore impacts on forest C dynamics.

These inconsistencies underscore the challenge of generalizing ungulate effects across forest types, especially in Mediterranean ecosystems, which are highly heterogeneous and underrepresented in global C studies. Moreover, the specific role of wild boar, an increasingly dominant species in many European forests, in shaping soil processes and overall ecosystem functioning remains poorly understood. A major limitation in the literature is the frequent focus on isolated components of the forest C cycle. Most studies have addressed only individual components of the C cycle, such as either SOC (Marks et al., 2024) or aboveground biomass (Lecomte et al., 2019) but rarely both. Even when both compartments are considered, aboveground C is typically estimated indirectly, for instance through canopy cover (Ibáñez-Álvarez et al., 2022), which limits the accuracy of ecosystem-scale assessments.

To address these knowledge gaps, this study investigates the role of wild ungulates in shaping C dynamics within a mature Mediterranean oak forest at the Castelporziano. We employed a paired-site design comparing an unfenced area (UN), subject to ongoing herbivore activity, with a fenced area (FE) that has been protected from ungulates for 11 years. Across both sites, we directly measured SOC, above- and below-ground living biomass, litter, and necromass. Together, these components constitute the total ecosystem C stock.

We hypothesized that ungulate disturbances, such as foraging, trampling, rooting, and fecal deposition, would enhance SOC through increased organic inputs and accelerated biomass turnover, while concurrently reducing understory C stocks (Penman et al., 2003). In contrast, we expected no significant change in overstory biomass due to the limited duration of exclusion which may not be sufficient to detect significant structural responses in mature forest stands. By integrating all C components, this study offers a comprehensive assessment of ungulate impacts on forest C storage, particularly within the Mediterranean ecosystems.

2. Materials and methods

2.1. Site description

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-hectares protected area within the Natura 2000 network. The estate includes sites of Community Importance, such as the lowland oak woodland (Recanatesi, 2015). Situated at the edge of Rome, in close proximity to urban infrastructure and the coastline, this peri-urban forest occupies a transitional zone where ecological and anthropogenic dynamics converge. Its location and multifunctionality support a wide range of key ecosystem services, including air pollution mitigation (Fares et al., 2016), C sequestration, coastal protection, and biodiversity conservation.

From a pedological perspective, the estate is predominantly composed of highly weathered Wurmian eolian sands, alongside recent sands, alluvial deposits, and pyroclastic materials. Soils range from Entisols and Inceptisols to more developed Alfisols, exhibiting a xeric moisture regime (Biondi et al., 2001). The Campo di Rota sector is specifically characterized by Alfisol, Ultic Haploxeralfs, coarse loamy, mixed, thermic, and Plinthic Haploxeralfs, coarse loamy. The site has a flat topography and a typical Mediterranean climate with average temperatures ranging from 7 °C in winter to 24 °C in summer, with annual precipitation between 700 and 1100 mm, mostly in spring and fall (Conte et al., 2021). The forest ecosystem is dominated by different ancient *Quercus* species forming a dominant layer, primarily *Quercus cerris*, *Quercus robur*, *Quercus frainetto*, *Quercus ilex*, and *Quercus suber*. Beneath this layer, the understory, characteristic of Mediterranean scrub ecosystems, is enriched by diverse genus including *Carpinus*, *Phillyrea*, *Erica*, *Myrtus*, *Arbutus*, *Genista*, and *Cytisus*, contributing to the structural and ecological complexity of the habitat. This remnant thermophilous forest is one of the most ecologically significant woodlands within the Castelporziano Estate (Giordano et al., 1995). The area gained scientific attention to study the impact of wild ungulates, particularly fallow deer (*Dama dama*), roe deer (*Capreolus capreolus italicus*), and wild boar (*Sus scrofa*), on forest ecosystem since the 1990s, due to their high population densities and the absence of natural predators (Focardi et al., 2002). Population estimates report densities of 17–35 individuals per km² for fallow deer and 8.5 individuals per km² for roe deer (Focardi et al., 2001). Additionally, wild boar populations showed density-independent fluctuations, primarily influenced by oak forest productivity, with densities ranging from 6 to 34 individuals/km². However, based on comprehensive monitoring data, a longitudinal study conducted between 1996 and 2002, estimated an average wild boar population of 5102 individuals within the estate (Focardi et al., 2008).

2.2. Experimental design

The experimental design focused on two adjacent deciduous oak forests (~10 ha each) in different locations of Campo di Rota, characterized by contrasting levels of wild ungulate disturbance (Fig. 1). The FE site has been fenced since 2012 to exclude wild ungulates, while the UN site has remained open, reflecting natural disturbance dynamics. The fence, standing 2 m high and buried approximately 0.5 m under the ground, serves as a non-electric physical barrier. It consists of a 10 × 10 cm welded wire mesh below ground and a 5 × 4 cm hexagonal double-twist mesh above ground, which allows the passage of small rodents while effectively excluding small herbivorous mammals. The setting offered an opportunity to assess the long-term effects of ungulates exclusion under controlled conditions.

Each 10-hectares forest was divided into three areas, for a total of six sampling plots. In the FE site (Fig. 1 left side), plots A, B, and C were assigned; in the UN site (Fig. 1 right side), plots D, E, and F. Plot selection was carried out in QGIS software (QGIS Development Team, 2019) using a random procedure overlaid on the forest polygons to ensure spatial precision, minimize edge effects, and avoid subjectivity in placement. These plots served as reference units for the quantification of SOC through soil sampling, and for the measurement of living plant biomass (above and belowground), litter, and necromass. The following sections describe the quantification methods for these C pools, which were used to estimate total ecosystem C stocks. [Supplementary Material 1 \(S1\)](#)

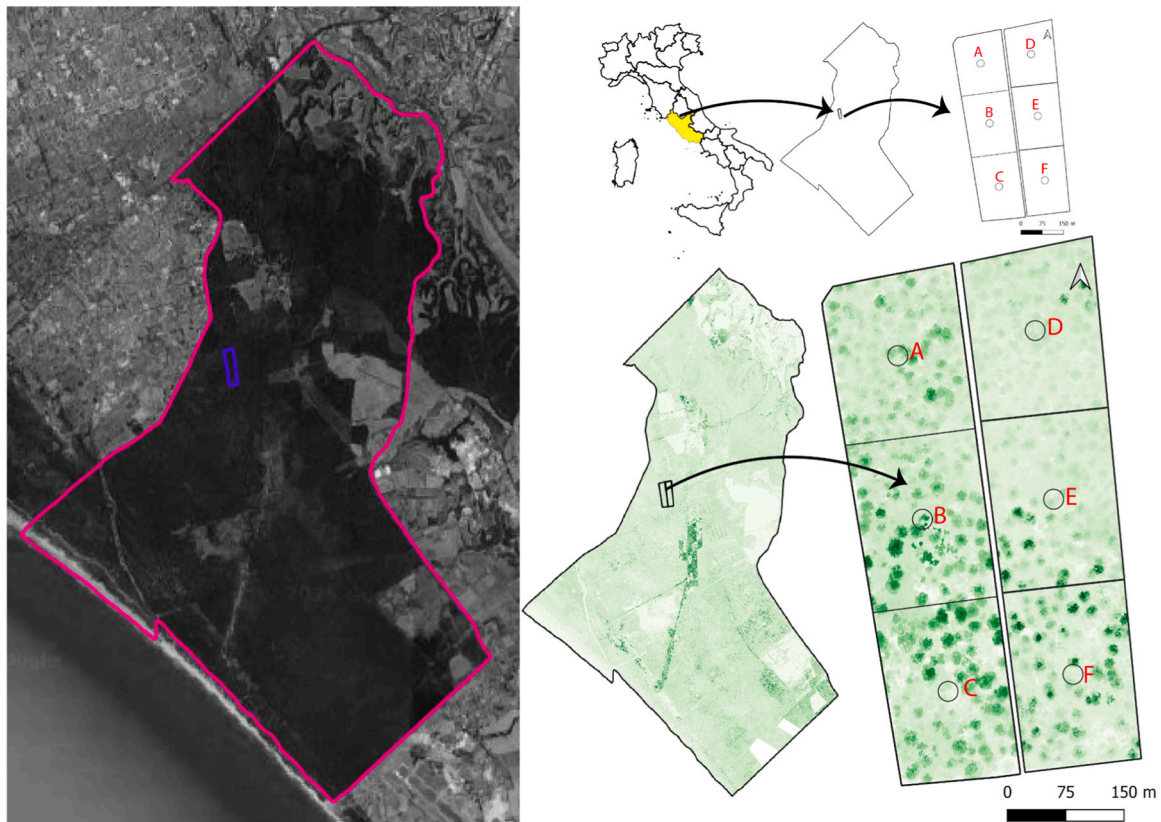


Fig. 1. Location of the Campo di Rota study site. The left panel presents an aerial view of the site (outlined in pink). The top-right panel shows its geographical position within the Lazio Region, Italy (highlighted in yellow). The bottom-right panel details the two experimental zones: fenced (FE; plots A, B, C) and unfenced (UN; plots D, E, F). Each plot was sampled for soil, biomass, and necromass within a 13 m radius circular area (black circles).

provides the complete protocols and plot coordinates.

2.3. Soil sampling

Soil sampling was conducted in May 2023 using a 7.0 cm diameter soil auger, following a modified protocol from the Joint Research Center of the European Commission (Stolbovoy et al., 2007). Within each plot, three non-contiguous square cells were selected through pseudo-random sampling. Samples were collected at three depths (0–10, 10–30, and 30–60 cm), resulting in a 9 samples per plot and 27 per site. Sampling depth followed IPCC guidelines (Aalde et al., 2006), with particular focus on the 0–30 cm layer, where SOC variation is most responsive to land use and management changes. To capture potential C dynamics in deeper soil horizons, sampling was extended to 30–60 cm. Considering soil homogeneity, a single soil profile was excavated to 0–60 cm soil depth at the center of each plot to determine bulk density (BD) (Blake, 1965). BD was measured using a steel cylinder of known volume (diameter = 5.0 cm, height = 5.0 cm, volume = 98.125 cm³) at the same depths intervals as soil sampling.

2.3.1. Soil sample processing and analysis

The soil samples were oven-dried at 60 °C in the laboratory to a constant weight, and sieved through a 2 mm mesh to separate the fine earth fraction. No rock fragments were detected in the soil. Further, the soil fractions were finely ground into a powder and analyzed for SOC and nitrogen (N) content using a CHN-Elemental Analyser (Thermo-Finnigan Flash EA112 CHN). Prior to analysis, inorganic C was removed by treating the samples with a 10 % hydrochloric acid solution. For BD measurements, samples were dried at 105 °C until a constant weight and then weighed. SOC stocks were calculated using the equation (Eq. (1)) outlined by Boone et al. (1999) as follows:

$$\text{SOC or TN stock (Mg ha}^{-1}\text{)} = \Sigma \left[(\text{SOC or TN}) \times \text{BD} \times \text{Depth} \times \left(1 - \frac{\text{Frag}}{100} \right) \right] \quad (1)$$

In this equation, SOC and TN (total N) stock, are expressed as megagrams per hectare (Mg ha⁻¹) representing the total organic C and N pool in the soil. BD is the bulk density in megagrams per cubic meter (Mg m⁻³), Depth (cm) is the thickness of the soil layer in centimetres, and Frag (%) indicates the proportion of rock fragments, if present in the soil.

2.4. Living biomass estimation

Above ground biomass (AGB) was systematically estimated across the forests, using a total of six sampling plots, each with a radius of 13 m. Three plots were located at the centers of the FE zones (A, B, and C), and three at the centers of the corresponding plot areas within the UN forest (D, E, and F). The methodology adopted for measuring AGB and dead biomass followed the guidelines provided by the Italian national forest inventory protocol (MPAF, 2006) and Bovio et al. (2014). Diameter and height of all trees with DBH > 9.5 cm were recorded within the entire plot, while smaller trees (2.5 cm ≤ DBH ≤ 9.5 cm) were measured in a concentric subplot placed at the center. Two 2 m radius subplots were positioned 10 m east and west of the plot center to sample shrub biomass. Herbaceous vegetation was collected separately in four 0.5 × 0.5 m quadrats placed along the N–S and E–W axes, 10 m from the center. All sampling protocols are described in detail in [Supplementary Material 1 \(S1\)](#). Biomass estimations for *Carpinus* spp. and *Q. ilex* were done using specific allometric equations derived from Tabacchi et al. (2011). *Erica arborea* and *Phillyrea angustifolia* were assimilated to *Q. ilex*

due to similar growth form, as they develop as small trees rather than shrubs, reaching an average height of 5.8 m and 10 m, respectively. This approach is consistent with Schirru (2013), as species-specific allometric models were considered inadequate (De Cáceres et al., 2019). *Q. suber* followed an allometric equation derived from Ruiz-Peinado et al., (2012), while Zianis et al. (2005) broader reference database of allometric equations from global studies. Specifically, *Arbutus unedo* was assessed using Italian data from Brandini and Tabacchi (1996). The allometric equation for *Pedunculata oak* (Dik, 1984), was applied to both *Q. robur* and *Q. frainetto*. These two species were assimilated based on their similar canopy architecture and size, and are classified in the area as “monumental trees” (Pignatti et al., 2001; Giordano et al., 2006). For volume-based models, wood density values were sourced from the Global Wood Density Database (Chave et al. 2009; Zanne et al., 2009), prioritizing Mediterranean studies. AGB was then converted to C, using the conversion factor of 0.475 as proposed by Magnussen and Reed (2004). Shoot-to-root ratio estimation is derived from values reported in the Italian National Inventory Reports 1990–2022 (ISPRA, 2024) for oaks and hornbeams. When species-specific data were not available, complementary references from Mediterranean forest systems were used. In particular, *Phillyrea angustifolia* from Marziliano et al. (2015), *Q. ilex* from Ruiz-Peinado et al. (2012), *Arbutus unedo* from Silva and Rego (2004), and *Erica arborea* were taken from Carrión-Prieto et al. (2017). Root-to-shoot ratio data for shrubs were obtained from Mokany et al. (2006). All allometric formulas used in this study are reported in Supplementary Material 2S.

2.5. Dead organic matter estimation

The sampling protocol described by Alberti et al. (2008) was followed for the estimation of dead organic matter (Table S2 in Supplementary Material 1). Dead organic matter was categorized into fine wood debris (FWD; $\varnothing < 5$ cm), collected in four 0.25 m² square frames, and coarse wood debris (CWD; $\varnothing > 5$ cm) sampled along a transect categorized both East-West and North-South within the 13 m radius plots used for AGB measurements (Fig. 2).

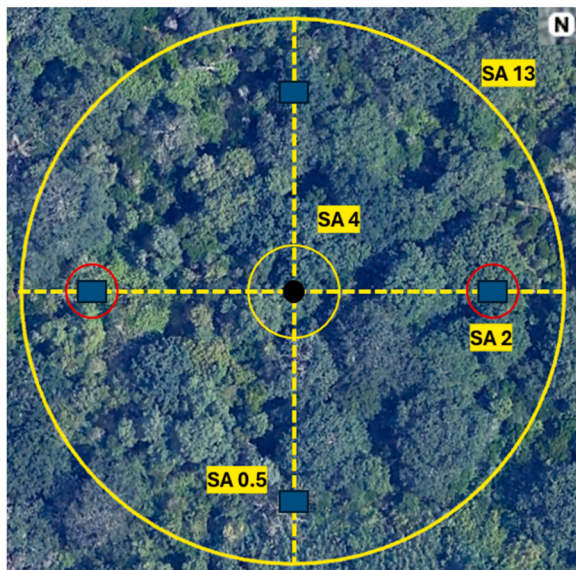


Fig. 2. Sampling design for biomass and necromass estimation. The black circular spot marks the central point also the location of litter collection, whereas the yellow area delineates the sampling unit. SA 13: 13 m radius circular area, including all live and dead standing trees with DBH > 9.5 cm. SA 4: concentric to SA 13, 4 m radius, includes trees with DBH between 2.5 and 9.5 cm. CWD: measured along N-S and E-W diameters. SA 2: two circular 2 m radius plots along the E-W axis for shrub collection. SA 0.5: four 0.5 × 0.5 m quadrants for fine wood debris (<5 cm) collection.

FWD mass was determined by oven-drying and weighing the collected samples in the laboratory. CWD volume (V CWD) was estimated using Eq. 2, as proposed by Harmon and Sexton (1996), and the decrease decay wood density class values described by Alberti et al. (2008).

$$VCWD = 9.869 \times \left(\frac{d^2}{L} \right) \quad (2)$$

The formula estimates the CWD volume in m³ ha⁻¹, where d represents the diameter of each fragment (m) and L corresponds to the combined length (m) of the North-South and East-West transects (26 m). Following Pellis et al., (2019), volume measurements were converted to mass using species specific fresh wood density volume from the Global Wood Density Database (Chave et al. 2009; Zanne et al., 2009), adjusted for decay class using the reduction factors proposed by Alberti et al. (2008). Carbon content was then estimated by applying a conversion factor of 0.475, as suggested by Magnussen and Reed (2004). The litter was collected at the center of each plot using a 20 × 20 cm frame. After oven-drying, the litter samples were analysed for C and N content via dry combustion using a Thermo-Finnigan Flash EA112 CHN. The instrumentation used for tube survey included a metric tape, a Haglof dendrometer, and the Haglof Vertex device, for measuring distances, heights, angles, and slopes.

2.6. Statistical analyses and calculations

All statistical analyses were performed using R software (version 4.4.3; R Core Team, 2025). For soil statistical analysis, a two-way analysis of variance (ANOVA) was conducted to test the effects of two independent factors: (i) wild ungulate presence and (ii) soil depth. SOC and N stocks were used as response variables. Model fit metrics, including F-statistics and associated p-values, were used to evaluate the effects of the factors and their interaction. The normality of the data was assessed using the Shapiro Wilk test, both for each treatment-depth combination and on the residuals of the ANOVA model. Pairwise comparisons between FE and UN plots at each soil depth were performed using independent-sample t-tests. Normality of residuals was also verified using the Shapiro Wilk test. Carbon stocks in aboveground and belowground biomass, as well as in deadwood and litter, were compared between treatments (FE vs. UN) using independent-sample t-tests performed on plot-level aggregated data. All data are expressed as means ± standard deviation and reported in megagrams of C per hectare (Mg C ha⁻¹). Differences at level (α) of 0.05 were considered significant between treatments and are represented by different lowercase letters.

3. Results

3.1. Soil C and N stocks

The two-way ANOVA on SOC showed significant effects of treatment ($F = 5.52$, $p = 0.023$) and soil depth ($F = 5.11$, $p = 0.010$), while the interaction term was marginally non-significant ($F = 2.44$, $p = 0.098$), indicating a potential depth-specific response to ungulate exclusion (Fig. 3). Residuals were normally distributed (Shapiro-Wilk $W = 0.957$, $p = 0.052$). For TN stock, soil depth had a strong effect ($F = 15.34$, $p < 0.001$), whereas treatment ($F = 0.55$, $p = 0.464$) and the interaction ($F = 0.67$, $p = 0.518$) were not significant. Despite a slight deviation from normality at the model level ($W = 0.917$, $p = 0.001$), five out of six treatment-depth groups met the normality assumption ($p > 0.05$), supporting the robustness of the analysis.

Pairwise t-tests conducted at each soil depth revealed a significant difference in SOC stocks between treatments only at 30–60 cm ($p = 0.035$), where unfenced plots exhibited markedly higher values than fenced ones (45.3 vs 24.2 Mg C ha⁻¹). For TN stocks, no statistically significant differences between treatments were found across any depth, although a near-significant trend was observed at 0–10 cm ($p = 0.055$),

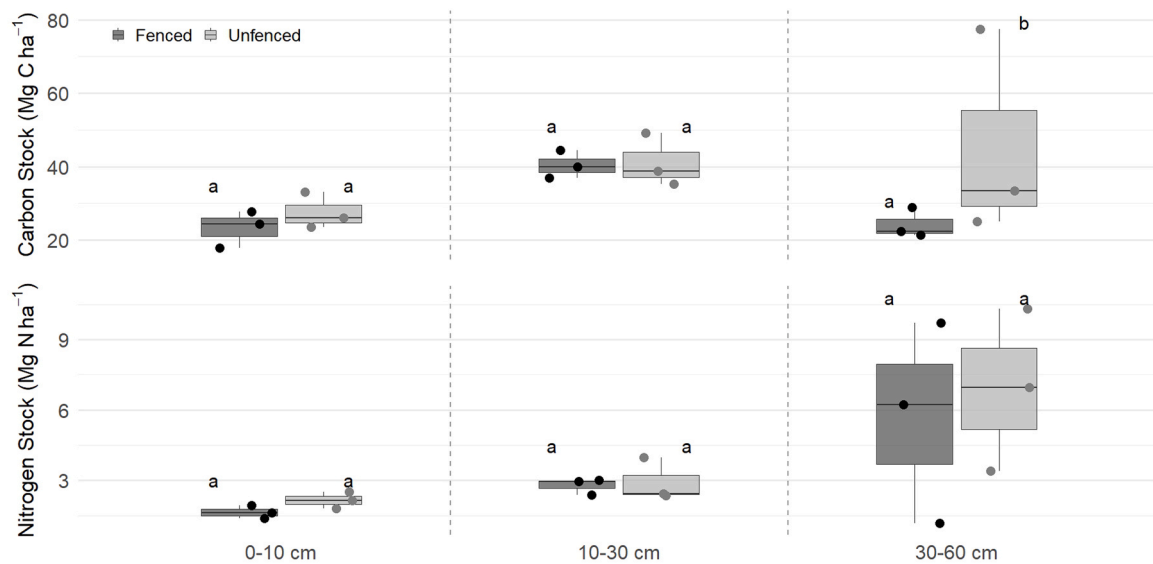


Fig. 3. Soil carbon (top) and nitrogen (bottom) stock (Mg ha^{-1}) across fenced (FE) versus unfenced (UN) areas and for the different soil depths (x-axis). Each box represents the interquartile range (IQR), with the horizontal line inside showing the median carbon and nitrogen stocks. Whiskers extend to the minimum and maximum values within 1.5 times the IQR. Dots inside the boxes represent the mean stock values for each sampled site within the respective treatment-depth combination. Letters above the boxes indicate the results of independent-sample *t*-tests comparing FE and UN plots at each soil depth.

with slightly higher values in unfenced plots. The increased variability in SOC stocks at the 30–60 cm depth within the UN treatment was largely attributable to plot E, which exhibited exceptionally high values ($77.4 \text{ Mg C ha}^{-1}$). Inclusion of this plot elevated the mean SOC stock at this depth by $16.1 \text{ Mg C ha}^{-1}$. Furthermore, BD tended to be higher in UN plots compared to FE plots, with significant differences at the 10–30 cm depth based on *t*-test results ($p = 0.008$), while differences at 0–10 cm and 30–60 cm were not significant. Linear regression analyses revealed a positive relationship between BD and both SOC and TN stocks. Specifically, SOC stock increased significantly with BD ($\beta = 44.9$, $p = 0.003$, $R^2 = 0.16$), although the model explained only a modest proportion of the variance. Similarly, TN stock was significantly associated with BD ($\beta = 9.15$, $p < 0.001$, $R^2 = 0.21$). These results indicate that BD partially

accounts for the spatial variability in SOC and TN stocks, although other ecological and management-related factors likely contribute to the observed patterns.

Across the 0–10 and 10–30 cm layers, mean SOC and TN stocks did not significantly differ between treatments, while C% and N% values also remained statistically similar. This suggests that minor stock differences in the upper soil were primarily driven by differences in bulk density. In contrast, at 30–60 cm, both C% and N% were significantly higher in UN plots, indicating that deeper stock increases were associated with combined effects of higher BD and increased organic matter accumulation.

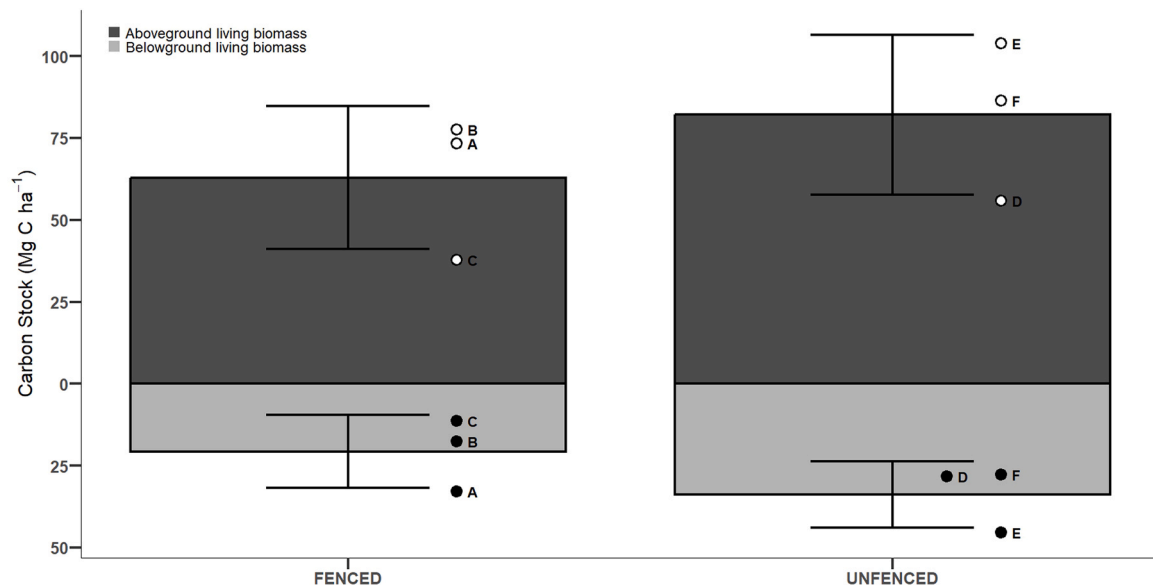


Fig. 4. Living biomass C estimation in the fenced (FE) versus unfenced (UN) areas. The Y-axis shows the mean carbon content \pm standard deviation (SD) in Mg C ha^{-1} in the aboveground (above zero) and belowground (below zero) biomass for the two study areas: FE on the left and UN on the right. The dots represent the carbon biomass averages for the three plots within each area. The horizontal line at zero represents the soil surface and serves as a visual reference to distinguish above-ground from below-ground living biomass carbon pools.

3.2. Living biomass C stock

Independent-sample *t*-tests revealed no statistically significant differences in either aboveground or belowground C stocks between FE and UN plots. On average, aboveground C stocks were $82.1 \pm 24.3 \text{ Mg C ha}^{-1}$ in UN plots and $62.9 \pm 21.8 \text{ Mg C ha}^{-1}$ in FE plots, while belowground C stocks amounted to $33.8 \pm 10.1 \text{ Mg C ha}^{-1}$ and $20.7 \pm 11.0 \text{ Mg C ha}^{-1}$, respectively (Fig. 4).

Despite an apparent trend, the high variability within each group indicates that differences in C storage are not consistent across all plots. C storage in ABG ranged between $37.8 \pm 11.7 \text{ Mg C ha}^{-1}$ and $103.9 \pm 86 \text{ Mg C ha}^{-1}$, while belowground C storage varied from 11.4 ± 3.9 – $45.5 \pm 17.6 \text{ Mg C ha}^{-1}$. These findings suggest that both fencing status and local stand structure influence C stock variation, although no statistically robust pattern emerged. In several plots, a limited number of very large trees disproportionately affected total C stock. Notably, in Plot E, trees within the 120–130 cm diameter class account for 83.8 % of the total C stock, underscoring the dominant role of very large trees in shaping both the mean C estimate and the observed high standard deviation ($103.9 \pm 86 \text{ Mg C ha}^{-1}$). Similarly, in Plot A, the 100–110 cm diameter class contributes 68.5 % of the total C stock, while in Plot B, trees in the 90–100 cm class represent 74.05 % of the total.

The C stocks associated with shrubs ($d < 2.5 \text{ cm}$), including both above and belowground biomass, were approximately 78 % lower in the UN area compared to the FE area, with mean values of $1.03 \text{ Mg C ha}^{-1}$ and $4.68 \text{ Mg C ha}^{-1}$, respectively. However, this pattern exhibited strong plot-level variability. In the FE area, C stocks ranged from 9.6 Mg C ha^{-1} (Plot A) to 1.6 Mg C ha^{-1} (Plot C), whereas in the UN area, values ranged from 1.2 Mg C ha^{-1} (Plot E) to 0.8 Mg C ha^{-1} (Plot D).

3.3. Total ecosystem C stock

Total ecosystem C stock (C_{Tot}), obtained by summing living biomass, deadwood (CWD + FWD), litter, and soil C pools, did not differ significantly between the two management types (Fig. 5). Although mean C_{Tot} was higher in the UN system ($245.7 \pm 39.6 \text{ Mg C ha}^{-1}$) than in the FE system ($194.6 \pm 26.4 \text{ Mg C ha}^{-1}$), this difference was not statistically significant. Deadwood and litter C stocks were consistently higher in FE plots. While deadwood showed a near-significant trend ($p = 0.09$), litter differences were less marked ($p = 0.327$). Specifically, deadwood averaged $13.6 \pm 4.6 \text{ Mg C ha}^{-1}$ in FE and $9.0 \pm 2.8 \text{ Mg C ha}^{-1}$ in UN

plots, while litter stocks were 9.7 ± 2.5 and $7.2 \pm 1.0 \text{ Mg C ha}^{-1}$ in FE and UN, respectively.

The substantial variability observed among replicates resulted in overlapping standard deviations and non-significant outcomes. Across both systems, the below-ground C component, comprising SOC and root biomass, represented more than half of the total ecosystem C. In particular, below-ground pools accounted for 55.7 % of total C in FE ($108.4 \pm 13 \text{ Mg C ha}^{-1}$) and 60 % in UN ($147.5 \pm 31.1 \text{ Mg C ha}^{-1}$).

4. Discussion

4.1. Soil C and N stocks

This study highlights the depth-dependent nature of SOC dynamics under contrasting conditions (FE vs. UN), emphasizing how different management practices influence C sequestration throughout the soil profile. Interestingly, the UN management showed a significant increase in SOC stock at the 30–60 cm depth relative to the soil managed under FE conditions. In contrast, the upper soil layers (0–10 and 10–30 cm) exhibited no significant differences between the two systems, underscoring that management effects on SOC are more pronounced in subsoil horizons. The marked accumulation in deeper soil layers may be attributed to multiple interacting mechanisms, including enhanced organic matter inputs, soil bioturbation, and vertical redistribution facilitated by animal activity (Dong et al., 2013; Lacki and Lancia, 1983; Malizia et al., 2000).

The observed increase in SOC in deeper soil layers under UN management likely reflects the ecological influence of wild ungulates, on soil processes. Their contributions include inputs of organic matter through excreta, physical soil redistribution via trampling, and microbial priming effects induced by dung deposition, all of which can enhance C cycling and promote SOC stabilization (Sitters & Andriuzzi, 2019; Wirthner et al., 2012; Andersen, 2022). Furthermore, ungulate activity and grazing behavior can generate nutrient-rich microsites, a phenomenon well documented in grazed ecosystems (Frank et al., 2000) that drives spatial heterogeneity in forest soils (Bardgett & Wardle, 2003). The increased integration of C and nitrogen N into mineral soil under UN management may, therefore, be attributed to these animal-driven processes.

Another key mechanism that could influence SOC and N in the deeper soil layers is the impact of ungulate trampling and the stabilizing

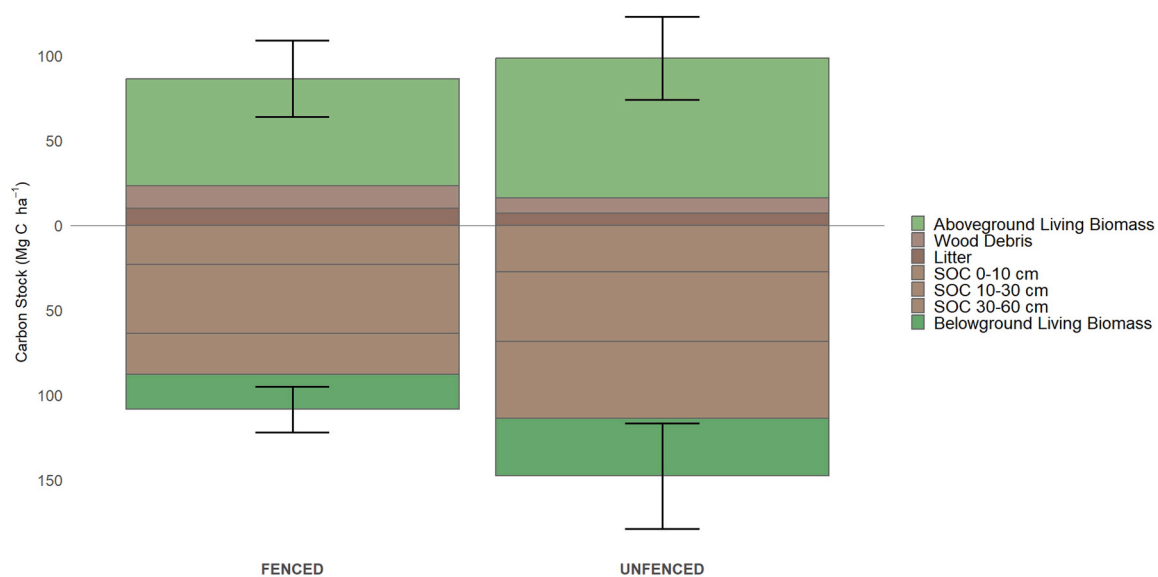


Fig. 5. Ecosystem carbon stocks are represented using bar plots for fenced and unfenced, with mean values \pm standard deviation (SD). The different carbon pools are indicated in the legend on the right. The horizontal line at zero represents the soil surface and serves as a visual reference to distinguish above-ground (litter, deadwood, living biomass) from below-ground (SOC and roots) carbon pools.

effect of BD. Trampling facilitates the vertical transport of organic matter through soil compaction and physical incorporation, thereby promoting SOC in subsoil layer, a process widely observed in both grazed (Bilotta et al., 2007; Howison et al., 2017) and forested systems (Kolstad et al., 2018).

Our findings align with those of Liu et al. (2020), who demonstrated in a two-year study that wild boars grubbing activities in an oak forest of central China led to SOC accumulation in both topsoil (0–10 cm) and subsoil (10–20 cm), supporting the role of soil distribution in modulating C dynamics.

In contrast, some studies report SOC depletion as a consequence of ungulate activities. Marks et al. (2024) observed a decline in SOC accumulation in woodland ecosystems subjected to intense wild herbivore activity. Similarly, Wang et al. (2021) found an increase in SOC stocks in temperate steppes under fenced conditions, suggesting that excluding grazing pressure may enhance C accumulation in certain contexts. Moreover, a long-term study by Gass and Binkley (2011) in the Rocky Mountain National Park, Colorado, USA, found that grazed riparian areas exhibited 25 % lower SOC and 23 % lower soil N compared to exclosures over a 12-year period. These contrasting results highlight the complexity of SOC and N dynamics and emphasize the importance of considering both biological and physical processes in understanding SOC sequestration in managed ecosystems. Our findings suggest that, in forested systems with high ungulate activity, nutrient redistribution by ungulates may enhance subsoil SOC storage rather than depleting surface C pools.

4.2. Living biomass C stock

The impact of ungulates on forest C dynamics in the Campo di Rota Forest appears to be primarily mediated through browsing pressure rather than direct alterations in species composition or total C stock of living biomass. Overall differences in C stock were not statistically significant, indicating that while ungulates may influence C storage, other environmental or ecological factors likely play a more prominent role in shaping the observed patterns.

The 77 % lower C stock (Mg C ha^{-1}) in the shrub layer ($d < 2.5$ cm) within the unfenced area suggests significant browsing pressure by wild ungulates. This result aligns with previous findings by Lecomte et al., (2019), who reported substantial structural changes in understory forest structure following 14 years of browsing exclusion. However, the sampling of our study (three plots per management) may limit statistical power, necessitating caution in interpretation.

Species composition remained relatively consistent between managements, with *Carpinus spp* emerging as a dominant in both UN (58 %) and in FE, (71 %) areas. Mediterranean species such as *Arbutus unedo* and *Phillyrea angustifolia* were also present, reflecting the characteristic floristic diversity of Mediterranean forests. This aligns partially with the findings of Allen et al. (2023), who reported no impact of invasive ungulates on total C stocks but observed changes in species composition in response to browsing pressure. Notably, large-diameter trees (>50 cm) contributed significantly to the total C stock of living biomass, accounting for 56 % of biomass in FE plots and 51 % in UN plots. Approximately 30 % of this biomass originated from trees exceeding 100 cm in diameters, highlighting the dominance of late-successional, large-diameter mature trees nearing the final stages of their life cycle in the experimental forests. This pre-existing dominance of mature, large-diameter trees, unaffected by the 11-year period of ungulate exclusion, may have masked potential treatment effects on total living biomass and ecosystems C stocks, thus contributing to the absence of statistically significant differences between FE and UN plots.

Such structural configuration reflects a forest dynamic in Campo di Rota primarily shaped by the senescence of mature oak cohorts, resulting in the formation of canopy gaps. These gaps have facilitated the expansion of *Carpinus spp.* a species previously confined to the subordinate forest layer now rapidly occupying the available space

thanks to its strong coppicing ability, vigorous stump sprouting, and competitive advantage under disturbance conditions. The coexistence of *Carpinus spp.* with Mediterranean maquis species such as *Q. ilex*, *Arbutus unedo*, *Phillyrea spp.*, and *Pistacia lentiscus*, contributing to the structural complexity and ecological resilience of the forest ecosystem.

One of the key factors contributing to oak decline in Mediterranean forests is summer water availability (Maselli, 2004). Emerging research increasingly links tree mortality in the forest ecosystems of this region to increasing water stress caused by shifting climate patterns (Ibáñez et al., 2017; Gentilesca et al., 2017). In the area, Scrinzi et al. (2016) identified three main factors limiting deciduous oak growth: forest senescence, lack of natural regeneration, and wildlife pressure. Romagnoli et al. (2018) also found evidence of oak decline in the same area through dendrochronological analysis, attributing it to intensifying drought conditions. Future forest trajectories in the region are likely to be shaped by the interaction between ungulate herbivory, stand dynamics, and climate change.

4.3. Total ecosystem C stock

Substantial variability in the measured C stocks resulted in overlapping values between the two systems, leading to statistically comparable outcomes despite observable differences in total biomass. When contextualized within the finding from Gratani et al. (2017), who studied C pools of forests within the same estate, our C_{Tot} values fall within the range reported for *Q. suber* evergreen forests (202 Mg C ha^{-1}) and Mediterranean high maquis ($168.8 \text{ Mg C ha}^{-1}$), although their study considered C only within the topsoil (0–20 cm).

Dead wood biomass (CWD + FWD), a key indicator of forest biodiversity and ecological integrity, showed values in both FE and UN comparable to those typically found in unmanaged ecosystems. For example, unmanaged Norway spruce forests have been reported to contain $11.3 \text{ Mg C ha}^{-1}$ of deadwood (Krueger et al., 2016). Finding within the UN area are comparable with data collected by Gratani et al., (2017) from the same estate for Broadleaf mixed forest and *Q. ilex* evergreen forest, with C_{Tot} values ranging from of 253.8 and 265 Mg C ha^{-1} while for FE area comparable to the values revealed within the *Q. suber* forest had a C_{Tot} of $202.1 \text{ Mg C ha}^{-1}$. However, deadwood accumulation in forest ecosystems represented high variability. Gough et al., (2007) reported total wood debris of 2.2 Mg C ha^{-1} for temperate forests, closely matching with the 2.4 Mg C ha^{-1} found by Makineci et al. (2017) in Coppice Oak Forests. The primary factor influencing deadwood accumulation is forest management practice implemented, which significantly regulates both the quantity and quality of deadwood and coarse wood debris (Paletto et al., 2014). Reduced deadwood and litter in UN plots provide evidence of ungulate-driven physical disturbance activity, influencing deadwood decomposition and litter mixing (Lecomte et al., 2019). Across both ecosystems, the below-ground C compartment, including SOC and root biomass, accounted for the majority of total C stocks. This underscores its critical role as a long-term C reservoir in Mediterranean forest ecosystems. These results provide a solid baseline for future diachronic analyses, which can be effectively integrated with paired plot designs and strengthened by long-term experimental trials, to better capture dynamics in SOC and wood C pools (Antoniella et al., 2024; Kumar et al., 2025; Petersson et al., 2024). The integrated use of standardized forest and soil protocols provides a replicable and efficient framework for C stock assessment, applicable to Mediterranean and temperate forest contexts.

5. Conclusions

Despite limited effects at the ecosystem scale, clear signals emerged at specific components of the C cycle. Ungulates had a significant impact on SOC at 30–60 cm soil depth and on understory biomass when comparing fenced and unfenced areas. The absence of statistically significant differences in total ecosystem carbon stocks may result from a

combination of methodological and ecological factors. Methodologically, the 11-year exclusion period may be insufficient to detect effects at the ecosystem scale. Moreover, the use of general allometric models for certain species, due to the lack of species-specific equations, may have introduced a systematic bias across all the plots. Ecologically, the presence of large, mature trees, evenly distributed across treatments, appears to be minimally affected by ungulate activity. Ecosystem C stocks in both treatments are consistent with typical values for Mediterranean mixed deciduous forests. Campo di Rota's Forest is undergoing a structural and compositional shift, driven by the decline of mature oaks and insufficient recruitment, which is facilitating the expansion of shade-tolerant, fast-growing, and previously suppressed coppice species, potentially leading to a transition toward a Mediterranean oak-hornbeam woodland.

The causes of oak regeneration failure remain unclear. Ongoing research is assessing the roles of climate change, interspecific competition, soil conditions, and herbivory. These findings underscore the complexity of forest dynamics, where legacy effects of past management and species-specific interactions may interact with, or amplify, the effects of climate-driven succession. Although ungulates may not be the primary drivers of ecosystem level C stock changes, their impact on belowground C pools suggests a more nuanced role in soil C cycling, warranting further study.

Funding

Funded by the European Union - Next Generation EU, Mission 4 Component 1 CUP J83C22000860007.

CRediT authorship contribution statement

Maurizio Sabatti: Writing – review & editing, Visualization, Validation, Supervision, Funding acquisition. **Tommaso Chiti:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Funding acquisition, Conceptualization. **Abhay Kumar:** Writing – review & editing, Visualization, Validation, Methodology, Investigation. **Federico Valerio Moresi:** Methodology, Conceptualization. **Anna-grazia Calò:** Software, Methodology. **Giuseppe Scarascia Mugnozza:** Validation, Supervision, Project administration, Investigation, Funding acquisition. **Gabriele Antoniella:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

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

Acknowledgments

Authors would like to thank the technicians of “Servizio Tenuta Presidenziale di Castelporziano” for their fruitful collaboration and support in field work activities.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ufug.2025.128967.

References

- Aalde, H., Gonzalez, P., Gytarsky, M., Krug, T., Kurz, W.A., Lasco, R.D., Martino, D.L., McConkey, B.G., Ogle, S., Paustian, K., Raison, J., Ravindranath, N.H., Schoene, D., Smith, P., Somogyi, Z., van Amstel, A., Verchot, L., 2006. Chapter 2: Generic methodologies applicable to multiple land-use categories. In: Eggleston, H.S., Buendia, L., Miwa, K., Ngara, T., Tanabe, K. (Eds.), IPCC Guidelines for National

- Greenhouse Gas Inventories, 4. Agriculture, Forestry and Other Land Use. Institute for Global Environmental Strategies (IGES), Hayama, Japan, p. 2006.
- Alberti, G., Peressotti, A., Piusi, P., Zerbi, G., 2008. Forest ecosystem carbon accumulation during a secondary succession in the Eastern Prealps of Italy. *Forestry* 81 (1), 1–11. <https://doi.org/10.1093/forestry/cpm026>.
- Allen, K., Bellingham, P.J., Richardson, S.J., Allen, R.B., Burrows, L.E., Carswell, F.E., Husheer, S.W., John, St., Peltzer, D.A., 2023. Long-term exclusion of invasive ungulates alters tree recruitment and functional traits but not total forest carbon. *Ecological Applications* 33 (5), e2836. <https://doi.org/10.1002/eap.2836>.
- Andersen, D.C., 2022. Deposition and decomposition of ungulate dung and associated nitrogen inputs on a Dryland River floodplain. *Southwest. Nat.* 66 (3), 213–224. <https://doi.org/10.1894/0038-4909-66.3.213>.
- Antoniella, G., Kumar, A., Chiarabaglio, P.M., Scarascia Mugnozza, G., Chiti, T., 2024. Do poplar plantations enhance organic carbon stocks in arable soils? A comprehensive study from northern Italy. *J. Environ. Manag.* 370, 122882. <https://doi.org/10.1016/j.jenvman.2024.122882>.
- Bardgett, R.D., Wardle, D.A., 2003. Herbivore-mediated linkages between aboveground and belowground communities. *Ecology* 84 (9), 2258–2268. <https://doi.org/10.1890/02-0274>.
- Barrios-Garcia, M.N., Ballari, S.A., 2012. Impact of wild boar (*Sus scrofa*) in its introduced and native range: a review. *Biol. Invasions* 14 (11), 2283–2300. <https://doi.org/10.1007/s10530-012-0229-6>.
- Bilotta, G.S., Brazier, R.E., Haygarth, P.M., 2007. The impacts of grazing animals on the quality of soils, vegetation, and surface waters in intensively managed grasslands. In: Sparks, D.L. (Ed.), *Advances in Agronomy*, 94. Elsevier, pp. 237–280. [https://doi.org/10.1016/S0065-2113\(06\)94006-1](https://doi.org/10.1016/S0065-2113(06)94006-1).
- Biondi, F.A., Dowgiallo, G., Gisotti, G., Tinelli, A., Figlioli, A., Scarascia Mugnozza, G., 2001. Supplemento al volume XXVI di “Scritti e Documenti”. Memoria illustrativa alla carta dei suoli della Tenuta di Castelporziano. Accademia Nazionale delle Scienze detta dei XL, Roma.
- Blake, G.R., 1965. Bulk Density. Methods of Soil Analysis. Part I: Physical and Mineralogical Methods. American Society of Agronomy, Madison, WI, pp. 374–390. <https://doi.org/10.2134/agronmonogr9.1.c30>.
- Boone, R.D., Grigal, D.F., Sollins, P., Ahrens, R.J., Armstrong, D.E., 1999. Soil sampling, preparation, archiving, and quality control. In: Robertson, In.G.P., Coleman, D.C., Bledsoe, C.S., Sollins, P. (Eds.), *Standard Soil Methods for Long-Term Ecological Research*. Oxford University Press, pp. 3–28. Retrieved from. (<https://andrewsforest.oregonstate.edu/pubs/pdf/pub2706.pdf>).
- Bovio, G., Corona, P., Leone, V., 2014. Gestione selvicolturale dei combustibili forestali per la prevenzione degli incendi boschivi. Compagnia delle For. ISBN 978-88-905577-9-8.
- Brandini, P., Tabacchi, G., 1996. Biomass and volume equations for holm oak and strawberry-tree in coppice stands of Southern Sardinia. *ISAF Commun. di Ric.* 96 (1), 59–69.
- Bueno, C.G., Azorin, J., Gómez-García, D., Alados, C.L., Badía, D., 2013. Occurrence and intensity of wild boar disturbances, effects on the physical and chemical soil properties of alpine grasslands. *Plant Soil* 373 (1–2), 243–256. <https://doi.org/10.1007/s11040-013-1784-z>.
- Busso, F., Pollastrini, M., 2020. Opportunities and threats of Mediterranean evergreen sclerophyllous woody species subjected to extreme drought events. *Appl. Sci.* 10 (23), 8458. <https://doi.org/10.3390/app10238458>.
- Carpio, A., Guerrero-Casado, J., Barasona, J., Tortosa, F., 2017. Ecological impacts of wild ungulate overabundance on Mediterranean basin ecosystems. In: Menendez, A., Sands, N. (Eds.), *Ungulates. Evolution, Diversity and Ecology*. NovaScience Publishers, Inc, pp. 111–157.
- Carrión-Prieto, P., Hernández-Navarro, S., Martín-Ramos, P., Sánchez-Sastre, L.F., Garrido-Launaga, F., Marcos-Robles, J.L., Martín-Gil, J., 2017. Mediterranean shrublands as carbon sinks for climate change mitigation: new root-to-shoot ratios. *Carbon Manag.* 8 (1), 67–77. <https://doi.org/10.1080/17583004.2017.1285178>.
- Caughley, G., 1970. Eruption of ungulate populations, with emphasis on Himalayan thar in New Zealand. *Ecology* 51 (1), 53–72. <https://doi.org/10.2307/1933599>.
- Cawson, J.G., Duff, T.J., Swan, M.H., Penman, T.D., 2018. Wildfire in wet sclerophyll forests: the interplay between disturbances and fuel dynamics. *Ecosphere* 9 (11), e02211. <https://doi.org/10.1002/ecs2.2211>.
- Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. *Ecol. Lett.* 12 (4), 351–366. <https://doi.org/10.1111/j.1461-0248.2009.01285.x>.
- Colomer, J., Massei, G., Roos, D., Rosell, C., Rodríguez-Teijeiro, J.D., 2024. What drives wild boar density and population growth in Mediterranean environments? *Sci. Total Environ.* 931, 172739. <https://doi.org/10.1016/j.scitotenv.2024.172739>.
- Conte, A., Otu-Larbi, F., Alivernini, A., Hoshika, Y., Paoletti, E., Ashworth, K., Fares, S., 2021. Exploring new strategies for ozone-risk assessment: a dynamic-threshold case study. *Environ. Pollut.* 287, 117620. <https://doi.org/10.1016/j.envpol.2021.117620>.
- De Cáceres, M., Casals, P., Gabriel, E., Castro, X., 2019. Scaling-up individual-level allometric equations to predict stand-level fuel loading in Mediterranean shrublands. *Ann. For. Sci.* 76 (3), 87. <https://doi.org/10.1007/s13595-019-0873-4>.
- Dik, E.J., 1984. Estimating the wood volume of standing trees in forestry practice. *Rijksinstituut voor onderzoek in de bos en landschapsbouw de Dorschkamp. Wagening. Uitvoerig Versl.* 19 (1), 1–114.
- Don, A., 2022. No threat to global soil carbon stocks by wild boar grubbing. *Glob. Change Biol.* 28, 685–686. <https://doi.org/10.1111/gcb.15990>.
- Dong, Q.M., Zhao, X.Q., Wu, G.L., Shi, J.J., Ren, G.H., 2013. A review of formation mechanism and restoration measures of “black-soil-type” degraded grassland in the Qinghai-Tibetan Plateau. *Environ. Earth Sci.* 70 (6), 2359–2370. <https://doi.org/10.1007/s12665-013-2338-7>.

- Fares, S., Savi, F., Fusaro, L., Conte, A., Salvatori, E., Aromolo, R., Manes, F., 2016. Particle deposition in a peri-urban Mediterranean forest. *Environ. Pollut.* 218, 1278–1286. <https://doi.org/10.1016/j.envpol.2016.08.086>.
- Focardi, S., Fanfani, A., Toso, S., Tinelli, A., Franceschini, G., Pucci, L., Ronchi, F., De Giacomo, U., Isotti, R., Pecchioli, E., Lombardi, S., 2001. Gli ungulati della Tenuta Presidenziale di Castelporziano. *Scr. e Doc.* 26, 187–199.
- Focardi, S., Gaillard, J.-M., Ronchi, F., Rossi, S., 2008. Survival of wild boars in a variable environment: unexpected life-history variation in an unusual ungulate. *J. Mammal.* 89 (5), 1113–1123. <http://www.jstor.org/stable/25145201>.
- Focardi, S., Isotti, R., Tinelli, A., 2002. Line transect estimates of ungulate populations in a Mediterranean forest. *J. Wildl. Manag.* 66 (1), 48–58. <https://doi.org/10.2307/3802870>.
- Frank, D.A., Groffman, P.M., Evans, R.D., Tracy, B.F., 2000. Ungulate stimulation of nitrogen cycling and retention in Yellowstone Park grasslands. *Oecologia* 123 (1), 116–121. <https://doi.org/10.1007/s004420050996>.
- Gass, T.M., Binkley, D., 2011. Soil nutrient losses in an altered ecosystem are associated with native ungulate grazing. *J. Appl. Ecol.* 48 (4), 952–960. <https://doi.org/10.1111/j.1365-2664.2011.01996.x>.
- Gentilesca, T., Camarero, J.J., Colangelo, M., Nolè, A., Ripullone, F., 2017. Drought-induced oak decline in the western Mediterranean region: an overview on current evidences, mechanisms and management options to improve forest resilience. *iForest Biogeosci. For.* 10, 796–806. <https://doi.org/10.3832/for2317-010>.
- Giordano, E., Capitoni, B., Eberle, A., Maffei, L., Musicanti, A., Recanatesi, F., Torri, V., 2006. Contributo alla realizzazione del Piano di Gestione del patrimonio forestale della Tenuta Presidenziale di Castelporziano. In: *Il II Sistema Ambientale della Tenuta Presidenziale di Castelporziano, III. Segretariato Generale della Presidenza della Repubblica Italiana – Accademia Nazionale delle Scienze detta dei XL*, pp. 1301–1529.
- Giordano, E., Scarascia Mugnozza, G., Tinelli, A., 1995. La rinnovazione naturale dei querceti caducifogli: dinamica temporale e interazione con i fattori ambientali. *Progett. di Monit. Ambient. della Tenuta Pres. di Castelporziano (SITAC)* 170–174.
- Gizicki, Z.S., Tamez, V., Galanopoulou, A.P., Avramidis, P., Foufopoulos, J., 2018. Long-term effects of feral goats (*Capra hircus*) on Mediterranean island communities: results from whole island manipulations. *Biol. Invasions* 20 (6), 1537–1552. <https://doi.org/10.1007/s10530-017-1645-4>.
- Gough, C.M., Vogel, C.S., Kazanski, C., Nagel, L., Flower, C.E., Curtis, P.S., 2007. Coarse woody debris and the carbon balance of a north temperate forest. *For. Ecol. Manag.* 244 (1–3), 60–67. <https://doi.org/10.1016/j.foreco.2007.03.039>.
- Gratani, L., Crescente, M.F., Varone, L., Puglielli, G., Catoni, R., Bonito, A., 2017. Carbon storage by Mediterranean vegetation developing inside a protected area. *Rend. Lince. Sci. Fis. e Nat.* 28 (2), 425–433. <https://doi.org/10.1007/s12210-017-0612-4>.
- Guidolotti, G., Papale, D., Mattioni, M., Nicolini, G., Sabbatini, S., Bonella, G., Calfapietra, C., Matteucci, G., Scarascia Mugnozza, G., 2025. the CastelPorziano Presidential Natural Reserve Research Team: exploiting a natural disaster for a comprehensive evaluation of different ecosystem recovery strategies: the example of Castelporziano network. *EGU25-8435 EGU Gen. Assem.* 2025. <https://doi.org/10.5194/egusphere-egu25-8435>.
- Harmon, M.E., Sexton, J., 1996. Guidelines for Measurements of Woody Detritus in Forest Ecosystems. In: *US LTER Publication*, 20. University of Washington, Seattle, WA, p. 73.
- Howison, R.A., Olff, H., van de Koppel, J., Smit, C., 2017. Biotically driven vegetation mosaics in grazing ecosystems: the battle between bioturbation and biocompaction. *Ecol. Monogr.* 87 (3), 363–378. <https://doi.org/10.1002/ecm.1259>.
- Ibáñez, B., Gómez-Aparicio, L., Ávila, J.M., Pérez-Ramos, I.M., Marañón, T., 2017. Effects of *Quercus suber* decline on woody plant regeneration: potential implications for successional dynamics in Mediterranean forests. *Ecosystems* 20 (3), 630–644. <https://doi.org/10.1007/s10021-016-0044-5>.
- ISPR. 2024. Italian Greenhouse Gas Inventory 1990–2022. National Inventory Report 2024. Istituto Superiore per la Protezione e la Ricerca Ambientale. <https://www.isprambiente.gov.it/en/publications/reports/italian-greenhouse-gas-inventory-1990-2022-national-inventory-report-2024>.
- Kolstad, A.L., Austrheim, G., Solberg, E.J., Venete, A.M.A., Woodin, S.J., Speed, J.D.M., 2018. Cervid exclusion alters boreal forest properties with little cascading impacts on soils. *Ecosystems* 21, 1027–1041. <https://doi.org/10.1007/s10021-017-0202-4>.
- Krueger, I., Schulz, C., Borken, W., 2016. Stocks and dynamics of soil organic carbon and coarse woody debris in three managed and unmanaged temperate forests. *European Journal of Forest Research* 135 (1), 151–167. <https://doi.org/10.1007/s10342-016-1013-4>.
- Kumar, A., Antoniella, G., Blasi, E., Chiti, T., 2024. Agronomic practices for storing soil carbon and reducing greenhouse gas emission in the Mediterranean region. Chapter 22. In: Prasad, M.N.V., Erickson, L.E., Nunes, F.C., Ramadan, B.S. (Eds.), *Decarbonization Strategies and Drivers to Achieve Carbon Neutrality for Sustainability*. Elsevier, pp. 445–480. <https://doi.org/10.1016/B978-0-443-13607-8.00024-9>. Chapter 22.
- Kumar, A., Antoniella, G., Blasi, E., Chiti, T., 2025. Recent advances in regenerative sustainable agricultural strategies for managing soil carbon and mitigating climate change consequences. *Catena* 258, 109208. <https://doi.org/10.1016/j.catena.2025.109208>.
- Lacki, M.J., Lancia, R.A., 1983. Changes in soil properties of forests rooted by wild boar. *Proc. Annu. Conf. Southeast. Assoc. Fish. Wildl. Agencies* 37, 228–236.
- Lecomte, X., Caldeira, M.C., Catri, F.X., Fernandes, P.M., Jackson, R.B., Bugalho, M.N., 2019. Ungulates mediate trade-offs between carbon storage and wildfire hazard in Mediterranean oak woodlands. *J. Appl. Ecol.* 56 (3), 683–694. <https://doi.org/10.1111/1365-2664.13310>.
- Liu, Y., Liu, X., Yang, Z., Li, G., Liu, S., 2020. Wild boar grubbing causes organic carbon loss from both top- and sub-soil in an oak forest in central China. *For. Ecol. Manag.* 464, 118059. <https://doi.org/10.1016/j.foreco.2020.118059>.
- Long, J.L., 2003. Introduced Mammals of the World: Their History Distribution and Influence. CSIRO Publishing. <https://doi.org/10.1071/9780643090156>.
- Magnussen, S., Reed, D., 2004. Modeling for estimation and monitoring. Rome: Food and Agriculture Organization of the United Nations (FAO) and International Union of Forest Research Organizations (IUFRO). Retrieved from https://www.fao.org/fileadmin/user_upload/national_forest_assessment/images/PDFs/English/KR2_EN_10.pdf.
- Makineci, E., Akburak, S., Özturk, A.G., Tolunay, D., 2017. Carbon stocks of fine woody debris in coppice oak forests at different development stages. *Forests* 8 (6), 199. <https://doi.org/10.3390/f8060199>.
- Malizia, A.I., Kittlein, M.J., Busch, C., 2000. Influence of the subterranean herbivorous rodent *Ctenomys talarum* on vegetation and soil. *Z. Saugtierk.* 65 (3), 172–182.
- Marks, E.A.N., Barbosa, J.M., García-Orenes, F., Mataix-Solera, J., Arcenegui, V., Albolafio, S., Velamazán, M., García-Carmona, M., Sánchez-Zapata, J.A., 2024. Ungulate herbivores promote contrasting modifications of soil properties and organic carbon stabilization in a grazed grassland versus rewilded woodland environment. *Agric. Ecosyst. Environ.* 367, 108983. <https://doi.org/10.1016/j.agee.2024.108983>.
- Martínez-Estévez, L., Balvanera, P., Pacheco, J., Ceballos, G., 2013. Prairie dog decline reduces the supply of ecosystem services and leads to desertification of semiarid grasslands. *PLOS One* 8 (10), e75229. <https://doi.org/10.1371/journal.pone.0075229>.
- Marziliano, P.A., Laforteza, R., Medicamento, U., Lorusso, L., Giannico, V., Colangelo, G., Sanesi, G., 2015. Estimating belowground biomass and root/shoot ratio of *Phillyrea latifolia* L. in the Mediterranean forestlandscapes. *Ann. For. Sci.* 72 (5), 585–593. <https://doi.org/10.1007/s13595-015-0486-5>.
- Maselli, F., 2004. Monitoring forest conditions in a protected Mediterranean coastal area by the analysis of multi-year NDVI data. *Remote Sens. Environ.* 89 (4), 423–433. <https://doi.org/10.1016/j.rse.2003.10.020>.
- Médail, F., 2008. Ecosystems: Mediterranean. In: Jørgensen, S.E., Fath, B. (Eds.), *Encyclopedia of ecology*, V. 3. Elsevier, Oxford, pp. 2296–2308.
- Médail, F., Myers, N., 2004. Mediterranean Basin. In: Mittermeier, R.A., Robles Gil, P. (Eds.), *Hotspots Revisited: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions*. CEMEX (Monterrey), Conservation International, Washington and Agrupación Sierra Madre, pp. 144–147.
- Ministero delle Politiche Agricole e Forestali (MPAF), 2006. Procedure di posizionamento e di rilievo degli attributi di terza fase INF.
- Mittermeier, R.A., Turner, W.R., Larsen, F.W., Brooks, T.M., Gascon, C., 2011. Global biodiversity conservation: the critical role of hotspots. In: Zachos, In.F.E., Habel, J.C. (Eds.), *Biodiversity Hotspots: Distribution and Protection of Conservation Priority Areas*. Springer Berlin Heidelberg, pp. 3–22. https://doi.org/10.1007/978-3-642-20992-5_1.
- Mokany, K., Raison, R., Prokushkin, A., 2006. Critical analysis of root:shoot ratios in terrestrial biomes. *Glob. Change Biol.* 12 (1), 84–96. <https://doi.org/10.1111/j.1365-2486.2005.001043.x>.
- Napoleitano, P., Maselli, V., Buglione, M., Arena, C., Zarrelli, A., Fulgione, D., De Marco, A., 2025. Wild boar grubbing affects soil carbon quantity and fractions under native, reforested and planted vegetation. *CATENA* 249, 108648. <https://doi.org/10.1016/j.catena.2024.108648>.
- Paletto, A., De Meo, I., Cantiani, P., Ferretti, F., 2014. Effects of forest management on the amount of deadwood in Mediterranean oak ecosystems. *Ann. For. Sci.* 71 (7), 791–800. <https://doi.org/10.1007/s13595-014-0377-1>.
- Pastor, J., Dewey, B., Naiman, R.J., McInnes, J., Cohen, Y., 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology* 74 (2), 467–480. <https://doi.org/10.2307/1939308>.
- Peco, B., Sánchez, A.M., Azcárate, F.M., 2006. Abandonment in grazing systems: consequences for vegetation and soil. *Agric. Ecosyst. Environ.* 113, 284–294. <https://doi.org/10.1016/j.agee.2005.09.017>.
- Pellis, G., Chiti, T., Rey, A., Curiel Yuste, J., Trotta, C., Papale, D., 2019. The ecosystem carbon sink implications of mountain forest expansion into abandoned grazing land: The role of subsoil and climatic factors. *Sci. Total Environ.* 672, 106–120. <https://doi.org/10.1016/j.scitotenv.2019.03.329>.
- Penman, J., Gyrtarsky, M., Hiraishi, T., Krug, T., Kruger, D., Pipatti, R., Buendia, L., Miwa, K., Ngara, T., Tanabe, K., Wagner, F., 2003. Good practice guidance for land use, land-use change and forestry. In: *Global Environmental Strategies. IPCC National Greenhouse Gas Inventories Programme and Institute for Kanagawa, Japan*.
- Petersson, T., Antoniella, G., Perugini, L., Chiriaco, M.V., Chiti, T., 2024. Carbon farming practices for European cropland: a review on the effect on soil organic carbon. *Soil Tillage Res.* 247, 106353. <https://doi.org/10.1016/j.still.2024.106353>.
- Pignatti, S., Bianco, P., Tescarollo, P., 2001. La vegetazione della Tenuta Presidenziale di Castelporziano. *Il Sist. Ambient. della tenuta Pres. di Castelporziano. Accad. Naz. delle Sci. detta dei Lx. "Scr. e Doc."* Xxvi. Roma 2 (468).
- Pulido, M., Schnabel, S., Lavado Contador, J.F., Lozano-Parra, J., González, F., 2018. The impact of heavy grazing on soil quality and pasture production in rangelands of sw Spain. *Land Degrad. Dev.* 29, 219–230. <https://doi.org/10.1002/ldr.2501>.
- QGIS Development Team. 2019. QGIS Geographic Information System (Version 3.10) [Software]. Available at: <https://qgis.org>.
- R Core Team 2025. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: <https://www.R-project.org/>.
- Recanatesi, F., 2015. Variations in land-use/land-cover changes (LULCCs) in a peri-urban Mediterranean nature reserve: the estate of Castelporziano (Central Italy). *Rend.*

- Lince. Sci. Fis. e Nat. 26 (3), S517–S526. <https://doi.org/10.1007/s12210-014-0358-1>.
- Recanatesi, F., Giuliani, C., Piccinno, M., Cucca, B., Rossi, C.M., Ripa, M.N., 2020. An innovative environmental risk assessment approach to a Mediterranean coastal forest: the Presidential Estate of Castelporziano (Rome) case study. *Ann. Silv. Res.* 4 (2), 80–85. <https://doi.org/10.12899/asr-1884>.
- Romagnoli, M., Moroni, S., Recanatesi, F., Salvati, R., Scarascia Mugnozza, G., 2018. Climate factors and oak decline based on tree-ring analysis. A case study of peri-urban forest in the Mediterranean area. *Urban For. Urban Green.* 34, 17–28. <https://doi.org/10.1016/j.ufug.2018.05.010>.
- Ruiz-Peinado, R., Montero, G., Montero, G., 2012. Biomass models to estimate carbon stocks for hardwood tree species. ISSN: 2171-5068, eISSN: 2171-9845 *For. Syst.* 21 (1), 42–52. <https://doi.org/10.5424/fs/2112211-02193>.
- Schirru, M.S., 2013. Valutazione del potenziale di sequestro del Carbonio forestale nella serie di vegetazione Galio scabri-Quercetum ilicis. Il caso di studio del Monte Arci – Sardegna centrale. Scuola di Dottorato di Ricerca in Scienze e Biotecnologie dei Sistemi Agrari e Forestali e delle Produzioni Alimentari – Indirizzo in Agrometeorologia ed Ecofisiologia dei Sistemi Agrari e Forestali. Ciclo XXVI. Università degli Studi di Sassari.
- Scrinzi, G., Presutti Saba, E., Colle, G., 2016. Indirizzi Gestionali e obiettivi d'intervento per le classi colturali della foresta della Tenuta Presidenziale Di Castelporziano. Accademia Nazionale delle Scienze, Roma, Italy.
- Silva, J.S., Rego, F.C., 2004. Root to shoot relationships in Mediterranean woody plants from Central Portugal. *Biologia* 59, 109–115.
- Sitters, J., Andriuzzi, W.S., 2019. Impacts of browsing and grazing ungulates on soil biota and nutrient dynamics. In: Gordon, I.M.R., Prins, H.H.T. (Eds.), *The Ecology of Browsing and Grazing II* (Chapter 9). Springer. https://doi.org/10.1007/978-3-030-25865-8_9.
- Stolbovoy, V., Montanarella, L., Filippi, N., Jones, A., Gallego, J., Grassi, G., 2007. Soil Sampling Protocol to Certify the Changes of Organic Carbon Stock in Mineral Soil of the European Union. Office for Official Publications of the European Communities, Luxembourg, p. 56 (Version 2. EUR 21576 EN/2.).
- Tabacchi, G., Di Cosmo, L., Gasparini, P., Morelli, S., 2011. Stima del volume e della fitomassa delle principali specie forestali italiane. Equazioni di previsione, tavole del volume e tavole della fitomassa arborea epigea. Consiglio per la Ricerca e la sperimentazione in Agricoltura. Unità di Ricerca per il Monitoraggio e la Pianificazione Forestale, Trento, p. 412.
- Tanentzap, A.J., Coomes, D.A., 2012. Carbon storage in terrestrial ecosystems: do browsing and grazing herbivores matter? *Biol. Rev.* 87, 72–94. <https://doi.org/10.1111/j.1469-185X.2011.00185.x>.
- Trotta, C., Menegoni, P., Manfredi Frattarelli, F.M., Iannetta, M., 2015. Assessing desertification vulnerability on a local scale: the Castelporziano study case (central Italy). *Rend. Lince.* 26, 421–450. <https://doi.org/10.1007/s12210-014-0362-5>.
- Underwood, E.C., Franklin, J., Molinari, N.A., Safford, H.D., 2018. Global change and the vulnerability of chaparral ecosystems. *Bull. Ecol. Soc. Am.* 99 (1), 1–10.
- Wang, Z.P., Han, S.J., Zheng, Y.H., Zhang, X.M., Wu, H.H., Cui, J.F., Xia, C.W., Han, X.G., 2021. Fencing facility affects plant species and soil organic carbon in temperate steppes. *Catena* 196, 104928. <https://doi.org/10.1016/j.catena.2020.104928>.
- Wirthner, S., Schütz, M., Page-Dumroese, D.S., Busse, M.D., Kirchner, J.W., Risch, A.C., 2012. Do changes in soil properties after rooting by wild boars (*Sus scrofa*) affect understory vegetation in Swiss hardwood forests? *Can. J. For. Res.* 42 (3), 585–592. <https://doi.org/10.1139/X2012-013>.
- Yu, C., Pang, X.P., Wang, Q., Jin, S.H., Shu, C.C., Guo, Z.G., 2017. Soil nutrient changes induced by the presence and intensity of plateau pika (*Ochotona curzoniae*) disturbances in the Qinghai-Tibet Plateau. *China. Ecol. Eng.* 106, 1–9. <https://doi.org/10.1016/j.ecoleng.2017.05.029>.
- Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R. B., Swenson, N.G., Wiemann, M.C. & Chave, J. (2009). Global Wood Density Database. Dryad Identifier. (<http://hdl.handle.net/10255/dryad.235>).
- Zianis, D., Muukkonen, P., Makipaa, R., Mencuccini, M., 2005. Biomass and stem volume equations for tree species in Europe. *Silva Fennica Monographs*. Finnish Society of Forest Science, p. 63. <https://doi.org/10.14214/sf.sfm4>.