

RESEARCH ARTICLE

Deer exclusion is necessary to promote post-fire herbaceous regeneration in the understorey of a Mediterranean forest

Andreu Cera^{1,2} , Miguel N. Bugalho¹, Filipe X. Catry¹

The frequency of severe wildfires is on the rise in the Mediterranean Basin as a result of climate change and land abandonment. Recurrent wildfires may retard or impede ecosystem recovery, frequently requiring the implementation of restoration practices. In that context, a post-fire deer exclusion experiment was conducted in a Mediterranean mixed forest ecosystem with high population densities of deer species (Fallow deer and Red deer). A deer exclusion area was established as a form of restoration intervention to promote post-fire vegetation recovery. We surveyed plant species during the second and third springs after fire in both deer-excluded and deer-allowed areas in order to detect changes in the community. We analyzed the plant species composition, species diversity, and structure of herbaceous and woody plant communities. We also compared the frequency of annual and perennial herb species, functional groups, and post-fire plant regeneration strategies. The main differences were due to differences between springs rather than of deer-excluded and deer-allowed plots. Deer consumed both woody and herbaceous species, favoring the assemblage of herbaceous over woody species. Deer favored the establishment of annual forbs, including unpalatable and/or exotic species, while limiting the abundance of graminoids. Observed deer impacts could have been magnified during the second spring by a drought. Our study demonstrates that deer exclusion can be an effective restoration practice for promoting post-fire herbaceous regeneration in forests with significant densities of wild ungulates, although seasonal effects may override restoration practice effects.

Key words: deer, forest, herbaceous, Mediterranean, post-fire, regeneration

Implications for Practice

- A density of 0.4 deer (primarily Fallow deer) per hectare had an impact on the post-fire regeneration of herbaceous species, and deer population control measures should be examined annually, as mitigation of effects may depend on climatic conditions.
- Sufficient rainfall in the years following the wildfire will likely reduce the impact of deer on herbaceous species.
- Excluding deer can prevent the spread of exotic species and promote the assemblage of graminoids after wildfires, particularly during dry periods.

Introduction

Fire and herbivory are two disturbances that characterize the Mediterranean Basin and strongly influence plant dynamics. Although Mediterranean plant species have evolved under these disturbances and developed multiple strategies to cope with them (Archibald et al. 2019), these may not be sufficient in the context of the increasing frequency of severe wildfires in the Mediterranean Basin (Nunes et al. 2016). Recurrent wildfires can lead to slow ecosystem recovery and may require management to ensure vegetation recovery and maintenance of ecosystem functionality and ecosystem services (Köbel et al. 2021). Fire and large ungulates can act synergistically to

influence vegetation recovery (Foster et al. 2015). While the consequences of pre-fire herbivory have been extensively studied (Rouet-Leduc et al. 2021), the effects of post-fire herbivory on plant communities are comparatively understudied, and can threaten plant recovery after fire (Clarke et al. 2021). Research on post-fire management and plant community restoration is gaining relevance in Mediterranean-type ecosystems (MTEs; Lucas-Borja et al. 2021). In particular, research on passive and assisted restoration practices, including the exclusion of wild ungulates in areas to be restored may be necessary to minimize the negative effects of wildfire on vegetation (Clark et al. 2016; Chard et al. 2022).

Fires consume plants, reducing biomass and increasing plant mortality, which may cause profound changes in plant communities. Fire-prone ecosystems are common in the Mediterranean Basin (Pausas et al. 2004), and plants have evolved to persist after

Author contributions: FXC conceived the research idea, collected data; AC performed statistical analyses, wrote the first draft of the manuscript with contributions from FXC, MNB; all authors discussed the results and participated in the manuscript writing-up.

¹Centre for Applied Ecology "Prof. Baeta Neves" (CEABN-InBIO), School of Agriculture, University of Lisbon, Tapada da Ajuda, 1349-017, Lisbon, Portugal

²Address correspondence to A. Cera, email andreucera@isa.ulisboa.pt

© 2024 Society for Ecological Restoration.

doi: 10.1111/rec.14208

Supporting information at:

<http://onlinelibrary.wiley.com/doi/10.1111/rec.14208/supinfo>

wildfire, even when all aboveground parts are burned (Keeley & Pausas 2022). Post-fire recovery of the vegetation depends strongly on the severity of wildfires (Catry et al. 2013; Rego et al. 2021), and the ability of plants to regenerate (Keeley et al. 2006). Herbaceous species generally re-initiate the ecological succession and often dominate the first years after a wildfire (Keeley et al. 2005), as herbaceous species tend to have higher growth rates than woody species and shorter life cycles (Grime 2006). Within herbs, annual and perennial species may differ in responses to fire (Noy-Meir 1995). Recovery of annual species in the early post-fire stages relies on the persistence and size of the seed banks in the burned area (Keeley et al. 2006), as colonization from other unburned populations is low during the first years (Keeley et al. 2005). These species, which mainly depend on the seed bank for persistence in the community, are called obligate seeders (Keeley et al. 2006). Conversely, herbaceous perennial species, especially grasses, can be obligate seeders or have the ability to resprout from vegetative buds to persist (Keeley & Pausas 2022). Herbaceous perennial species may have aboveground regenerative structures, namely stolons, or belowground structures such as bulbs, lignotubers, and rhizomes, that allow resprouting, which may also occur from the root crown (Pausas & Paula 2020). Hence, the development of plant community structure during early post-fire succession depends on the success of these plant regeneration strategies. In addition, post-fire succession can be modified by the interaction with stressors (Keeley et al. 2005), such as droughts that may contribute to filter the assembly of annual species (Luzuriaga et al. 2015), or by the interaction with disturbances, such as herbivory, which may cause selective plant mortality. However, despite the current knowledge on post-fire herbaceous responses in various MTEs, the impact of wild herbivores on the recovery of herbaceous species after wildfires in forest ecosystems remains understudied, as most research on post-fire recovery in MTEs has been conducted on woody plant species (Pausas et al. 2016).

Deer populations are increasing across their range in some MTE regions, such as the Mediterranean Basin (Côté et al. 2004; Acevedo et al. 2008). Deer consume plants, directly impacting plant growth and indirectly impacting interspecific plant competition, ultimately shaping the plant community (Gordon & Prins 2019). The effects of deer on plant communities depend in part on their foraging behavior (e.g. browsers or grazers or intermediate feeders; Hofmann & Stewart 1972), population density, availability of enough preferable plant food, and interaction with other disturbances (Wisdom et al. 2006). Deer species are generally intermediate feeders (that is, have a mixed diet of woody, forbs, and graminoid species sensu Hoffman & Stewart 1972), although species have different dietary preferences and levels of selectivity, exhibiting seasonal foraging behavior. For example, Bruno and Apollonio (1991) observed that Fallow deer (*Dama dama*) preferred graminoids to forbs or legumes in a sub-Mediterranean coastal area in Northern Italy. Other studies in temperate forests in northern Europe have similarly found that Fallow deer prefer graminoids (e.g. Rautiainen et al. 2021). Conversely, one-third of the diet of Red deer (*Cervus elaphus*) was found to consist of graminoids (Gebert & Verheyden-Tixier 2001) in a temperate forest in

France. Bugalho and Milne (2003) found in Mediterranean oak woodlands in Portugal that Red deer feed mainly on grasses in spring and early summer but switch to browsing woody species in summer and early autumn, when green herbaceous vegetation is not available.

In the early post-fire stages in MTEs, there is a flush of annual plant species and resprouter species that initiate regeneration, which provides food for deer and other vertebrate herbivores (Keeley et al. 2006). Mediterranean herbaceous species have adaptations that influence the impact of herbivores. There are many frameworks in the literature regarding plant responses to herbivory, but Archibald et al. (2019) suggest three major strategies: avoidance (having traits that reduce consumption), resistance (protecting particular plant parts), and tolerance (ability to grow and reproduce in spite of herbivory). For example, a plant species with an annual life span or with structures such as rhizomes or stolons can be more resistant and tolerant (Noy-Meir et al. 1989; Briske & Richards 1995). In contrast, unpalatable species tend to depend largely on avoidance (Wisdom et al. 2006; Royo et al. 2010). Therefore, the impact of deer on herbaceous communities after a wildfire depends on deer species, deer population density, and foraging behavior, which plant species regenerate after fire, and whether these species have traits that enable them to avoid, resist, or tolerate consumption by herbivores. However, few studies have addressed the effects of deer herbivory on post-fire regeneration in the Mediterranean Basin (but see Paula & Ojeda 2011; Silva et al. 2014, 2015, studying only woody species). Filling this knowledge gap is important to facilitate wildlife conservation management and ecosystem restoration in the MTEs after wildfire.

Our study area is an enclosed estate in central Portugal with a relatively high ungulate density composed mainly of two deer species. This area was affected by a severe crown fire in 2003 (Catry et al. 2010). Following this fire, an experimental area of 4 ha was fenced and used to assess the effects of deer exclusion on post-fire vegetation recovery. Previously, in our investigation and in the same experiment, the short-term effects of exclusion on the woody community were analyzed (Catry et al. 2007a, 2007b; Silva et al. 2014, 2015). These studies reported that deer exclusion did not result in improvements in the ecological diversity of the woody community, although the complexity of vegetation structure increased as well as the abundance of some woody species. The objective of our study was to build upon these prior investigations by examining the effects of deer on the post-fire recovery of the herbaceous community. In particular, we aimed to assess whether deer exclusion is an effective post-fire restoration practice for the herbaceous community. Additionally, we wanted to understand how deer exclusion affects early post-fire plant succession and mitigates the impact of deer on plant communities. To achieve this, we analyzed species composition, species diversity indices, and the structure of the herbaceous plant community after a wildfire in deer-excluded and deer-allowed areas. We also used the information about diversity and the structure of the woody community to compare with the herbaceous community, reanalyzing the same dataset used by Silva et al. (2015). We also evaluated whether there were differences between annual and perennial species in the frequency of

functional groups and of herbaceous species with different regeneration strategies during two consecutive years after a wildfire. We hypothesized that deer exclusion would increase herbaceous recovery in the early stages after wildfire. Specifically, we hypothesized that deer, as plant consumer, would: (1) affect the structure of the herbaceous and woody plant communities by reducing the cover, height, and phytovolume; (2) reduce the species richness and diversity of the herbaceous community in the context of low food resources as a recent post-fire scenario, and increase the dominance of grazing and browsing avoidance and resistance species. Additionally, since Fallow deer is the main species in the study area and prefers perennial graminoids, we also hypothesized that (3) deer would promote the assemblage of: (1) annual herbs over perennial herbs; (2) legumes and forbs over graminoids; (3) species with belowground sources of regeneration (i.e. rhizomes, storage organs or seeds) as opposed to aboveground regeneration sources (i.e. stolons), because belowground structures are less exposed to herbivory.

Methods

Study Area

This study was conducted in the Tapada Nacional de Mafra (TNM; lat 38°N 58'30", long 9°W 15'52") (Fig. 1). TNM is a public enclosed estate located in central-western Portugal, 8 km from the Atlantic Ocean, at an elevation between 100 and 350 m. The climate is Mediterranean with wet, cool winters and dry, hot summers. Average annual rainfall is 767.7 mm, and the average annual temperature is 14.9°C (data from the nearest weather station at Sintra-Base Aérea 38°50'N, 9°20'W, 8 km from TNM, 10 km from the Atlantic Ocean, at an elevation of 140 m, data from the years 1971 to 2000 and extracted from Instituto Português do Mar e da Atmosfera-IPMA, <http://www.ipma.pt>). The main soil types are humic cambisols derived from sandstone. Tree cover is dominated by *Pinus* spp. and *Quercus* spp., while the dominant shrubs are *Erica* spp. and *Ulex jussiaei* Webb (Silva et al. 2015). Fallow deer and Red deer co-occur in TNM at an estimated combined density of 0.4 deer/ha (Silva et al. 2014). Approximately 85% of the deer population consisted of Fallow deer and 15% of Red deer. TNM is surrounded by a 3-m-high stone-wall (formerly a royal hunting estate), which prevents the animals from escaping to neighboring areas. In September 2003, a crown-fire burned the area. This fire affected nearly 70% of the area, and most animals could escape the fire. The severity of the fire was high and most trees were top-killed (Catry et al. 2010). Approximately 1.5 years after the fire, in March 2005, an experimental area of 4 ha was fenced by TNM managers as part of a management plan to improve plant regeneration and vegetation recovery. The fenced area was selected as representative of the existing conditions in terms of vegetation and fire severity in the overall site. The fenced area used to monitor the effects of deer exclusion on post-fire recovery. The fence excluded deer but not other mammals such as wild boar (*Sus scrofa*), which could pass through a very narrow opening in a small ditch on a watercourse, or rabbits which were able to pass through the

mesh size. The population density of wild boars was approximately 0.17 individuals/ha (Catry et al. 2007a, 2007b), and we do not have any estimation for the rabbit population. The fence was 190 cm high with a mesh size of 30 × 13 cm (2.5 mm wire).

Experimental Design and Surveys

We evaluated the effects of deer on post-fire recovery during the two springs following fire. We compared the deer-excluded area (fenced area, approximately 4 ha) and the deer-allowed area to understand the effects of deer on the plant communities after fire. In each area, we randomly located 5 plots of 50 × 4 m (2 areas × 5 plots = 10 plots) in the deer-excluded and in the deer-allowed areas. Plots in the deer-allowed area were located close to the fence, between 10 and 25 m, to replicate as closely as possible the vegetation and fire conditions found in the plots in the deer-excluded area. Our experimental design lacks true experimental replication, as we only studied one fenced area. However, it is a large fenced area that allows us to accurately capture the full set of ecological interactions. This is very rare in the literature, as most previous studies only looked at the impact on individual plants or used cages, which does not allow us to understand the effect of animals on plant communities. (e.g. Frazer & Davis 1988; Moreno & Oechel 1993; Arévalo et al. 2009; Paula & Ojeda 2011; Leverkus et al. 2015).

We designed two different surveys, one to study the herbaceous plant community and the other to study the woody plant community. To study the herbaceous plant community, fifty 1 m² quadrats were established within each plot (50 quadrats × 10 plots; $n = 500$ quadrats). In each quadrat, we recorded which herbaceous species were present during the two consecutive springs after the fire; note that this means the fence had excluded deer for approximately 2 months at the time of the first survey. Additionally, we visually estimated the live herbaceous total cover (0–100%) and estimated the modal height (the most common height) of this plant community in each quadrat. To study the woody plant community, we established a longitudinal transect along the central axis of each plot. We measured the intercepts of the canopy of each woody species along the transect to assess woody species cover. We also measured the individual's total height at each intercept with the transect.

We conducted the plant surveys in the spring of 2005 and 2006 (between late April and early June, mainly in May), corresponding to the second (hereafter spring 2) and third (hereafter spring 3) years after the fire, with one and two full growing seasons, respectively. Drought conditions occurred during spring 2 (SPEI = −1.69), but not in spring 3 (SPEI = 0.58), based on a multiscale drought index (SPEI; Vicente-Serrano et al. 2017), where SPEI values less than 0 indicate a drought. All herbaceous species were identified and classified according to their lifespan (annual vs. perennial), functional group (graminoid, legume, and non-legume forb), and regeneration strategy (seed, storage organ, root crown, stolon, and rhizome) using the BROTH 2.0 database (Tavşanoğlu & Pausas 2018) and Flora Iberica (Castroviejo 1986).

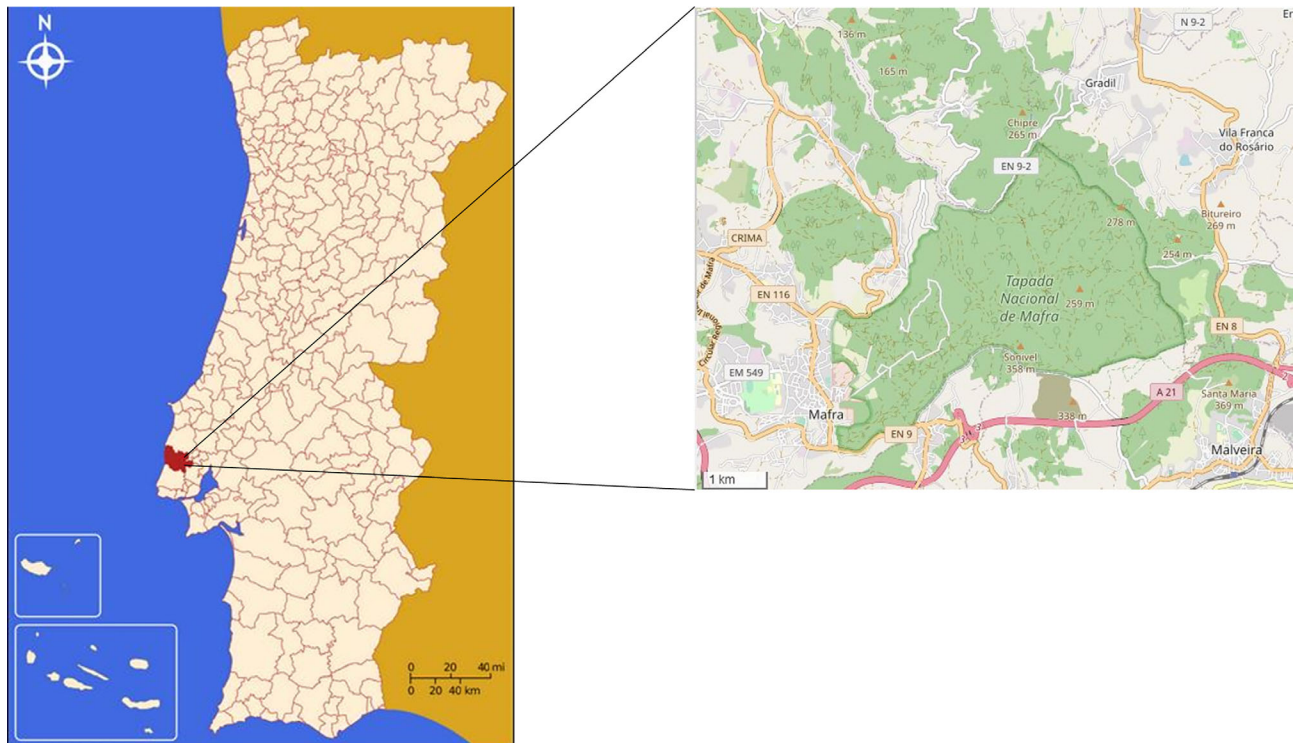


Figure 1. On the left, map of Portugal with the municipality of Mafra in red (© Rei-artur/Obersachse, <http://commons.wikimedia.org>). On the right, the Tapada Nacional de Mafra (© OpenStreetMap).

Facultative seeders were classified according to their vegetative regeneration strategy.

Data Analyses

In all of the following statistical analyses, we performed plot-level analyses by averaging data from the quadrats (herb data) or from the intercepts (woody data) to generate a single data point for each plot in each spring. Although this approach reduces the statistical power to detect significant differences, it homogenizes the two different surveys at the same level (plot) and thus allows statistical tests. We used a repeated measures design because we analyzed the plant communities in the same plots during two consecutive springs (e.g. Céspedes et al. 2014).

We used the frequency of herbaceous species and the cover of woody species as proxies of species abundance. We calculated the frequency of herbaceous species (%) per plot as the number of quadrats where the species was present, divided by the total number of quadrats in each plot. We calculated woody species cover (%) as the sum of cover intercepts along the transect divided by the length of the transect. We separately assessed the diversity of the plant community (herbaceous and woody species, separately) per plot using three common species diversity indices: Species richness, Shannon–Wiener index, and the inverse of Simpson. Species richness was calculated as the number of species per plot. Shannon–Wiener and Simpson indices considered the species richness and relative abundance of species in each plot. The Shannon–Wiener index emphasizes the

importance of species richness and therefore the presence of rare species, while the Simpson’s index emphasizes the importance of relative abundance, and therefore the presence of dominant species (Garnier et al. 2016). We calculated species diversity indices using the *diversity* function in vegan R package version 2.4-6 (Oksanen et al. 2022). We also calculated the herbaceous and woody phytovolumes of the plot (m^3/ha) as the product of cover (%) and height (cm).

To assess changes in herbaceous species composition (as the proportions of various plant species in relation to the total in a given area), a permutational analysis of variance (PERMANOVA) based on Bray–Curtis distances and type III sum of squares was performed using the *adonis2* function in vegan. To prepare the data for PERMANOVA, species frequency data were square root-transformed to avoid statistical bias for rare species. Spring (spring 2 and spring 3), area (deer-excluded vs. deer-allowed) and the interaction between spring and area were considered as categorical fixed factors. We used a restricted permutation within repeated measures (spring) with the parameter “strata.” *F*-statistic was used to test the significance of PERMANOVA. Nonmetric multidimensional scaling was used to represent relationships among species composition at the plot level. We used frequency data of the 101 species from the 20 plots and *metaMDS* functions in vegan.

To evaluate the impact of deer on the herbaceous and woody community properties (structure and diversity indices), we carried out two different analyses of variance (ANOVA) using generalized linear mixed models (GLMM) with repeated measures

included as random factors. For the diversity indices, we carried out GLMMs for each response variable (diversity indices) with spring, area, and the interaction between spring and area as categorical fixed factors. Residuals were examined for normality and homoscedasticity using the DHarma package (version 0.4.6; Hartig & Lohse 2022). Models with normal residuals were fitted to a Gaussian distribution using the *lmer* function (Bates et al. 2023), while models without normal residuals were fitted with *glmer* functions (lme4 package version 1.1-15; Bates et al. 2023). We report selected families of GLMMs in the results tables or in the results figures. For frequency data, when residuals were not normally distributed, we used a negative binomial family, because our data were not adjusted to a Poisson distribution (it was not count data), and we assumed that the mean followed a gamma distribution. Significance of differences was evaluated using a Wald test with the *Anova* function in the car package (Fox et al. 2023). When differences were statistically significant, multiple comparisons between levels of fixed factors were assessed using the *emmeans* function in emmeans package version 1.4-13 (Lenth et al. 2023). In terms of structure, we carried out GLMMs for each response variable (cover, height, and phytovolume) with community type (herbaceous vs. woody), spring and area as categorical fixed factors, and also the interactions between them. We also observed the performance of residuals, as we described above. In this case, we assessed whether there were differences between herb and woody species structure in the study plots in both years using estimated marginal means from a linear regression model, and we did not analyze the significance of the differences.

To evaluate whether annual herbs were more frequent than perennial herbs in deer-allowed areas and what plant functional group was more frequent in open areas, a four-way repeated measures ANOVA was performed using GLMM. The response variable was group frequency per plot, calculated as the mean of the species frequency of each type per quadrat. Explanatory variables were life cycle (annual vs. perennial), plant functional group (legume, forb, and graminoid), with area and spring as fixed factors, and the interaction between them. We included repeated measures as a random factor. To evaluate whether species with a hidden belowground regeneration source were more frequent in open areas, we carried out a one-way nested ANOVA using a GLMM with regeneration strategy (obligate seeders, sprouters regenerating from storage organs, root crown, rhizomes, or stolons) and area and spring as fixed factors, and the interaction between them. In both cases, we selected a negative binomial regression model, after following the same

procedure described above for the assumptions of residual normality and homoscedasticity. We also assessed the significance of differences using a Wald test, and we described the differences between groups using the estimated marginal means using the *emmeans* function.

All calculations, statistical analyses and graphics were made using R v.4.0.2 (R Core Team 2023).

Results

Herbaceous Species Composition, Ecological Diversity, and Community Structure

In total, we found 101 herbaceous species in both spring 2 and spring 3 after the wildfire (see Table S1 for the list of species). Although deer presence (area factor) explained only 6% of the variation in herbaceous species composition (Fig. S1), there were significant differences in plant species composition between deer-excluded and deer-allowed plots (F -ratio = 1.82, $p = 0.004$). Time since fire (spring factor) explained more than 35% of the variation in herbaceous composition, and there were significant differences between spring 2 and spring 3 (F -ratio = 10.20, $p = 0.002$). The interaction between spring and area factors was not significant (F -ratio = 0.87, $p = 0.561$), indicating similar trends in each spring and each type of area.

Although species diversity indices showed higher values in deer-excluded plots, these differences were not significant, suggesting no effects of deer on herbaceous diversity (Table 1). In contrast, species diversity indices differed significantly between sampled springs. Herbaceous species richness increased five-fold from spring 2 to spring 3, Shannon–Weiner diversity increased almost three-fold, indicating an increase of rare species, and inverse of Simpson increased almost six-fold (Fig. 2), indicating less frequency of dominant species. Notably, woody diversity indices (see Table S2 for the list of woody species) were not significantly different between springs, nor between deer-excluded and deer-allowed plots (Table S3), with an average value of 1.25/plot for the Shannon–Weiner diversity index.

Deer and time since fire significantly affected the structure of the plant community (Table S4; Fig. 3). Overall, the exclusion of deer resulted in an increase in plant cover, height, and phytovolume compared to the deer-allowed area. Herbaceous cover decreased from spring 2 to spring 3 in both deer-excluded and deer-allowed plots, whereas woody cover and both herbaceous and woody height and phytovolume increased from spring 2 to

Table 1. Herbaceous species community. ANOVAs (type II) with species diversity indices per plot as response variable, using Gaussian LMMs with area (deer-excluded vs. deer-allowed) and spring (spring 2 vs. spring 3), and repeated measures based on spring as random factors. *df*: degrees of freedom. $n = 20$ observations.

| | df | Spring | | Area | | Spring \times area | |
|------------------|----|----------|---------------|----------|---------------|----------------------|---------------|
| | | χ^2 | $Pr(>\chi^2)$ | χ^2 | $Pr(>\chi^2)$ | χ^2 | $Pr(>\chi^2)$ |
| Species richness | 1 | 132.75 | <0.001 | 3.11 | 0.078 | 1.35 | 0.245 |
| Shannon–Weiner | 1 | 108.23 | <0.001 | 1.65 | 0.199 | 0.00 | 0.986 |
| Inverse Simpson | 1 | 110.17 | <0.001 | 2.40 | 0.122 | 1.58 | 0.208 |

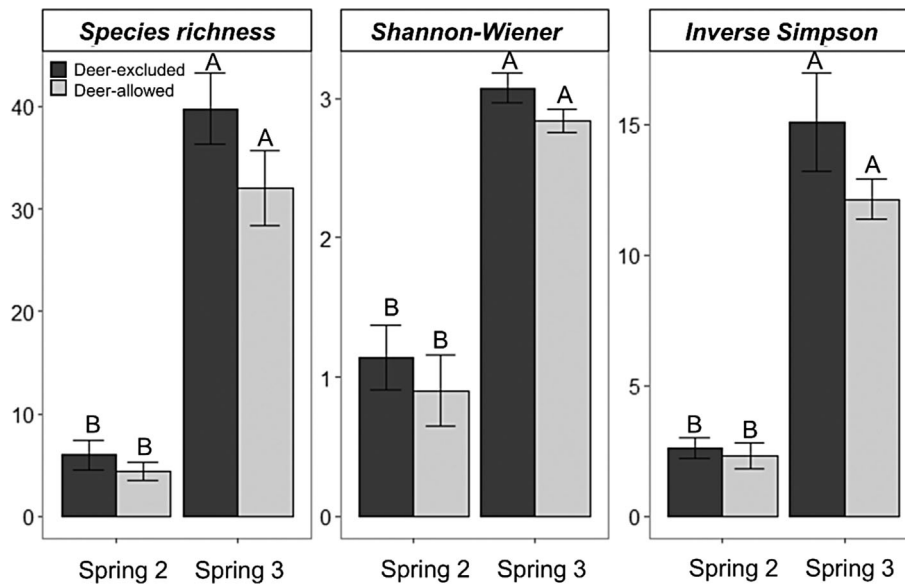


Figure 2. Herbaceous community properties through time (second and third spring). Average of species diversity indices per plot type (deer-allowed vs. deer-excluded) \pm SE. Letters indicate significant differences after GLMM, and multiple comparisons ($p < 0.05$).

spring 3. Furthermore, herbs were more abundant and taller than woody plants in spring 2, especially in deer-excluded plots, but not in spring 3.

Variation in Life Span, Functional Groups, and Regeneration Strategy of Herbaceous Plants

Deer affected the frequency of annual and perennial herbs differently in the early post-fire stage (Table S5; Fig. 4), although this difference was only marginally significant ($\chi^2 = 6.99$, $p = 0.072$). Furthermore, deer did not affect the frequency of legumes,

graminoids and non-legume forbs ($\chi^2 = 4.36$, $p = 0.499$). Herbs overall were almost six-fold more frequent in deer-excluded plots than in deer-allowed plots ($\chi^2 = 8.58$, $p = 0.004$). Regardless of deer impact, forbs showed a higher frequency than graminoids, and legumes showed the lowest frequency ($\chi^2 = 128.22$, $p < 0.001$). In addition, there were differences between springs. Herbs showed higher frequencies in spring 3 than in spring 2 ($\chi^2 = 38.59$, $p < 0.001$), although the frequency of functional and life form groups did not vary between springs (Table S4). However, there were some different trends between groups in each spring (Fig. 4). In spring 2, annuals were very limited, and perennials

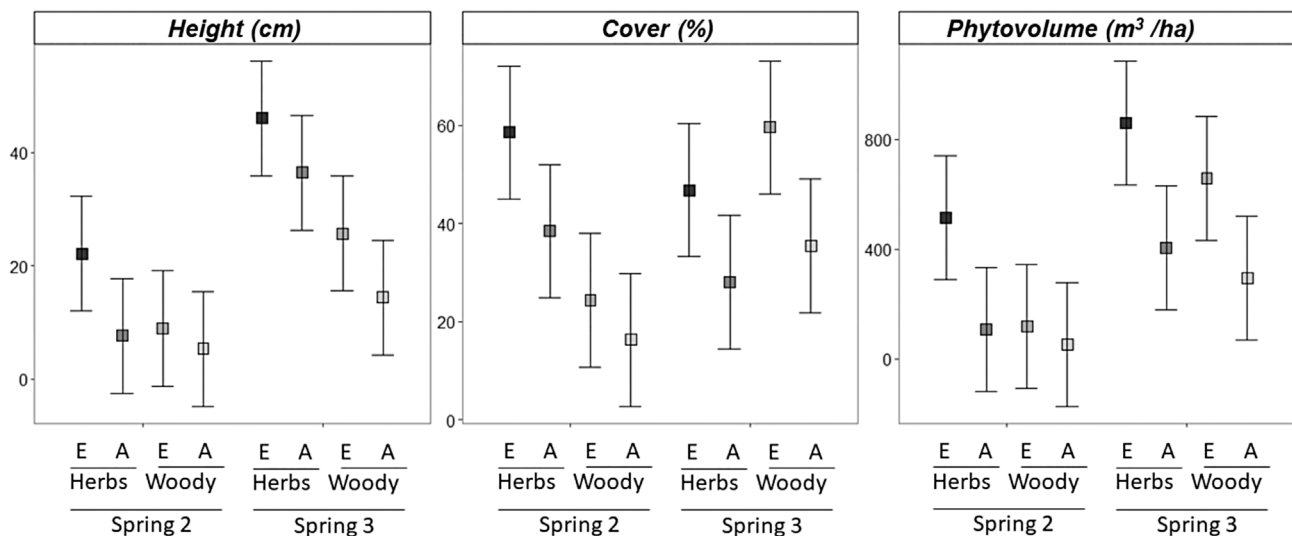


Figure 3. Height, cover, and phytovolume of herbaceous and woody plants through time per plot (deer-allowed and deer-excluded). Points are estimated marginal means (95% CI) of frequencies per plot. Means were estimated on the interaction among type of community (herb vs. woody species), area and spring using a linear regression model. E: Deer-excluded plots. A: Deer-allowed plots.

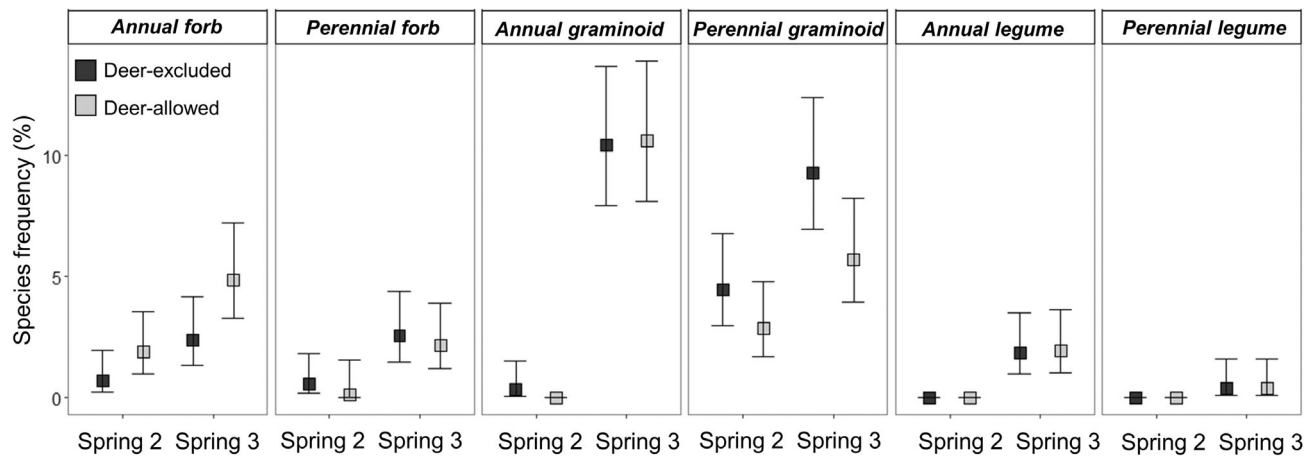


Figure 4. Frequency of functional groups according to life span in deer-allowed and deer-excluded plots through time. Points are estimated marginal means (95% CI) of frequencies per plot. Means were estimated on the interaction among four factors (life span, functional group, area, and spring) using a negative binomial regression model.

were more frequent, due to the high frequency of perennial graminoids. Legumes were absent in spring 2, and annual graminoids were also absent, but only in deer-allowed plots in spring 2. Conversely, in spring 3, annuals were more frequent than perennial herbs in deer-allowed plots, where they were almost three times more frequent, although both showed similar frequencies in deer-excluded plots. In summary, forbs and graminoids accounted for these differences between deer-allowed versus deer-excluded plots and between spring 2 versus spring 3, as legumes were almost absent. Annual graminoids were the most frequent group, regardless of deer disturbance. Annual forbs tended to be more frequent in deer-allowed plots than in deer-excluded plots, while perennial graminoids tended to be less frequent in deer-allowed plots.

Plant regeneration strategy explained the assemblage of the herbaceous community in the early post-fire stages ($\chi^2 = 51.85$, $p = <0.001$; Table S6; Fig. 5). Species with stolons were four times more frequent than species with storage organs or obligate seeders in both study years. Similarly, species with rhizomes were three times more frequent than species with storage organs or obligate seeders. Species with root crown were absent in year 2. All groups were more frequent in spring 3 than in spring 2 ($\chi^2 = 38.60$, $p = <0.001$). In addition, deer significantly affected the species frequency ($\chi^2 = 14.03$, $p = <0.001$), independent of regeneration strategy and spring. There was no significant interaction between deer and plant regeneration strategy, nor any other interaction between spring, deer disturbance, and regeneration strategy. Species with rhizomes, species with root crown regeneration and obligate seeders were equally frequent in deer-allowed and deer-excluded plots. However, species with stolons tended to be more frequent in deer-excluded than in deer-allowed plots, as were species with storage organs.

Discussion

In accordance with our general expectations, during the initial years of post-fire recovery, excluding deer can significantly

impact vegetation dynamics. However, the impact of deer is influenced by time since the fire and weather conditions, which may be more important than herbivory in shaping the recovery trajectory of herbaceous composition. Based on our first hypothesis, deer exclusion or population control could be effective management interventions for increasing the volume of woody and herbaceous vegetation, particularly in dry years. Contrary to our second hypothesis, excluding deer does not seem to affect plant diversity or composition. Therefore, it is not a useful management strategy for enhancing biodiversity. Our third hypothesis is partially supported by the fact that the exclusion of deer promotes the assemblage of graminoids and does not seem to affect annual species. Unexpectedly, the exclusion can also prevent the spread of exotic species due to deer disturbance.

Weather Conditions Explain the Post-Fire Recovery of Herbaceous Species in Early Stages

Early post-fire vegetation stages were dominated by herbaceous plants in our study, as also observed in other MTEs (Keeley et al. 2006). The crown-fire killed most of the aboveground plant parts (Catry et al. 2010), opening an opportunity for herbaceous species, which, without any disturbance, typically decrease in cover over ecological succession as woody species increase (Coulter et al. 2010). In MTEs, post-fire recovery is often a gradual succession from an herbaceous to a shrub community and finally woodland in a few years, following the “self-regulatory” hypothesis (Keeley et al. 2005). However, recovery is also context-dependent (Keeley et al. 2005). Indeed, we observed a shift between the second and the third spring, with a notable increase in annual herbs. This unexpected behavior could be explained by a drought year in 2005 (the second spring after the wildfire), which mainly affected the rainy months of spring (quantified by the multiscale drought index; Vicente-Serrano et al. 2017). This dry year likely limited the flush of annual species, which typically occur in MTEs after a wildfire (Keeley et al. 2006). In the same experiment, drought may

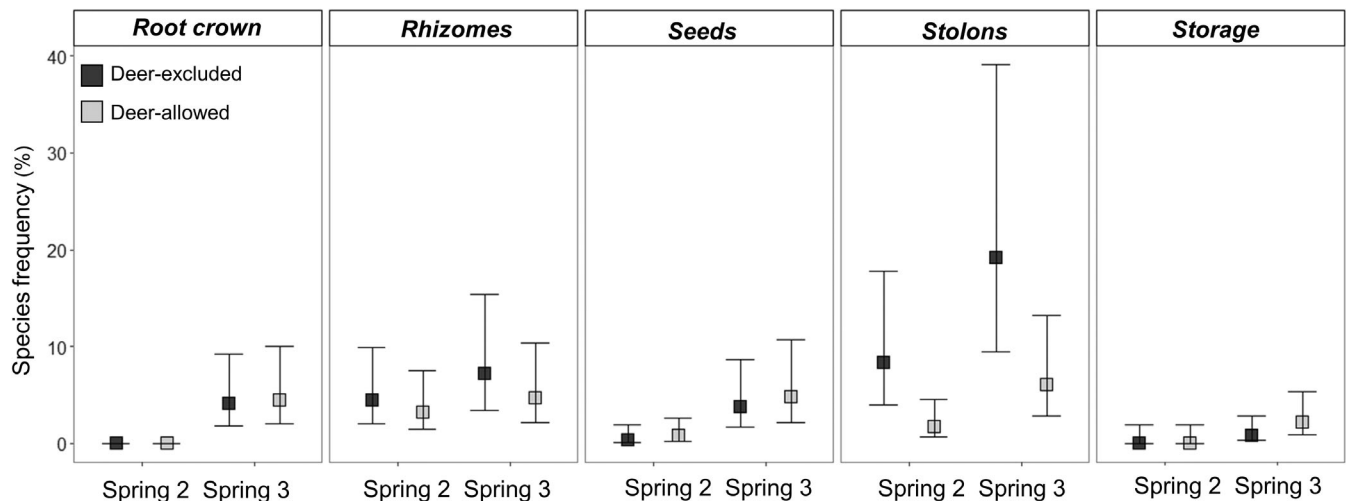


Figure 5. Frequency of herbaceous species of each regeneration group in deer-allowed and deer-excluded plots through time. Points are estimated marginal means (95% CI) of frequencies per plot. Means were estimated on the interaction among regeneration strategy, area, and spring using a negative binomial regression model.

reduce the frequency of some woody species compared to other early post-fire years, but without producing changes in the dominance of functional groups (Silva et al. 2014).

Deer as a Driver in the Post-Fire Recovery Assembly

Herbivores can limit the recovery of plant species in recently burned areas by feeding on seeds, seedlings, and resprouts, delaying plant regeneration and growth, while also indirectly benefiting other species, producing shifts in plant communities (Foster et al. 2020). In our study, minimal differences between deer-excluded and deer-allowed plots could be expected in the first monitored spring, given the recent installation of fences. However, significant differences between areas were observed in both springs, including the first one studied. By consuming herbaceous species, deer reduced plant cover, height, and phytovolume of the herbaceous community in both springs. In contrast, there were no differences in the species diversity indices of either the herbaceous or the woody plant community between deer exclusion and deer-allowed areas. This was also previously reported for the woody community in the same experiment (Silva et al. 2015). These results might be explained by the time of fence installation. Indeed, the fence was installed 1.5 years after the fire, which may have been sufficient time for deer together with wild boars to impact the plant community (Leverkus et al. 2015).

Herbivorous mammals tend to be very selective when feeding by choosing between different plant species and parts (Pringle et al. 2023), as plants present numerous resistance and resilience adaptations, such as spines or hidden meristems, which determine the impact of these herbivores (Archibald et al. 2019). In our study, we look at the impact of deer at the plant functional group level and also at the species level. Annuals were not affected by deer in our experiment, as we predicted. Annuals were successful, probably due to the fact that wildfires, and to a lesser extent, deer, reduced competition for light and resources

by eliminating the woody plant cover. Plant community disturbances, such as fire, usually favor annuals over perennials, and short perennials over tall perennials (Belsky 1992). Additionally, perennial species may have been more vulnerable to deer herbivory as usually they are more nutritious (Noy-Meir 1995). Graminoids and non-leguminous forbs were the main functional groups explaining deer-induced changes in the post-fire assemblage. Conversely, legumes had similar frequencies in both deer-excluded and deer-allowed areas. It has been reported that Fallow deer prefer graminoid herbs to forbs and legumes (Bruno & Apollonio 1991). Fallow deer was the most abundant deer species in our study area, comprising approximately 85% of the deer population. This may explain the lower abundance of perennial graminoids in the deer-allowed area, and the very low impact on the assembly of perennial forbs. This result also highlights the importance of knowing herbivore foraging behavior and, if possible, diets to understand the potential effects of herbivores on the post-fire vegetation recovery (Royo et al. 2010). However, perennial graminoid species responded differently to deer depending on their regeneration strategies. Stoloniferous species, such as *Agrostis castellana* or *Poa trivialis*, appeared to be more vulnerable than rhizomatous species, such as *Brachypodium phoenicoides*. A hidden belowground bud bank can resprout after the aerial part of the plant suffers vertebrate grazing (Pausas & Paula 2020). In addition to regeneration strategies, different nutritional value among grasses or forbs, and therefore differences in deer feeding preferences, may also contribute to the differences found between deer-excluded and deer-allowed areas. Many annual forbs such as *Anagallis arvensis*, *Gnaphalium uliginosum*, and *Senecio sylvaticus* were more abundant in deer-allowed areas, possibly because they are unpalatable or of low nutritional value, as observed for sika deer in Japan (Takahashi & Kaji 2001). In addition, as forbs in our study area were mainly short ruderal plant species favored by disturbance, they may have also benefited from reduced competition

for light and resources resulting from an overall lower plant biomass in the deer-allowed areas (Belsky 1992).

Feeding activity of herbivores is determined by the availability of forage (Bugalho & Milne 2003; Royo et al. 2010). The first year of our study coincided with a dry spring, during which the plant community was dominated by perennial graminoids with a very low frequency of annual species, and during which woody species may have had low growth rates. A dry spring could have resulted in low food abundance for deer, which may have induced an overgrazing (Royo & Carson 2006). In this case, the effects of deer on the plant community could be intensified, in particular toward perennial grasses, the most abundant form during drought and also one of the forms most preferred by deer. Furthermore, deer foraging behavior may have favored the success of forb species but also allowed the establishment of exotic plant species such as *Conyza* spp. Assessing the impacts of vertebrate herbivores on post-fire plant community assembly is thus crucial, not only in relation to the effects on native plant communities but also on exotic species. A similar situation where post-fire grazing stimulated the propagation of exotic plant species was described by Keeley et al. (2003) and Coulter et al. (2010) for chaparral habitats in the United States, such as species of *Erodium* and *Torilis* in both studies. In our study, however, the frequency of *Conyza* spp. decreased considerably during the third spring, probably because of its lower competitive ability as compared to native annual grasses (Prieur-Richard et al. 2002). Conversely, in the non-dry spring, the plant community was rich in annual and perennial species, which may have provided higher food availability for deer. During the dry spring, deer reduced the abundance of perennial grasses, but not that of other grasses and other annual species, nor forbs such as the exotic *Gamochaeta subfalcata*. In the non-dry spring, deer had little or no effect on the herbaceous plant community, namely on annual species. Additionally, deer affected the abundance of woody species, such as *Rubus ulmifolius* and *Cistus salviifolius* (Silva et al. 2014), and that of perennial graminoids in springs whose abundance decreased in deer-allowed areas. Deer therefore delayed the post-fire recovery of the woody plant community (Silva et al. 2015), favoring herbaceous over woody species, and annual over perennial herbs.

Deer Exclusion as Post-Fire Restoration Action

The establishment of post-fire deer exclusion zones or control populations may be appropriate management practices to support ecosystem restoration, depending on the objective. First, if the restoration aim is to increase the cover, height, and phytovolume of woody and herbaceous vegetation, deer exclusion would be appropriate in the first few years after the fire. This action would be especially important to buffer the recovery of herbaceous species against interannual variation in weather, such as droughts. However, this may at the same time increase fire risk (e.g. Lecomte et al. 2019), because deer prevent plant biomass and fuel load accumulation (Catry et al. 2007a, 2007b; Silva et al. 2015). Second, if the restoration aim is to increase biodiversity, deer exclusion appears to have no impact on plant diversity or composition in our study. Although deer act as biotic assembly filters at

the species-specific level or even at the functional group level with relevance to ecosystem restoration. Deer exclusion can enhance the assemblage of graminoids, which are important components of perennial vegetation cover and reduce soil erosion in the first post-fire years (Beyers 2004). In addition, deer can potentially increase the abundance of unpalatable and sometimes exotic species, which are already favored in degraded areas such as post-fire sites (Coulter et al. 2010). Deer exclusion can also promote the recovery of species that are sensitive to trampling, such as *Pteridium aquilinum*, which deer do not seem to feed on (e.g. Marozas et al. 2009). However, these species are observed at low frequency in deer-allowed areas.

In summary, we found that deer affect the recovery of herbaceous and woody plant communities. Further work is needed to better understand the impact of deer on post-fire recovery. Despite the logistical challenges, more studies with the exclusion of deer rather than simply studying damage to individual plants or using cages are needed to observe a broad impact of deer on community structure. In addition, the inclusion of drought experiments would be interesting to unravel the interaction between disturbances, particularly in the context of climate change in MTEs.

Acknowledgments

We are very grateful to C. Santos, M. Cardoso, and T. Lopes for their collaboration in the field work. This research was funded by FEDER funds through the Operational Competitiveness Factors Program—COMPETE and by national funds through FCT—Portuguese Foundation for Science and Technology within the scope of the project UID/BIA/50027/2019. A.C. was funded by the postdoctoral grant FCT, UID/50027/2020. M.N.B. was funded by contract DL 57/2016/CP1382/CT0030. F.X.C. was funded by the research contract CEECIND/01378/2017/CP1430/CT0005. We thank Dr. K. Veblen for coordinating the editing and Prof. E. W. Schupp and two anonymous reviewers for their careful reading of our manuscript and their many insightful comments and suggestions.

LITERATURE CITED

- Acevedo P, Ruiz-Fons F, Vicente J, Reyes-García AR, Alzaga V, Gortázar C (2008) Estimating red deer abundance in a wide range of management situations in Mediterranean habitats. *Journal of Zoology* 276:37–47. <https://doi.org/10.1111/j.1469-7998.2008.00464.x>
- Archibald S, Hempson GP, Lehmann C (2019) A unified framework for plant life-history strategies shaped by fire and herbivory. *New Phytologist* 224: 1490–1503. <https://doi.org/10.1111/nph.15986>
- Arévalo JR, Álvarez P, Narvaez N, Walker K (2009) The effects of fire on the regeneration of a *Quercus douglasii* stand in quail ridge reserve, Berryessa Valley (California). *Journal of Forest Research* 14:81–87. <https://doi.org/10.1007/s10310-008-0107-3>
- Bates D, Maechler M, Bolker B, Walker S, Christensen RHB, Singmann H, et al. (2023) lme4: linear mixed-effects models using 'Eigen' and S4. <https://cran.r-project.org/web/packages/lme4/index.html>. 2023.01.015
- Belsky AJ (1992) Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. *Journal of Vegetation Science* 3:187–200. <https://doi.org/10.2307/3235679>

- Beyers JL (2004) Postfire seeding for erosion control: effectiveness and impacts on native plant communities. *Conservation Biology* 18:947–956. <https://doi.org/10.1111/j.1523-1739.2004.00523.x>
- Briske DD, Richards JH (1995) Plant responses to defoliation: a physiological, morphological and demographic evaluation. Pages 635–710. In: *Wildland plants: physiological ecology and developmental morphology*. Society for Range Management, Denver, USA
- Bruno E, Apollonio M (1991) Seasonal variations in the diet of adult male fallow deer in a submediterranean coastal area. *Revue d'Ecologie, La Terre et la Vie* 46:349–362. <https://doi.org/10.3406/revec.1991.2045>
- Bugalho MN, Milne JA (2003) The composition of the diet of red deer (*Cervus elaphus*) in a Mediterranean environment: a case of summer nutritional constraint? *Forest Ecology and Management* 181:23–29. [https://doi.org/10.1016/S0378-1127\(03\)00125-7](https://doi.org/10.1016/S0378-1127(03)00125-7)
- Castroviejo S (1986) Flora iberica 1–8, 10–15, 17–18, 21. Real Jardín Botánico, CSIC, Madrid, Spain
- Catry FX, Bugalho MN, Lopes T, Rego F, Moreira F (2007a) Post-fire effects of ungulates on the structure, abundance and diversity of vegetation in a Mediterranean ecosystem. Pages 43–44. In: Rokich D, Wardell-Johnson G, Yates C, Stevens J, Dixon K, McLellan R, Moss G (eds) *Proceedings of the International Mediterranean Ecosystems Conference – Medecos XI 2007*. Kings Park and Botanic Garden, Perth, Australia
- Catry FX, Pausas J, Moreira F, Fernandes P, Rego F (2013) Post-fire response variability in Mediterranean Basin tree species in Portugal. *International Journal of Wildland Fire* 22:919–932. <https://doi.org/10.1071/WF12215>
- Catry FX, Rego F, Lopes T, Bugalho MN, Silva JS, Moreira F (2007b) Recuperação da Floresta após o Fogo. O caso da Tapada Nacional de Mafra. Centro de Ecologia Aplicada Prof. Baeta Nieve, Lisboa, Portugal
- Catry FX, Rego F, Moreira F, Fernandes PM, Pausas JG (2010) Post-fire tree mortality in mixed forests of central Portugal. *Forest Ecology and Management* 260:1184–1192. <https://doi.org/10.1016/j.foreco.2010.07.010>
- Céspedes B, Luna B, Pérez B, Urbieto IR, Moreno JM (2014) Burning season effects on the short-term post-fire vegetation dynamics of a Mediterranean heathland. *Applied Vegetation Science* 17:86–96. <https://doi.org/10.1111/avsc.12053>
- Chard M, Foster CN, Lindenmayer DB, Cary GJ, MacGregor CI, Blanchard W (2022) Post-fire pickings: large herbivores alter understory vegetation communities in a coastal eucalypt forest. *Ecology and Evolution* 12:e8828. <https://doi.org/10.1002/ece3.8828>
- Clark PE, Williams CJ, Pierson FB, Hardegree SP (2016) Postfire grazing management effects on mesic sagebrush-steppe vegetation: spring grazing. *Journal of Arid Environments* 132:49–59. <https://doi.org/10.1016/j.jaridenv.2015.10.022>
- Clarke MF, Kelly LT, Avitabile SC, Benshemesh J, Callister KE, Driscoll DA, et al. (2021) Fire and its interactions with other drivers shape a distinctive, semi-arid 'Mallee' ecosystem. *Frontiers in Ecology and Evolution* 9. <https://doi.org/10.3389/fevo.2021.647557>
- Côté SD, Rooney TP, Tremblay J-P, Dussault C, Waller DM (2004) Ecological impacts of deer overabundance. *Annual Review of Ecology, Evolution, and Systematics* 35:113–147. <https://doi.org/10.1146/annurev.ecolsys.35.021103.105725>
- Coulter CT, Southworth D, Hosten PE (2010) Prescribed fire and post-fire seeding in brush masticated oak-chaparral: consequences for native and non-native plants. *Fire Ecology* 6:60–75. <https://doi.org/10.4996/fireecology.0602060>
- Foster CN, Banks SC, Cary GJ, Johnson CN, Lindenmayer DB, Valentine LE (2020) Animals as agents in fire regimes. *Trends in Ecology & Evolution* 35:346–356. <https://doi.org/10.1016/j.tree.2020.01.002>
- Foster CN, Barton PS, Sato CF, MacGregor CI, Lindenmayer DB (2015) Synergistic interactions between fire and browsing drive plant diversity in a forest understory. *Journal of Vegetation Science* 26:1112–1123. <https://doi.org/10.1111/jvs.12311>
- Fox J, Weisberg S, Price B, Adler D, Bates D, Baud-Bovy G, et al. (2023) car: companion to applied regression. <https://cran.r-project.org/web/packages/car/index.html.2023.01.015>
- Frazer JM, Davis SD (1988) Differential survival of chaparral seedlings during the first summer drought after wildfire. *Oecologia* 76:215–221. <https://doi.org/10.1007/BF00379955>
- Garnier E, Navas M-L, Grigulis K (2016) *Plant functional diversity: organism traits, community structure, and ecosystem properties*. Oxford University Press, Oxford, United Kingdom
- Gebert C, Verheyden-Tixier H (2001) Variations of diet composition of Red Deer (*Cervus elaphus* L.) in Europe. *Mammal Review* 31:189–201. <https://doi.org/10.1111/j.1365-2907.2001.00090.x>
- Gordon IJ, Prins HH (2019) The ecology of browsing and grazing in other vertebrate taxa. In: Gordon IJ, Prins HH (eds) *The ecology of browsing and grazing II*. Springer International Publishing, Cham Switzerland
- Grime JP (2006) *Plant strategies, vegetation processes, and ecosystem properties*. John Wiley & Sons Ltd, Chichester, United Kingdom
- Hartig F, Lohse L (2022) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. <https://cran.r-project.org/web/packages/DHARMa/index.html.2023.01.015>
- Hofmann RR, Stewart DRM (1972) Grazer or browser: a classification based on the stomach-structure and feeding habits of East African ruminants. *Mammalia* 36:226–240.
- Keeley JE, Fotheringham CJ, Baer-Keeley M (2005) Determinants of postfire recovery and succession in Mediterranean-climate shrublands of California. *Ecological Applications* 15:1515–1534. <https://doi.org/10.1890/04-1005>
- Keeley JE, Fotheringham CJ, Baer-Keeley M (2006) Demographic patterns of postfire regeneration in Mediterranean-climate shrublands of California. *Ecological Monographs* 76:235–255. [https://doi.org/10.1890/0012-9615\(2006\)076\[0235:DOPRIJ\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2006)076[0235:DOPRIJ]2.0.CO;2)
- Keeley JE, Lubin D, Fotheringham CJ (2003) Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. *Ecological Applications* 13:1355–1374. <https://doi.org/10.1890/02-5002>
- Keeley JE, Pausas JG (2022) Evolutionary ecology of fire. *Annual Review of Ecology, Evolution, and Systematics* 53:203–225. <https://doi.org/10.1146/annurev-ecolsys-102320-095612>
- Köbel M, Listopad CMCS, Príncipe A, Nunes A, Branquinho C (2021) Temporary grazing exclusion as a passive restoration strategy in a dryland woodland: effects over time on tree regeneration and on the shrub community. *Forest Ecology and Management* 483:118732. <https://doi.org/10.1016/j.foreco.2020.118732>
- Lecomte X, Caldeira MC, Catry FX, Fernandes PM, Jackson RB, Bugalho MN (2019) Ungulates mediate trade-offs between carbon storage and wildfire hazard in Mediterranean oak woodlands. *Journal of Applied Ecology* 56:699–710. <https://doi.org/10.1111/1365-2664.13310>
- Lenth RV, Bolker B, Buurkner P, Giné-Vázquez I, Herve M, Jung M, Love J, Miguez F, Riebl H, Singmann H (2023) Emmeans: estimated marginal means, aka least-squares means. <https://cran.r-project.org/web/packages/emmeans/index.html.2023.01.015>
- Leverkus AB, Rojo M, Castro J (2015) Habitat complexity and individual acorn protectors enhance the post-fire restoration of oak forests via seed sowing. *Ecological Engineering* 83:276–280. <https://doi.org/10.1016/j.ecoleng.2015.06.033>
- Lucas-Borja ME, Delgado-Baquerizo M, Muñoz-Rojas M, Plaza-Álvarez PA, Gómez-Sánchez ME, González-Romero J, Peña-Molina E, Moya D, de las Heras J (2021) Changes in ecosystem properties after post-fire management strategies in wildfire-affected Mediterranean forests. *Journal of Applied Ecology* 58:836–846. <https://doi.org/10.1111/1365-2664.13819>
- Luzuriaga AL, González JM, Escudero A (2015) Annual plant community assembly in edaphically heterogeneous environments. *Journal of Vegetation Science* 26:866–875. <https://doi.org/10.1111/jvs.12285>
- Marozas V, Pételis S, Brazaitis G, Baranaukaitė J (2009) Early changes of ground vegetation in fallow deer enclosure. *Baltic Forestry* 15:268–272
- Moreno JM, Oechel WC (1993) Demography of *Adenostoma fasciculatum* after fires of different intensities in southern California chaparral. *Oecologia* 96:95–101. <https://doi.org/10.1007/BF00318035>

- Noy-Meir I (1995) Interactive effects of fire and grazing on structure and diversity of Mediterranean grasslands. *Journal of Vegetation Science* 6:701–710. <https://doi.org/10.2307/3236441>
- Noy-Meir I, Gutman M, Kaplan Y (1989) Responses of Mediterranean grassland plants to grazing and protection. *Journal of Ecology* 77:290–310. <https://doi.org/10.2307/2260930>
- Nunes A, Oliveira G, Mexia T, Valdecantos A, Zucca C, Costantini EAC, et al. (2016) Ecological restoration across the Mediterranean Basin as viewed by practitioners. *Science of the Total Environment* 566–567:722–732. <https://doi.org/10.1016/j.scitotenv.2016.05.136>
- Oksanen J, Simpson GL, Blanchet FG, Kindt R, Legendre P, Minchin PR, et al. (2022) Vegan: community ecology package. <https://cran.r-project.org/web/packages/vegan/index.html.2023.01.015>
- Paula S, Ojeda F (2011) Response to recurrent disturbance in two co-occurring resprouter heath species: the ecological consequences of withstanding herbivores. *Plant Ecology* 212:2035–2045. <https://doi.org/10.1007/s11258-011-9927-x>
- Pausas JG, Bradstock RA, Keith DA, Keeley JE (2004) Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology* 85:1085–1100. <https://doi.org/10.1890/02-4094>
- Pausas JG, Paula S (2020) Grasses and fire: the importance of hiding buds. *New Phytologist* 226:957–959. <https://doi.org/10.1111/nph.15964>
- Pausas JG, Pratt RB, Keeley JE, Jacobsen AL, Ramirez AR, Vilagrosa A, Paula S, Kaneakua-Pia IN, Davis SD (2016) Towards understanding resprouting at the global scale. *New Phytologist* 209:945–954. <https://doi.org/10.1111/nph.13644>
- Prieur-Richard A-H, Lavorel S, Linhart YB, Dos Santos A (2002) Plant diversity, herbivory and resistance of a plant community to invasion in Mediterranean annual communities. *Oecologia* 130:96–104. <https://doi.org/10.1007/s004420100774>
- Pringle RM, Abraham JO, Anderson TM, Coverdale TC, Davies AB, Dutton CL, et al. (2023) Impacts of large herbivores on terrestrial ecosystems. *Current Biology* 33:R584–R610. <https://doi.org/10.1016/j.cub.2023.04.024>
- R Core Team (2023) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Rautiainen H, Bergvall UA, Felton AM, Tigabu M, Kjellander P (2021) Nutritional niche separation between native roe deer and the nonnative fallow deer—a test of interspecific competition. *Mammal Research* 66:443–455. <https://doi.org/10.1007/s13364-021-00571-w>
- Rego FC, Morgan P, Fernandes P, Hoffman C (2021) Fire regimes, landscape dynamics, and landscape management. Pages 421–507. In: Rego FC, Morgan P, Fernandes P, Hoffman C (eds) *Fire science: from chemistry to landscape management*. Springer textbooks in Earth sciences, geography and environment. Springer International Publishing, Cham, Switzerland. https://doi.org/10.1007/978-3-030-69815-7_12
- Rouet-Leduc J, Pe'er G, Moreira F, Bonn A, Helmer W, Shahsavani Zadeh SAA, Zizka A, van der Plas F (2021) Effects of large herbivores on fire regimes and wildfire mitigation. *Journal of Applied Ecology* 58:2690–2702. <https://doi.org/10.1111/1365-2664.13972>
- Royo AA, Carson WP (2006) On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Canadian Journal of Forest Research* 36:1345–1362. <https://doi.org/10.1139/x06-025>
- Royo AA, Collins R, Adams MB, Kirschbaum C, Carson WP (2010) Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. *Ecology* 91:93–105. <https://doi.org/10.1890/08-1680.1>
- Silva JS, Catry FX, Moreira F, Bugalho MN (2015) The effects of deer exclusion on the development of a Mediterranean plant community affected by a wildfire. *Restoration Ecology* 23:760–767. <https://doi.org/10.1111/rec.12242>
- Silva JS, Catry FX, Moreira F, Lopes T, Forte T, Bugalho MN (2014) Effects of deer on the post-fire recovery of a Mediterranean plant community in Central Portugal. *Journal of Forest Research* 19:276–284. <https://doi.org/10.1007/s10310-013-0415-0>
- Takahashi H, Kaji K (2001) Fallen leaves and unpalatable plants as alternative foods for sika deer under food limitation. *Ecological Research* 16:257–262. <https://doi.org/10.1046/j.1440-1703.2001.00391.x>
- Tavşanoğlu Ç, Pausas JG (2018) A functional trait database for Mediterranean Basin plants. *Scientific Data* 5:180135. <https://doi.org/10.1038/sdata.2018.135>
- Vicente-Serrano SM, Tomas-Burguera M, Beguería S, Reig F, Latorre B, Peña-Gallardo M, Luna MY, Morata A, González-Hidalgo JC (2017) A high resolution dataset of drought indices for Spain. *Data* 2:22. <https://doi.org/10.3390/data2030022>
- Wisdom MJ, Vavra M, Boyd JM, Hemstrom MA, Ager AA, Johnson BK (2006) Understanding ungulate herbivory—episodic disturbance effects on vegetation dynamics: knowledge gaps and management needs. *Wildlife Society Bulletin* 34:283–292. [https://doi.org/10.2193/0091-7648\(2006\)34\[283:UUHDEO\]2.0.CO;2](https://doi.org/10.2193/0091-7648(2006)34[283:UUHDEO]2.0.CO;2)

Supporting Information

The following information may be found in the online version of this article:

Table S1. Observed herbaceous taxa in our study.

Table S2. Observed woody species in our study.

Table S3. Woody species community.

Table S4. ANOVAs (type II) with plant structure variables (cover, height, and phytovolume).

Table S5. ANOVA (type II) with species frequency per plot as response variable, and life span (annual vs. perennial), functional group (legume, forb, graminoid), area and spring as fixed factors.

Table S6. ANOVA (type II) with species frequency per plot as response variable, and regeneration source, area and spring as fixed factors.

Figure S1. Biplot of nonmetric multidimensional scaling.

Coordinating Editor: Kari Veblen

Received: 28 June, 2023; First decision: 25 August, 2023; Revised: 23 May, 2024; Accepted: 23 May, 2024