

RESEARCH ARTICLE

The effects of deer exclusion on the development of a Mediterranean plant community affected by a wildfire

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Despite the resilience of Mediterranean ecosystems to fire, the ecological restoration of burned plant communities can be hindered by ungulate herbivores, particularly in areas with high population densities. This study compares the postfire development of a shrub community with and without deer, after a wildfire occurred in 2003 in a protected area in Central Portugal. We monitored 12 fenced and 12 unfenced plots 2, 3, 4, and 8 years after fire. Within each plot, we established a linear transect and measured the monospecific canopy projections (plant patches). Five plant community indicators (patch number, average patch length, average patch height, patch cover, and patch phytovolume per square meter) were obtained. The diameter and height of individuals of the most abundant shrub species (*Cistus salvifolius*, *Erica scoparia*, *Myrtus communis*, *Pistacia lentiscus*, *Rubus ulmifolius*, and *Ulex jussiaei*) were also measured. These measurements were used as response variables in generalized linear mixed models in order to assess the effects of time-after-fire and fencing, on the development of the plant community. Patch height and phytovolume had a significantly higher growth in fenced plots. At the species level, *C. salvifolius*, *M. communis*, *R. ulmifolius*, and *U. jussiaei* showed a higher growth across time both in height and in diameter, in the absence of herbivory. This work shows that deer exclusion needs to be considered when aiming at the postfire restoration of Mediterranean shrub communities.

Key words: browsing, ecosystem restoration, Mediterranean ecosystems, plant growth, postfire management, ungulates

Implications for Practice

- Fencing may be an effective strategy to accelerate the restoration of a burned plant community browsed by a deer population, but the decision to invest in a fence will depend on management objectives.
- Deer browsing can contribute to retard fuel buildup; as a consequence deer exclusion may harm fire prevention objectives in fire-prone areas.
- Likewise, in the absence of deer thorny shrubs such as *Rubus ulmifolius* and *Ulex jussiaei* may be favored, eventually leading to the need of specific management addressed to these species.

Introduction

The Mediterranean Basin is a hotspot for climatic changes. This region shows an increased probability of occurrence of hot and dry summers as well as drought events and severe wildfires (Amatulli et al. 2013; Venäläinen et al. 2014). On average, approximately 500,000 ha of Mediterranean forests burn every year in Southern Europe. Nearly 24% of this area is located in Portugal (San-Miguel & Camia 2009). Wildfires frequently occur in valuable and protected ecosystems, as for example in 2012 when 22,000 ha of the Portuguese Natura 2000 network of protected areas, burned (JRC 2013).

Although many Mediterranean plant species and communities are fire-adapted and resilient to disturbances such as grazing

or browsing, cutting and fire (Perevolotsky & Seligman 1998), the postfire restoration of Mediterranean protected areas has become an important conservation issue. Considering the conservation aims of protected areas and the dominant fire-adaptive traits in the plant community (e.g. seeders or resprouters), how to balance postfire passive and active ecological restoration in these regions? Such management decision is particularly relevant if grazing or browsing, by domesticated or wild herbivores, occurs. It is known that grazing and fire frequently interact in Mediterranean ecosystems (Bond & Keeley 2005). Plant resprouts are usually more palatable and have higher digestibility and nitrogen content in burned than in unburned areas (Hobbs et al. 1991). As a consequence, both domesticated and wild herbivores are attracted to recently burned areas for feeding (Moe & Wegge 1997; Laterra et al. 2003), which may retard ecological succession. Given the sensitivity of recently burned areas to feeding by large herbivores, fencing out these areas (or parts of them), to avoid grazing and browsing, is a

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possible management option. Exclusion of larger herbivores may be economically and ecologically preferable to other more active restoration strategies, such as reforestation or the protection of individual trees.

Deer populations have recently expanded both in number and geographical distribution in Northern Hemisphere including the Mediterranean countries (Fuller & Gill 2001; Côté et al. 2004). Lack of predators and land use changes, including land abandonment, with consequent increase of shrub and woodland areas, have driven recent expansion of deer populations (Côté et al. 2004). Deer can affect the structure, the species composition, and the ecological functioning of ecosystems (Bugalho et al. 2011; Hidding et al. 2012; Speed et al. 2013). Although considerable work has been conducted on the effects of deer on forest ecosystems (Rooney & Waller 2003; Gordon et al. 2004; Edenius et al. 2011), fewer address the cumulative effects of fire and browsing on plants (Thomas-Van Gundy et al. 2014).

This study was conducted in a public protected area in central Portugal, hosting an overabundant deer population. The area was ravaged by an intense wildfire in September 2003. After the fire, local managers observed a high grazing and browsing pressure over the plant community. A 6-year experiment was established to assess the midterm effect of fencing on postfire plant recovery and restoration. A previous work resulting from this experiment (Silva et al. 2014) suggested a shift in floristic composition as a result of browsing preference over different species. Here, we test the existence of a retarding effect of browsing on plant growth and recovery. This effect was assessed at the community and at the species levels, using several plant development indicators.

Methods

Study Area

This study was conducted in Tapada Nacional de Mafra (TNM), a 827-ha public protected area located in central west Portugal (38°58'30" N, 9°15'52" W), 8 km from the Atlantic Ocean. The altitude ranges from 100 to 350 m and the soils are humic cambisols derived from sandstone. The climate is Mediterranean with dry and hot summers. The mean annual precipitation and temperature are 798 mm and 14.6°C, respectively. The main vegetation types are forests dominated by *Quercus* spp. and *Pinus* spp., and shrublands dominated by *Erica* spp. and *Ulex jussiaei*. Two species of deer—*Dama dama* (fallow deer) and *Cervus elaphus* (red deer)—occur in the area, with an estimated density of around 40 deer/km². Approximately 85% of the deer population is composed of fallow deer (TNM deer counts 2004–2010; unpublished data). TNM is surrounded by a 3-m-high stone wall, preventing the animals from escaping to neighboring areas. In September 2003, a large wildfire burned nearly 70% of the study area. Fire severity was high and most trees were top-killed (Catry et al. 2010).

Sampling

In March 2005, an experimental area of 4 ha was fenced to assess the effects of deer exclusion on the postfire recovery

of woody plants. This option was preferred to the alternative of fencing out individual plots all across the burned area, in order to minimize the influence of other variables (e.g. soil or topography) besides those under study. Fencing excluded deer, not other mammals such as wild boars or rabbits. The fence was 190 cm high with 30 × 13 cm mesh size (2.5 mm wire). It was checked on a regular basis and fixed whenever a problem was detected. Fencing proved effective against the intrusion of deer, although, because of a landslide in December 2009, one fallow deer entered the fenced area and presumably remained inside during the final stage of the study.

We established 24 plots of 10 × 4 m in the study area, half of which were installed inside the fenced area (fenced plots) and the remaining outside (open plots). Fenced plots were randomly distributed inside the fenced area. Open plots were established close to the fence within a 25-m buffer, in order to match as much as possible the conditions of fenced plots, particularly topography, soil cover, and plant species composition. Mean elevation in fenced and open plots was 166 and 179 m and average slopes were 19° and 26°, respectively. The prefire vegetation of fenced plots was very similar to open plots. It was dominated by a mixed forest of pines and oaks (*Pinus* spp. and *Quercus* spp.; around 70% cover) with a shrub understory. Smaller trees included *Olea europaea* var. *sylvestris*, *Quercus coccifera*, *Crataegus monogyna*, and *Pistacia lentiscus*. Fire severity of fenced plots was also similar to open plots and almost all trees in their vicinity were completely scorched, and logged 6 months later. Given the protection status of the area, salvage logging was restricted to bigger logs, leaving the remnant twigs and branches on site. Although heavy machinery has been used, particular care was taken in order to minimize soil and vegetation damage. The generalized destruction of mature plant formations by fire across the protected area prevented the possibility of installing control plots of undisturbed vegetation.

Each plot was divided into 80 quadrats of 0.5 m² each (1 × 0.5 m grid). We identified all plant species found within each quadrat, and recorded total height and the basal diameter of one randomly chosen individual from each woody species. In the case of multistemmed plants, only one stem, randomly chosen, was measured. In addition, we established a longitudinal transect along each plot. The transect was used to identify and characterize all plant patches, that is all monospecific canopy projections intersected by the transect. Overlapping plant patches of the same species were recorded as one single patch. For each patch, we measured the average height and the intersected length. Monitoring was conducted four times after fire, in 2005, 2006, 2007, and 2011 (hereafter postfire years 2, 3, 4, and 8). The first field survey was conducted in April 2005.

Data Analysis

Transect data were used to assess the postfire recovery at the plant community level, whereas quadrat data were used to assess the postfire recovery at the species level. We used transect data to estimate the number of intersected plant patches (patch number), the average patch length in meters (patch length), the average patch height in meters (patch height), the proportion

of transect length intercepting plant patches (patch cover), and the phytovolume per square meter (phytovolume). Phytovolume was simply computed as the product of patch cover by patch height and expressed in meters. Patch number was used as an indicator of plant establishment. Patch length and patch height were used as indicators of vegetation growth after fire. Patch cover was used as an indicator of soil cover. Phytovolume was used as a proxy for plant biomass. We used the quadrat data to obtain the average height (height, cm) and the average diameter (diameter, cm) by species for each plot over time. Species abundance (F_i) was calculated as the number of quadrats where each species was present, divided by the overall sum of presences (in quadrats from all plots, from both treatments and from all years). We analyzed only species with $F_i > 5\%$. The six species that met this criterion corresponded to 82% of all quadrat records: *Cistus salvifolius* (sage-leaved rock rose), *Erica scoparia* (besom heat), *Ulex jussiaei* (small-flowered gorse), *Rubus ulmifolius* (elmleaf blackberry), *Myrtus communis* (myrtle), and *P. lentiscus* (mastic tree). Overall, we analyzed 17 dependent variables: five obtained from transects and 12 obtained from quadrat sampling.

We used generalized linear mixed models (GLMM) to minimize the risk of spatial pseudoreplication in our experimental design. Spatial pseudoreplication has been often addressed in ecological studies through the use of mixed models (e.g. Millar & Anderson 2004; Chaves 2010), where sampling units can be included as a random effect in addition to the variables of interest (fixed effects). GLMM were used to analyze the effect of time-after-fire (TAF; continuous variable) and fencing (factor with two levels: fenced or open) on the 17 response variables. Plots were included as a random effect. For obtaining more robust results, we estimated 95% confidence intervals of model parameters, through parametric bootstrapping using 500 simulations for each model. We included in the models the interaction TAF × Fencing, allowing to account for initial differences between open and fenced plots. The squared transformation of TAF was included in the models to take into account possible quadratic or curve-shaped effect of TAF. All response variables were modeled using a Gaussian distribution, except for patch number that was modeled using a Poisson distribution. Following Zuur et al. (2009), model building started with all variables and a subsequent removal of variables that did not significantly contribute to the explained deviance, using a likelihood-ratio test. The analysis was run in R (R Development Core Team 2013), using the package lme4 (Bates et al. 2014). Assessment of model performance was based on the fraction of total deviance explained by the fixed part of the model, estimated using the marginal r^2 (Nakagawa & Schielzeth 2013). Mann–Whitney U -tests were used to assess the statistical significance of differences between open and fenced plots for each of the four monitoring years.

Results

With the exception of patch number, the plant community models explained a high proportion of the observed variance (between 68.8 and 81.1%) and all indicators increased across

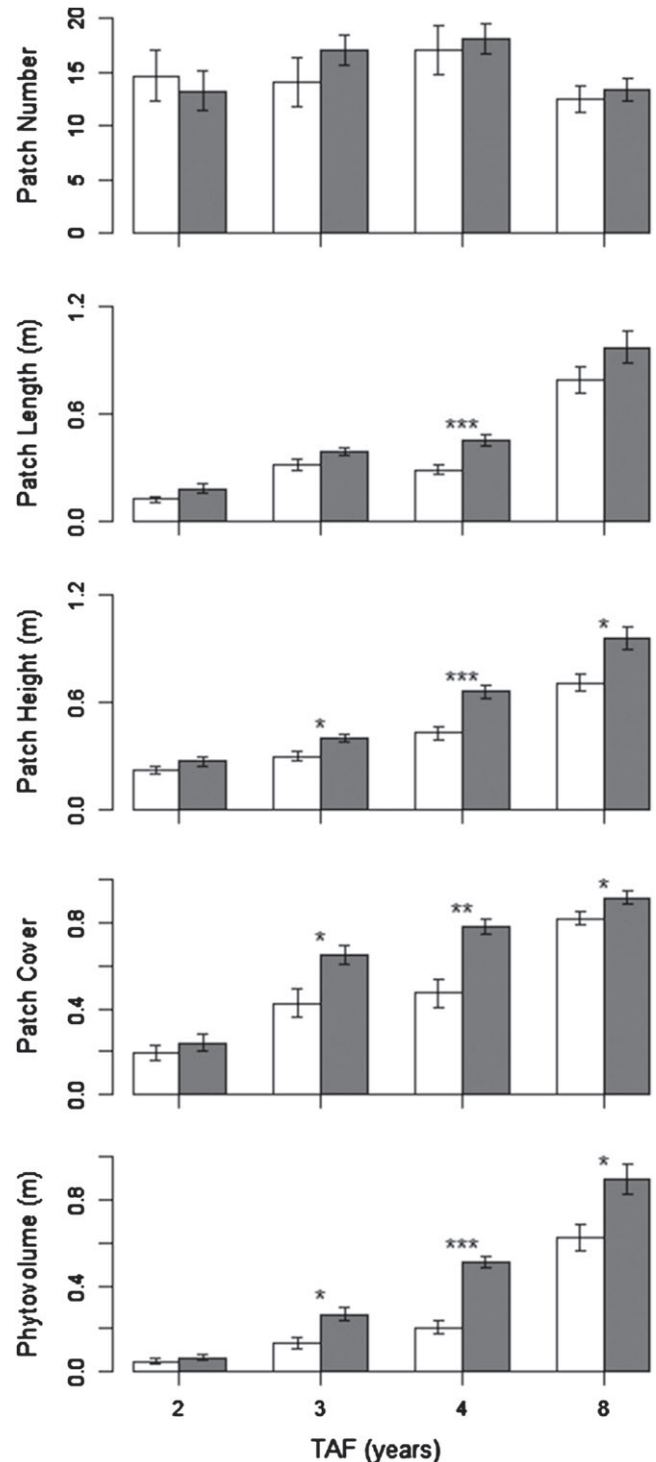


Figure 1. Development of the plant community in open (white bars) and fenced (gray bars) plots, 2, 3, 4, and 8 years after fire (TAF) according to five indicators (mean ± SE): patch number, patch length, patch height, patch cover, and phytovolume. Asterisks represent the significance of Mann–Whitney U -tests comparing open with fenced plots for each year (p values: * <0.05 , ** <0.01 , *** <0.001).

time, both in open and fenced plots (Supporting Information Table S1; Fig. 1). The interaction TAF × Fencing was significant for patch height ($p = 0.003$) and phytovolume ($p = 0.001$), showing that fencing significantly influenced the development of these two indicators during the 6-year study period. Patch height increased 3.2 times in open plots and 3.6 times in fenced plots, reaching 0.71 ± 0.05 and 0.96 ± 0.06 m, respectively (mean ± SE), by the end of the study. Phytovolume increased 12.4 times in open plots and 12.9 times in fenced plots reaching 0.62 ± 0.06 and 0.90 ± 0.07 m, respectively, by the end of the study. However, the growth pattern of the vegetation was not similar between treatments across years; in year 4, fenced plots presented an average phytovolume 2.4 times higher than open plots ($p < 0.001$). With the exception of patch number, all indicators have shown a significantly higher development of the plant community in fenced plots in most years. No differences were observed in year 2 and the highest differences were

observed in year 4 ($p = 0.002$ for patch cover and $p < 0.001$ for the other three indicators). In years 3 and 8, differences were either nonsignificant or significant only at the 0.05 level for the five indicators.

There were significant TAF × Fencing interactions in the height models of *C. salvifolius*, *M. communis*, *R. ulmifolius*, and *U. jussiaei*, with marginal r^2 values ranging between 60.8 and 84.6% (Supporting Information Table S2). *Ulex jussiaei*, *R. ulmifolius*, and *C. salvifolius* had the highest growth difference between treatments (Fig. 2). Average height of *U. jussiaei* increased 2.8 and 8.1 times in open and fenced plots, respectively, with plants reaching 43.1 ± 5.4 m in open and 154.3 ± 11.2 m in fenced plots in year 8. *Rubus ulmifolius* increased 1.7 and 3.2 times in open and fenced plots reaching 32.3 ± 5.0 and 72.6 ± 5.8 m respectively, in year 8. *Cistus salvifolius* increased 2.6 and 4.4 times in open and in fenced plots, reaching 39.6 ± 3.2 and 72.1 ± 3.4 m, respectively, in

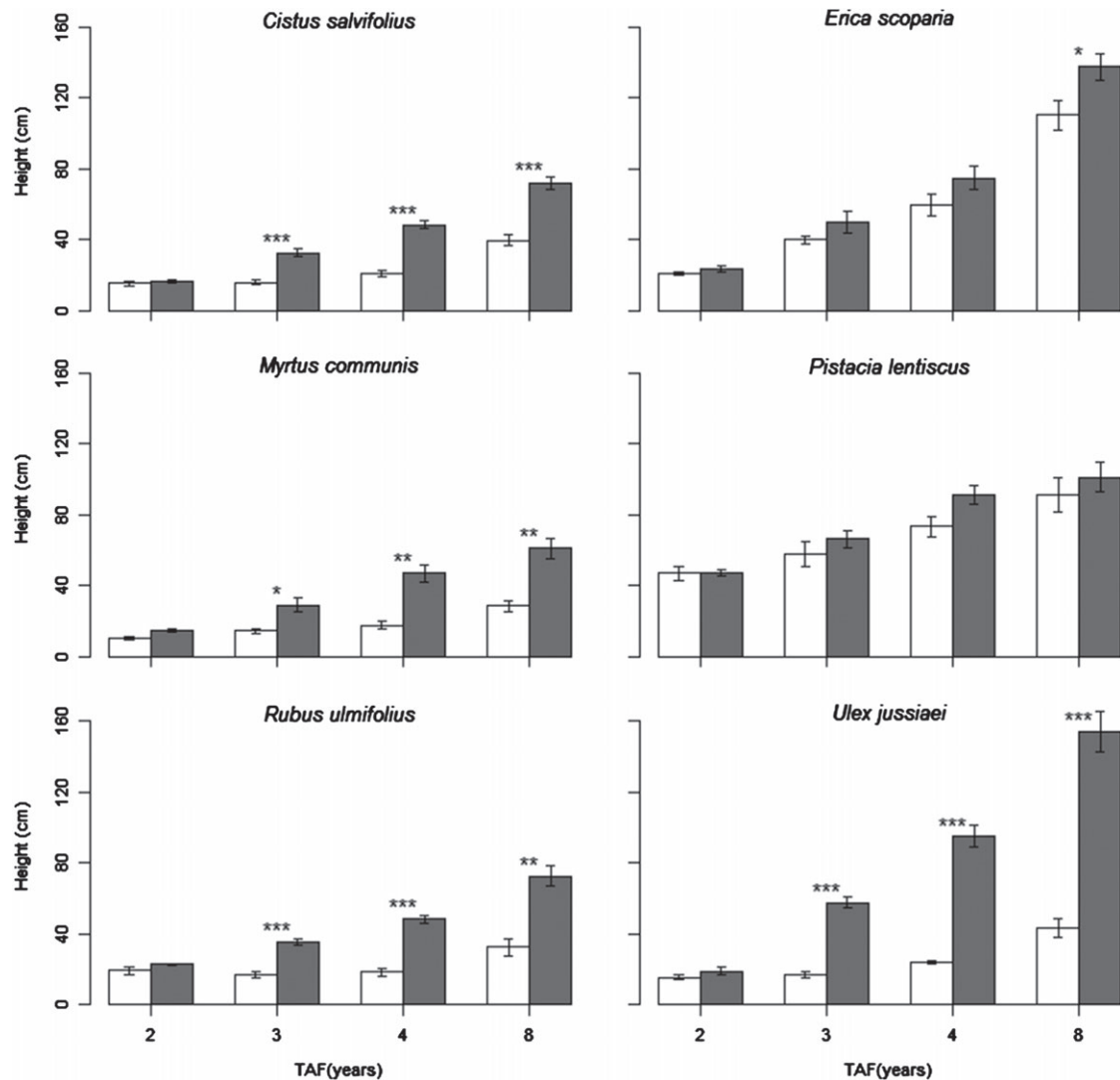


Figure 2. Height of the six most abundant species (mean ± SE; $n = 12$) at 2, 3, 4, and 8 years after fire (TAF) in open (white bars) and fenced (gray bars) plots. Asterisks represent the significance of Mann–Whitney U -tests comparing open with fenced plots for each year (p values: * < 0.05 , ** < 0.01 , *** < 0.001).

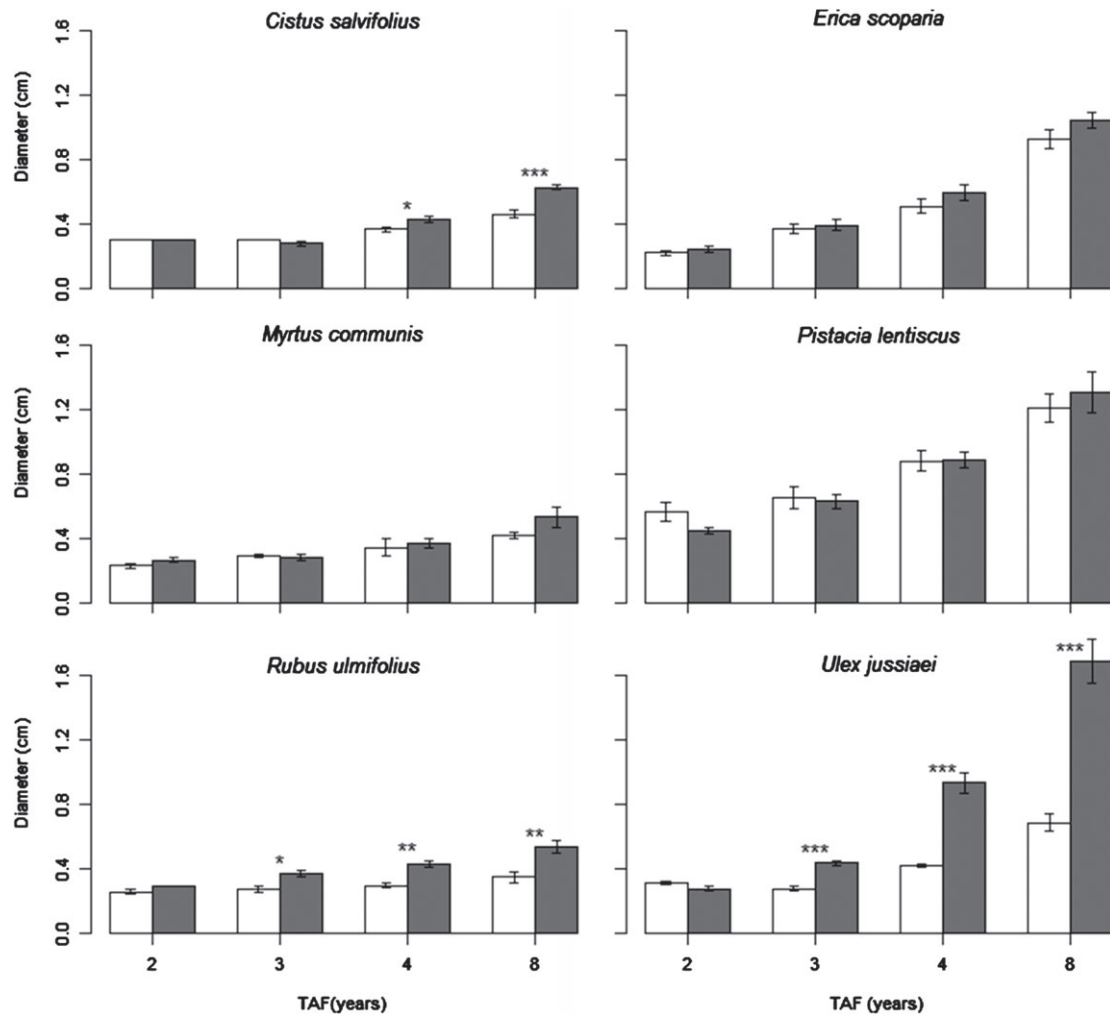


Figure 3. Diameter of the six most abundant species (mean \pm SE; $n = 12$) at 2, 3, 4, and 8 years after fire (TAF) in open (white bars) and fenced (gray bars) plots. Asterisks represent the significance of Mann–Whitney U -tests comparing open with fenced plots for each year (p values: * <0.05 , ** <0.01 , *** <0.001).

year 8. Height differences between the two treatments were significant for all years except in year 2 where no differences could be detected. *Pistacia lentiscus* was the only species with no significant height differences and *Erica scoparia* presented only a significant height difference at the end of the study ($p = 0.014$). *Myrtus communis* had an intermediate response with significant differences in years 3, 4, and 8 ($p = 0.010$, $p = 0.002$, and $p = 0.002$, respectively).

There were significant TAF \times Fencing interactions in the diameter models of *C. salvifolius*, *M. communis*, *R. ulmifolius*, and *U. jussiaei* (Supporting Information Table S3). However, model coefficients for this interaction were less significant than in the height models (p values between <0.001 and 0.039) and the marginal r^2 values were also lower (between 31.5 and 80.9%). *Ulex jussiaei* was the species showing the highest difference in diameter growth across time between the two treatments (Fig. 3). The average diameter of this species increased 2.2 times in open

plots and 6.0 times in fenced plots, reaching 0.69 ± 0.06 and 1.69 ± 0.13 cm, respectively, in year 8. All the other species presented much lower differences of diameter increase. In terms of absolute values, the only significant differences between open and fenced plots were observed for *C. salvifolius* ($p = 0.025$ in year 4 and $p < 0.001$ in year 8), *R. ulmifolius* ($p = 0.014$ in year 3, $p = 0.002$ in year 4, and $p = 0.0099$ in year 8), and *U. jussiaei* ($p < 0.001$ in years 3, 4, and 8).

Discussion

The number of plant patches did not increase across time in both fenced and open plots. However, the consistent increase in patch length across the study period in both open and fenced plots suggests the coalescence of plant patches, which may have counterbalanced the emergence of new patches. Development of these two indicators across time was not significantly different between fenced and open plots. Different results were obtained

by Seifan and Kadmon (2006), who observed a change in the distribution pattern of shrubs in areas grazed by cattle. Patch height and patch cover increased consistently along the study period, both in open and fenced plots, but the interaction TAF × Fencing was significant only for patch height, showing higher values in fenced plots. Other studies have shown a detrimental effect of animals in plant cover and plant height: Raffaele et al. (2011) registered a decrease in the cover of woody species in areas grazed by cattle and hares; Relva et al. (2010) found a decrease in plant cover due to deer browsing; Pellerin et al. (2006) found a decrease in plant height, due to deer browsing and trampling. In the literature review presented by Crête et al. (2001), deer had a detrimental effect on plant cover in 26 out of 30 studies and a detrimental effect on plant height in 13 out of 16 studies. In this study, there was also a significantly higher development of phytovolume across time in fenced plots. Assuming phytovolume as a proxy for biomass, our results show that fencing allowed a faster buildup of woody biomass. However, differences between treatments in year 8 were not as important as in year 4, a trend which was verified for all indicators except patch number. This apparent converging trend of the two treatments at the community level may have different explanations. As time passed and vegetation developed, more forage became available for deer browsing in the open area. This in turn may have led to a lower browsing pressure in the open plots. On the other hand, there may have been a decrease in plant growth rate in fenced plots as the plant community became more mature. Another possible contribution could have been the intrusion of one fallow deer during the last stage of the study. An additional aspect of the impact of deer on phytovolume is fuel reduction. Browsers and mixed feeders can be used for fuel management aiming at wildfire prevention. Most studies about the effects of browsing on fuels refer to goats (e.g. Zimmerman & Neuenschwander 1984; Tsiouvaras et al. 1989; Torres-Manso et al. 2014), and most of them concluded that browsing had a significant effect on fuel reduction. We suggest that browsing by deer may also have significant effects on fuel reduction through control of woody plant communities. This effect may also have implications for ecological restoration in Mediterranean fire-prone ecosystems.

The results obtained for plant height differed according to species, which may suggest a balance between animal preference and consumption of some species and their productivity and growth rates. Plant growth and height may have also been affected by facilitative or competitive interactions with surrounding vegetation (Weiner & Thomas 1986; Dudley & Schmitt 1996). Different growth rates between fenced and open plots in species such as *C. salvifolius*, *M. communis*, *R. ulmifolius*, and *U. jussiaei* can be explained by different reasons. Species of genus *Rubus* are known for being strongly preferred by deer because of the palatability and the high protein content of its leaves (Bugalho & Milne 2003; Mazzoleni et al. 2004; Boulanger et al. 2009). *Ulex jussiaei* has also been referred to be part of deer diet at TNM (Mazzoleni et al. 2004). Similarly *M. communis* was also mentioned by Lovari et al. (2007) as strongly preferred by deer, and Ammar et al. (2005) classify it as a medium–high digestibility species. Although these three

species present strong resprouting capability, apparently this was not sufficient to overcompensate the effect of browsing, contrarily to what has been suggested by Focardi and Tinelli (2005) for *R. ulmifolius*. *Cistus salvifolius* has opposite characteristics: it does not resprout and it does not present the same fodder qualities of the three previous species (Fernández-Olalla et al. 2006). Nonetheless, our results clearly show that *C. salvifolius* has equally benefited from fencing, which is supported by field observations of browsed individuals. On the contrary, *E. scoparia* and *P. lentiscus* did not present a significantly different development across time, suggesting that these species were less preferred by deer. *Pistacia lentiscus* is known for its low digestibility due the chemical composition of its leaves (Massei et al. 2000; Ammar et al. 2005), and *E. scoparia* is referred as a nonpreferred species by Mazzoleni et al. (2004). Besides being less preferred, these species are strong resprouters able to withstand natural disturbances like fire and browsing (Paula & Ojeda 2011).

Although the effect observed on plant height can be directly associated with browsing, the effect on stem diameter is not a direct consequence of animal activity. It is relevant the fact that all four species that had their height development significantly affected by fencing, had also their diameter development significantly affected. We may reasonably assume that this difference in diameter development was probably caused by a reduction in physiological activity (Pallardy 2008), which in turn could have been caused by higher browsing activity in the open plots. A similar detrimental effect of herbivores on stem diameter was observed in browsing simulation experiments by Bergstrom and Danell (1987) and Bee et al. (2007). The results of this study are also in line with those obtained by Silva et al. (2014), who assessed deer impact on plant frequency and floristic composition in the same area. Browsing seems to have affected both the number of individuals and their development for some species, therefore influencing the ecological succession.

This study used a sampling design that may be considered pseudoreplicated (Hurlbert 1984), as plots were distributed within one single fenced area, rather than using individual fences for each plot. The drawbacks of such a design were considerably minimized by choosing a homogeneous study area and by adopting an analytical approach that has been largely employed in similar designs (e.g. Millar & Anderson 2004; Chaves 2010). Despite these precautions, we should remark that the generalization of our results is obviously limited by the specific conditions of the study site, namely species composition, fire severity, logging practices (Lindenmayer et al. 2008), and browsing pressure.

Passive restoration of disturbed areas has been criticized for its direct and indirect costs (e.g. Zahawi et al. 2014). However, in the specific case of a burned area submitted to intense browsing such as the TNM area, the short- to middle-term benefits of passive restoration may eventually compensate the costs, given the much faster regrowth of some dominant species and the overall plant community. This effect was observed for both plant height and stem diameter, particularly in more palatable/preferred species. The higher development of phytovolume in the fenced area reveals the advantage of fencing from a

restoration point of view, but it also shows that deer may significantly contribute to reduce fuel buildup, eventually decreasing fire hazard. Likewise, the strong effect of deer browsing over thorny shrubs such as *R. ulmifolius* and *U. jussiaei* may be an advantage from a management point of view, as these species may retard ecological succession toward more mature stages (e.g. Ferris & Purdy 2003) and hamper vegetation monitoring by local managers. Therefore, the decision of fencing out a recently burned area will ultimately depend on the specific management objectives associated with the restoration of the disturbed vegetation.

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Supporting Information

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

Table S1. Results of GLMM analysis using plant community indicators as response variables. Model coefficients and respective standard errors are provided, except for nonsignificant variables. The *p* values resulting from model comparison are included, except when nonapplicable (na) or nonsignificant (ns). Parametric bootstrap was used to compute 95% confidence intervals of model coefficients.

Table S2. Results of GLMM analysis using the average height of the six most abundant species, as response variables. Model coefficients and respective standard errors are provided, except for nonsignificant variables. The *p* values resulting from model comparison are included, except when nonapplicable (na) or nonsignificant (ns). Parametric bootstrap was used to compute 95% confidence intervals of model coefficients.

Table S3. Results of GLMM analysis using the average diameter of the six dominant species, as response variables. Model coefficients and respective standard errors are provided, except for nonsignificant variables. The *p* values resulting from model comparison are included, except when nonapplicable (na) or nonsignificant (ns). Parametric bootstrap was used to compute 95% confidence intervals of model coefficients.

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