RESEARCH ARTICLE

JOURNAL OF Applied Ecology | BRITISH ECOLOGICAL SOCIETY

Ungulates mediate trade-offs between carbon storage and wildfire hazard in Mediterranean oak woodlands

Xavier Lecomte[1] [iD] | Maria C. Caldeira[1] [iD] | Filipe X. Catry[2] [iD] |
Paulo M. Fernandes[3] [iD] | Robert B. Jackson[4] [iD] | Miguel N. Bugalho[2] [iD]

[1]Forest Research Centre, School of Agriculture, University of Lisbon, Lisbon, Portugal

[2]Centre for Applied Ecology "Prof. Baeta Neves" (CEABN-InBIO), School of Agriculture, University of Lisbon, Lisbon, Portugal

[3]Centre for the Research and Technology of Agro-Environmental and Biological Sciences (CITAB), University of Trás-os-Montes and Alto Douro (UTAD), Vila Real, Portugal

[4]Department of Earth System Science, Woods Institute for the Environment, and Precourt Institute for Energy, Stanford University, Stanford, California

Correspondence
Xavier Lecomte
Email: xlecomte@isa.ulisboa.pt

Abstract

1. Ungulates influence ecosystem services in important ways, including by altering the amount of standing plant biomass and species composition. Browsing, for example, removes biomass and, in consequence, can decrease the risk of wildfires. The influence of ungulates on carbon storage is more complicated. Browsers reduce carbon stocks directly by consuming biomass, but if browsing reduces fine fuel loads, then long-term carbon storage may increase.

2. We investigated how wild ungulates mediate trade-offs between carbon stocks and wildfire hazard in a Mediterranean oak woodland. We assessed the effects of deer (*Cervus elaphus* and *Dama dama*) on the colonization by gum cistus (*Cistus ladanifer*), a highly flammable Mediterranean shrub, through a long-term ungulate exclusion experiment.

3. We established fenced (unbrowsed) and open (browsed) plots in areas where shrubs were previously cleared, and compared shrub density, height, biomass, and above-ground carbon stocks 6 and 14 years after fencing.

4. There were no significant differences in shrub density between treatments after 6 years of browsing exclusion but, by this point, height was already significantly greater in fenced plots. At the end of the experiment, shrub density and height were both significantly greater in fenced plots. Biomass and carbon stocks of gum cistus increased and reached a plateau in fenced plots, while in open plots biomass and carbon stocks increased initially but then decreased. Ungulates also prevented accumulation of litter carbon stocks, which was significantly higher in fenced plots after 14 years of browsing exclusion.

5. We also modelled fire behaviour in fenced and open plots. Browsing reduced fine fuel load, an important contributor to fire spread, by 80%. In browsed plots, modelled wildfire rate of spread, flame length, and fireline intensity decreased by 50%, 65%, and 90%, respectively, which also decreased the probability of canopy fire and of oak mortality.

6. *Synthesis and applications*. By decreasing fire hazard and the probability of canopy fire, ungulates may ultimately increase ecosystem carbon stocks through improved adult oak survival. These critical, indirect trade-offs need to be assessed when addressing the effects of ungulates on ecosystems and the management of their populations.

1 | INTRODUCTION

Woody encroachment into grasslands has been increasingly documented world-wide (Sala & Maestre, 2014) and associated with climate and land-use changes, including altered fire and grazing regimes (Briggs et al., 2005; D'Odorico, Okin, & Bestelmeyer, 2012; Sankaran, Ratnam, & Hanan, 2008). Shrublands provide a wide range of ecosystem services, including carbon storage and sequestration, and livestock forage (Janssens et al., 2003; McKinley et al., 2011; Pacala et al., 2001; Piao et al., 2009). Increased carbon stocks, however, may increase wildfire hazard, particularly in Mediterranean environments (Fernandes, 2009). Although dependent on factors such as precipitation (Jackson, Banner, Jobbagy, Pockman, & Wall, 2002), increased net primary productivity, biomass accumulation, and consequent increase in carbon stocks can be substantial in shrub encroached ecosystems (Hughes et al., 2006). For example, above-ground carbon stocks in six shrublands along a climate gradient in Europe ranged from 1.4 to 18.2 Mg carbon ha^{-1} (Beier et al., 2009) and in a dryland ecosystem, in northern Texas, USA, carbon stocks increased from 3.8 to 5 Mg carbon ha^{-1}, during 60 years of *Prosopis glandulosa* encroachment (Archer & Predick, 2014; Asner, Archer, Hughes, Ansley, & Wessman, 2003). After soils, trees are a major carbon stock component of the ecosystems (Pan et al., 2011; Zomer et al., 2016). Mediterranean Basin oak woodlands, for example, with a tree cover of 30%, may sequester up to 140 g C m^{-2} year^{-1} (Pereira et al., 2007), a value within the range of productive savannas in California (Xu & Baldocchi, 2004). A decrease in shrub moisture content during the warm and dry summer, (Dennison & Moritz, 2009; Dennison et al., 2003; Pellizzaro, Duce, Ventura, & Zara, 2007), however, increases shrub flammability and fire hazard in Mediterranean shrublands (Keeley, 2013; Pausas & Bradstock, 2007; Rego & Silva, 2014). Additionally, the properties (e.g., proportion of fine fuels) and structure of vegetation (e.g., plant density and height), also affect fire behaviour. For example, the rate of fire spread and fire intensity both increase with shrub population height and density (Anderson et al., 2015; De Luis, Baeza, Raventos, & Gonzalez-Hidalgo, 2004; Fernandes, 2001).

Woody plants are also important sources of forage for large ruminant herbivores, especially in drylands, such as Mediterranean environments (Azorit, Tellado, Oya, & Moro, 2012; Bugalho & Milne, 2003; López-Díaz, Rolo, Benítez, & Moreno, 2015; Papanastasis, Yiakoulaki, Decandia, & Dini-Papanastasi, 2008). Therefore, fuel loads can be effectively reduced in fire-prone landscapes through grazing and browsing (Briggs et al., 2005; Hobbs, 2006; van Langevelde et al., 2003). By ingestion and trampling, livestock alters the horizontal and vertical structure of shrublands and reduces fine fuel loads (Davies, Boyd, Bates, & Hulet, 2016; Ingram, Doran, & Nader, 2013; Nader, Henkin, Smith, Ingram, & Narvaez, 2007; Strand, Launchbaugh, Limb, & Torell, 2014). This reduction decreases the probability of ignition, spread, and intensity of wildfires (De Luis et al., 2004). Both wild and domestic ungulates, such as deer or goats, have been shown to disrupt fuel ladders, breaking the vertical continuity of biomass between ground and tree canopy, and decreasing litter depth and fine fuel loads (Hobbs, 2006; Lovreglio, Meddour-Sahar, & Leone, 2014).

Here, we investigated how wild ungulates mediate trade-offs between the ecosystem services of fire hazard mitigation and increased carbon stocks in a Mediterranean oak ecosystem. As part of a 14-year exclusion experiment, we assessed the effects of red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) in halting ecological succession and the encroachment of gum cistus (*Cistus ladanifer*), a fire-prone Mediterranean shrub, into oak woodland areas that had been previously cleared from shrubs. Specifically, we compared carbon stocks and modelled wildfire behaviour in oak stands either browsed (open plots) or protected from ungulates (fenced plots) over the last 14 years. We hypothesized that protection from deer browsing would increase (a) average plant height, volume, and density of *C. ladanifer* stands; (b) total above-ground biomass and carbon stocks, namely of *C. ladanifer*; and (c) fine fuel load accumulation. Finally, we hypothesized that ungulates would decrease modelled fire spread, intensity, and severity, as well as the probability of crown fires and adult oak mortality. Ultimately, through prevention of severe wildfires, ungulates could potentially increase long-term ecosystem carbon stocks (Figure 1).

2 | MATERIALS AND METHODS

2.1 | Site and species

The experiment was conducted in Tapada Real de Vila Viçosa (Tapada de Baixo), an enclosed estate of approximately 900 ha, located in southeast Portugal (38°49′N, 07°24′W). The study site was an open woodland of evergreen holm (*Quercus rotundifolia*) and cork oak (*Quercus suber*). Woodland understorey was dominated by *C. ladanifer*, a Mediterranean shrub species, and annual grasslands primarily composed of grasses (e.g., *Bromus madritensis*, *Gaudinia fragilis*), with smaller proportions of forbs (e.g., *Andryala integrifolia*, *Leontodon taraxacoides*) and legumes (e.g., *Vicia disperma*, *Ornithopus compressus*). *Cistus ladanifer* is a highly flammable species because of the terpene-derived resin that impregnates its leaves and branches

FIGURE 1 Conceptual figure illustrating trade-offs among above-ground C stocks, fuel loads, and fire hazard in unbrowsed and browsed oak ecosystems. Browsing decreases understorey C stocks and fine fuel load, potentially decreasing the probability of crown fires and of oak mortality. Ultimately, ungulates may enhance long-term ecosystem C stocks, but trade-offs need to be assessed against potential negative effects on oak regeneration
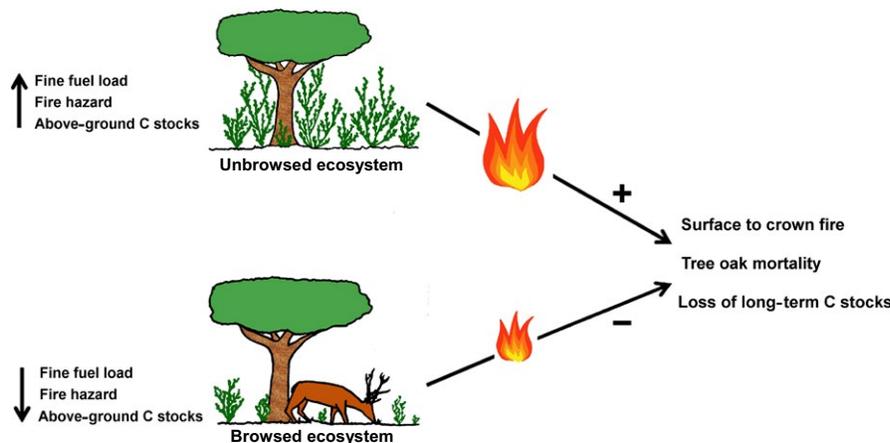
(Núnez-Regueira, Rodríguez-Anón, Proupín, Mourino, & Artiaga-Diaz, 2005), which may also lessen litter decomposition and accelerate fine fuel accumulation (Horner, Gosz, & Cates, 1988). Population densities of red and fallow deer, estimated at the beginning of the experiment, were 0.4 and 0.1 individuals per ha, respectively. The climate is typically Mediterranean with warm and dry summers and cool and wet winters. The mean annual precipitation is 585 mm, mostly distributed between October and May, and the mean annual temperature is 15.9°C (maximum of 31.1°C in July and minimum of 5.8°C in January).

2.2 | Experimental design and sampling

We established five blocks of paired fenced and open (control) plots of 25 × 25 m in July 2001. Plots were fenced with a 2.20 m tall fence, to exclude browsing by deer, and established in homogeneous grassland areas, where *C. ladanifer* was cleared through tillage. There were between two and four cork oak trees and two and four holm oak trees in each open and fenced plot. Tree density was 98 ± 6 trees/ha, within the range of other Iberian oak woodlands (Caldeira et al., 2015; Moreno & Pulido, 2008) which can go up to 120 trees/ha (Pinto-Correia & Godinho, 2013). Each 25 × 25 m plot was further divided into 40 subplots of 2 × 4 m. Eighteen of these subplots were then randomly selected for *C. ladanifer* measurements. In July 2004, one open plot was lost; hence, only the remaining four pairs of plots were used in data analysis.

2.2.1 | Shrub layer structure and biomass

In March 2007 and 2015, we counted all live and dead *C. ladanifer* individuals in the 18 randomized subplots and measured maximum height of 10–19 randomly selected individuals per plot, for a total of 40 shrubs per treatment. Furthermore, in 2015, we also measured the basal stem diameter of all *C. ladanifer* individuals occurring in the subplots. To estimate above-ground biomass of *C. ladanifer* stands, we used plant biomass–volume allometric equations as follows. In 2007, we randomly tagged 15 *C. ladanifer* individuals per plot (60 individuals per browsing treatment). We then estimated *C. ladanifer*

volume for all tagged individuals, assuming an elliptical cone shape for the species:

$$V = \left(\frac{1}{3}\right) \times \pi \times \left(\frac{D1}{2}\right) \times \left(\frac{D2}{2}\right) \times H$$

where V was the shrub volume (m^3), $D1$ the maximum diameter of shrub canopy projection (m), $D2$ the diameter perpendicular to $D1$ (m), and H the maximum shrub height (m). We estimated dry above-ground shrub biomass by cutting to ground level 16 and 19 of the total tagged shrubs in the fenced and open plots respectively. We oven-dried samples at 60°C to constant mass and weighed them (e.g., Lecomte et al., 2016).

Because of a high number of juvenile plants of *C. ladanifer* observed in the fenced plots in 2015, we estimated *C. ladanifer* above-ground biomass in a stratified manner in that year. We randomly selected 6–10 *C. ladanifer* living individuals per plot (30 shrubs per treatment) according to 10-mm stem diameter classes (between 6 and 86 mm). We then estimated total above-ground biomass of each measured individual shrub using allometric equations considering class stem diameters. We estimated biomass of dead shrubs in a similar way, excluding leaves, as the branch structure and volume of dead *C. ladanifer* individuals were similar to that of living individuals without leaves.

To assess *C. ladanifer* fuel load and modelling fire behaviour, we separated shrub biomass into dead and living components by stem diameter classes (Anderson, 1982) as: live woody fuel, that is, living components of shrubs including the foliage and very fine stems <0.64 cm in diameter; 1-hr fuel, that is, dead components including leaves and fine dead stems <0.64 cm in diameter; 10-hr fuel, that is, dead components with 0.64–2.54 cm in diameter; and 100-hr fuel, that is, dead components with diameters of 2.54–7.62 cm.

2.2.2 | Herb and litter biomass

We estimated biomass of herbs during the first week of June 2007 and 2015, the peak of grassland production in the study area. We randomly selected four subplots within each of the fenced and open plots and clipped to ground level all above-ground herb plant

material within a 50 × 25 cm quadrat. For estimating litter biomass, we collected all dead plant material within the 50 × 25 cm quadrat that was located in eight randomly selected subplots per plot. For modelling fire behaviour, we separated the litter samples by diameter class, as described for shrub biomass (see Section 2.3). These samples were oven-dried at 60°C to constant mass and weighed.

2.2.3 | Tree layer structure and biomass

In 2015, we measured tree diameter at breast height, maximum tree height, and height of the tree canopy base of all individual oak trees occurring in fenced and open plots. In the case of cork oak, because its bark (cork) is fire resistant, we also measured bark thickness of all trees using a bark gauge.

We estimated tree canopy area by measuring the longest (D1) axis of width and its perpendicular (D2) length projections on the ground and considering an elliptical canopy shape (canopy area = $\pi \times (D1/2) \times (D2/2)$). We estimated canopy cover as the percentage of the plot occupied by the tree canopy projection using IMAGEJ software (version 1.51p, NIH, Bethesda, MD, USA).

For estimating total above-ground oak tree biomass, we used the equations of Ruiz-Peinado, Montero, and Del Rio (2012). Canopy bulk density, that is, the mass of available canopy fuel (diameter <0.6 cm) per unit canopy volume, was determined for fire modelling purposes (Scott & Reinhardt, 2001). We estimated cork and holm oak canopy bulk density in each of the plots as follows. First, we randomly clipped a thin branch (diameter smaller than 2 cm) at middle height of each tree canopy from eight cork oak trees and eight holm oak trees. All biomass with a diameter <0.6 cm (including leaves) and biomass with diameter between 0.6 and 2 cm was separated from these thin branches, oven-dried at 60°C to constant mass and weighed. Finally, for estimating canopy bulk density, we used the equation of Ruiz-Peinado et al. (2012), to determine the total biomass of thin branches per oak species, based on tree diameter at breast height and total tree height, and using the equation relating biomass of thin branches and total biomass with a diameter <0.6 cm (and leaves) that we had determined.

We measured biometric parameters of 49 oak trees (28 cork and 21 holm oaks) in all plots. There were no significant differences in biometric parameters for each oak species and also at the whole tree layer between fenced and open plots (Supporting Information Appendices S1 and S2). For the overall oak population canopy cover, canopy height, canopy base height, canopy bulk density, and diameter at breast height were, respectively, (M ± SEM): 59.9 ± 3.3%, 8.0 ± 0.2 m, 2.30 ± 0.09 m, 0.11 ± 0.02 kg m^{-3}, and 42.4 ± 1.4 cm. For cork oak trees, the mean bark thickness was 3.50 ± 0.02 cm.

2.2.4 | Carbon stocks estimates

We estimated above-ground carbon stocks of C. ladanifer using the conversion factor of 0.51 g of carbon per g of dry biomass determined for C. ladanifer (Ruiz-Peinado, Moreno, Juarez, Montero, & Roig, 2013), 0.50 g of carbon per dry biomass for herbs and litter (Fonseca, de Figueiredo, & Bompastor Ramos, 2012), and 0.47 g of carbon per dry biomass for oaks (Gil, Blanco, Carballo, & Calvo, 2011).

2.3 | Fire behaviour modelling

We modelled fire behaviour using the SURFACE, CROWN, and SCORCH models of BEHAVEPLUS 5.0.5 fire modeling software (Andrews, 2009). BEHAVEPLUS estimates fire behaviour using as data input, vegetation fuel characteristics, weather, and topographic slope (Andrews, 2014). In our case, for fire modelling purposes, we used shrub and tree cover and heights, and total dead fuel load, from shrubs, herbs, and litter, separated by time-lag classes (i.e., 1, 10, and 100 hr, see above) and live woody fuel load. Herbs were included in the 1-hr class as most grassland species in the study area are annuals that dry out during summer. We followed Burgan and Rothermel (1984) recommendations and developed two fuel models: One for the open and another for the fenced plots using respective vegetation fuel characteristics. We run simulations to compare predicted fire spread rates with those predicted by a reference empirical shrubland model (Anderson et al., 2015). Then, we fine-tuned the fuel models by adjusting fuel depth until obtaining agreement between the two model estimates.

Fire behaviour simulation were run with fuel moisture contents values of 4%, 5%, and 6%, respectively, for 1-, 10-, and 100-hr dead fuels, and 75% and 80% for live woody fuels, respectively, in the understorey and in the overstorey (Chuvieco, González, Verdú, Aguado, & Yebra, 2009; Fernandes, 2009).

We set air temperature at 31°C as a baseline, as wildfires usually occur in summer in Mediterranean regions, and varied wind speed from 0 to 30 km/h, at 5 km/h steps, aligned with a 5° slope, which is within the range of slopes for our plots (M ± SEM: 4.6 ± 0.5°, range: 1.4–7.5°). Fire modelling outputs were flame length (m), surface rate of spread (m/min), and fireline intensity (MW/m).

We estimated the probability of oak tree mortality using the results of fire behaviour simulations, along with tree biometric characteristics and existing fire-effects models for cork and holm oaks (Catry et al., 2012; Catry, Pausas, Moreira, Fernandes, & Rego, 2013; Catry, Rego, Moreira, Fernandes, & Pausas, 2010). These models are based on tree biometrics (DBH, height, bark thickness) and fire severity descriptors (maximum char height expressed as percentage of total tree height). To estimate fire severity, we considered char height as flame length plus the height of the fuel bed. Additionally, when flame length was over 50% of tree height indicating a transition to crown fire and crown torching, we assumed that char height was 100%.

2.4 | Statistical analysis

We used GLMMs to compare C. ladanifer population density, height, and carbon stocks as well as herb and litter biomass, between fenced and open plots. Due to the high number of zero values in C. ladanifer

counts for shrub density, we used a negative binomial error and log-link function (see Lecomte et al., 2016). For shrub height and above-ground carbon stocks, herbaceous carbon stocks, litter carbon stocks, and shrub fuel load, we specified a normal error and identity-link function. Ungulate exclusion was specified in the models as a fixed effect, as well as year and interaction between ungulate exclusion and year. Plot and replicate (nested within plot) were included as random factors. We fitted nonlinear regression models to determine the best relationship between volume and biomass (i.e., dry weight) of *C. ladanifer*.

We used *t* tests for data collected in 2015 to compare tree canopy cover, tree canopy height, tree canopy bulk density, tree diameter at breast height, as well as biomass of herbs and litter (1-hr dead fuel load) between browsing treatments. We used a Mann–Whitney *U* test to compare litter (10-hr dead fuel load) because of the lack of normality of distribution and homogeneity of variance. We conducted statistical analyses in SPSS® software package (PASW Statistics, v. 23.0.0.0, 2015).

3 | RESULTS

3.1 | Effects of ungulates on the structure of *C. ladanifer* understorey

Ungulates substantially altered the structure and affected the patterns of the *C. ladanifer* colonization of the plots. In fenced plots, *C. ladanifer* continuously increased, seeming to have reached a plateau by the end of the experiment. Conversely, in open plots and after a first period of *C. ladanifer* increase, ungulates were able to halt and revert encroachment (Figure 2a). Results substantiate this interpretation: shrub colonization of the plots started in 2001, at the beginning of the experiment, but in 2007 there were no differences in *C. ladanifer* plant density between browsing treatments ($F_{2,142}$ = 1.736, *p* = 0.180) (Figure 2a). Shrub height, however, was already significantly higher in fenced plots ($F_{2,78}$ = 1441,02, *p* < 0.001) highlighting a strong effect of ungulates on the vertical structure of the *C. ladanifer* stands (Figure 2b).

Between 2007 and 2015, ungulates substantially altered both the horizontal and the vertical structure of the *C. ladanifer* understorey. Plant density ($F_{2,142}$ = 4.765, *p* = 0.010) and height ($F_{2,78}$ = 109.55, *p* < 0.001) were significantly higher in the fenced plots in 2015.

Moreover, while living *C. ladanifer* plant density and height increased between 2007 and 2015 in fenced plots ($F_{2,142}$ = 27.494, *p* < 0.001; $F_{2,78}$ = 216.21, *p* < 0.001, respectively), it decreased in open plots over the same period ($F_{2,143}$ = 3.463, *p* = 0.034 and $F_{2,78}$ = 127.03, *p* < 0.001 for shrub density and shrub height respectively) (Figure 2). These results emphasize the ability of wild ungulates to halt ecological succession and hamper *C. ladanifer* encroachment into the system.

3.2 | Effects of ungulates on above-ground carbon stocks

Ungulate exclusion had a strong effect on above-ground carbon stocks of *C. ladanifer.* Such an effect was already observed in 2007, 6 years after the beginning of the experiment, with significant differences between browsing treatments ($F_{2,118}$ = 266.98, *p* < 0.001) and accentuated in 2015 ($F_{2,142}$ = 38.88, *p* < 0.001) (Figure 3a). Moreover, there was a significant interaction between ungulate exclusion and year ($F_{1,260}$ = 5.52, *p* = 0.020) showing that carbon stocks of *C. ladanifer* increased in fenced plots but decreased in open plots between 2007 and 2015.

Although there was a tendency for higher biomass of herbs, and therefore higher herb carbon stocks, within fenced plots, these differences were not significant neither in 2007 or 2015 (Figure 3b). Biomass of herbs and above-ground carbon stocks, however, varied significantly between 2007 and 2015 ($F_{1,60}$ = 142.92, *p* < 0.001) suggesting that the annual grasslands in our study are mainly responding to climatic variability between years (Figure 3b).

Litter biomass and carbon stocks were significantly higher within fenced plots both in 2007 ($F_{2,62}$ = 45.70, *p* < 0.001) and 2015 ($F_{2,62}$ = 41.85, *p* < 0.001) (Figure 3c).

Ungulates, therefore, strongly affected the overall understorey above-ground carbon stocks, that is, total carbon stocks of shrubs, herbs, and litter, which was already significantly different between browsing treatments in 2007 (i.e., 2007; $F_{2,6}$ = 9.03, *p* = 0.015) and which differences accentuated in 2015 (i.e., 2015; $F_{2,6}$ = 55.99, *p* < 0.001; Figure 4). Moreover, carbon stocks of shrubs, herbs, and litter significantly increased within the fenced plots between 2007 and 2015 ($F_{2,6}$ = 21.47, *p* = 0.002) but decreased within the open plots during the same period ($F_{2,6}$ = 55.42, *p* < 0.001), as shown by a significant interaction between ungulate exclusion and year ($F_{1,12}$ = 8.32, *p* = 0.014).
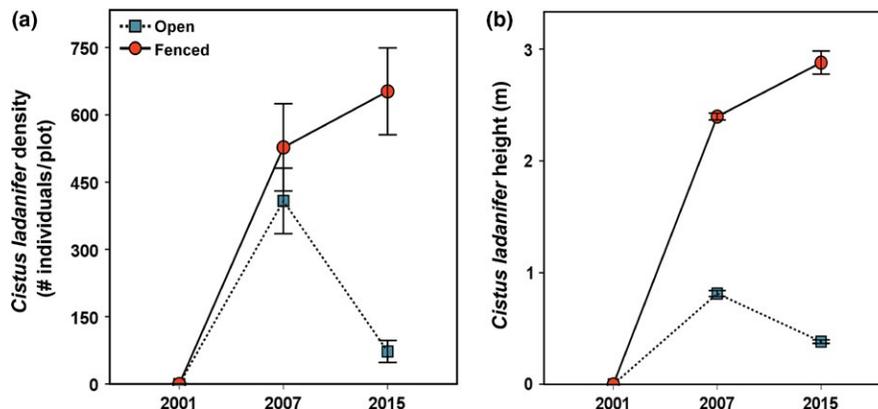
FIGURE 2 Change in (a) density and (b) height of living *Cistus ladanifer* in fenced and open plots between 2001 and 2015 (*M ± SEM*)

There were no significant differences, between browsing treatments, in relation to above-ground carbon stocks of oak trees estimated in 2015. The carbon stocks of cork oak trees were 0.27 ± 0.04
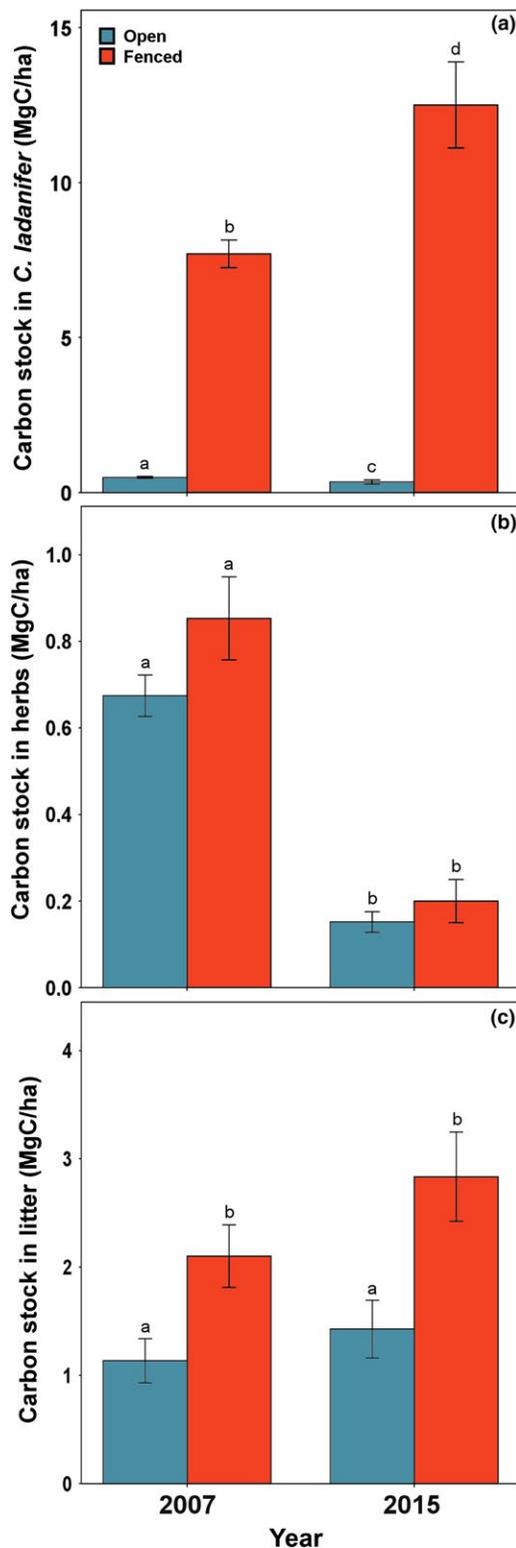

FIGURE 3 Above-ground C stocks in fenced and open plots in 2007 and 2015 ($M \pm SEM$): (a) *Cistus ladanifer*, (b) herbs, and (c) litter. Different letters indicate significantly (GLMM, $p < 0.05$) different values between treatments. Note that the scale range differs between graphs

and 0.21 ± 0.02 Mg carbon ($t(26) = 1.386$, $p = 0.177$) and of holm oak trees were 0.43 ± 0.07 and 0.44 ± 0.07 Mg carbon ($t(19) = 0.086$, $P = 0.933$) in fenced and open plots, respectively. Considering oak tree species density per plot and carbon stocks, the average tree aboveground carbon stock was estimated as 31.8 ± 4.1 Mg carbon ha^{-1}, that is, 67% and 94% of the total above-ground carbon stocks (i.e., oak trees, shrubs, herbs, and litter), in fenced and open plots respectively. After 14 years of browsing exclusion, total above-ground carbon stock was 40% higher in the fenced plots compared to open plots ($M \pm SEM = 47.3 \pm 2.2$ and 33.7 ± 0.2 Mg carbon ha^{-1} respectively).

3.3 | Long-term effects of ungulates on fuel loads

Ungulate exclusion altered fuel load characteristics in a number of ways, namely through halting of ecological succession and *C. ladanifer* encroachment. Therefore, in 2015, at the end of the experiment, live woody fuel load of *C. ladanifer* in fenced plots was significantly and dramatically higher than in open plots ($F_{2,142} = 19.35$, $p < 0.001$). Concomitantly, 1-hr ($F_{2,142} = 26.43$, $p < 0.001$), 10-hr ($F_{2,142} = 21.82$, $p < 0.001$), and 100-hr ($F_{2,142} = 20.67$, $p < 0.001$) fuel loads were also significantly higher in fenced plots (Figure 5).

Contrastingly, browsing exclusion did not significantly alter herb fuel load (i.e., 1-hr dead fuel load) or litter 10-hr fuel loads ($M \pm SEM$: 0.40 ± 0.10 vs. 0.30 ± 0.05 t/ha and 0.18 ± 0.08 vs. 0.19 ± 0.07 t/ha in fenced and open plots respectively). However, ungulate exclusion did have a significant effect on litter 1-hr fuel load, which was significantly higher in fenced plots (5.49 ± 0.78 vs. 2.66 ± 0.48 t/ha; Mann–Whitney U test, $U = 751$, $p = 0.01$). No 100-hr litter fuels occurred in open plots.

3.4 | Modelled fire behaviour and tree survival

Fire modelling shows that ungulate exclusion causes a strong increase in potential flame length, that exceeded 1.3 m, a critical threshold implying surface-to-crown fire transition and crown torching, regardless of the wind speed considered (Figure 6a). In open plots, in contrast, modelled flame length required a wind speed >20 km/h to surpass the critical flame length threshold (Figure 6a). In the fenced plots, modelled surface rate of fire spread and fireline intensity are 2- and 10-fold higher, respectively, as compared to open plots (Figure 6b,c).

The probability of oak tree mortality varied between 3% and 6% and between 0% and 2%, in fenced and open plots, respectively, as estimated from combining tree and fire characteristics, with the models of post-fire tree responses (e.g., Catry et al., 2013). The maximum char height on trees was estimated to be 100% in fenced plots and 20% in open plots. Moreover, in the case of cork oak trees, which are harvested every 9–12 years for their bark (cork), the probability of mortality decreased significantly with cork regrowth after harvesting (Figure 7). Our cork oak tree modelled mortality estimates considered a bark thickness of 3.5 cm, measured in 2015, which corresponds to the end of the bark growing cycle, immediately before cork harvest. For recently debarked trees, the probability of tree mortality would increase to 45% in open plots and to 65% in fenced plots (Figure 7).

4 | DISCUSSION

4.1 | Effects of ungulates on ecosystem structure and carbon stocks

Our study revealed substantial effects of ungulate browsing on the plant density and height of the *C. ladanifer* understorey. Ungulates hampered ecological succession, halted shrub encroachment and consequently affected negatively above-ground carbon stocks of the shrub understorey. Reductions in shrub biomass and in shrub
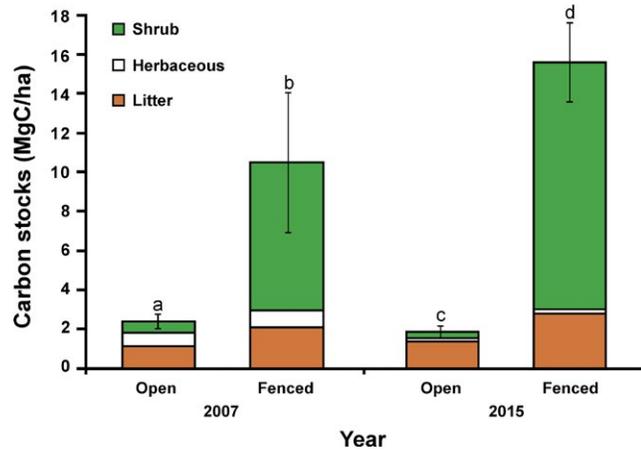
carbon stocks have been observed in other ecosystems browsed by wild ungulates in North America (e.g., mule deer *Odocoileus hemionus* (Huffman & Moore, 2003); wapiti *Cervus canadensis*, pronghorn

FIGURE 4 Above-ground C stocks of shrubs, herbs, and litter in fenced and open plots, in 2007 and 2015 (*M ± SEM*). Different letters indicate significantly different (GLMM, *p* < 0.05) values between treatments for total C stocks
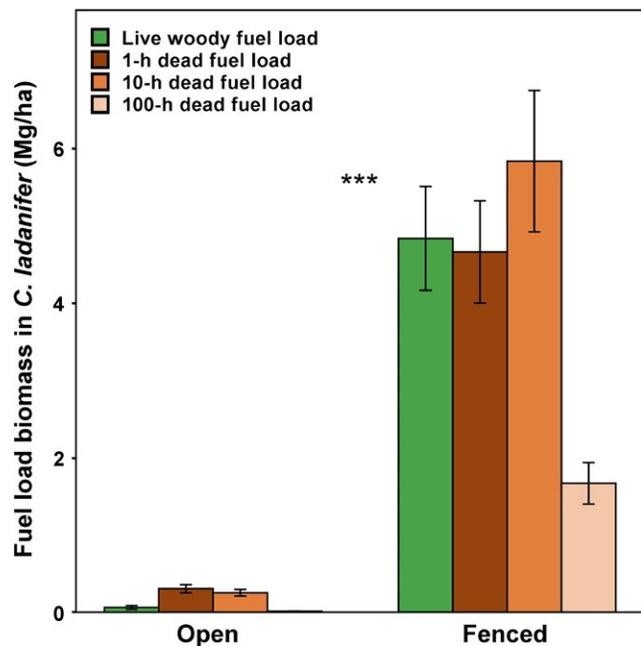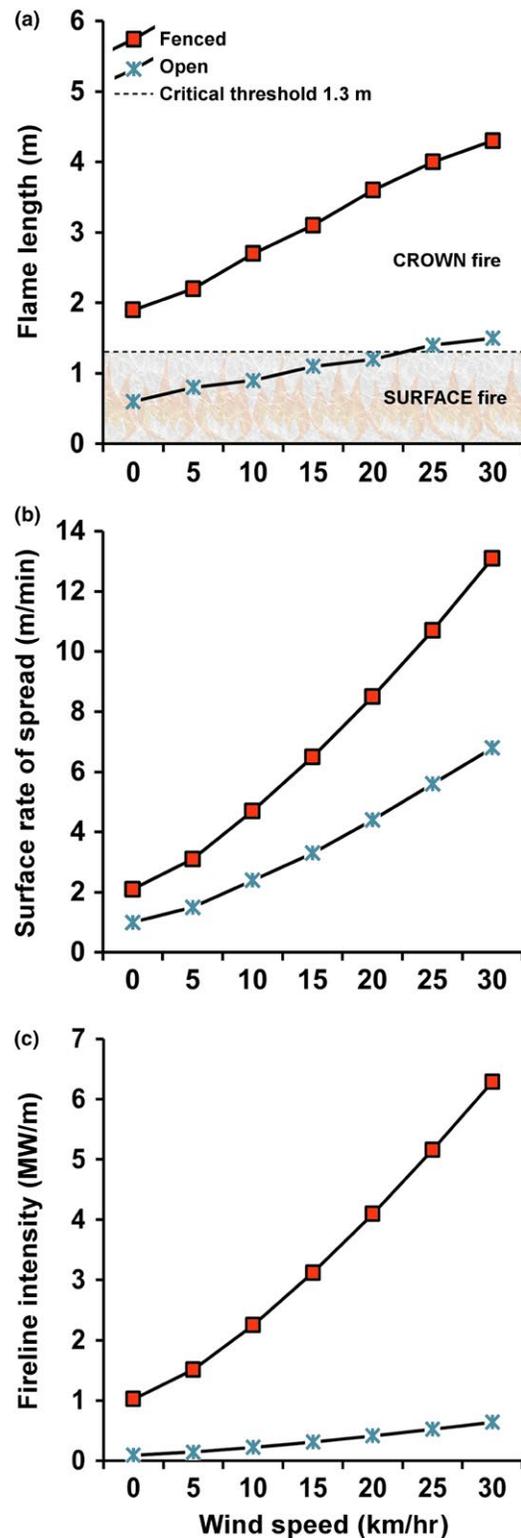
FIGURE 5 Fuel load of *Cistus ladanifer* by size class in fenced and open plots in 2015 (*M ± SEM*), after 14 years of browsing exclusion. ***All differences in fuel load size classes between treatments were highly significant (GLMM, *p* < 0.001). Data on herbs and litter are not presented here

FIGURE 6 Fire behaviour characteristics in fenced and open plots under increasing wind speed and constant slope of 5° as estimated with BehavePlus fire modelling system: (a) flame length, (b) surface rate of spread, and (c) fireline intensity

Antilocapra americana, and mule deer *Odocoileus hemionus* (Singer & Renkin, 1995)) and Europe (e.g., reindeer *Rangifer tarandus*; Vowles, Molau, Lindstein, Molau, & Björk, 2016); roe deer *Capreolus capreolus*, and red deer *Cervus elaphus* (González Hernández & Silva-Pando, 1996). Our results also showed that ungulate browsing significantly reduced the accumulation of twigs and leaves in litter, and therefore litter carbon stocks. Reduction in biomass and in rates of accumulation of litter by ungulates has been reported by other authors (Pajunen, Virtanen, & Roininen, 2012). Consumption of plant material (leaves and twigs) and animal trampling contribute to explain reduction in litter accumulation, which can potentially decrease carbon stocks (Hughes et al., 2006).

In our sites, browsing had a strong negative effect on shrub and litter above-ground carbon stocks, as observed in other studies (e.g., Tanentzap & Coomes, 2012). By feeding selectively on plants and by avoiding the less palatable plant parts, ungulate herbivores may also induce a more recalcitrant litter, which may indirectly slow down plant matter composition and therefore affect soil carbon stocks (Tanentzap & Coomes, 2012). Future research, therefore, should address how decomposition of such dead plant material affects estimates of long-term balance of carbon stocks (Keith, Mackey, & Lindenmayer, 2009). Although in our work we did not consider below-ground carbon, other studies have shown that encroachment by *C. ladanifer* can increase soil organic carbon (SOC) (Gomez-Rey, Madeira, Gonzalez-Prieto, & Coutinho, 2013). Trade-offs resulting from shrub encroachment and potential increase in SOC and recalcitrant but lower litter accumulation in areas browsed by wild ungulates, need to be considered when addressing the effects of browsing in carbon stocks. Moreover, the increased density and above-ground biomass of *C. ladanifer* in fenced plots is likely associated with an increase of carbon stocks in the shrub roots (Barger et al., 2011). Conversely, in browsed and grazed areas, ungulates may reduce below-ground carbon stocks. For example, in a study in eastern Australian in a semi-arid woodland of mulga *Acacia aneura*, 20 years of grazing by sheep reduced below-ground carbon stocks (Daryanto, Eldridge, & Throop, 2013). In our study, shrub encroachment, through browsing exclusion, led to an increment

FIGURE 7 Probability of cork oak mortality (%) in relation to bark thickness, based on Catry et al. (2012), model of effects of fire on mortality of oak trees

of above-ground carbon inputs into the ecosystem, as shown by other authors (Knapp, 2008; Throop & Archer, 2007; Zhou, Brandle, Schoeneberger, & Awada, 2007). Conversely, ungulates reduced above-ground carbon stocks and litter accumulation, which negatively affected this regulating ecosystem service (sensu Millenium Ecosystem Assessment, 2005). Carbon stocks of oak trees, however, were not affected by ungulate exclusion. Although in our study we focused on the above-ground carbon, from a whole ecosystem carbon balance perspective, adding to the soil carbon, the emission of greenhouse gases from ungulates (e.g., Perez-Barberia, 2017) should also be considered in the future.

4.2 | Effects of ungulates on fire behaviour

Our results demonstrated a strong fuel load reduction by ungulates, namely of fine fuels. Domestic and wild ungulates, such as deer, may effectively be used as management tools for reducing fuel load (Davies, Bates, Svejcar, & Boyd, 2010; Hobbs, 2006; Ingram et al., 2013). Although the effects likely vary with animal and plant species and with population densities, ungulates can contribute to decrease fire hazard in Mediterranean regions (Ingram et al., 2013). For example, domestic ungulates, such as goats, can disrupt the vertical continuity and accumulation of biomass of grasses and shrubs (Lovreglio et al., 2014). In Spain, goats were found to reduce the volume of *C. ladanifer* by 45%, over a period of 24 months (Mancilla-Leytón & Vicente, 2012) and decreased understorey flammability by 25% after 4 years (Mancilla-Leytón, Mejias, & Vicente, 2013). In California, goats reduced shrub understorey height between 40% and 82% and decreased 1- and 10-hr fuel load by 33% and 58%, respectively (Tsiouvaras, Havlik, & Bartolome, 1989). There is a dearth of information on the effects of wild ungulates on fire behaviour, although Kramer, Groen, and van Wieren (2003) showed, through modelling, that both wild (red and row deer and wild boar *Sus scrofa*) and domestic (cattle and horses) ungulates reduced fuel load and the occurrence of wildfires.

Our fire modelling results also showed a clear reduction in potential fire spread rate and intensity (50% and 90%, respectively) in the open plots. In particular, browsing decreased the flame length and the likelihood of crown fire. Crown fires are severe fires that are more likely to induce tree mortality, in contrast to the lower intensity surface fires (Agee & Skinner, 2005). Numerous studies have shown a negative impact of high-intensity fire on tree survival (Hoffmann & Solbrig, 2003; Ritchie, Skinner, & Hamilton, 2007; Williams, Cook, Gill, & Moore, 1999). We show that severe crown fires can thus be hindered in areas browsed by ungulates, which may ultimately favour adult tree survival. Our estimates indicated that fire-induced tree mortality can be up to threefold greater in fenced plots. In the case of recently debarked cork oak trees, however, tree mortality will likely increase in both fenced and open plots (Catry et al., 2012), impacting tree and ecosystem above-ground carbon storage.

Although soil is the main reservoir of carbon, contribution of trees to both above- and below-ground carbon stocks is critical in these ecosystems (Ruiz-Peinado et al., 2013). Fire-derived black
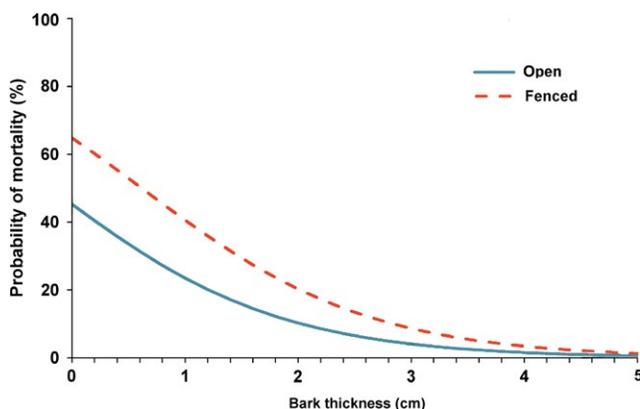
carbon also contributes to the overall carbon balance of the ecosystems although in Mediterranean fire-prone ecosystems it may not be the dominant fraction in the soil organic carbon (Rovira, Duguy, & Vallejo, 2009). Nevertheless, in our study, we only addressed aboveground carbon stocks.

Indirect positive effects of ungulates on adult tree survival may be critical to maintain carbon stocks of trees. If ungulates reduce the likelihood of crown fires and therefore increase the probability of tree survival during a wildfire event, than ungulates may be ultimately contributing to the carbon balance of the ecosystem by enhancing reservoirs of carbon in trees. These effects need to be balanced with potential long-term negative effects of ungulates on tree regeneration (Bugalho, Ibáñez, & Clark, 2013) or adult trees (e.g., Ramos, Bugalho, Cortez, & Iason, 2006; White, 2012). However, while management practices such as fencing may be used to protect tree seedlings and saplings from ungulate browsing, protection of tree regeneration from wildfire may prove more challenging (Díaz-Delgado, Lloret, Pons, & Terradas, 2002). Paradoxically, in this study, we show that ungulates, which are usually associated with negative effects on trees, may also contribute positively to oak tree survival and to the sustainability of the system.

The effects of land abandonment, with subsequent encroachment by flammable shrubs and increased stand tree densities, associated with lack of forest management such as thinning, are implicated in the fire regime changes observed in Mediterranean and other regions during the last decades (e.g., Fernandes et al., 2014; Pausas & Fernández-Muñoz, 2012; Taylor et al., 2017). Moreover, weather extreme conditions, which are now more common under current climatic changes (Rego & Silva, 2014; Trigo et al., 2006), also contribute to increase frequency and intensity of wildfires (IPCC, 2013). Mitigation of wildfire severity is thus a crucial ecosystem service in Mediterranean regions. In the Iberian Peninsula, where severe wildfires are increasing in frequency, ungulate hunting is also widespread. Although in ungulate hunting estates, such as those occurring in Iberia, shrub cover is usually high, we show in our study that wild ungulates can prevent encroachment of flammable shrubs. Thus, ungulate populations may act as effective tools for fuel reduction and maintenance of long-term carbon stocks.

5 | IMPLICATIONS FOR ECOSYSTEM PROPERTIES AND MANAGEMENT

Our study, based on a 14-year browsing exclusion experiment showed that ungulate browsing mediates carbon storage and wildfire severity trade-offs. Ungulates may halt ecological succession and reduce rates of shrub encroachment. Mainly through the effects on shrub plant biomass and litter, ungulates may prevent sudden carbon losses resulting from severe wildfires and death of adult trees, induced by canopy fires. Within the context of climate change scenarios, with predicted increased frequency of severe wildfires

in Mediterranean ecosystems, research on the effects of different ungulate communities on ecosystem services trade-offs is clearly needed in the future.

AUTHORS' CONTRIBUTIONS

M.N.B. and M.C.C. conceived and designed methodology; X.L. and M.N.B. collected the data; X.L. analysed the data; X.L., F.X.C., and P.M.F. performed fire simulations; X.L., M.C.C., and M.N.B. led the writing of the manuscript. R.B.J., F.X.C., and P.M.F. contributed critically to the conception and writing of the manuscript. All authors gave final approval for publication.

DATA ACCESSIBILITY

Data available via the Zenodo repository https://doi.org/10.5281/zenodo.1481953 (Lecomte et al., 2018).

ORCID

Xavier Lecomte https://orcid.org/0000-0003-3518-5490

Maria C. Caldeira http://orcid.org/0000-0002-3586-8526

Filipe X. Catry http://orcid.org/0000-0003-0668-9323

Paulo M. Fernandes http://orcid.org/0000-0003-0336-4398

Robert B. Jackson http://orcid.org/0000-0001-8846-7147

Miguel N. Bugalho http://orcid.org/0000-0002-7081-657X

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SUPPORTING INFORMATION

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