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Selective and taxon-dependent effects of semi-feral cattle grazing on tree regeneration in an old-growth Mediterranean mountain forest

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Abstract

Background: In Mediterranean mountain socio-ecosystems, both grazing by livestock and the dry season may influence tree regeneration. However, the relative contributions of these drivers are poorly known, even though present and future canopy composition might result from past and present variations in climate and herbivore density. This study aims to test how semi-feral cattle presence and season affect tree regeneration.

Methods: The study was conducted using permanent plots inside and outside a cattle exclosure in an old-growth Mediterranean forest. Saplings and seedlings were counted five times per year (winter, early spring, middle spring, summer, fall) and monitored over 7 yrs.

Results: Semi-feral cattle exclusion increased *Acer*, *Fagus, Ilex, Pinus, Prunus* and *Quercus* sapling densities and increased *Acer*, *Fraxinus, Ilex, Quercus* and *Sorbus* seedling densities. Interestingly, the dry season did not exert any noticeable effects on the sapling or seedling densities of any of the studied taxa.

Discussion: Semi-feral cattle presence may limit tree regeneration through taxon-dependent effects, which suggests that the current decrease in grazing livestock across the Mediterranean basin will modify recruitment processes and, likely, future forest composition.

Conclusions: Semi-feral cattle presence acts as a selective driver of tree community composition.

Keywords: Cattle, Climate, Experiment, Herbivory, Forest pastoralism

Background

Summer grazing in Mediterranean mountain areas has historically been an important socio-economical activity, as it provides livestock with essential nutritional supplements during the dry and warm seasons (Casasùs et al. 2007). Although forest grazing is still used by farmers in some areas, the last decades have been characterised by a net decrease in forest pastures across northern Mediterranean countries, a dynamic which is mainly explained by the abandonment of low productivity areas that are widespread in mountain regions. However, the consequences of these large-scale land-use changes, which include effects on long-term community diversity, remain unclear. The presence of large domestic mammals may influence the recruitment of species through selection of palatable seedlings and saplings, foraging on competing species, trampling, and modification of organic matter turnover and biogeochemical fluxes (McEvoy et al. 2006; Marquardt et al. 2009; Wassie et al. 2009). The community structure and functioning of forest socio-ecosystems should thus differ based on

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whether domestic herbivores are present or not (for a review of effects see Öllerer et al. 2019).

Seedling emergence can be negatively affected by both direct mechanisms, such as the destruction and burial of seeds (Hulme and Borelli 1999; Smit et al. 2006), and indirect mechanisms, such as soil compaction, solifluction and erosion (McEvoy et al. 2006; Wassie et al. 2009). Livestock may also hamper seedling growth and survival via the direct consumption of entire seedlings or their shoots, mainly leaves and buds (Kuiters and Slim 2002; Wassie et al. 2009). However, the magnitude of the impact on species and community structure depends on plants, productivity, grazing system and ungulate density (Plieninger et al. 2004; Teich et al. 2005; Carmona et al. 2013; Chauchard et al. 2018, Ramirez et al. 2018). In some cases, even low livestock density can have consequences for tree demography (Cierjacks and Hensen 2004; Casasùs et al. 2007; Tremblay et al. 2007, Smit et al. 2015). The regeneration impacts attributed to livestock also vary based on grazer characteristics (Marquardt et al. 2009). These differences may stem from both animal diet selection and seedling/sapling species characteristics like compensatory growth ability after defoliation (Kupferschmid 2017). These differences can skew species distributions so that resilient species are favoured over sensitive species. On the other hand, herbivore presence may facilitate seedling emergence, growth and survival by removing competitive or inhibiting plants, e.g. grass and shrubs, or exposing bare ground though trampling, which can create regeneration niches (Kuiters et al. 1996; Perrin et al. 2006).

Studies with a focus on how livestock influence tree regeneration in Mediterranean regions have generally focussed on oaks (e.g. Henkin et al. 2005; Plieninger 2007; Papachristou and Platis 2011), which dominate forests (FAO 2018). Nevertheless, little is known about how semi-feral cattle presence impacts the regeneration of entire tree communities, especially in mixed forests. The present paper describes how grazing by large semi-feral cattle affects tree regeneration in a mixed old-growth Mediterranean mountain forest in which cattle have been present for centuries (Fortuny et al. 2014, 2017). Cattle presence is certainly not the sole factor affecting tree regeneration. For example, the Mediterranean climate is characterised by dryness during summer months - a result from both high temperatures and low precipitation - which is known to hamper seedling establishment (Castro et al. 2005; Mendoza et al. 2009). Water stress, which affects both water use efficiency and carbon allocation, strongly influences seedling survival (Kolb and Robberecht 1996). The issue of water-stress is important to the Mediterranean, as the region is expected to be strongly affected by increased temperatures caused by global warming (Christensen and Christensen 2007). Precipitation is also expected to decrease, and this will be particularly evident during summer months (Giorgi and Lionello 2008). The resulting increase in summer dryness could affect long-term forest productivity (Van der Moelen et al. 2011), as well as the tree recruitment processes and diversity. Dry and hot summers may also be a factor that interacts with cattle grazing. For example, sapling species that are better adapted to the changing climate could also be highly resistant to herbivory. In this case, the effect of summer dryness would override the grazing effect.

The study aims to test the effects of semi-feral cattle presence and season on tree regeneration through experiments that excluded cattle using permanent plots. The experiments investigated two components of tree regeneration: the number of seedlings and the number of saplings available for regeneration (Arista 1995). We hypothesise that (1) semi-feral cattle presence reduces regeneration potential, yet this driver of community composition varies between tree species, and (2) stressful summer conditions and cattle presence have a combined negative effect on tree regeneration. Because grazing by cattle is decreasing locally and climate change is expected to exert significant effects, this study may help highlight future consequences for tree regeneration in Mediterranean mountain socio-ecosystems.

Methods

Study area

The study was carried out in the Massane Natural Reserve (42.5° N, 03.0° E), which covers the whole upper valley of the Massane River in the Albères Massif of the eastern French Pyrenees (Supplementary material S1). The southern crests of the upper valley mark the French-Spanish border. The valley has an altitude ranging from 600 to 1200 m above sea level (a.s.l.) and is characterised by generally steep slopes (ca. 40°). The bedrock is composed of acidic shale and gneiss, and the soil belongs to the brunisol category (Servant 1970). The area has a typical Mediterranean mountain climate, with warm and dry summers and cool and windy winters (Garrigue and Magdalou 2010). Mean annual precipitation is 1140 ± 327 mm (period 1976–2017, meteorological station in the Massane Nature Reserve [NR]), with the rain mainly concentrated to the spring and autumn. The dry season occurs between June and August (with mean monthly precipitation of 37 ± 26 mm, 31 ± 27 mm and 33 ± 19 mm, respectively, between 1976 and 2017). Mean annual temperature (1976–2017) is 11.9 ± 1.0 °C, with January (5.1 ± 1.7 °C) and July (20.1 ± 1.8 °C) as the coldest and warmest months, respectively.

The valley includes two ecological zones: forests and woodlands below 900–1000 m a.s.l., and grassland on the crests. Forests cover over 50% of the NR. The forest type is dominated by beech (*Fagus sylvatica* L.) with other broad-leaved trees present, namely, white oak (*Quercus pubescens* Willd.), whitebeam (*Sorbus aria* L.), wild cherry-tree (*Prunus avium* L.), maples (*Acer campestre* L., *A. monspessulanum* L., *A. opalus* Mill.) and holm oak (*Q. ilex* L.). Individual occurrences of ash tree (*Fraxinus excelsior* L., *F. angustifolia* Vahl), Austrian black pine (*Pinus nigra subsp. nigra* Arn.) and yew (*Taxus baccata* L.) are scattered throughout the reserve. The understory is dominated by European holly (*Ilex aquifolium* L.). The Austrian pine was introduced and naturalised during the nineteenth century (Chauchard et al. 2006).

The upper Massane valley (336 ha) was designated as a NR in 1973, but was already protected since the early 1950's. A French NR entails high protection status (category IV and category 1a, UICN) that bans economic exploitation (except traditional activities with little impact on species and their habitats, e.g. pastoralism) and most recreational activities like hunting and fishing. Approximately 10 ha of the inner forest zone has been fenced off since 1954 to exclude cattle (category 1a, UICN). The fence consists of wire netting 1.10 m in height (mesh-size of 10 cm) with no anchor in the soil. The rest of the reserve (category IV, UICN) is browsed and grazed by semi-feral cattle (*Bos taurus* L.). Wild boar (*Sus scrofa* L.) and roe deer (*Capreolus capreolus* L.) are the only other two wild large herbivores that have been recorded in the forest. A permanent roe deer population does not currently exist in this mountain massif. Even though no quantitative data about these two wild ungulates are available, their impacts on tree regeneration were considered negligible because the estimated densities of both herbivores in the area were low.

The semi-feral cattle can freely enter the higher altitudes at the beginning of the spring (post-calving period) and then remain there until autumn. During these five to six months they browse and graze freely. Some cattle, generally bulls, are present in the area even during winter months, but at very low densities. During the sampling period, cattle were present at noticeably different densities in the winter (~ 0.08 heads·ha^{-1}) and spring-summer (0.46 heads·ha^{-1}). Cattle densities, provided by the NR administration, can be influenced by an unknown number of erratic cattle that enter the area from the south-facing slopes of the mountain massif (i.e., Spanish side) to visit the fresher north-facing slopes, including the Natural Reserve. This occurrence of erratic cattle was mainly noted during the hot and dry summer months, which make the south-facing slopes more arid, and affect the crest grasslands and upper forest more than the lower forests in which the experimental site was situated. Even though the exact number of erratic cattle cannot be reliably quantified, this occurrence has little influence on the cattle density observations provided by the NR administration.

Experimental design

Four permanent 50 m^2 (1 m × 50 m; total 200 m^2) transects were established in the forest in 2006 (Table 1) and monitored until 2012. The mean distance between each transect was about 190 ± 104 m, and the transects were established at altitudes ranging from 661 to 728 m a.s.l. The transect locations were chosen based on two criteria: (1) minimal risk of disturbances like runoff and soil erosion; and (2) a site that is representative of the main forest microhabitats. Transect 1 (Tr 1), near the river, is in the wettest part of the forest. Transect 2 (Tr 2) is located in a patchy population of pine mixed with beeches and white oaks. Transects 3 and 4 are located in the main part of the forest, i.e. more homogeneous and mainly dominated by beech trees of different ages and shapes (Tr 3: taller and younger; Tr 4: smaller but older trees).

Each transect was divided into two 25 m^2 (1 m × 25 m) sub-transects: one was located in a single cattle exclosure (fenced area) from which cattle have been excluded since 1954, while the second was located in an unfenced area. Thus, four of the eight sub-transects were located in the same cattle exclosure. The sub-transects (inside and outside the fence) of each transect included equivalent environmental conditions. The mean distance between each sub-transect was around 20 m. A 1 m × 1 m quadrat was used to count the seedlings and saplings in each transect. The quadrat was sub-divided into a hundred 10 cm × 10 cm sub-quadrats that allowed the monitoring of individual seedlings over the course of the year. In total, 20,000 sub-quadrats with an area of 100 cm^2 were monitored.

Between 2006 and 2012, tree seedlings and saplings in each of the 20,000 sub-quadrats were counted five times per year: late winter (March–April transition); early spring (April–May transition); middle spring (May–June transition); early summer (June–July transition); and early autumn (middle October).

Table 1 Transect description. UNF: unfenced area (grazed), FEN: fenced area (ungrazed)

Transect	Coordinates		Altitude (m, a.s.l.)	Slope (°)	Vegetation cover (%)		
	Long. (°E)	Lat. (°N)			Tree	Shrub	Grass
1 UNF	3.02855	42.48765	661	18	25–50	5–25	5–25
1 FEN	3.02861	42.48772	661	25	25–50	5–25	50–75
2 UNF	3.03001	42.48741	713	22	50–75	< 5	5–25
2 FEN	3.02992	42.48748	713	22	50–75	< 5	25–50
3 UNF	3.03137	42.48895	728	16	50–75	< 5	< 5
3 FEN	3.03083	42.48892	711	20	50–75	< 5	25–50
4 UNF	3.03230	42.49102	689	17	50–75	< 5	5–25
4 FEN	3.03206	42.49111	697	21	50–75	5–25	25–50

This study considers both first-year seedlings, hereafter “seedlings”, and saplings over a year old and < 20 cm in height. The seedlings can be easily distinguished from the saplings by the presence of cotyledons. Because the study was conducted in a NR, individual marking and tracking was not possible.

While the precipitation levels observed in 2008 and 2012 were close to historical levels, they were lower than average in 2006, 2007 and 2009 (Fig. 1a). The summers of 2006 and 2009 were hot and dry whereas the summer of 2007 was only dry (Fig. 1b and c). In 2009, the autumn and spring were also dry (Fig. 1b). The precipitation levels observed in 2010 and 2011 were higher than average, with 2010 and 2011 showing very wet spring and autumn periods (Fig. 1b). These observations translate to high inter-annual variability in seasonal features.

Data analyses

The community structure of the seedlings and saplings were investigated in the first step of the analyses. During the second step, we analysed the effect of semi-feral cattle presence and season on seedling and sapling density (individual no. per m^2). The observed tree seedling and sapling densities of *Acer* sp., *Fagus sylvatica*, *Fraxinus* sp., *Ilex aquifolium*, *Pinus nigra*, *Prunus avium*, *Quercus pubescens* and *Sorbus aria* were included in the analyses. The seedling and sapling densities of *Quercus ilex* and *Taxus baccata* were excluded because these species showed extremely low abundance. The three species of maple were analysed at the genus level because a high level of hybridization makes seedling identification at the species level almost impossible. The ash seedlings were also analysed at the genus level because *F. excelsior* and *F. angustifolia* seedlings are difficult to differentiate.

Community analysis

The relationships between seedling and sapling community structures and the explanatory variables (transect, year, season, fencing) were assessed by a constrained ordination of the seedling and sapling counts data using

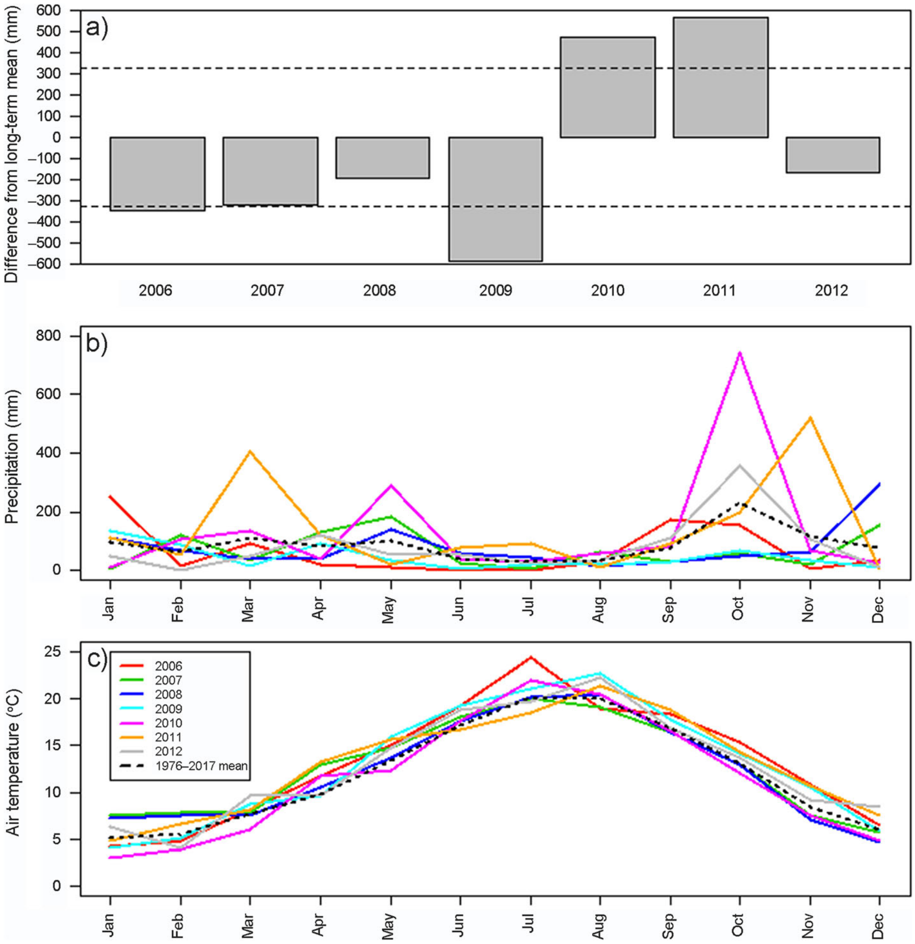

Fig. 1 (**a**) Precipitation anomalies for the experimental period 2006–2012 relative to historical average (1140 mm, 1976–2017); horizontal dashed lines indicate standard deviations (327 mm). Monthly total precipitation (**b**) and average air temperature (**c**) for 2006, 2007, 2008, 2009, 2010, 2011, 2012, with the historical values (1976–2017) shown for comparison

redundancy analysis (RDA). This analysis was performed using the package "vegan" (Oksanen et al. 2019). The RDA response matrix was a taxa matrix composed with the data records as rows and the eight taxa as columns. Each record in this matrix corresponded to the seedling and sapling count combined in each sub-transect, for each sampling season, over the study duration. A Hellinger pre-transformation of the data was performed (Legendre and Gallagher 2001). In this transformation, the abundance values were first divided by total recorded abundance, after which the result was square-root transformed. After the first RDA, a forward selection was run using the ordiR2step function (package "vegan", Oksanen et al. 2019) by permutation tests based on adjusted R^2 using 199 permutations. The model that maximized the adjusted R^2 was retained. Transect, year, season and fencing contributions to seedling and sapling community structures were then assessed through variance partitioning.

Due to variability in tree regeneration between years, which was particularly evident in species or taxa that show masting years (*Fagus sylvatica*, *Quercus pubescens* and *Fraxinus excelsior*), and the strong effect of each transect's forest canopy on seedling taxa composition, a conditioned RDA was performed to isolate the effects of cattle presence and season from the effects of year and transect (which were not considered in the analysis). To facilitate the visualisation of RDA results, records were clustered in term of classes in the scatter diagrams. Each cluster groups records that belong to a specific transect and the sub-transect (fenced or grazing area).

Effect of cattle presence and season on seedling and sapling density

A generalised linear mixed-effect model (GLMM), which allowed crossed random effects and employed a negative binomial distribution and a log-ratio link function (package "lme4", Bates et al. 2015), was used to test how the interaction between taxa and semi-feral cattle presence (inside versus outside the fenced area) and the interaction between taxa and season (winter, early spring, middle spring, early summer and autumn) affected seedling density, sapling density and overall seedling and sapling density. Count data were generally analysed using Poisson distributions, but when variance exceeded the mean (overdispersion) negative binomial distributions were preferred (Krebs 1999). The interactions between taxa and years (taxon: year) and between taxa and transects (taxa: transect) were included as crossed random effects in the GLMM model. This is because transects and years had varying effects on different taxa over the study period.

The GLMM was tested for over-dispersion using the "blmeco" package (Korner-Nievergelt et al. 2015), using $\Phi > 0.7$ and $\Phi < 1.4$ as thresholds for potential overdispersion. The normality of residuals was visually checked using a histogram and normal q–q plot. We also checked that the residuals are centred around zero throughout the range of fitted values. We used the dredge function in the "MuMln" package (Barton 2019), which automatically fits all of the different combinations of fixed predictor variables to the data and calculates Akaike Information Criterion (AIC) values, to identify the optimal model. The subset of models identified for the input data were then used to calculate the final model. The "MuMln" package was also used to calculate marginal R^2 (representing only fixed effects) and conditional R^2 (representing both fixed and random effects) so that we could determine how much of the variation was explained by fixed and random effects, respectively (Nakagawa and Schielzeth 2013). The significance of fixed effects in the best model was assessed by Wald-tests applying χ^2 probabilities in the "car" package (Fox and Weisberg 2019). Post-hoc tests, predicted marginal means, and standard errors for fixed effects were calculated using the "lsmeans" package (Lenth 2016).

Results

The densities of seedlings and saplings varied according to taxa. *Fagus sylvatica* was the dominant taxon of the regeneration community, representing, on average, around 44% of the saplings and 25% of the seedlings in the fenced area (Supplementary material S2). The second most abundant taxon was *Ilex aquifolium*, which corresponded to 27% and 25% of the saplings and seedlings in the fenced area, respectively (Supplementary material S2). Seedling and sapling densities also varied between years (Supplementary material S2). Intra-annual variations in seedling and sapling density, which were mainly linked to differences between transects, were also important (Supplementary material S2).

Community structure

The redundancy analysis (RDA) model that maximised adjusted R^2 included transect, year and cattle exclosure (fencing) but did not include season (adj. $R^2 = 0.45$). In this model, transect, year and fencing explained 49.9%, 9.7% and 2.1% of the variance, respectively. The first two RDA axes captured 49.8% of the variance (Fig. 2a). The first RDA axis (36.4% of the total variance) separated *Fagus sylvatica* and *Pinus nigra* (positive values) from *Acer* sp. (negative values). The second RDA axis (13.4% of the total variance) included *Quercus pubescens* on the positive side. *Fraxinus* sp. was located on the negative sides of both axes 1 and 2. *Ilex aquifolium* demonstrated negative and positive values for axes 1 and 2, respectively. The first RDA axis isolated: i) transect 1 (high abundance of *Fraxinus*, *Ilex* and *Acer*) on the negative

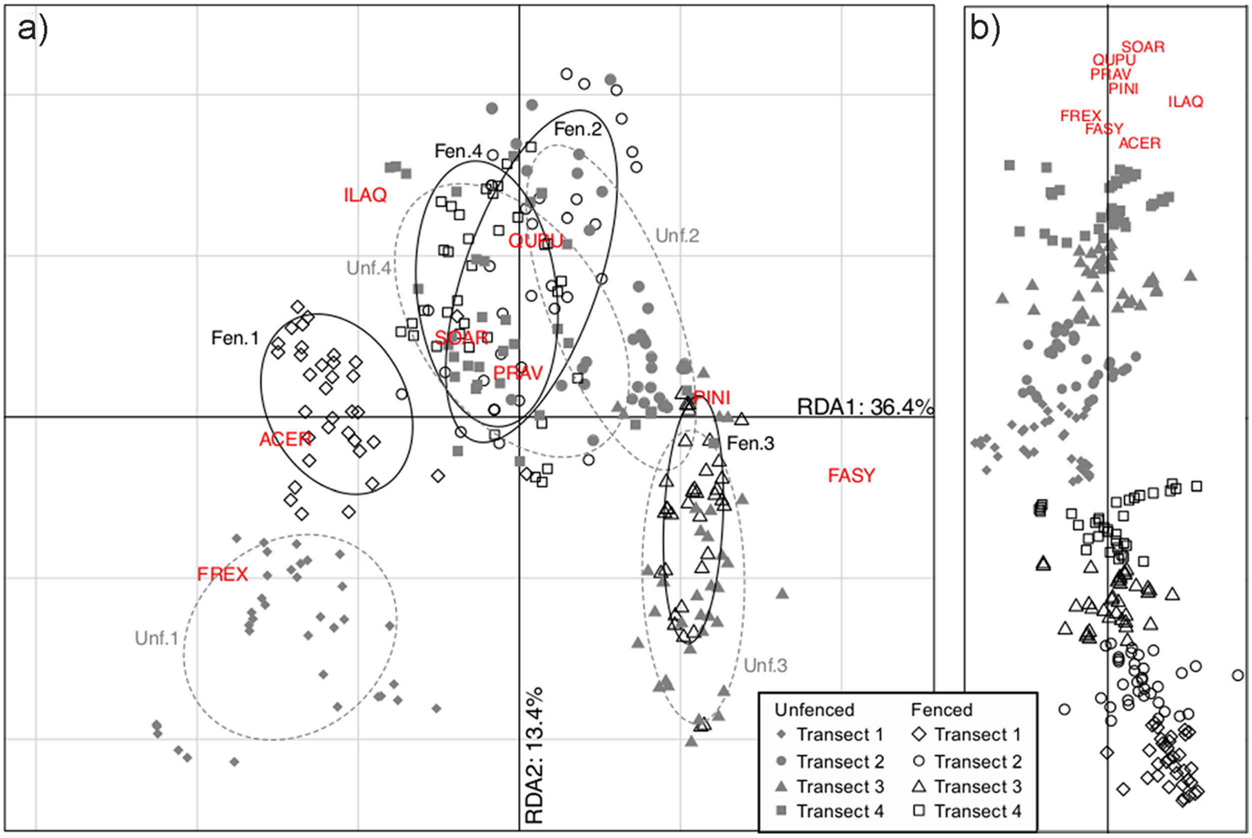

Fig. 2 (**a**) Redundancy analysis (RDA) ordination diagram of both seedling and sapling communities, with a scatter diagram of sample scores clustered in terms of transect number and livestock presence (unfenced vs fenced). FASY: *Fagus sylvatica*; QUPU: *Quercus pubescens*; SOAR: *Sorbus aria*; PRAV: *Prunus avium*; ACER: *Acer* sp.; FREX: *Fraxinus* sp.; PINI: *Pinus nigra*; ILAQ: *Ilex aquifolium*; Unf: unfenced area (presence of semi-feral cattle); Fen: fenced area (absence of semi-feral cattle); 1 to 4: transect number. The ellipses correspond to confidence intervals of 1.5× standard deviation for the average coordinates of samples. (**b**) Scores along the first axis of a conditioned redundancy analysis ordination (horizontal axis) diagram of seedling and sapling communities that only includes the effect of cattle presence (the effects of transect and year were excluded)

side of the plot; and ii) transect 3 (high abundance of *Fagus* and *Pinus*) on the positive side of the plot. When interpreting the second RDA axis, we noticed that coordinates representing the cattle exclosures of Tr 1 and Tr 3 were located noticeably higher on the plot than the coordinates from unfenced areas of the same transects. The coordinates for the other two transects (2 and 4) did not differ noticeably based on whether they represented fenced or unfenced areas.

After removing transect and year effects, the conditioned RDA axis (including only cattle presence) explained 5.5% of the total variance (Fig. 2b). The conditioned RDA axis clearly isolated the cattle exclosure sub-transects (positive values, and associated with a higher abundance of *Ilex*, *Acer* and *Sorbus*) from the unfenced sub-transects (negative values).

Effect of cattle presence versus season on density

The best regression model for overall seedling and sapling densities included interaction between taxon and cattle presence (‘taxon:fence’, Table 2), while interaction between taxon and season (‘taxon:season’) was excluded.

Table 2 General linear mixed models (GLMM) for overall seedling and sapling densities, seedling density and sapling density. Only the results of the best models are displayed. ‘Taxon:Fence’: interaction between taxa and cattle presence; ‘Taxon:Season’: interaction between taxa and season. R^2_m: marginal R^2 (fixed effects only), R^2_c: conditional R^2 (fixed and random effects)

	Seedling + Sapling ($R^2_m = 0.36$, $R^2_c = 0.85$)			Seedling ($R^2_m = 0.30$, $R^2_c = 0.78$)			Sapling ($R^2_m = 0.44$, $R^2_c = 0.87$)		
	Chisq	Df	Pr (>Chisq)	Chisq	Df	Pr (>Chisq)	Chisq	Df	Pr (>Chisq)
Taxon: Fence	197.5	15	< 0.001	80.9	15	< 0.001	357.8	15	< 0.001
Taxon: Season	–	–	–	214	32	< 0.001	80.7	32	< 0.001

Cattle presence significantly affected the overall seedling and sapling density (SSD) of *Acer*, *Fagus*, *Fraxinus*, *Ilex*, *Prunus*, *Quercus* and *Sorbus* (Figs. 3a, b and 4a). Transects within cattle exclosures showed higher seedling and sapling densities than transects outside of exclosures (Figs. 3a, b and 4a). The extent to which cattle presence affected SSD differed between species, namely, *Acer*, *Ilex*, *Quercus* and *Sorbus* regeneration was more affected by cattle presence than the regeneration rates observed for *Fagus*, *Fraxinus* and *Prunus* (Fig. 4a).

The best regression model for seedling densities included both 'taxon:fence' and 'taxon:season' interactions (Table 2). Cattle presence significantly affected *Acer*, *Fraxinus*, *Ilex*, *Quercus* and *Sorbus* seedling density (Figs. 3c, d and 4b). Each of these five taxa showed significantly higher seedling densities within cattle exclosures than in unfenced areas (Figs. 3c, d and 4b). However, the extent to which cattle presence affected seedling density varied between taxa: *Quercus* and *Sorbus* were the most affected, showing slightly higher marginal mean differences than *Ilex* and *Acer*, while *Fraxinus* seedling densities were the least affected by cattle presence (Fig. 4b). The interaction 'taxon:season' also had a significant effect on seedling density (Table 2). These effects were not linked to the dry season, but rather seedling emergence, which occurs between late winter and early spring for all taxa (Fig. 5a).

The best regression model for sapling densities included both 'taxon:fence' and 'taxon:season' interactions (Table 2). The presence of cattle had a significant effect on *Acer*, *Fagus*, *Ilex*, *Pinus*, *Prunus* and *Quercus* sapling densities (Figs. 3e, f and 4c). Furthermore, sapling densities were generally higher inside the cattle exclosure than in unfenced areas. As was the case for seedling densities, the extent to which cattle presence affected sapling density differed between taxa (Figs. 3e, f and 4c). *Acer* and *Ilex* were the most affected, and showed higher marginal mean differences than *Fagus*, *Pinus* and *Prunus* (Fig. 4c). The interaction 'taxon:season' significantly influenced sapling density (Table 2), but no differences between successive seasons were found (Fig. 5c).

Discussion

The present study reports that semi-feral cattle presence has a selective impact on regeneration of Mediterranean mountain trees due to taxon-specific effects. The dry season (summer) effect was not observed in the analyses, which contrasts our working hypothesis. Although this study does not consider processes that influence juvenile tree survival prior to the adult stage (i.e. recruitment), which can diminish the seedling/sapling stock, the results provide solid evidence for how the current climate and semi-feral cattle presence can affect seedling and sapling densities. These effects are first discussed in terms of tree community and populations dynamics under the effect of grazing, after which the implications for forest conservation management are covered.

The seedling and sapling community structure

The seedling and sapling communities both showed strong spatial clustering based on transect location, which explained 49.9% of the observed variance. Spatial heterogeneity can be expected in old Mediterranean mountain forests (e.g., Fournier et al. 2012), and is likely connected to soil thickness, terrain variation or tree cover composition. For instance, transect 1 is close (ca. 25 to 50 m) to a winding stream that traverses the Nature Reserve. This transect also showed the lowest tree cover (25%–50%). Seedling composition in the unfenced part of this transect differed strongly from what was observed in other transects, especially in terms of *Fraxinus* seedlings. *Fraxinus* trees are more abundant in the riparian forest than in the rest of the forest. Furthermore, *Fraxinus* is a light-demanding taxon that would be favoured in areas with low tree cover. For both of these reasons, it is not surprising that the unfenced sub-transect of transect 1 was dominated by *Fraxinus* seedlings (Table 1). As the mean distance between pairs of 25-m sub-transects was ~ 20 m, we cannot rule out that edge effects influenced our results. Both sub-transects in each site were at 10 m from the fence.

Strong variability was observed between the years (SM S2); for example, the year explained 9.7% of the community variance. The variation observed in seedling densities may be the result of irregular seed production between years; for example, *Fagus*, *Quercus* and *Fraxinus* are known to be masting taxa (Tapper 1996; Piovesan and Adams 2001; Alejano 2011; Vacchiano et al. 2017), which may lead to interannual pollen limitation (Schermer et al. 2019). As highlighted by Alejano (2011), masting clearly influences the regeneration success of trees and the demography of seed consumers. Moreover, the weather can directly impact germination and survival, e.g., extreme precipitation or drought (the year 2009 at the study site was noticeably drier than the historical average) can increase the mortality of seedlings and saplings.

Interestingly, variation in the structure of the seedling and sapling communities in relation to cattle presence was less obvious than expected. Cattle presence explained only 2.1% of the community variance, even though the seedling communities in the sub-transects (fenced and unfenced) of transects 1 and 3 could be differentiated. These observed differences, which are illustrated in the RDA plot, may be due to other mechanisms, e.g., tree-cover composition, which varied between transects. It is important to note that other predators of seedlings, including invertebrates or rodents, could also underlie this result, as they could affect

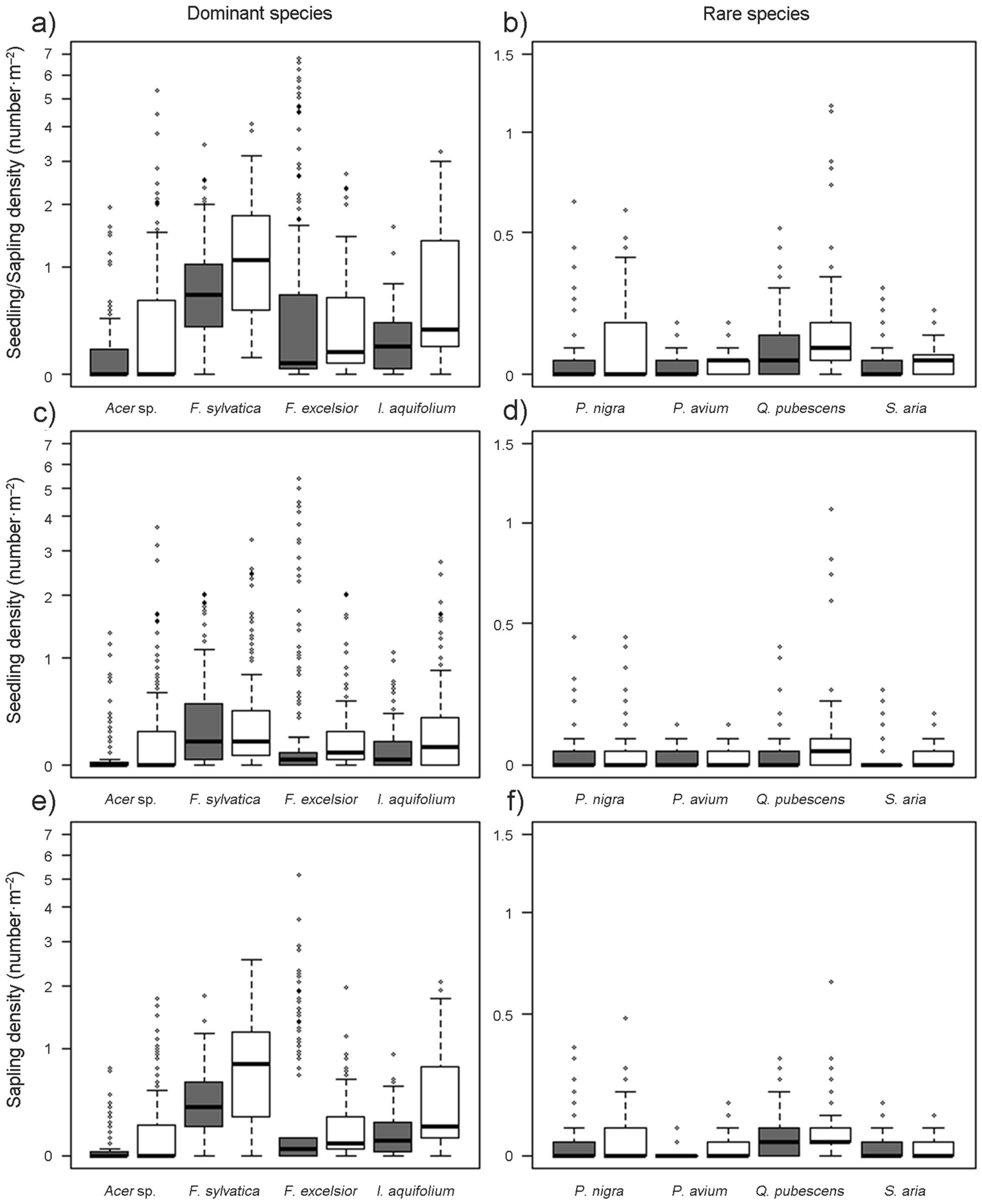

Fig. 3 Box-plot representation of seedling + sapling (**a**, **b**), seedling (**c**, **d**), and sapling densities (**e**, **f**) both inside (white box, fenced) and outside (grey, unfenced) the cattle exclosure. The black line indicates the median value of seedling and sapling density, while upper extent of the box indicates the 75th percentile and the lower extent indicates the 25th percentile. The whiskers indicate the lower and upper adjacent values. Dots are outliers

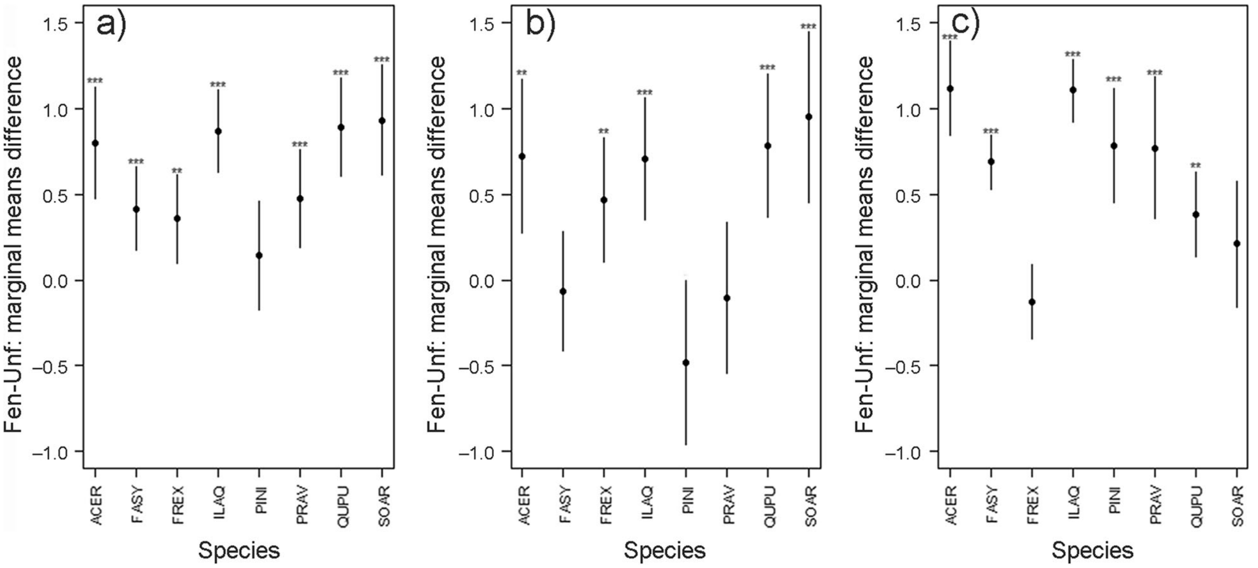

Fig. 4 Estimated differences in marginal means, including 95% confidence intervals, for the (**a**) overall, (**b**) seedling and (**c**) sapling densities of each species with (Unf) and without the presence (Fen) of semi-feral cattle (Fen). Comparison of pairwise marginal mean (Fen-Unf): * $p < 0.05$, ** $p < 0.01$, ***$p < 0.001$

all sub-transects in a similar manner because the wire mesh of this experiment does not exclude small animals. Complex insect-seedling interactions that are linked to herb cover and tree cover were reported, with the interactions differing between seedling tree species and involving different levels of herbivory, competition and facilitation (Vaz et al. 2019).

Cattle presence alters tree regeneration and community composition

Cattle exclosure had a highly positive effect on the sapling densities of six of the eight studied taxa (Fig. 4c), but a less significant positive effect on the seedling densities of five of eight taxa (Fig. 4b). Based on a wide body of literature (e.g., Dufour-Dror 2007), grazing is traditionally expected

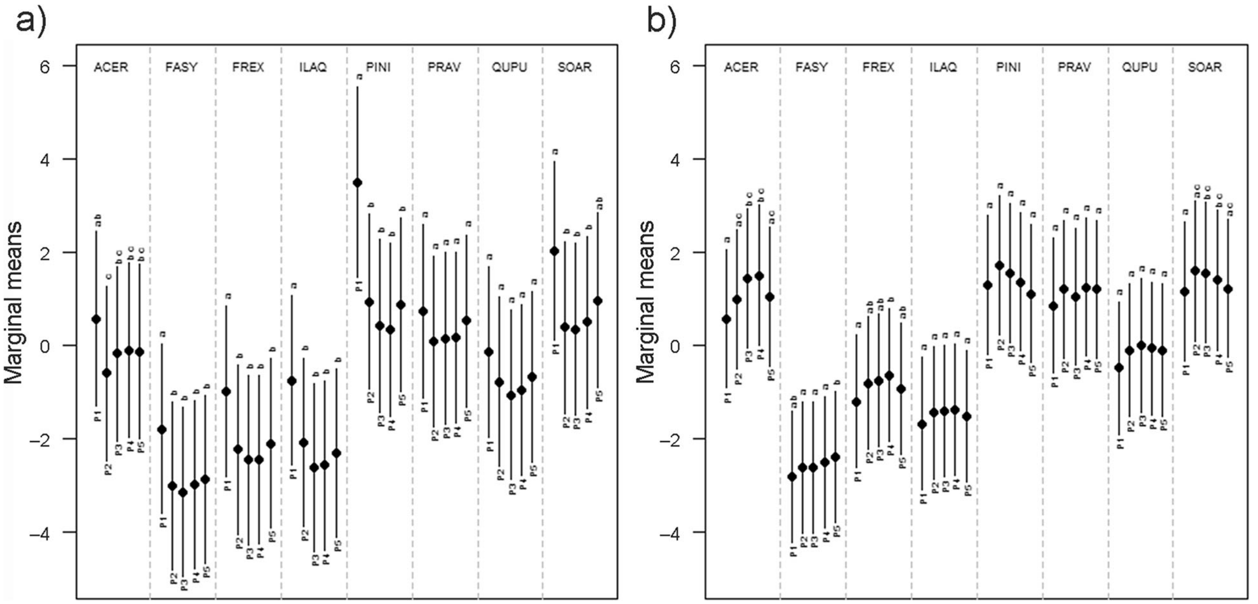

Fig. 5 Estimated marginal means, including 95% confidence intervals, for the (**a**) seedling and (**b**) sapling densities of each species between seasons; P1: late winter, P2: early spring, P3: middle spring, P4: early summer, P5: early autumn. Within a species, periods marked with different letters significantly differ ($p < 0.05$)

to negatively impact seedling and sapling densities. Although a positive effect of grazing on seedling density is less obvious, it has also been reported in some studies (e.g., González-Hernández and Silva-Pando 1996). For example, higher seedling emergence rates are generally related to suitable habitat characteristics, such as an available seedbed which results from trampling by livestock (Szwagrzyk et al. 2001). Cattle can thus exert opposing effects on young trees, either indirectly favouring seedling establishment through foraging for herbs and trampling moss cover, or directly reducing the abundance of certain species of plants through seedling grazing and sapling browsing. The overall effect of cattle presence on seedling density depends on the relative prevalence of both these processes, and can occasionally be negligible (meaning that both processes are in equilibrium), as observed here for *Fagus* and *Prunus* seedlings (Fig. 4b). Ultimately, the effect of cattle exclosure on sapling communities in old-growth Mediterranean forest was found to be taxon-specific (Fig. 4c).

Based on the presented research, the impact of cattle on forest regeneration was found to be taxon-specific. The observed variation in sensitivity to grazing probably resulted from animals' diet selection or foraging behaviour (Marquardt et al. 2009). A study that investigated the dietary composition of the cattle population in the same forest was examined in the present study showed that woody species form the bulk of the animals' diet, from ca. 70% in spring and summer to ca. 90% in winter (Bartolomé et al. 2011). This study suggests that the diet selection of these semi-feral cattle is closely related to which plants are available rather than animal preference. It has been found that the two main species consumed by cattle were *Ilex* and *Fagus*, mostly in a mixture with herbs (Travé 1993). Our results partially support this foraging behaviour. *Ilex* saplings and seedlings were strongly impacted by cattle presence (Fig. 4b and c), whereas only *Fagus* saplings were weakly affected (Fig. 4c). However, we reported that other species with lower canopy density were also highly impacted at their seedling (i.e. *Acer*, *Quercus* and *Sorbus*) or sapling stages (i.e. *Acer*, *Pinus*, *Prunus*). The results concerning *Pinus* confirm previous empirical research which found cattle to be a primary driver of black pine population dynamics (Chauchard et al. 2006). Differences in sensitivity to grazing may depend on species characteristics, such as compensatory growth ability after defoliation (Kupferschmid 2017). For example, *Fraxinus* has strong compensatory growth ability after defoliation, which may make these plants better suited to surviving grazing (Collin et al. 2000). The observed differences in tree regeneration under grazing pressure demonstrate that cattle presence promotes changes in tree composition, as has already been shown for other large herbivores in temperate forests (Putman 1996; Hester et al. 2000). As such, the presented results highlight the "biotic driver" role of herbivores in forest dynamics and composition (Bond 2005). Since the presented experiments concluded, the spring-summer cattle density in the area has been reduced from 0.46 to ca. 0.10 head·ha^{-1} to maintain an equal density throughout the year. This reduction should favour the recruitment of *Acer*, *Ilex*, *Quercus* and *Sorbus* and, to a lesser extent, the recruitment of *Fagus*, *Fraxinus* and *Prunus*.

Effects of season and cattle-season interactions on seedling and saplings densities

Season affected the seedling densities of six species (Table 2 and Fig. 5a). However, this effect was not linked to the dry season, but rather to changes that occur during the late winter-early spring period (late March and early April). This finding was not in line with our working hypothesis, as we assumed that water stress during the dry summer months would increase mortality (Ibáñez and Schupp 2001; Pulido and Diaz 2005). Hence, our initial working hypothesis – that survival differences among species will be linked to summer water stress response – did not receive experimental support. Although the dry season did not influence seedling and/or sapling densities in this study, increased aridity in southern Europe, which is expected to occur due to climate change, remains a major issue for the conservation of mixed beech forests in the Mediterranean mountains (Cheaib et al. 2012).

Cattle presence and season do not interact to alter seedling and/or sapling densities (Table 2), although such an interaction was expected due to increased grazing pressure in the summer when herbs become rare or less palatable. This lack of interaction means that one driver's impact on regeneration does not depend on the other. This result is not in line with what has been previously reported, as multiple studies (e.g. Ibáñez and Schupp 2001) have identified a linkage between cattle presence and drought conditions on seedling survival.

The experimental setting and measurements applied in this study make it impossible to accurately distinguish effects that are derived from season (e.g., drought during summer months) and interannual variability in grazing intensity, which is inherent to the ecosystem. In this study, grazing intensity between seasons was not quantified. This was not because these types of measurements are impossible, as several methods for this type of quantification exist, for instance, dung measurements serve as a grazing proxy (e.g., Burkepile et al. 2016) or a camera trap can be used to capture images of animals feeding on seedlings and/or saplings (Rovero and Marshall 2009). Such methods would have enabled reliable measurements of grazing intensity at different times of the year, which could have helped us disentangle the effect of season from the effect of grazing intensity at a certain time of the year.

Conservation issues

Our regeneration monitoring during 7 yrs showed that (i) grazing and browsing by cattle exerts taxon-dependent effects on the early stages of tree regeneration and, surprisingly, (ii) seedling and sapling densities were not noticeably affected by the dry conditions of summer months. Therefore, our results indicate that cattle grazing is an important driver of seedling and sapling densities in this old-growth forest. Thus, managing a forest with or without the presence of cattle, a decision that depends on the conservation issue (rewilding, dung insect diversity, functionality, fire management, etc.), will have significant consequences for tree composition and dynamics. This means that any changes to the factor of livestock grazing will not have a neutral effect on the ecosystem based on the mass-ratio hypothesis (Grime 1998).

The decrease in cattle density since this study was performed might influence the regeneration of certain tree species and, in turn, the future composition of the tree community. However, such a trend might be balanced by increasing aridity, which is expected to occur in the Mediterranean in the near future (Giorgi and Lionello 2008; van Der Molen et al. 2011). Certain offset mechanisms can be expected to occur in the community once a certain drought threshold is exceeded. As such, the increased regeneration caused by reduced cattle pressure may be balanced by the impending increase in arid conditions. Greater aridity would favour drought-sensitive species in the Mediterranean mountain forests, with drought-resistant species becoming dominant as a result (Mendoza et al. 2009). As a result, certain species that are common to the Mediterranean, yet not currently abundant in the Massane forest holly oak (*Quercus ilex*) and white oak (*Q. pubescens*), may become noticeably more abundant in the area.

Conclusion

This seven-year study demonstrated that the presence of semi-feral cattle can influence the seedling/sapling community dynamics and structure of a Mediterranean mountain forest under current climatic conditions. The presented research found that grazing by cattle affected tree regeneration in a taxon-dependent manner. As such, the current exclusion of semi-feral cattle and other ungulates from most Euro-Mediterranean mountains would threaten the conservation of such socio-ecosystems, which have developed as a result of centuries of complex land uses. If we are to identify sustainable models for how to manage Mediterranean forest socio-ecosystems, forest pastoralism and climate change should be considered at the regional level.

Nomenclature

Flora Europaea (Tutin et al. 1976).

Supplementary information

Supplementary information accompanies this paper at https://doi.org/10.1186/s40663-020-00222-7.

Additional file 1. Supplementary material S1: Location of the study area. **Supplementary material S2:** Mean seedling and sapling densities per 100 m^2 outside (Unf) and inside (Fen) cattle exclosures between 2006 and 2012. **Supplementary material S3:** Estimated differences in marginal means for (a) overall, (b) seedling and (c) sapling densities of each species with (Unf) and without the presence of semi-feral cattle (Fen). The corresponding post-hoc test results (estimate, standard error, *z*-ratio and *p*-value) are shown.

Abbreviations

GLMM: Generalised Linear Mixed-effect Model; RDA: Redundancy Analysis

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Legal statement

All of the research work reported in this study was performed in accordance with all relevant legislation and guidelines.

Authors' contributions

C.C. conceived the study. X.F., S.C. and C.C. monitored the plant materials. X.F. and S.C. carried out the statistical analyses. X.F. wrote the first draft of the manuscript. S. C and C.C. provided feedback and completed the manuscript.

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Availability of data and materials

The materials described in the manuscript - including all relevant raw data - will be freely available upon request from the corresponding author.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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