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Habitat protection and removal of encroaching shrubs support the recovery of biodiversity and ecosystem functioning

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Abstract

Livestock overgrazing causes environmental degradation, species invasion, biodiversity loss, and productivity decline, with profound consequences for ecological sustainability and human livelihoods. Habitat protection can mitigate such impacts, but we know little about how the long-term recovery of plant communities from livestock overgrazing depends on the presence of encroaching shrubs. Here, we explored how shrub encroachment mediates the effects of habitat protection (i.e., livestock exclusion and creation of UNESCO protected areas) on biodiversity recovery and ecosystem functioning (i.e., biomass productivity). We leveraged a long-term (15–25 years) experiment of livestock exclusion and complemented it with the removal of an encroaching shrub species in pasture areas and protected areas. We reveal that habitat protection has positive effects on patterns of recovery. Yet, the effects of habitat protection are mediated by shrub encroachment. Encroaching shrubs have net positive effects on plant diversity in pasture areas but inhibit biodiversity recovery in protected areas. The combination of habitat protection and the removal of encroaching shrubs best enhances the recovery of plant diversity and biomass productivity. A potential underlying mechanism is the shift in plant interactions from facilitation for recruitment and associated resistance to competition for water. Understanding species interactions is key to guiding conservation and restoration actions which can turn degraded ecosystems back into functional, species-rich communities.

KEYWORDS

biodiversity–ecosystem functioning, biological invasion, conservation actions, facilitation, indirect effects, land degradation, livestock overgrazing, plant communities, resilience

1 | INTRODUCTION

Exploitation of natural resources and changes in land use cause rapid land degradation and erosion of biodiversity (Isbell et al., 2017; Pimm et al., 2014; Vitousek et al., 1997). The current decline in biodiversity has profound implications for critical ecosystem functions (Dirzo et al., 2014; Pereira et al., 2010; Wright et al., 2017) and the sustainability of socio-ecological systems (Komatsu et al., 2019; Naeem et al., 2012). Halting biodiversity loss, protecting biological communities, and supporting ecosystem recovery are fundamental for human wellbeing (Bradshaw et al., 2021). Ecosystem recovery (i.e., resilience) is the ability to absorb and maintain stable relationships from change and disturbance (Holling, 1973). The recovery of functional, species-rich ecosystems from the impact of multiple stressors is poorly understood, even though this knowledge is key for ecological restoration (Genes & Dirzo, 2022).

A widespread driver of land degradation is livestock overgrazing (Sala et al., 2000). Although grassland biomes have been associated with native mammalian herbivores for millions of years, pastures have been created in prehistoric and recent times with livestock grazing (Wilkinson & Sherratt, 2016). In some cases, livestock can replace grazing by native herbivores (Hempson et al., 2017; Veblen et al., 2016) and support biodiversity in defaunated ecosystems (Dirzo et al., 2014; Price et al., 2022). Moderate density of livestock grazing may be beneficial for specialized grasses and herbs adapted to grazing that could not withstand competition with shrubs and trees (Lázaro et al., 2016; Petanidou & Ellis, 1993; Price et al., 2022; Wang et al., 2019). However, livestock grazing has increased in stocking density and extension of grazed areas during the last decades (Steinfeld et al., 2006). Current livestock practices are leading to land degradation, impairing the sustainability of pasture ecosystems in many parts of the world (Herrero & Thornton, 2013; Steinfeld et al., 2006).

Livestock overgrazing decreases biodiversity and productivity (Eldridge et al., 2016, 2017; Losapio et al., 2024; Pimm et al., 2014) by exposing ecosystems and biological communities to different stressors that persist for prolonged periods (Briske et al., 2005; Komatsu et al., 2019; Sala et al., 2000; Westoby et al., 1989). The threats to plant communities caused by livestock overgrazing include soil erosion, acidification, and nitrogen input (Evans et al., 2015; Lindenmayer et al., 2018), spread of novel invasive species, and encroachment of unpalatable plants (Filazzola et al., 2020; Sala et al., 2000; Walsh et al., 2016). The encroachment of unpalatable species which dominate degraded pastures is the classic symptom of livestock overgrazing (Eldridge et al., 2013). However, how those stressors interact—whether the effects of overgrazing and encroachment are additive, antagonistic, or synergistic—is still poorly understood.

Halting livestock overgrazing, when a feasible option, can limit desertification (Eldridge et al., 2016), increase biodiversity (Filazzola et al., 2020), and support ecosystem recovery (Lindenmayer et al., 2018). Nonetheless, the consequences of livestock exclusion are often nuanced, largely depending on broad-scale environmental drivers (e.g., biome and climate) but especially on the local context given by grazing history and the occurrence of unpalatable, encroaching species (Price et al., 2022). Likewise, removing encroaching species can provide multiple ecological benefits (Davis et al., 2019; Losapio et al., 2024). There is some evidence that encroaching, grazing-resistant species can promote animal biodiversity (Losapio et al., 2024) and plant biodiversity (Holzapfel et al., 2006; Segoli et al., 2012). These studies evidence that species interaction between livestock grazing and encroaching shrubs is key for biodiversity patterns and ecosystem recovery. However, predicting and anticipating the consequences of conservation actions is challenged by the interactions and potential synergistic impacts of overgrazing and encroachment. These relationships are frequently not considered in conservation programs (Genes & Dirzo, 2022), despite their importance for understanding the resilience of degraded lands. Improving our knowledge of the interactions between livestock exclusion and encroachment is key to devise specific recommendations for ecosystem management and for restoring functional, species-rich systems.

Three decades of biodiversity experiments indicate that more diverse ecosystems are more productive and may be more resilient to environmental perturbations through redundancy of functions carried out by different species (Naeem et al., 2012; Sala et al., 2000; Tilman et al., 2001). Biodiversity experiments also show that greater numbers of species within communities are associated with lower invasion success and higher functioning such as productivity (Isbell et al., 2017). This positive diversity–productivity (BEF) relationship has been reported across different systems and scales, from grasslands to forests and from microcosmos to regional landscapes (Wright et al., 2017). Such a positive BEF relationship can be accomplished, for instance, by acquiring more effectively a wider spectrum of resources or by defending against a broader spectrum of threats. However, our understanding of the ways in which habitat protection contributes to the ability of ecosystems to recover to positive BEF relationships after prolonged exposure to multiple anthropogenic stressors remains far from complete.

Here, we asked the following research questions: How do plant biodiversity and biomass respond to the combined effects of livestock exclusion and shrub encroachment? Do encroaching shrubs facilitate or inhibit plant community recovery following livestock exclusion? In this study, our goals were to (i) understand the recovery of plant communities and biomass productivity in response to long-term habitat protection and (ii) examine how the effects of habitat protection are mediated by shrub encroachment. Given that protected areas in which livestock has been excluded for decades are still in a degraded state, we hypothesize that livestock exclusion is not enough to support ecosystem recovery. We hypothesize that such a lack of recovery is due to interactions between herbaceous plants and encroaching shrubs. An improved understanding of these processes is necessary for managing, conserving, and restoring ecosystems.

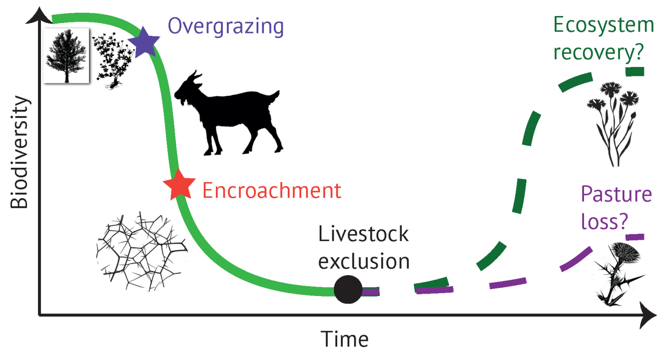

FIGURE 1 Livestock overgrazing causes loss of biodiversity and triggers encroachment of grazing-resistant species. Together, they decrease productivity and may lead to pasture loss. Habitat protection and livestock exclusion can halt biodiversity loss and support ecosystem recovery. However, the effects of livestock exclusion are difficult to anticipate due to multiple interacting stressors that influence ecosystem recovery.

FIGURE 2 View of pasture areas and adjacent protected areas, separated by a fence, encroached by *Sarcopoterium spinosum* (the grayish shrub).

2 | METHODS

2.1 | Study system

The study was conducted on Lesvos Island, Greece. The original (potential) vegetation is Mediterranean woodlands and forests within grassland–forest mosaics. Here, as in many other areas of the Mediterranean Basin, livestock overgrazing with sheep increased desertification (Arianoutsou-Faraggitaki, 1985; Iosifides & Politidis, 2006; Seligman & Henkin, 2002), reduced diversity and productivity by substituting Mediterranean scrublands and woodlands with pastures composed mainly of annual herbaceous species (Arianoutsou-Faraggitaki, 1985; Bazos, 2005) Table S1).

On Lesvos Island, livestock overgrazing enhanced the spread and dominance of "prickly burnet" (*Sarcopoterium spinosum* (L.) Spach, Rosaceae). This is an unpalatable dwarf shrub that is avoided by livestock thanks to its thorny, dense canopy overgrazing (Perevolotsky et al., 2001; Seligman & Henkin, 2002). *S. spinosum* is native to the Southeast Mediterranean and Middle East (Mohammad & Alseekh, 2013; Seligman & Henkin, 2002). Its dominance is facilitated by livestock, while its germination and resprouting are facilitated by prescribed fire (Perevolotsky et al., 2001; Seligman & Henkin, 2002). Shrub encroachment has made many pastures nearly unusable on Lesvos Island, causing severe problems for the local human population that relies heavily on livestock grazing for their food production and livelihood (Iosifides & Politidis, 2006).

Given the status of land degradation, UNESCO protected areas (Lesvos Petrified Forest Parks in Sigri and Plaka; Figure S1) were created in 1994 and 2002 to protect ecosystems as well as to enhance the sustainability of Lesvos socio-economic systems (Zouros, 2010; see also https://whc.unesco.org/en/tentativelists/5858/ for more information on these protected areas). The establishment of these protected areas led to the exclusion of livestock (Figure 1 and Figures S2). Nevertheless, these protected areas are still in a degraded state as *S. spinosum* continues to dominate the plant community as of 2018 (Figure 2 and Figure S3). To the best of our knowledge, those areas have been grazed with sheep for centuries, but we do not have information on when exactly overgrazing began.

2.2 | Field experiment

The establishment of these two protected areas created a long-term (i.e., 15–25 years), large-scale field experiment. Here, livestock grazing was excluded on 15 ha of pasture lands, while livestock overgrazing continued on adjacent lands that were otherwise similar (Figure 2 and Figure S2). This system allows us to address the effects of habitat protection as well as the recovery of biodiversity and ecosystem functioning after halting livestock overgrazing. Communities inside protected areas are considered as "under recovery" as they should be recovering from overgrazing following long-term livestock exclusion. In addition to taking advantage of this experiment at the landscape scale, we implemented local short-term (i.e., one growing season) livestock exclusion in pasture lands. The exclusion of livestock in current pasture lands allowed us to assess the short-term recovery of biodiversity and account for the direct effects of livestock on biomass productivity.

To assess the recovery of plant communities once livestock overgrazing ceased, we have chosen two contiguous areas differing only in land-use management: (1) pasture areas where livestock grazing was still occurring at the time of our study (i.e., 2018), henceforth "livestock grazing in pasture areas"; (2) protected areas where livestock has been excluded for decades, henceforth "livestock exclusion in protected areas"; and (3) pasture areas where livestock was excluded, henceforth "livestock exclusion in pasture." We will refer to these treatment designations as land management.

To test whether and how shrub encroachment mediates the effects of livestock exclusion on patterns of recovery of plant biodiversity and biomass, we coupled land management treatments with a removal experiment. We removed the encroaching shrubs of *S. spinosum* at the local scale by clipping the canopy. We refer to this factor as "removed" for the encroachment treatment. We carefully avoided disturbing the community when clipping the shrubs so as not to disturb the soil or trample the plot. Then, we also considered communities where the encroaching species was absent or where it was present. Thus, encroachment treatments are (1) absent, (2) present, and (3) removed.

We adopted a variant of a randomized complete block design with a sub-plot restriction on randomization (Figure 2). Land management types (livestock grazing in pasture, livestock exclusion in pasture, and livestock exclusion in protected areas) were the main-plot treatments. Shrub encroachment manipulation (absent, present, and removed) were the sub-plot treatments implemented in each main plot (Figure 2).

For livestock exclusion in pasture, we installed 5×5 m fences (1.5 m height) within pastures in randomly selected main plots (Figure S3). For livestock exclusion in protected areas, we took advantage of the already installed fence system. For livestock grazing in pasture, we took no action and agreed with shepherds to continue livestock grazing as usual. Eight fences were randomly established on pasture lands at the Sigri Park site and four at the Plaka Park site. Adjacent to each fence, we selected and marked with strings 5×5 m plots in randomly defined positions 3 m from fences. Inside protected areas, we randomly selected 5×5 m plots and marked them with strings. This resulted in 36 (5×5 m) main plots in total. The sub-plots were 1×1 m quadrats marked with strings. We selected prickly burnet individuals of ca. 1 m of canopy diameter to control for shrub age and to fit the sub-plots within main plots. In total, we installed $n = 36$ main plots for land management treatments and $n = 108$ sub-plots for encroachment treatments.

The experiment was installed at the start of the vegetative season (February 2018) and lasted for the whole growing season, which in this Mediterranean ecosystem goes from mid-February to mid-May. Although the removal treatment lasted for one growing season, the time frame and length of the experiment match the growth form of the annual plant species that characterize this vegetation (Bazos, 2005). We surveyed the composition and richness of plant species within each sub-plot and estimated the visual plant species cover (April 2018). Visual estimates of plant cover were conducted by a single observer dividing virtually the 1 m^2 quadrat into four parts, then estimating visually the relative cover in each quarter (approximation of 10%) prior to summing them up. Plant species nomenclature follows Bazos (2005). Finally, we measured the productivity of the plant communities by harvesting the aboveground biomass of each plot at the end of the season (May 2018). The entire 1×1 m sub-plot was harvested, except for the *S. spinosum* canopy. Harvested material was dried for 72 h at 70°C prior to measuring plant biomass. We looked at aboveground biomass productivity (g m^{-2} $year^{-1}$) given by annual herbaceous communities, as this measure is a widely used proxy of ecosystem functioning (Isbell et al., 2017; Tilman et al., 2001).

2.3 | Data analysis

After assessing the robustness of our biodiversity sampling via the species accumulation curve (Figure S4), we focused on the levels of biodiversity: alpha (α) diversity and beta (β) diversity.

First, we quantified biodiversity within communities, that is, α-diversity at the local, community scale. We compared α-diversity for each encroachment treatment among different land management treatment. For each sub-plot, we calculated α-diversity by means of the Shannon index. We used the Shannon diversity index as $H = -\sum_{i=1}^{S} p_i \ln p_i$, where p is the relative cover of plant species i occurring in the community with S species. This index accounts for both abundance and evenness of plant species. It was computed using the *diversity* function of the *vegan* R package (Oksanen et al., 2019). The influence of treatments on plant α-diversity were tested by means of linear mixed-effects models, using the *lmer* function of *lme4* R package (Bates et al., 2015). In this model, the response variable was α-diversity; land management treatment (factor with three levels, livestock grazing in pasture as reference level), encroachment treatment (factor with three levels, absent as reference level), and their statistical interaction were fixed effects; site (Plaka or Sigri) and main-plot id nested within site were considered as a random effect. The significance of treatments was assessed with a Wald chi-square test using the *Anova* function of *car* R package (Fox & Weisberg, 2018). Model parameters and p-values were estimated with restricted maximum likelihood using the *summary* function of the *lmerTest* R package (Kuznetsova et al., 2017). Contrasts between combinations of treatment levels were computed with least-squares mean estimation, using the *emmeans* function of the *emmeans* R package (Lenth, 2019).

Second, we considered biodiversity between communities, that is, plant β-diversity. This diversity measurement refers to the dissimilarity (heterogeneity) in species composition among communities. This diversity index indicates how many different and unique species there are between each pair of sub-plots. We used the Sørensen dissimilarity index (Koleff et al., 2003) as $\beta = 2a/(2a+b+c)$, where a is the number of shared plant species between two sub-plots, while b and c are the numbers of plant species unique to each sub-plot. It ranges between 0 and 1, with values close to 1 indicating low dissimilarity (i.e., high homogeneity) and values close to 0 indicating high dissimilarity (i.e., high heterogeneity) in terms of plant species composition. We quantified β-diversity between each pair of sub-plots across main-plots for each unique combination of land management treatment and species removal treatment. This resulted in $n = 3 \times 3 = 9$ matrices, each one containing $n = 12!/(2!(12-2)!) = 66$ pairwise dissimilarity values between sub-plots pairs under the same encroachment treatment across different land management treatments. It was computed using the *vegdist* function of the *vegan* R package (Oksanen et al., 2019). We then tested how β-diversity changed with shrub encroachment and land management using linear mixed-effects model (*lmer* function of *lme4* R package; Bates et al., 2015). We fitted β-diversity as response variable and land management treatment (factor with three levels, livestock grazing in pasture as reference level), invasive species treatment (factor with three levels, absent as reference level), and their statistical interactions as fixed effects; site was considered as random effect. The significance of treatments was assessed with a Wald test using the *Anova* function of *car* R package (Fox & Weisberg, 2018). Model parameters and p-values were estimated with restricted maximum likelihood (*summary* function of the *lmerTest* R package; Kuznetsova et al., 2017). Contrasts between combinations of treatment levels were computed with least-squares mean estimation, using the *emmeans* function of the *emmeans* R package (Lenth, 2019).

Finally, to understand the recovery of ecosystem functioning, we analyzed the response of aboveground biomass productivity to different land management treatments and encroachment treatments. Furthermore, we analyzed how the diversity–productivity relationship between plant species richness (α-diversity) and biomass productivity changed across treatments. We did so by fitting a single linear mixed-effects model with biomass productivity as the response; land management treatment (factor with three levels, livestock grazing in pasture as a reference level), invasive species treatment (factor with three levels, absent as a reference level), biodiversity (plant α-diversity), and their statistical interactions as fixed effects; main-plot id as a random effect. The significance of treatments was assessed with Wald test; model parameters and p-values were estimated with restricted maximum likelihood; contrasts and linear trends resulting from BEF relationship were computed with marginal mean estimation using the *emtrends* function of the *emmeans* R package (Lenth, 2019). Data analysis was performed in R ver. 4.1.3 (R Core Team, 2018).

3 | RESULTS

3.1 | Effects of habitat protection on biodiversity recovery

First, we addressed the effects of land management treatments, shrub encroachment treatments, and their interactions on plant α-diversity (Figure 3; Table S2). Plant α-diversity changed among land management treatments (variance explained $p = .006$, $F_2 = 10.30$). Livestock exclusion in both pasture areas and protected areas increased plant α-diversity by 5% and 13%, respectively (estimate = 0.442 ± 0.146 SE, $p = .003$; estimate = 0.569 ± 0.146 SE, $p < .001$; respectively).

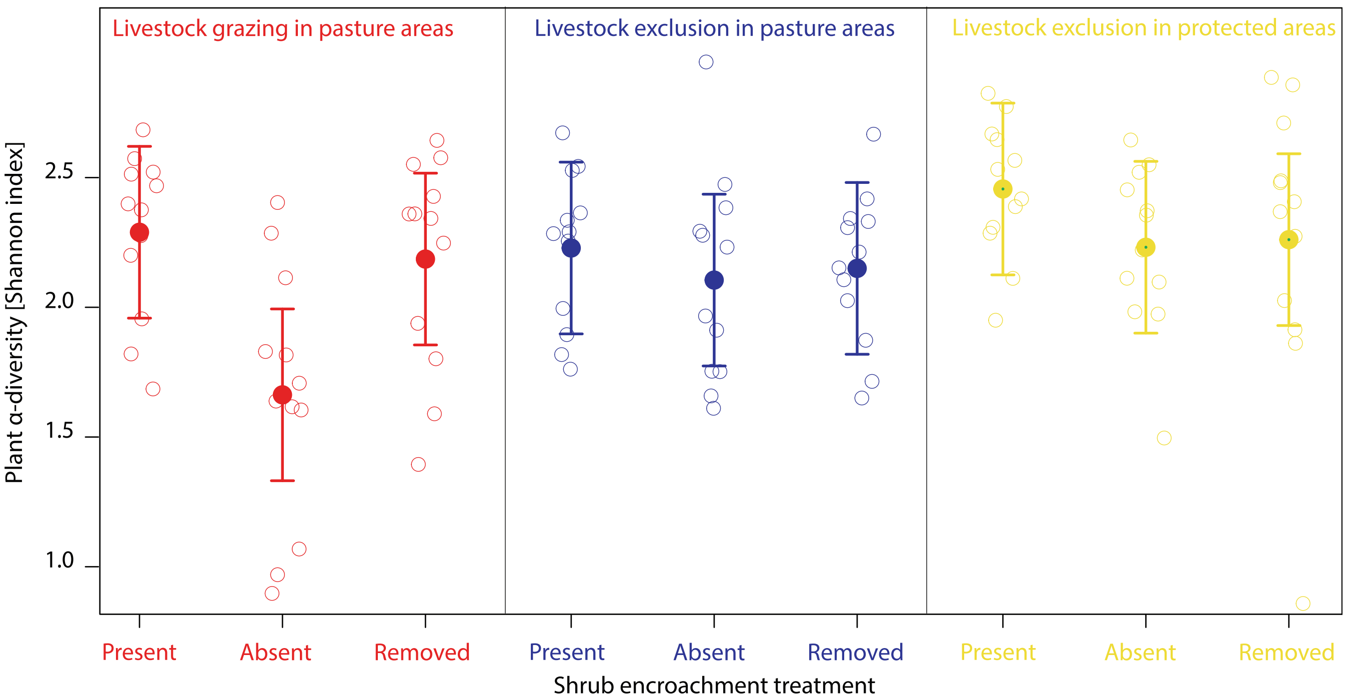

FIGURE 3 Effects of land management (livestock grazing in pasture areas, livestock exclusion in pasture areas, and livestock exclusion in protected areas) and shrub encroachment (present, absent, and removed) treatments on plant α-diversity (Shannon index). We report predicted marginal means with 95% CI.

Shrub encroachment affected plant α-diversity (variance explained $p < .001$, $F_2 = 15.05$). Plant α-diversity was 16% higher in the presence of encroaching shrubs (estimate $= 0.627 \pm 0.144$ SE, $p < .001$) and 10% higher after shrub removal (estimate $= 0.523 \pm 0.144$ SE, $p < .001$).

Yet, the effects of livestock exclusion changed depending on shrub encroachment (interaction term variance explained $p = .048$, $F_4 = 0.56$). The presence of encroaching shrubs or their removal had positive effects in pasture areas (contrast $= 0.63 \pm 0.15$ SE, $p = .002$; contrast $= 0.52 \pm 0.15$ SE, $p = .016$; respectively), whereas shrub encroachment or removal had no effects inside protected areas (contrast $= 0.22 \pm 0.15$ SE, $p = .836$; contrast $= -0.20 \pm 0.15$ SE, $p = .918$; respectively). Furthermore, plant diversity increased by 34% inside protected areas only in the absence of encroaching shrubs but not in their presence (contrast $= 0.57 \pm 0.15$ SE, $p = .006$; contrast $= 0.17 \pm 0.15$ SE, $p = .966$).

Second, we addressed how plant β-diversity changed with land management and species invasion (Figure 4; Table S3). Land management treatments had no effects per se on plant β-diversity (variance explained $p = .287$, $F_2 = 2.49$). On the contrary, shrub encroachment had significant effects on plant β-diversity (single term variance explained $p < .001$, $F_2 = 42.06$) depending on land management treatments (interaction term variance explained $p = .004$, $F_4 = 15.46$). While the removal of encroaching shrubs increased plant β-diversity by 11% overall (estimate $= 0.054 \pm 0.018$ SE, $p = .016$), the effects of removal where larger in protected areas than pastures as plant β-diversity increased by 21% (estimate $= 0.056 \pm 0.026$ SE, $p = .031$).

3.2 | Consequences for ecosystem functioning

We considered biomass productivity as indicator of ecosystem functioning and addressed how it changed with land management and shrub encroachment treatments (Figure 5; Table S4). Productivity recovered inside parks as livestock exclusion in protected areas increased biomass productivity by 21% on average (estimate $= 49.69 \pm 12.94$, $p < .001$), whereas livestock exclusion did not change productivity in pasture areas (Table S5). This indicates that ecosystem functioning recovered inside protected areas only. In contrast, as productivity was similar between pastures and exclosures, productivity was independent of biomass removal by livestock or their short-term exclusion (one growing season).

Furthermore, shrub encroachment decreased productivity by 28% on average (estimate $= 27.69 \pm 13.29$, $p = .040$), while removal marginally increased by 19%

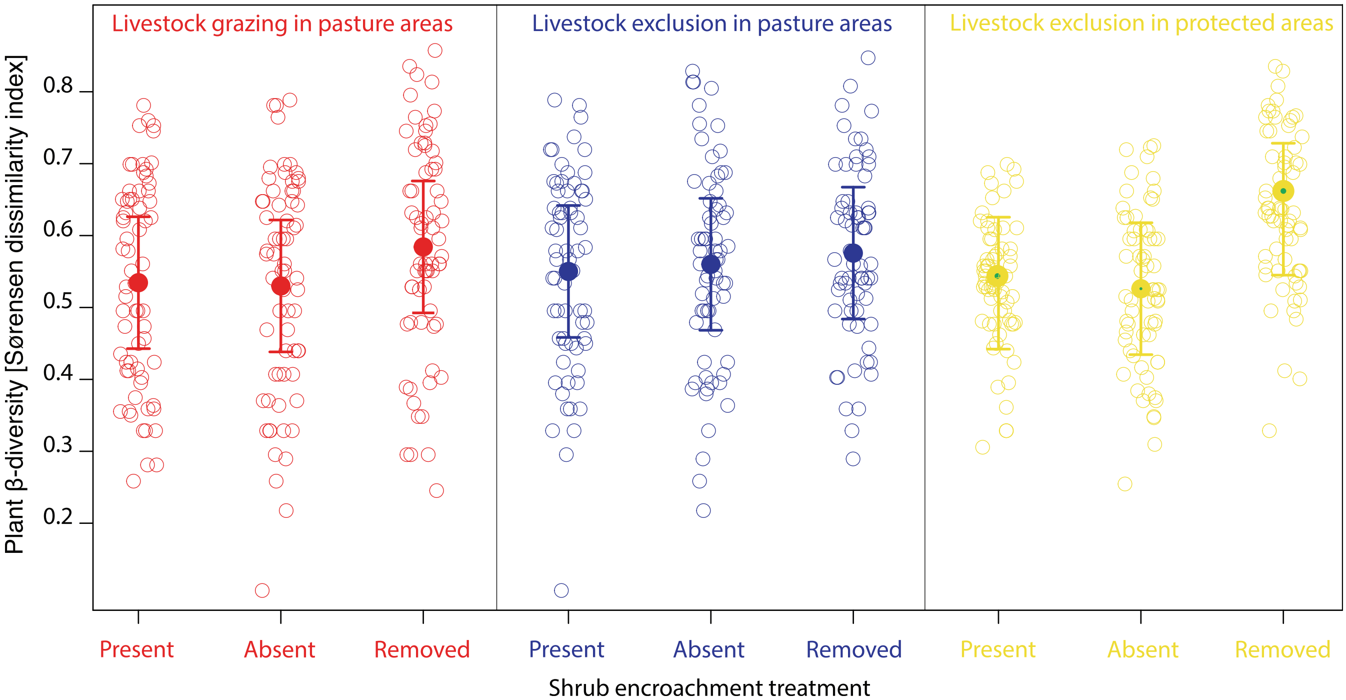

FIGURE 4 Effects of land management (livestock grazing in pasture areas, livestock exclusion in pasture areas, and livestock exclusion in protected areas) and shrub encroachment (present, absent, and removed) treatments on plant β-diversity (Sørensen dissimilarity index). We report predicted marginal means with 95% CI.

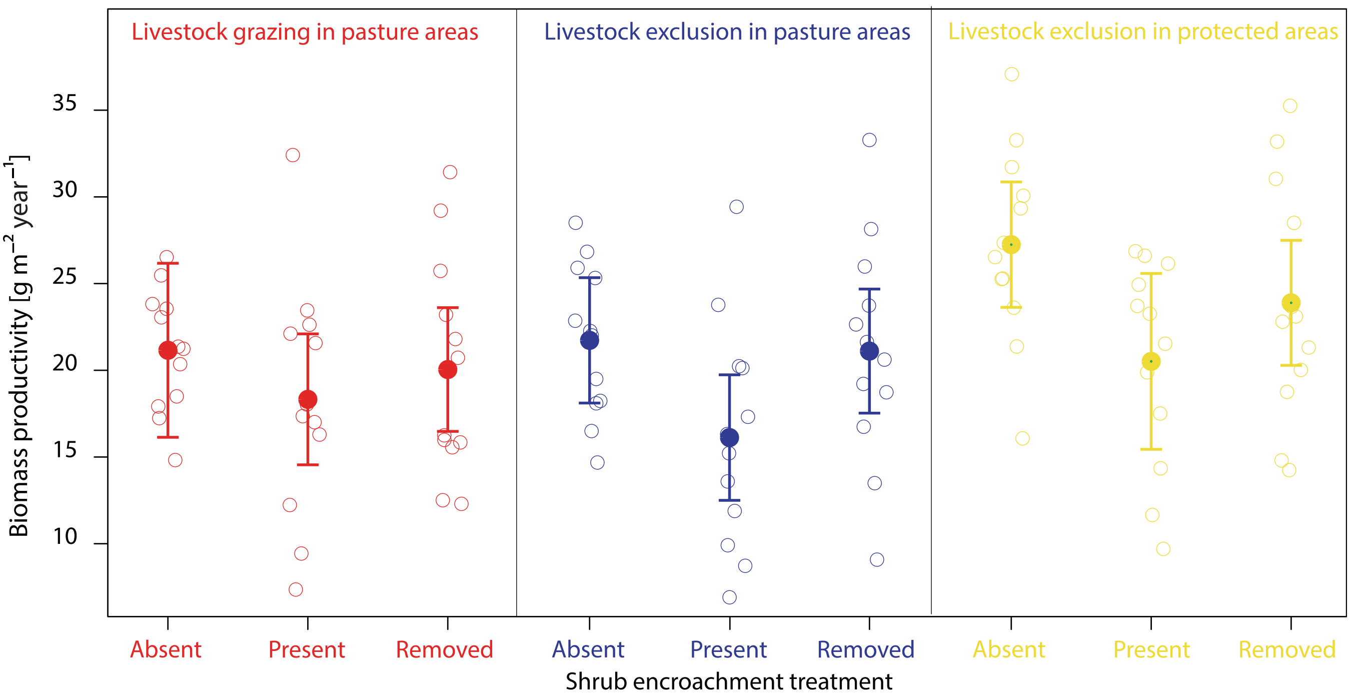

FIGURE 5 Effects of shrub encroachment treatment on biomass productivity across land management treatments. Dots represent estimated marginal means with 95% CI.

(estimate $= 18.34 \pm 10.66$, $p = .089$). No statistical interaction was observed between land management treatments and encroachment treatments for plant productivity ($p = .694$, $F_4 = 2.23$; Table S5).

Finally, we addressed the BEF relationship looking at how biomass productivity changed in relation to plant diversity (Figure 6; Table S6). On average, biomass productivity increased with increasing plant α-diversity

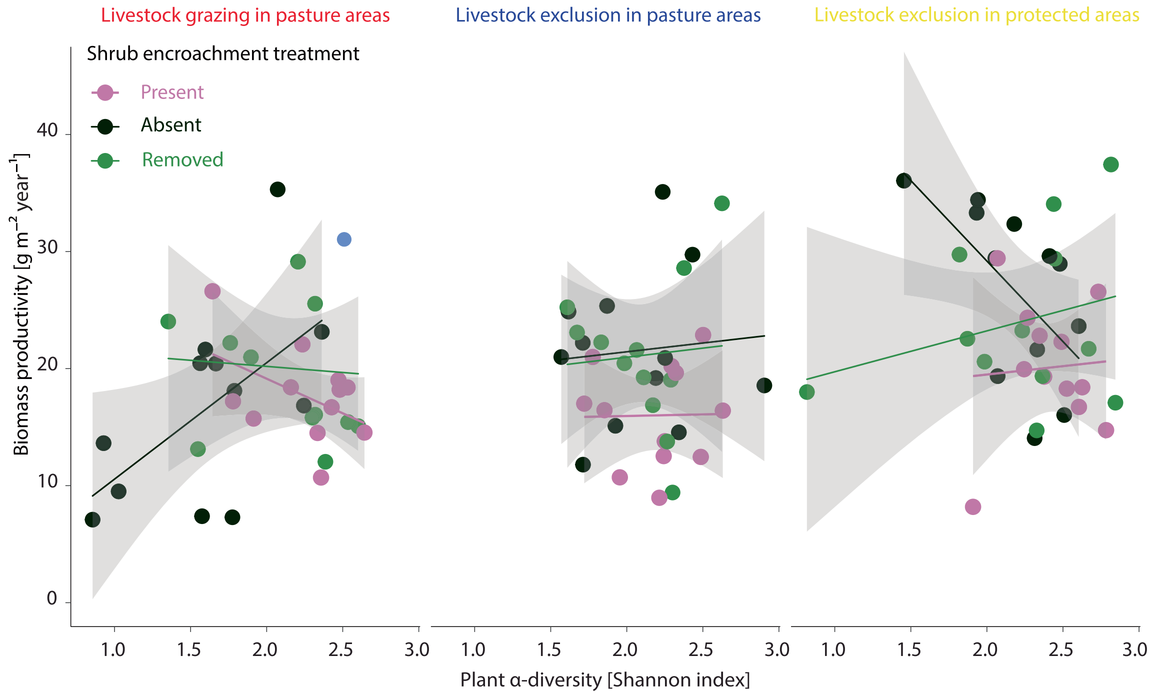

FIGURE 6 Biodiversity–ecosystem functioning relationship (plant α-diversity and biomass productivity) across land management treatments (livestock grazing in pasture, livestock exclusion in pasture, and livestock exclusion in protected areas) and shrub encroachment treatments (present, absent, and removed) treatments. Lines represent estimated marginal trends with 95% CI.

(estimate $= 8.63 \pm 3.47$, $p = .015$). Yet, the strength and direction of the BEF relationship changed from positive to negative with land management treatments and shrub encroachment (estimate $= 22.09 \pm 8.04$, $p = .007$). Specifically, the BEF relationship was negative either inside protected areas (estimate $= -20.44 \pm 6.27$, $p = .002$) or in the presence of encroaching shrubs (estimate $= -14.31 \pm 6.26$, $p = .025$), while it was positive in pasture areas and in the absence of encroaching shrubs (Table S6).

4 | DISCUSSION

We addressed the poorly understood effects of habitat protection on the recovery of plant community diversity and productivity from livestock overgrazing, which are mediated by shrub encroachment. We found that shrub encroachment mediates the effects of livestock exclusion on the recovery of plant communities. Local diversity, heterogeneity, and biomass productivity increased with the removal of encroaching shrubs and livestock exclusion. Looking at the relationship between plant diversity and biomass productivity, we found that this BEF relationship changed across treatments. Taken together, our results indicate that the combination of habitat protection and encroachment mitigation best supports the recovery of biodiversity and ecosystem functioning.

By reducing livestock pressure, habitat protection can prevent further ecosystem degradation and desertification (Arianoutsou-Faraggitaki, 1985; Eldridge et al., 2016; Filazzola et al., 2020). As observed in our study system, livestock overgrazing erodes biodiversity by favoring only grazing-resistant species that dominate the community and ultimately limit communities' ability to recover. Our results also indicate that livestock overgrazing and shrub encroachment tend to homogenize plant communities. Taken together, our findings highlight the potential for prolonged exposure to multiple anthropogenic stressors to cause major impoverishment of biological communities. Such biodiversity decline alters ecosystem functioning as well as compromise conservation efforts in support of ecosystem restoration. Habitat protection combined with the removal of encroaching shrubs proved to be effective for supporting ecological resilience.

We documented that shrub encroachment had net positive effects on plant diversity in pasture areas but net negative effects in protected areas. Therefore, knowledge of the ecological context and interactions between species is key to successful biodiversity conservation programs. Our findings also highlight the potential for shrub encroachment to reverse the positive effects of habitat protection. Yet, shrub encroachment may in the first instance prevent further ecosystem degradation and desertification by indirectly reducing grazing pressure (Callaway et al., 2005; Segoli et al., 2008).

The mechanisms associated with net positive effects are improving soil conditions, such as soil humidity and organic matter content, and providing unique microhabitat and shelter against livestock for herbaceous plant species that better germinate and grow beneath *S. spinosum* thorny, protective canopy (Holzapfel et al., 2006; Segoli et al., 2012). Such facilitative interactions are common in pasture ecosystems (Callaway, 2007), which are frequently invaded or encroached by single, highly resistant species when overgrazed (Callaway et al., 2005; Wilkinson & Sherratt, 2016). A possible underlying mechanism is related to the shift in the balance of facilitation and competition between shrub species and associated plants (Callaway et al., 2005; Holzapfel et al., 2006; Losapio et al., 2021; Segoli et al., 2012). Consistently, the resilience of plant communities was probably limited by competitive effects once overgrazing disturbance ceased.

Although biodiversity increased in protected areas, the persistence of degraded state and lack of transition to another state is probably due to deforestation. Indeed, as the encroaching species examined here does not grow below tree canopy (Seligman & Henkin, 2002), the eradication of tree species from the landscape is a further factor favoring shrub encroachment and precluding woodland recovery. We suggest that restoration practices that include native tree regeneration would help suppress shrub encroachment (Seligman & Henkin, 2002), recover biodiversity (Aronson et al., 1993; Chazdon & Brancalion, 2019; Hall et al., 2011), and re-establish a positive BEF relationship (Isbell et al., 2017). Major efforts to facilitate not only passive tree dispersal but also active reintroduction and assisted establishment are clearly warranted.

Contrary to previous claims regarding the positive effects of livestock grazing on biodiversity (Petanidou & Ellis, 1993; Wang et al., 2019) but consistent with current evidence on the impact of such land-use practice (Eldridge et al., 2013, 2016; Evans et al., 2015; Losapio et al., 2024), our experiment documented detrimental impacts of overgrazing on plant communities and ecosystem functioning. We foresee that effective conservation and management measures to improve ecosystem resilience in this and similar systems will need to include both the reduction of grazing pressure and the removal of encroaching species. Outside protected areas, this measure would likely also enhance the resilience and productivity of pastures since a drastic reduction in livestock overgrazing is needed to halt and reverse the process of desertification and support productivity recovery. These implications are possibly generalizable to other local and landscape scales in Mediterranean systems or otherwise grazed systems in different climates such as in temperate zones. Our recommendations need to be framed considering the regional socio-ecological context and evaluated locally. For instance, different results may emerge in naturally treeless systems.

In conclusion, species interactions between livestock and encroaching shrubs drive the recovery of plant communities and ecosystem functioning. These interactive stressors have long-term detrimental effects. Multiple targeted interventions are needed to recover desirable levels of biodiversity, re-establish positive BEF relationships, and ultimately improve human livelihoods. Proactive conservation actions are key to revert the mechanism by which encroachment of livestock-resistant species impacts biodiversity recovery. We suggest that protection along with active removal and woodland restoration would better support ecosystem resilience.

POSITION STATEMENT

We conducted thorough literature research. We made use of conservationevidence.com.

AUTHOR CONTRIBUTIONS

G.L., C.M.D.M., T.T., and M.C.M. conceived the study. G.L., C.M.D.M., T.T., N.Z., and M.C.M designed the research. G.L. performed research, analyzed data, and wrote the article. C.M.D.M., R.D and M.C.M contributed to discussing results and edited the manuscript. All authors contributed to the interpretation of results and provided input on the article.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data collected for this study have been deposited on the ETH Research Collection server at https://doi.org/10.3929/ethz-b-000309353 and https://doi.org/10.3929/ethz-b-000311948. The R script to reproduce the analyses and figures is freely accessible on GitHub at https://github.com/losapio/Conservation-Science-and-Practice.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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