



## The effects of shrub encroachment on arthropod communities depend on grazing history

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### ABSTRACT

Unsustainable grazing is a major driver of biodiversity loss worldwide. Conservation actions such as grazing exclusion are effective strategies for halting such decline. However, we still know little how the long-term impact of grazing exclusion depends on plant–animal interactions such as those between encroaching unpalatable shrubs and ground arthropods. Here, we assessed how encroaching, unpalatable shrub species (*Sarcopoterium spinosum*) mediates the effects of grazing exclusion on the recovery of arthropod communities. We used a large-scale, long-term (15–25 years) grazing exclusion experiment complemented with local-scale treatments that consider the presence or absence of shrubs. We found that halting overgrazing supported the recovery of biodiversity in the long-term. Notably, the impacts of shrubs on arthropod diversity vary with grazing history. Shrubs decreased arthropod abundance by three folds, affecting particularly flies, butterflies, hymenopteran, and beetles in protected areas. Yet, shrubs had positive effects on animal diversity, particularly centipedes and millipedes in grazed areas. On the one hand, shrubs may enhance biodiversity recovery in overgrazed systems; on the other hand, shrubs may be detrimental in protected areas, in the absence of grazing. Understanding how plant–animal interactions vary with historical land-use change is key for biodiversity conservation and recovery and for integrated management of agroecosystems.

### 1. Introduction

Exploitation of the environment is causing rapid changes in Earth's ecosystems (Sala et al., 2000; Naeem et al., 2012), leading to defaunation and unprecedented biodiversity loss (Dirzo et al., 2014; Pimm et al., 2014; Ceballos et al., 2015). Disturbance, livestock overgrazing, and related species invasion are altering the structure and functioning of biodiversity (Vazquez and Simberloff, 2003; Tylianakis et al., 2007). These drivers pose a threat to key plant and animal communities that are essential for human livelihood and economies (Potts et al., 2016; Isbell et al., 2017). To address such challenges, it is crucial to understand how animal communities respond to and recover from the combined impact of multiple stressors over time.

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In the Mediterranean Basin, the widespread conversion of woodlands into pastures and unsustainable livestock management (e.g., overgrazing) have led to land degradation (Arianoutsou-Faraggitaki, 1985; Hobbs et al., 1995; Reynolds et al., 2007). The reduction in natural habitats is a major driver of defaunation and erosion of biodiversity (Dirzo et al., 2014; Losapio et al., 2020; Sala et al., 2000; Underwood et al., 2009). Furthermore, livestock overgrazing reduces pasture and animal productivity due to land degradation, soil erosion, nutrient depletion, and ecological invasion (Kairis et al., 2015; Lindenmayer et al., 2018). Conservation actions such as grazing exclusion may limit the decline of biodiversity and support the recovery of ecosystem functioning (Sala et al., 2000; Dirzo et al., 2014; Young et al., 2016; Losapio et al., 2020). However, evidence supporting the positive role of grazing exclusion for biodiversity recovery in the long-term remains scattered.

A classic problem of unsustainable livestock grazing is the elimination of forage plants and their substitution with thorny and unpalatable species (Crawley, 1997; McNaughton, 1993; Wilkinson and Sherratt, 2016). The encroachment of unpalatable species, such as *Sarcopoterium spinosum*, which dominate pastures is the classic symptom of livestock overgrazing (Eldridge et al., 2013). As a matter of facts, shrub encroachment is the consequences rather than the cause of land degradation due to unsustainable practices. Yet, we have poor knowledge of how interactions between unpalatable, encroaching shrubs and arthropods may change with grazing history. Understanding how grazing history mediates plant–arthropod interactions and the recovery of arthropod communities is key to informing decision-making to manage and restore ecosystems, particularly in human-dominated, degraded and defaunated lands.

In this study, we examine how the recovery of arthropod communities after long-term grazing exclusion is influenced by encroaching, unpalatable shrubs. We aim to answer the following research questions: (i) How do grazing history and shrub encroachment jointly shape arthropod diversity? (ii) How does the recovery of arthropod communities from livestock overgrazing depend on encroaching unpalatable shrubs? (iii) Do different groups of arthropods respond differently to grazing exclusion and unpalatable shrubs? We hypothesize that grazing exclusion supports the recovery of animal diversity while shrub encroachment hinders it.

## 2. Materials and methods

### 2.1. Study site

Our study was conducted in Mediterranean-type ecosystems on Lesvos Island, Greece. Increasing overgrazing and consequent encroachment of unpalatable shrubs have dramatically changed the structure and composition of the landscape (Arianoutsou-Faraggitaki, 1985; Iosifides and Politidis, 2006; Kizos and Vakoufaris, 2012), pushing lands towards irreversible degradation (Arianoutsou-Faraggitaki, 1985; Kizos et al., 2013; Mohammad and Alseekh, 2013; Kairis et al., 2015). In the western part of Lesvos, where this study was carried out, herds (sheep and goat) range from 30 to 300 on average according to self-reporting interviews (Iosifides and Politidis, 2006). In this area, livestock size accounts more than 230,000 animals, c 13.5 livestock units per hectare, which is more than six times the sustainable levels of carrying capacity (Kizos et al., 2013).

Heavily degraded pastures are encroached by the unpalatable prickly burnet (*Sarcopoterium spinosum* (L.) Spach; Rosaceae). This species, native to the Eastern Mediterranean and Western Asia (Mohammad and Alseekh, 2013), is an unpalatable dwarf shrub that is highly resistant to grazing due to its thorny dense canopy and is facilitated by livestock overgrazing and fire practices (Seligman and Henkin, 2002).

The work was carried out at two protected-areas sites (UNESCO Lesvos Geoparks of Plaka and Sigri, Greece; for more information, visit <https://whc.unesco.org/en/tentativelists/5858/>). The creation of protected areas in 1994 and 2002 was an attempt to remove livestock and enhance recovery of these agroecosystems. These sites were chosen as they host a unique long-term field experiment where livestock has been excluded for 15–25 years surrounded by ongoing livestock overgrazing.

Protected areas that were previously grazed are still in a degraded state as the grazing-resistant species keeps dominating in comparable density and cover in both protected areas and pasture (Fig. 1). Notably, there was no tree growth since the establishment of the protected area 25 years ago (Losapio et al., 2020). This is the case as land is extremely degraded and vegetation has reached a state characterized by the dominance of this thorny, unpalatable species (Arianoutsou-Faraggitaki, 1985; Kizos et al., 2013). For example,



**Fig. 1.** Summary of the study design. On the left, areas where grazing has been excluded for c 20 years and adjacent overgrazed pasture areas. Shrub encroachment is evident in both areas. In the center, fence for short-term grazing exclusion (recently ungrazed treatment). On the right, the unpalatable shrubs (*Sarcopoterium spinosum*) and surrounding “open” areas with a pitfall trap.

(Losapio et al., 2020) showed that plant diversity is higher inside protected areas than in pasture, but the effects of livestock exclusion on plant diversity and plant productivity are mediated by shrubs. In particular, they showed that *S. spinosum* has net positive effects on plant diversity in pasture areas but inhibits plant diversity recovery after livestock exclusion in protected areas. Plant communities have a higher degree of heterogeneity inside protected areas than in pasture (Losapio et al., 2020).

## 2.2. Field experiment

This research entails a local-scale treatment replicated over a large-scale field experiment at these two sites. We addressed the local-scale effects of shrub encroachment by comparing animal communities below the canopy of unpalatable plants with surrounding open areas (Fig. 1). This treatment followed a split plot design in which the unpalatable shrub species was either present or absent. We randomly selected plants of *S. spinosum* (c 1 m diameter size each) and adjacent areas devoid of this species at a random direction with 1 m distance from each other (Fig. 1).

This local-scale treatment was replicated across three land management types: pasture, enclosure, protected areas. Areas where overgrazing is ongoing in pasture were randomly selected adjacent (c 20–100 m) to protected areas. In addition, the field experiment also entails the short-term, localized exclusion of grazing by means of livestock enclosures (Losapio et al., 2020). Enclosure fences of 5 m x 5 m were randomly installed in pasture (grazed) areas using metal poles and fences before the beginning of the growing season (February 2018). Twelve enclosures were installed at c 20–100 m from protected areas fences, eight in Sigri Park and four in Plaka park. Although this sampling design was replicated over two sites only, pasture and protected areas have the same geological, climatic, biogeographic, and historical characteristics. We are therefore confident that the main difference between pasture and protected areas is the livestock exclusion factor initiated in 1994. Yet, it may be possible that some overlooked factor is covarying with livestock exclusion between pasture and protected areas. However, the design for sampling animal biodiversity included replication at the level of local-scale treatment, which makes it robust against pseudo replication.

Pitfall traps were installed below the canopy (ground level) and outside the canopy of *S. spinosum*. Pitfall traps consisted of plastic cups (250 ml, 8 cm diameter, 10.4 cm height,  $n = 288$ ) filled with water diluted with vinegar and in later rounds with ethylene glycol. Pitfall trapping measures the density of ground-dwelling arthropods, but can also attract flying insects (Torma et al., 2023). Specimens of flying insects were considered in the analysis too as they may anyhow provide good information on biodiversity.

Split-plots were replicated twelve times over the three land management types (i.e., pasture, enclosure, and protected habitat) in the two different protected area sites, for a total of  $n = 2 \times 3 \times 12 = 72$  traps. Traps were emptied every c two weeks from the beginning until the end of the Mediterranean growing season (March 2018–May 2018), resulting in four-times samples. In total, we examined  $n = 72 \times 4 = 288$  traps. Unfortunately, we lost 8 traps (i.e., 2.8%), which left us with a total of  $n = 280$  replicates. All arthropods collected in the traps were counted and identified to order level. Nomenclature for insects follows Chinery (2004). In total, we sampled and identified 53,299 arthropod specimens belonging to 23 orders. For this reason, we focused our analysis on abundance data and order level.

## 2.3. Data analysis

Statistical analysis was conducted in R, version 4.1.3 (R Core Team, 2022).

We assessed whether shrubs provide habitat for ground active invertebrates and how such effects differ with levels of grazing. We used mixed-effects models to test the effects of shrubs (categorical variable with two levels: present as treatment or absent as reference level), grazing history (categorical variable with three levels: currently grazed as reference, recently ungrazed and long-term ungrazed as treatment levels), and their statistical interaction on the overall abundance and diversity of arthropods (response variables; two separate models). Plots within sites over time were considered as random effects.

For arthropod abundance, measured as number of collected specimens, we used generalized linear mixed-effects models with a negative binomial distribution to account for data overdispersion (Brooks et al., 2017). For arthropod diversity, we calculated the Shannon diversity index of arthropod higher-taxa as  $H = -\sum_i p_i \ln p_i$ , where  $p_i$  is the proportional abundance of order  $i$  in a sample. A normal distribution was fitted for modelling arthropod diversity. Then, estimated marginal means were used for comparisons and post-hoc contrasts between single-level combinations in each model (Lenth, 2019). Results of contrasts are presented as  $\gamma$  in the results section.  $P$ -values were adjusted with Tukey method (Lenth, 2019).

To assess the recovery of arthropod communities, we further analyzed the joint effects of shrubs and grazing history on single arthropod groups. The abundance of each arthropod order was modelled using zero-inflated mixed-effects models with a negative binomial distribution (Brooks et al., 2017). Split plots within site over time were considered as random effects to account for multiple re-sampling. Only orders with abundances higher than 100 specimens were retained in the analysis ( $n = 11$ ). As above, estimated marginal means were used for comparisons and post-hoc contrasts between single-level combinations in each model (Lenth, 2019).  $P$ -values were adjusted with Tukey method (Lenth, 2019).

Finally, to quantify the multivariate response of different arthropod groups to constraining factors, i.e., environmental variables including shrubs and grazing history, we used canonical correspondence analysis (CCA, Oksanen et al., 2019). In particular, we fit CCA with (1) order abundance by samples as community data matrix, and (2) shrubs and grazing treatments as environmental variables. Only orders occurring in more than 5% of samples were retained in the CCA ( $n = 14$ ). We additionally performed Nonmetric Multidimensional Scaling (*metaMDS* function of *vegan* R package, Oksanen et al., 2019) to reveal differences in arthropod community composition among treatments; these additional results are reported in the SI.

### 3. Results

We found that shrubs, grazing history, and their interaction had significant effects on arthropod abundance (all  $p < 0.001$ , SI Table 1, Fig. 2a). Since shrubs by grazing interaction term was significant, we proceed with assessing posthoc comparisons among levels. Shrubs decreases arthropod abundance in grazed areas ( $\gamma = -1.21 \pm 0.10$  SE,  $p < 0.0001$ ) as well as in recently ungrazed areas ( $\gamma = -1.25 \pm 0.09$  SE,  $p < 0.0001$ ). In long-term ungrazed areas, the effects of shrubs were smaller as compared to grazed and recently ungrazed areas ( $\gamma = -0.74 \pm 0.10$  SE,  $p < 0.0001$ ).

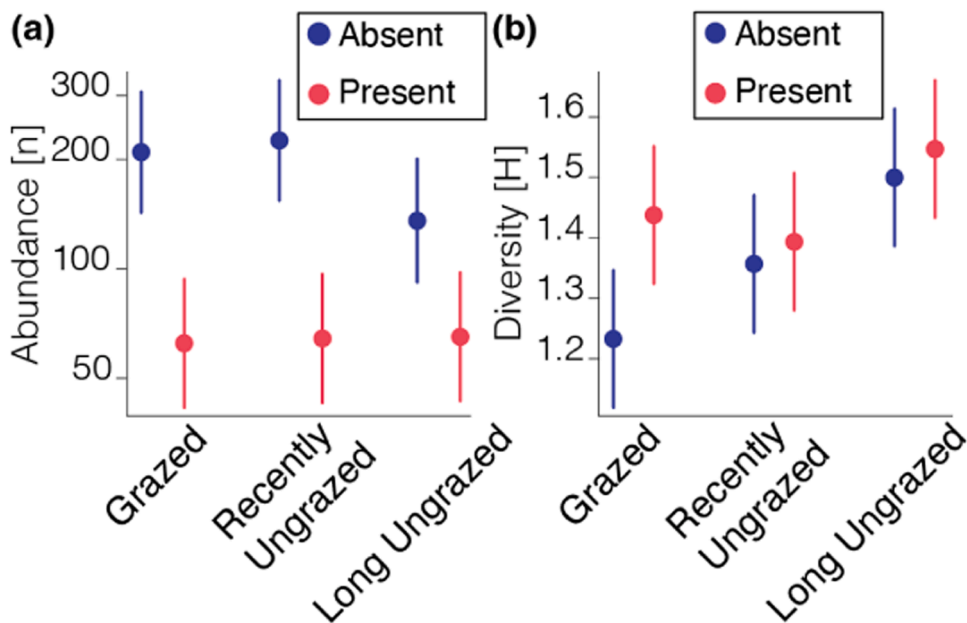
In the absence of shrubs, arthropod abundance was significantly higher in grazed areas than in long-term ungrazed areas ( $\gamma = 0.43 \pm 0.08$  SE,  $p < 0.0001$ ). On the contrary, the presence of shrubs attenuates such differences between grazed and long-term ungrazed areas ( $\gamma = -0.04 \pm 0.12$  SE,  $p = 0.9993$ ). The same occurred between recently ungrazed and long-term ungrazed areas. No differences were observed between grazed and recently ungrazed areas in the absence of shrubs ( $\gamma = -0.07 \pm 0.07$  SE,  $p = 0.8973$ ) nor in the presence of shrubs ( $\gamma = -0.03 \pm 0.12$  SE,  $p = 0.9998$ ).

Shrubs and grazing history had significant effects on arthropod diversity ( $p = 0.035$  and  $p = 0.002$ , respectively, SI Table 1, Fig. 2b). In particular, livestock exclusion increased arthropod diversity, in the long-term in protected areas ( $\gamma = 0.19 \pm 0.06$  SE,  $p = 0.002$ ) as well as in the short-term inside enclosures ( $\gamma = 0.15 \pm 0.06$  SE,  $p = 0.023$ ). Notably, arthropod diversity was significantly higher below the canopy of shrubs than in their absence ( $\gamma = 0.10 \pm 0.05$  SE,  $p = 0.036$ ). Whereby there is no difference in diversity between shrubs and open for recent ( $\gamma = -0.04 \pm 0.08$  SE,  $p = 0.9973$ ) and long-term ungrazed areas ( $\gamma = -0.05 \pm 0.08$  SE,  $p = 0.9914$ ), invertebrate diversity is marginally greater below shrubs than in the open at currently grazed sites ( $\gamma = 0.21 \pm 0.08$  SE,  $p = 0.1022$ ). Furthermore, differences were much greater in the absence of shrubs ( $\gamma = -0.27 \pm 0.08$  SE,  $p = 0.0106$ ) but not below shrubs ( $\gamma = -0.11 \pm 0.08$  SE,  $p = 0.7389$ ) between currently grazed and long-term ungrazed areas.

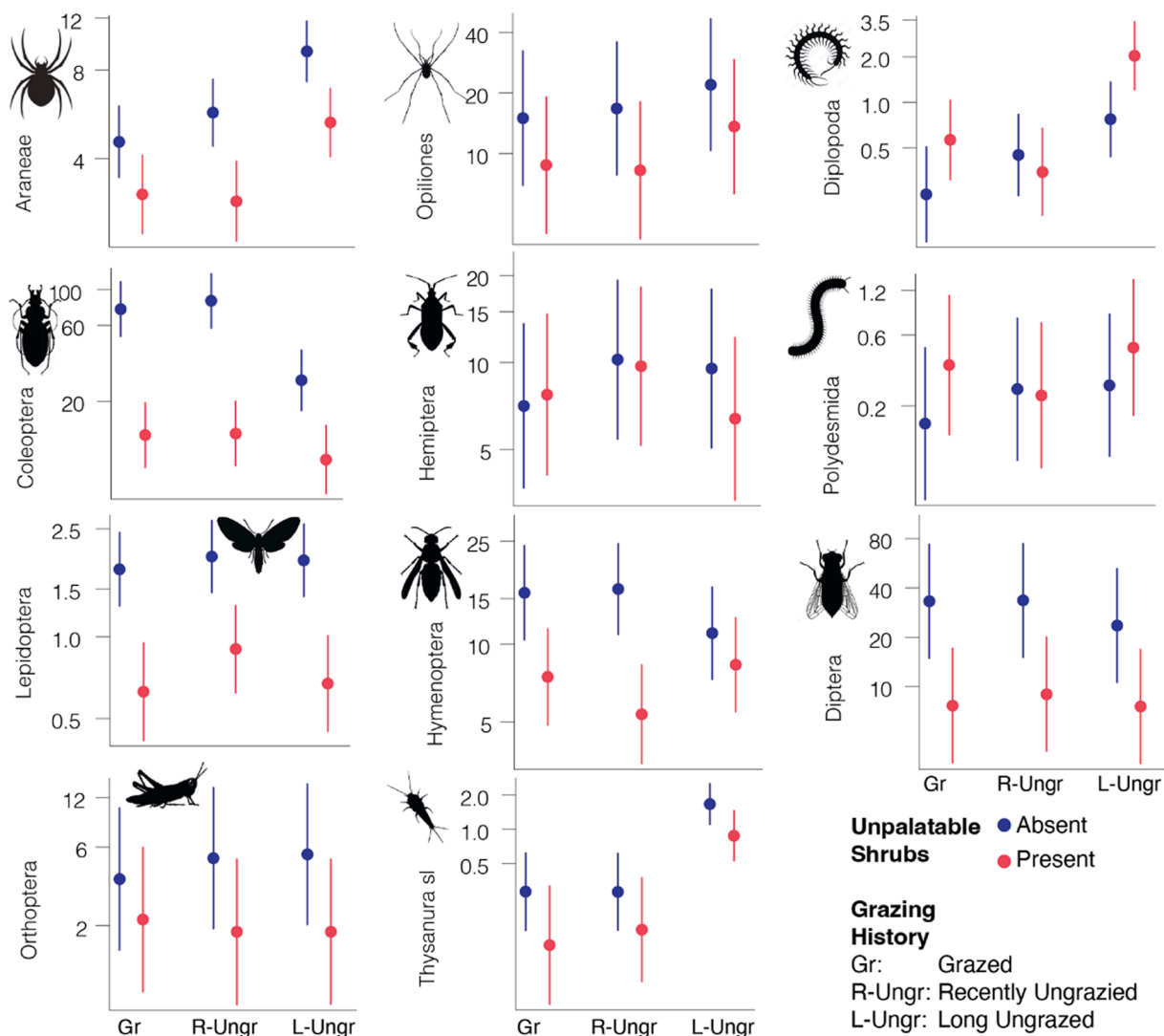
Shrubs and grazing had idiosyncratic effects across different arthropod groups (SI Table 2). On one hand, short-term grazing removal significantly increased the abundance of Hemiptera and Orthoptera (Fig. 3), and long-term removal inside protected habitats increased the abundance of Araneae, Hemiptera, Opiliones, Orthoptera, and Thysanura (Fig. 3). On the other hand, shrubs increased the abundance of Diplopoda and Polydesmida, whereas Araneae, Coleoptera, Diptera, Hymenoptera, Lepidoptera, Opiliones, and Orthoptera were more abundant in open areas than underneath shrubs (SI Table 2). Hymenoptera was the sole group equally abundant in both pastures and protected areas.

Furthermore, the effects of shrubs changed with grazing for Diplopoda and Orthoptera (SI Table 2, Fig. 3). Diplopoda significantly increased with shrubs after long-term grazing removal ( $\gamma = 0.97 \pm 0.28$  SE,  $p = 0.0081$ ), whereas shrubs had no effects in currently grazed areas ( $\gamma = -0.83 \pm 0.40$  SE,  $p = 0.2908$ ). The differences between currently grazed and long-term ungrazed areas were twice as strong in the presence of shrubs ( $\gamma = -2.11 \pm 0.37$  SE,  $p < 0.0001$ ) as compared to shrub absence ( $\gamma = -1.14 \pm 0.38$  SE,  $p = 0.0353$ ). Considering Orthoptera, we found that the effects of shrubs were twice as strong in long-term ungrazed areas ( $\gamma = 1.09 \pm 0.18$  SE,  $p < 0.0001$ ) and short-term ungrazed areas ( $\gamma = 1.03 \pm 0.19$  SE,  $p < 0.0001$ ) as compared to currently grazed areas ( $\gamma = 0.57 \pm 0.18$  SE,  $p = 0.0238$ ).

Finally, results of multivariate analysis (Fig. 4) show that the distribution of arthropod groups was positively driven by grazing



**Fig. 2.** Combined impact of unpalatable shrubs (shrub absent in blue, shrub present in red) and grazing history on arthropod abundance (a) (number of specimens) and arthropod diversity (b) (Shannon index). Estimated means and 95% confidence intervals are shown.



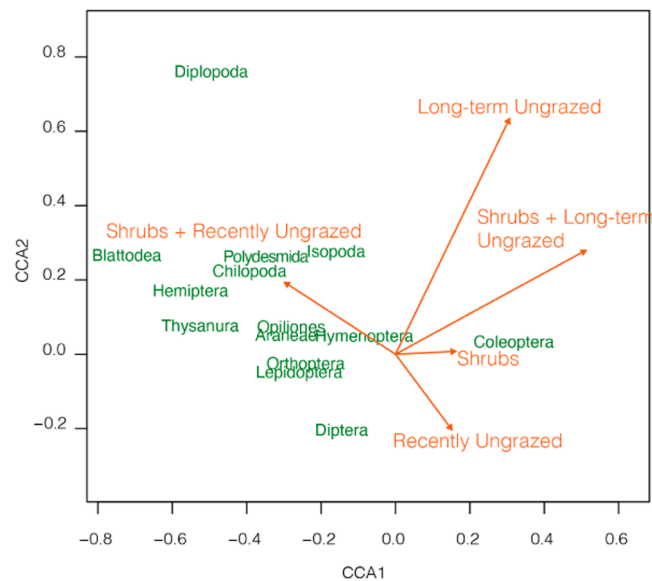
**Fig. 3.** Combined impacts of unpalatable shrubs (shrub absent in blue, shrub present in red) and grazing history (currently grazed, recently ungrazed, long ungrazed) on abundance of arthropods (different orders). Estimated means and 95% confidence intervals are shown.

history ( $F = 5.97, p < 0.001$ ) and its interaction with shrubs ( $F = 7.71, p < 0.001$ ). The first axis of CCA significantly explained  $c$  10% of the variance in arthropod distribution ( $F = 22.66, p < 0.001$ ) and was positively constrained by shrub presence (inertia = 0.20), recently ungrazed (inertia = 0.19), long-term ungrazed (inertia = 0.38), and most importantly the interaction between shrubs and long-term livestock removal (inertia = 0.63). Coleoptera was the main order positively associated with shrubs in long-term ungrazed areas (correlation with first axis = 0.30).

#### 4. Discussion

Our study addressed how unpalatable shrubs mediate the effects of grazing exclusion on biodiversity recovery. Animal diversity increased from pastures to ungrazed areas in a stronger way in the absence of shrubs than in their presence. The abundance of arthropods was the most heavily impacted by shrubs and, in some cases, their dependency on overgrazing. Yet, arthropod diversity was consistently higher beneath the canopy of unpalatable shrubs after grazing exclusion than in the absence of shrubs in pasture areas.

The microhabitat created by unpalatable shrubs may have contributed to the increase in arthropod diversity overall. A possible mechanism underlying observed biodiversity recovery is that unpalatable shrubs in overgrazed landscapes provided a broader niche for fauna. We suggest the following non-exclusive processes: (1) mitigation of disturbance via sheltering from trampling and protections from predators (Noemí Mazía et al., 2006; Shelef and Groner, 2011); (2) amelioration of microclimate via thermal cover and increasing moisture (Mohammad and Alseekh, 2013); and (3) broadening resource availability via fruit trapping and higher litter accumulation favoring both detritivores and higher prey availability (Li et al., 2012). The combination of these microclimatic and



**Fig. 4.** Biplot of multivariate analysis (i.e., Canonical Correspondence Analysis) relating the distribution of arthropod orders across treatments of unpalatable shrubs, grazing history, and their interaction. Arrows show the component scores for contrasting variables (capital letter). Arthropod orders are distributed according to their loadings.

biotic factors may explain how unpalatable shrubs can act as ecosystem engineer and favor biodiversity. Our results are in accordance with previous studies from other Mediterranean and semi-arid systems that highlight positive interactions between shrubs and arthropods (Eldridge et al., 2013; Lortie et al., 2016; Ruttan et al., 2016; Losapio et al., 2018, 2021). Our study therefore suggests that in overgrazed landscapes, encroaching unpalatable species may actually reduce further defaunation and prevent biodiversity loss.

Overgrazing generally reduces arthropod diversity (Gibson et al., 1992; Kruess and Tschardtke, 2002; Cole et al., 2007; Eldridge et al., 2013). Disturbance associated with trampling directly increases the mortality of arthropods, meanwhile deterioration of abiotic conditions and reduction of resource availability for herbivorous arthropods are indirect causes of arthropod diversity decline with grazing (van Klink et al., 2015). According to this general evidence, we found that unsustainable grazing substantially reduced the diversity of arthropods in our system. Indeed, long-term grazing exclusion inside protected habitats favored animal diversity. The response of biodiversity to conservation measures was weak in the short-term enclosures, indicating that there was a time lag in its recovery. Whereas moderate density of grazing may favor specialist organisms that characterize sustainable pasture lands, it is not the case in this examined overgrazed system.

Our study also found a taxa-specific response to the combination of shrubs encroachment and grazing history. Although arthropod abundance was higher in the absence of shrubs than in their presence or in pastures than in protected areas, some groups of arthropods were favored by both grazing exclusion and unpalatable shrubs. Millipedes and centipedes were positively associated with shrubs, but only inside enclosures in the short-term. Millipedes are detritivores usually found in litter where they feed on decaying plant material, while centipedes are predators that inhabit the soil (Sierwald and Bond, 2007; Voigtländer, 2011; David, 2015). Our results suggest that unpalatable shrubs may enhance both millipedes by providing a suitable microhabitat with abundant plant litter and centipedes by increasing prey diversity.

On the other hand, grazed areas without unpalatable shrubs favored flies, butterflies, and grasshoppers. Although flies and butterflies can move and disperse over large distances, we nevertheless found that local scale conditions or localized grazing exclusion may still contribute to influence their spatial distribution. Accordingly, the dense canopy of unpalatable shrubs may limit the access to these flying insects. Furthermore, local-scale conditions including plant community composition and flower richness can influence the abundance and diversity of flying insects (Losapio et al., 2021). Hence, other factors controlled by shrubs such as diversity of flowers and biomass productivity may also have contributed to the decrease of flies and butterflies. As grasshoppers tend to prefer sun exposed areas and herbaceous vegetation (Greatorex-Davies et al., 1993), we accordingly found that they were more abundant in grazed areas outside the canopy of shrubs.

Our results indicate unpalatable shrubs can reduce the abundance and diversity of species with preferences for warm and open habitats. As some flies, butterflies, and grasshoppers can serve as pollinators and herbivores, our study suggests that unpalatable shrubs can compromise the functioning of pasture ecosystems via impact on these communities with key roles in ecological networks and ecosystem services. Furthermore, these results point out that there is no general rule we can derive, stressing the importance of considering taxa-specific responses to livestock exclusion and plant–animal interactions in overgrazed landscapes. Future studies shall address microhabitat improvement and animal functional traits to better understand mechanisms driving biodiversity recovery after grazing exclusion.

Although grazed and long-term ungrazed areas have the same geological, climatic, biogeographic, and historical characteristics, it

may still be possible that some overlooked factor is covarying with grazing exclusion. Furthermore, the observed differences can be attributed to the trait combination of this species (low shrub with dense thorny canopy). Future studies shall address the role of plant diversity in driving animal diversity and examine other systems. Previous research in the study area highlighted those unpalatable shrubs had positive effects on plant diversity in grazed areas but negative effects with grazing exclusion (Losapio et al., 2020). This current study suggests that the recovery of animal communities may be also driven by changes in plant communities.

It is not easy to infer ecological processes from the current study to assess whether the positive shrub–arthropod associations would result in net-positive or net-negative effects on other ecological communities and on ecosystem service provision to humans in this landscape. Yet, the substantial patterns observed in key groups such as beetles, spiders and millipedes may potentially reflect changes in ecosystem functioning (Dirzo et al., 2014; Graham et al., 2019). Future studies should address the direct and indirect role these shrub–animal interactions play in the larger food web and the functioning of these ecosystems.

## 5. Conclusions

We found positive plant–animal interactions suggesting that encroaching, unpalatable shrubs can facilitate the recovery of arthropod communities in overgrazed landscapes. There are many challenges for sustainable pasture management and, at the same time, conserving and restoring ecological communities in protected areas. Sometimes, livestock exclusion is not pursuable or feasible. Nonetheless, our findings support the effectiveness of creating protected areas with interdicted access to livestock for conserving and supporting biodiversity and allowing biodiversity to recover. In addition to usual problems associated with overgrazing (land degradation, reduced livestock productivity, soil erosion, loss of forage plants, loss of profit) we also highlight a biodiversity decline across different arthropod taxa, but also a recovery within *c* 20 years. Considerations of future efforts to reduce the loss of Mediterranean biodiversity and improve sustainability may require abandoning short-term benefits while proactively restoring ecosystems and grant suitable habitats to diverse animal communities.

## Authors' contributions

GL conceived the study with inputs from CMDM, MCM, TT, and NZ. GL and VN run the study. VN carried out data collection, arthropod identification, and data processing. GL analyzed the data and drafted the manuscript. All authors commented the results and edited the manuscript.

## Declaration of Competing Interest

The authors declare that they have no competing financial interests nor personal relationships that could have influenced the work reported in this paper.

## Data Availability

Data are publicly available online at the ETH Research collection (<https://doi.org/10.3929/ethz-b-000311956>). R script to reproduce the results and figures is publicly available at <https://github.com/losapio/GECCO2024>.

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## Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors did not use generative AI or AI-assisted technologies in the writing process.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2024.e02819](https://doi.org/10.1016/j.gecco.2024.e02819).

## References

- Arianoutsou-Faraggitaki, M., 1985. Desertification by overgrazing in Greece: the case of Lesvos island. *J. Arid Environ.* 9, 237–242.
- Brooks, M.E., et al., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R. J.* 9 (2), 378–400.
- Ceballos, G., et al., 2015. Accelerated modern human-induced species losses: entering the sixth mass extinction. *Sci. Adv.* 1, 1–5.

- Cole, L.J., McCracken, D.I., Baker, L., Parish, D., 2007. Grassland conservation headlands: their impact on invertebrate assemblages in intensively managed grassland. *Agric., Ecosyst. Environ.* 122, 252–258.
- Crawley, M.J., 1997. Plant–herbivore dynamics. In: Crawley, M.J. (Ed.), *Plant Ecology*. Blackwell Science.
- David, J., 2015. Diplopoda – ecology. In: Minelli (Ed.), *Treatise on Zoology - Anatomy, Taxonomy, Biology. The Myriapoda, Volume 2*. Brill, Leiden, Niederlande.
- Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J., Collen, B., 2014. Defaunation in the Anthropocene. *Science* 345, 401–406.
- Eldridge, D., Soliveres, S., Bowker, M.A., Val, J., 2013. Grazing dampens the positive effects of shrub encroachment on ecosystem functions in a semi-arid woodland. *J. Appl. Ecol.* 50, 1028–1038.
- Gibson, C.W.D., Brown, V.K., Losito, L., McGavin, G.C., 1992. The response of invertebrate assemblages to grazing. *Ecography* 15, 166–176.
- Graham, S.I., Kinnaird, M.F., O'Brien, T.G., Vagern, T.G., Winowiecki, L.A., Young, T.P., Young, H.S., 2019. Effects of land-use change on community diversity and composition are highly variable among functional groups. *Ecol. Appl.* 29, e01973.
- Hobbs, R.J., Richardson, D.M., Davis, G.W., 1995. Mediterranean-type ecosystems: opportunities and constraints for studying the function of biodiversity. In: Davis, G.W., Richardson, D.M. (Eds.), *Mediterranean-Type Ecosystems*. Springer.
- Iosifides, T., Politidis, T., 2006. Socio-economic dynamics, local development and desertification in western Lesvos, Greece. *Local Environ.* 10, 487–499.
- Isbell, F., et al., 2017. Linking the influence and dependence of people on biodiversity across scales. *Nature* 546, 65–72.
- Kairis, O., Karavitis, C., Salavati, L., Kounalaki, A., Kosmas, K., 2015. Exploring the impact of overgrazing on soil erosion and land degradation in a dry mediterranean agro-forest landscape (Crete, Greece). *Arid Land Res. Manag.* 29, 360–374.
- Kizos, T., Vakoufaris, H., 2012. "there is no overgrazing or desertification of fields, but depopulation of the villages": analysis of the views of stakeholders for overgrazing and desertification on Western Lesvos. *Hell. Assoc. Agric. Econ.* 17, 317–330.
- Kizos, T., Plieninger, T., Schaich, H., 2013. "Instead of 40 sheep there are 400": traditional grazing practices and landscape change in Western Lesvos, Greece. *Landsc. Res.* 38, 476–498.
- van Klink, R., van der Plas, F., van Noordwijk, C.G.E., WallisDeVries, M.F., Olf, H., 2015. Effects of large herbivores on grassland arthropod diversity. *Biol. Rev.* 90, 3347–3366.
- Kruess, A., Tschamtkke, T., 2002. Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. *Conserv. Biol.* 16, 1570–1580.
- Lenth, R. (2019). *emmeans: Estimated Marginal Means, aka Least-Squares Means*. R package version 1.4.1.
- Li, F.-R., Liu, J.-L., Liu, C.-A., Liu, Q.-J., Niu, R.-X., 2012. Shrubs and species identity effects on the distribution and diversity of ground-dwelling arthropods in a Gobi desert. *J. Insect Conserv.* 17, 319–331.
- Lindemayer, D.B., Blanchard, W., Crane, M., Michael, D., Sato, C., 2018. Biodiversity benefits of vegetation restoration are undermined by livestock grazing. *Restor. Ecol.* 26, 1157–1164.
- Lortie, C.J., Filazzola, A., Sotomayor, D.A., 2016. Functional assessment of animal interactions with shrub-facilitation complexes: A formal synthesis and conceptual framework. *Funct. Ecol.* 30, 41–51.
- Losapio, G., Pugnaire, F.I., O'Brien, M.J., Schöb, C., 2018. Plant life history stage and nurse age change the development of ecological networks in an arid ecosystem. *Oikos* 128, 1390–1397.
- Losapio, G., De Moraes, C.M., Dirzo, R., Dutoit, L.L., Tschewlin, T., Zouros, N., Mescher, M.C., 2020. An invasive plant species enhances biodiversity in overgrazed pastures but inhibits its recovery in protected areas. *bioRxiv*, 2020. 08. 16. 227066.
- Losapio, G., Norton Hasday, E., Espadaler, X., Germann, C., Ortiz-Sanchez, F.J., Pont, A., Sommaggio, D., Schöb, C., 2021. Facilitation and biodiversity jointly drive mutualistic networks. *J. Ecol.* 109, 2029–2037.
- McNaughton, S.J., 1993. Grasses and grazers, science and management. *Ecol. Appl.* 3, 17–20.
- Mohammad, A.G., Alseekh, S.H., 2013. The effect of *Sarcopoterium spinosum* on soil and vegetation characteristics. *CATENA* 100, 10–14.
- Naeem, S., Duffy, J.E., Zavaleta, E., 2012. The functions of biological diversity in an age of extinction. *Science* 336, 1401–1406.
- Noemí Mazía, C., Chaneaton, E.J., Kitzberger, T., 2006. Small-scale habitat use and assemblage structure of ground-dwelling beetles in a Patagonian shrub steppe. *J. Arid Environ.* 67, 177–194.
- Oksanen, J., et al., 2019. *vegan: Community Ecol. Package R. Package Version 2*, 5–6.
- Pimm, S.L., et al., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344, 1246752.
- Potts, S.G., et al., 2016. Safeguarding pollinators and their values to human well-being. *Nature* 540, 220–229.
- R Core Team, 2022. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria (URL). (<https://www.R-project.org/>).
- Ruttan, A., Filazzola, A., Lortie, C.J., 2016. Shrub-annual facilitation complexes mediate insect community structure in arid environments. *J. Arid Environ.* 134, 1–9.
- Sala, O.E., et al., 2000. Global biodiversity scenarios for the year 2100. *Science* 287, 1770–1774.
- Seligman, N., Henkin, Y.Z., 2002. Persistence in *Sarcopoterium spinosum* dwarf-shrub communities. *Plant Ecol.* 164, 95–107.
- Shelef, O., Groner, E., 2011. Linking landscape and species: effect of shrubs on patch preference of beetles in arid and semi-arid ecosystems. *J. Arid Environ.* 75, 960–967.
- Sierwald, P., Bond, J.E., 2007. Current status of the myriapod class diplopoda (Millipedes): taxonomic diversity and phylogeny. *Annu. Rev. Entomol.* 52, 401–420.
- Torma, A., Révész, K., Gallé-Szpisjak, N., Šeát, J., Szél, G., Kutasi, C., Malenovský, I., Batáry, P., Gallé, R., 2023. Differences in arthropod communities between grazed areas and grazing exclosures depend on arthropod groups and vegetation types. *Agric., Ecosyst. Environ.* 341, 108222.
- Tylianakis, J.M., Tschamtkke, T., Lewis, O.T., 2007. Habitat modification alters the structure of tropical host-parasitoid food webs. *Nature* 445, 202–205.
- Underwood, E.C., Viers, J.H., Klausmeyer, K.R., Cox, R.L., Shaw, M.R., 2009. Threats and biodiversity in the Mediterranean biome. *Divers. Distrib.* 15, 188–197.
- Vazquez, D.P., Simberloff, D., 2003. Changes in interaction biodiversity induced by an introduced ungulate. *Ecol. Lett.* 12, 1077–1083.
- Voigtländer, K., 2011. *Chilopoda – Ecology*. Brill, Leiden, Niederlande.
- Wilkinson, D.M., Sherratt, T.M., 2016. Why is the world green? the interactions of top-down and bottom-up processes in terrestrial vegetation ecology. *Plant Ecol. Divers.* 9, 127–140.
- Young, H.S., McCauley, D.J., Galetti, M., Dirzo, R., 2016. Patterns, causes, and consequences of Anthropocene defaunation. *Annu. Rev. Ecol., Evol., Syst.* 47, 333–358.