1   **An invasive plant species enhances biodiversity in overgrazed pastures but**

2   **inhibits its recovery in protected areas**

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16

17 **Abstract**

18 Anthropogenic environmental change exposes biological communities to concurrent

19 stressors (e.g., changes in climate and land-use, overexploitation, biotic invasions) that

20 frequently persist over prolonged periods. Predicting and mitigating the consequences

21 of human action on nature therefore requires understanding how exposure to multiple

22 interacting stressors alters biological communities over relevant (e.g., multi-decadal)

23 time periods. Here, we explore the effects of overgrazing and plant species invasion on

24 plant community diversity and ecosystem functioning (productivity), as well as the

25 patterns of recovery of plant communities following cessation of grazing pressure. In a

26 Mediterranean pasture system, we utilized a "natural" experiment involving long-term

27 exclusion of grazers (for 15–25 years in parks) and also conducted short-term grazing-

28 exclusion and invasive species removal experiments. Our results reveal that invasion by

29 a grazing-resistant plant (prickly burnet) has net positive effects on plant diversity

30 under overgrazing conditions but inhibits the recovery of biodiversity once grazing

31 ceases. Furthermore, while the diversity–productivity relationship was found to be

32 positive in pastures, the interactive effects of overgrazing and species invasion appear to

33 disrupt ecosystem functioning and inhibit the recovery of pasture productivity. These

34 findings highlight the potential for prolonged exposure to anthropogenic stressors, such

35 as overgrazing, to cause potentially-irreversible changes in biological communities that,

36 in turn, compromise ecosystem functioning and resilience. In such cases, sustainable

37 ecosystem management may require direct intervention to boost biodiversity resilience

38 against centennial overgrazing.

39

40   Human activities are causing rapid environmental change at local and global scales (1-3),

41   leading to dramatic increases in the frequency and intensity of ecological disturbance

42   (4,5). As a consequence, global biodiversity is rapidly declining, with potentially

43   profound implications for critical ecosystem functions (6,7) and ecological sustainability

44   (8–10). A key feature of anthropogenic environmental disturbance is the coincident

45   occurrence of multiple stressors that persist over long periods of time, for example

46   when changes in land use are accompanied by the introduction of novel species (4) or

47   loss of native ones (10). Furthermore, the interaction between such stressors can have

48   serious implications for important ecosystem functions, such as productivity, as well as

49   the ability of natural systems to tolerate or recover from disturbance events (7,11–13).

50   To predict and mitigate the long-term effects of anthropogenic environmental change on

51   ecological sustainability, it is therefore crucial to understand how biological

52   communities are altered by, and recover from, simultaneous exposure to multiple

53   perturbations (3,6).

54   The ability of an ecosystem to recover from disturbance is termed resilience (14).

55   In the face of anthropogenic environmental change, ecosystem resilience can be strongly

56   influenced by changes in biodiversity and ecosystem functioning that arise from the

57   interaction of multiple stressors acting across different spatial and temporal scales (3,

58   10,15). For instance, local-scale perturbations such as fire exacerbate the negative

59   effects of large-scale deforestation (12). However, we currently have limited

60   understanding of the processes that determine whether, and how, biological

61   communities recover from prolonged exposure to multiple stressors or shift to a new

62   state. Improved understanding of these processes is necessary for managing, conserving

63   and restoring ecosystems.

64   In the European Mediterranean Basin, severe overgrazing across centuries of

65   human habitation has dramatically altered ecosystem composition, structure, richness,

66   and productivity (16-18). While some studies suggest that moderate grazing may be

67   beneficial for the maintenance of some plant species (19,20), overgrazing is currently

68   pushing ecosystems towards desertification in many areas, including on the Greek island

69   of Lesvos, where this study was conducted (16). Heavily overgrazed pasture lands in

70   Lesvos have also experienced widespread invasion by prickly burnet (*Sarcopoterium*

71   *spinosum* (L.) Spach, Rosaceae), a thorny dwarf-shrub that, because of its unpalatability

72   and high grazing resistance, has come to dominate vast areas of rangeland throughout

73   the eastern Mediterranean Basin (18,21) (Fig. 1a and *SI Appendix*, Figure S1). This

74   invasion has made many pastures on Lesvos nearly unusable, causing severe problems

75   for the local human population, which rely heavily on livestock grazing for their

76   livelihood and food production.

77   By reducing grazing pressure, however, prickly burnet invasion may prevent

78   further ecosystem degradation and desertification. Indeed, there is some indication that

79   prickly burnet can promote plant diversity by improving soil conditions and providing

80   shelter against livestock grazing to other plants that grow beneath its thorny, protective

81   canopy (22). Such facilitative interactions are common to pasture ecosystems,

82   worldwide, which are frequently invaded by single, highly resistant species (23,24).

83   However, less is known about the consequences of species invasion for ecosystem

84   recovery once livestock grazing is halted and pastures are abandoned or set aside to

85   become protected areas (e.g., national parks). Despite their importance, these

86   relationships are frequently not considered in conservation programs (21).

87   To address whether and how species invasion mediates the impact of land-use

88   change and overgrazing on ecosystem resilience, we studied a pasture ecosystem and

89   adjacent protected parks on Lesvos (see Methods). Our overarching goals were to

90   examine the long-term effects of combined overgrazing and species invasion on plant

91   diversity and productivity and the resilience of local plant communities in the face of

92   these stressors. Lesvos offers a unique opportunity to address these questions, since the

93   establishment of two parks in 1994 and 2002 (UNESCO Lesvos Petrified Forest Parks in

94   Sigri and Plaka) created a "natural" long-term exclosure experiment in which grazing

95   was abruptly terminated on fifteen hectares of pasture lands, while intense grazing

96   continued on adjacent lands that were otherwise similar. In addition to taking advantage

97   of this long-term exclusion at the landscape scale, we implemented short-term exclosure

98   and invasive-species removal experiments at the local community scale (Fig. 1, see

99   Methods).

100   To assess the recovery of plant communities once overgrazing ceased, in 2018 we

101   laid out 5 x 5 m experimental blocks for plant community surveys in: (i) grazed pastures,

102   (ii) adjacent parks where grazing had ceased 16 or 24 years before, and (iii) fenced

103   enclosures within the pastures. We will henceforth refer to these different areas as "land

104   management types". To test the consequences of species invasion and its interaction

105   with land management, we performed a removal experiment in each block with the

106   following treatments implemented in 1 x 1 m plots: (a) prickly burnet removed by

107   clipping ('removal'), (b) open areas without prickly burnet ('open'), and (c) prickly

108   burnet left intact ('invasive'). Our experimental blocks were replicated twelve times at

109   two different sites for a total of 108 1 x 1 m plots. At the end of the growing season, we

110   measured the composition, richness, and productivity of the plant communities, which

111   mainly comprised annual plants.

112

113   **Results and discussion**

Interactive effects of species invasion and overgrazing at landscape scale

114

115   We addressed the effects of species invasion on biodiversity resilience against

116   overgrazing at the landscape scale. To do so, after checking for sampling completeness

117   (*SI Appendix*, Figure S2) and standardizing by sample-based extrapolation (25,26), we

118   quantified the effect of prickly burnet on plant diversity (γ-diversity) by means of a

119   relative interaction index (27) (see Methods). When comparing plant communities in

120   'invasive' and 'open' areas, we found that the impact of species invasion on plant

121   diversity differed between land management types (*SI Appendix*, Table S1). Specifically,

122   the presence of the invader had positive effects on plant diversity in pastures but

123   negative effects inside exclosures and parks (Fig. 2 and *SI Appendix*, Table S2). This

124   pattern highlights the potential for one environmental stressor to revert the effects of

125   another on ecological communities in a context-dependent way. In this case, an invasive

126   species protects and facilitates otherwise vulnerable plants experiencing overgrazing,

127   but also inhibits the recovery of biodiversity once such disturbance ceases.

128   Next, we explored a potential mechanism for the idiosyncratic effects of invasion

129   on diversity described above by experimentally removing the invader. When comparing

130   plant communities in 'removal' and 'invasive' areas, we found that removing prickly

131   burnet had consistently positive effects on plant diversity (Fig. 2; *SI Appendix*, Table S2),

132   indicative of a net negative (competitive) effect of prickly burnet on associated plants.

133   Furthermore, these findings suggest a legacy effect (22,28), in which the prior presence

134   of prickly burnet has a constructive impact on soil conditions as compared with those of

135   open, grazed communities.

136   Together with our previous findings, these results suggest that species invasion

137   enhances biodiversity maintenance in the presence of livestock but inhibits its resilience

138   once such pressure ceases. A possible underlying mechanism is related to the shift in the

139   balance of facilitation and competition between shrub species and associated plants

140   (29), where net positive and negative effects prevail in pasture and in parks,

141   respectively (Fig. 1). A similar pattern has been observed in overgrazed plant

142   communities in Caucasus mountain ecosystems (23), suggesting that the facilitative role

143   of unpalatable invaders for biodiversity maintenance is more relevant and widespread

144   than previously thought.

145

146   **Persistent effects of grazing and species invasion on plant diversity and turnover**

147   When we assessed the resilience of local-scale diversity (α-diversity) and

148   community composition (β-diversity) against the combination of grazing and invasive

149   species, we found that overgrazing significantly decreased biodiversity; moreover, in the

150   absence of prickly burnet, plant communities could recover locally once grazing ceased

151   (*SI Appendix*, Figure S3a and Table S3). In particular, local diversity increased inside

152   exclosures (i.e., after short-term livestock exclusion from pasture lands) and increased

153   even further in parks (i.e., after long-term livestock exclusion; $p < 0.001$).

154   The presence of prickly burnet also had strong effects on diversity: in pasture lands,

155   local diversity was higher in the presence of prickly burnet and after its removal in

156   comparison to open communities, whereas diversity was similar across these

157   treatments inside both exclosures and parks (*SI Appendix*, Table S4). Consistent with our

158   previous results, these findings further suggest that the positive effects of the invader on

159   local plant diversity occur only in the presence of livestock, whereas the resilience of

160   biodiversity may be limited by competitive effects that prevail once overgrazing

161   disturbance ceases. Considering bottom-up and top-down drivers of plant diversity (24),

162   our results suggest that the resilience of plant communities is regulated by both

163   processes.

164   While community composition was similar in both prickly burnet and open

165   communities across land management types, removal of the invasive species increased

166   species turnover in parks (*SI Appendix*, Fig. S3b and Table S5). These results indicate

167   that the presence of both livestock and invader tend to promote homogeneous plant

168   communities, while long-term grazing exclusion combined with invader removal leads

169   to increased community heterogeneity.

170   Contrary to previous claims regarding the positive effects of livestock grazing on

171   biodiversity (16,20) but consistent with current evidence on the impact of such land-use

172   practice (4,9,12), our experiment documented detrimental impacts of overgrazing on

173   plant communities. Livestock grazing erodes biodiversity by favoring a few dominant

174   species (15,23,24) and triggering invasion by unpalatable plants that ultimately limit the

175   ability of communities to recover. Consequently, we foresee that effective management

176   measures to improve ecosystem resilience in this and similar systems will need to

177   include both the reduction of grazing pressure and exclusion of the invasive species.

178

179   **Grazing and species invasion jointly alter the biodiversity–ecosystem functioning**

180   **(BEF) relationship**

181   Having found positive effects of prickly burnet on plant diversity in the presence of

182   livestock, but negative effects in its absence, we examined the combined effects of the

183   invader and grazing pressure on ecosystem functioning. Here, we found that the

184   resilience of productivity against the invasive species varied with land management (Fig.

185   3 and *SI Appendix*, Table S6). In particular, livestock grazing significantly decreased

186   productivity, which recovered with long-term livestock exclusion in parks (*SI Appendix*,

187   Table S7). Notably, productivity was similar between pastures and exclosures, indicating

188   that it was independent of biomass removal (Fig. 3 and *SI Appendix*, Table S7).

189   Furthermore, the presence of prickly burnet decreased productivity, while its removal

190   had positive effects, particularly in parks (*SI Appendix*, Table S7). These results indicate

191   that putting pastures under protection and removing invasive species increases

192   productivity.

193   Finally, we explored how the biodiversity–productivity relationship (3,6,11)

194   changed under the combined impact of species invasion and land management (see

195   Methods). Although pasture productivity generally increased with increasing plant

196   diversity (*SI Appendix*, Table S6), the nature of this BEF relationship differed between

197   removal treatments depending on land management (Fig. 4). Specifically, the BEF

198   relationship was negative in the presence of prickly burnet, while it became more

199   positive with the removal of prickly burnet. Furthermore, this trend was consistent

200   across land management types (*SI Appendix*, Table S7 and Table S8).

201   This finding was most likely due to the previously discussed legacy effect and partial

202   recovery, indicating that species invasion erodes the positive effects of biodiversity on

203   ecosystem functioning. In contrast, in the absence of prickly burnet, productivity

204   increased with plant diversity in pastures but decreased in parks. This pattern might be

205   related to nutrient input by livestock (20), which may help maintain a positive BEF

206   relationship. Taken together, these results indicate that changes in land management

207   systematically alter the relationship between biodiversity and ecosystem functioning,

208   with species invasion mediating the magnitude and sign of the diversity–productivity

209   relationship.

210

211   **Implications for the sustainable management of Mediterranean pastures and**

212   **parks**

213   Three decades of biodiversity research suggest that more diverse ecosystems are

214   more productive and may be more resilient to environmental perturbations through

215   redundancy of functions carried out by different species (3,7). Furthermore, recent

216   theoretical studies of plant networks predict that certain foundation species are critical

217   for maintaining biodiversity as they increase community robustness (15,29). Yet,

218   despite these advances, our understanding of the ways in which biodiversity

219   concurrently contributes to the ability of ecosystems to recover functioning after

220   prolonged exposure to multiple anthropogenic stressors remains far from complete.

221   Biodiversity experiments show that greater numbers of species within communities are

222   associated with lower invasibility (9) and higher productivity (7). Here, we show that

223   conserving biodiversity alone may not be sufficient to ensure the long-term recovery of

224   pasture productivity even 15–25 years after the cessation of overgrazing. This is likely

225   due to disruption of the positive relationship between biodiversity and ecosystem

226   functioning by species invasion.

227   A striking feature of our study system is the extent to which prickly burnet

228   continues to dominate the plant community in parks, where grazing ceased decades ago.

229   A possible explanation for this dominance is the total absence of any trees and shrubs in

230   the landscape, which, once established, might well exclude prickly burnet from the

231   community by limiting its recruitment. Indeed, it has been observed that prickly burnet

232   germinates only in the absence of an overhead canopy (18,21). The observation that

233   simply placing former pasture areas under protection is insufficient strongly suggests

234   that proactive measures of conservation and restoration are essential (6,10).

235   Restoring native shrubs and trees might be an effective strategy for suppressing

236   species invasion and boosting ecosystem resilience. Since grazing impacts ecosystem

237   functioning and the associated canopy removal increases soil erosion and water loss (4),

238 tree and shrub restoration may help recover multiple ecosystem functions such as

239 productivity, soil erosion control and water retention (30). Restoring shrublands and

240 woodlands with diverse species would also boost ecosystem resilience through the re-

241 establishment of a positive BEF relationship. Outside parks, this measure would likely

242 also enhance the resilience and productivity of pastures, since a drastic reduction in

243 livestock overgrazing is needed to halt and reverse the process of desertification.

244   In sum, our results provide evidence that biodiversity and ecosystem functioning

245 have limited resilience against multiple anthropogenic stressors in overgrazed

246 landscapes. In the presence of livestock, we found that an invasive plant species helps

247 reduce the severity of biodiversity loss at both local and landscape scales by protecting

248 plants under its canopy. In contrast, once grazing ceases, the same invasive species

249 inhibits biodiversity recovery, indicating potentially-irreversible biodiversity loss in the

250 absence of targeted restoration efforts. These findings indicate that creating parks

251 without proactive intervention is necessary but insufficient to restore desirable levels of

252 biodiversity and ecosystem functioning due to the long-lasting detrimental effects of

253 multiple stressors. Rather, interventions such as the restoration of native shrub and tree

254 species may be needed to mitigate anthropogenic impact, enhance resilience and restore

255 desirable ecosystem functioning.

256

257 **Materials and Methods**

258 **Field experiment**

259 The study was carried out in an overgrazed ecosystem in the western part of Lesvos

260 Island, Greece. In this area, intense long-term grazing pressure of livestock (mainly

261 sheep and goat) has led to domination of the plant community by a spiny invasive shrub,

262 *Sarcopoterium spinosum* (L.), 'prickly burnet'. *S. spinosum* is a thorny, unpalatable dwarf-

263   shrub highly resistant to grazing (Fig. 1). It is native to the Southeast Mediterranean and

264   Middle East (17,18,21). The establishment in some areas of UNESCO Lesvos Petrified

265   Forest Parks in 1994 (Sigri Park) and 2002 (Plaka Park) led to the removal of

266   overgrazing disturbance and maintenance of the ecosystem in a "natural" state.

267   Nevertheless, prickly burnet continues to dominate the plant community inside the

268   parks as of 2018 (Fig. 1). This system in itself constitutes a "natural" experiment

269   allowing us to address whether and how biodiversity was able to recover from long-

270   term overgrazing.

271   We therefore chose two adjacent communities differing in land-use management:

272   pasture lands where overgrazing is still ongoing, and the above-mentioned parks where

273   overgrazing ceased 15–25 years previously. A third land type was created with the

274   localized exclusion of grazing in pasture lands. By excluding livestock, we could assess

275   the direct short-term recovery of biodiversity and ecosystem functioning from

276   overgrazing. In pastures, we randomly installed 5 x 5 m fences (1.5 m height) and

277   selected adjacent 5 x 5 m areas. In parks, we randomly selected 5 x 5 m areas. For each

278   land type, eight blocks were established at the Sigri Park site and four at the Plaka Park

279   site, for a total of 36 blocks.

280   The field experimental manipulation also included the removal of prickly burnet. By

281   removing prickly burnet, we could assess the effects of species invasion on the resilience

282   of biodiversity and ecosystem functioning. The following three treatments were

283   conducted: i) community without prickly burnet (open areas); ii) community with

284   prickly burnet; and iii) removal of prickly burnet by clipping its canopy. We followed a

285   fully-factorial, randomized block design by replicating and making blocks of the three

286   treatments together (i.e., open areas, prickly burnet and prickly burnet removal) in each

287   land management type (i.e., pasture, exclosure and park) (Fig. 1).

288   The treatment plots measured 1 x 1 m. In total, we installed $n = 108$ plots at the start

289   of the vegetative season (February 2018). Then, we visually recorded the occurrence

290   and cover of plant species within each plot (April 2018), using the nomenclature of

291   Bazos (2005). Finally, we harvested the aboveground biomass of each entire plot at the

292   end of the season (May 2018). Biomass was dried for 72 h at 70°C.

293

294   **Data analysis**

295   First, we measured biodiversity at the landscape scale, i.e., gamma (γ) diversity. This

296   measure of biodiversity refers to the species richness in a landscape, i.e., species pool. In

297   order to cover the highest possible extent of biodiversity, we quantified the species pool

298   by integrating the observed species richness with the estimated number of unseen

299   (missing) species in each treatment. We used the bootstrap estimator $\hat{f}_o =$

300    $\sum_{i=1}^{S_o}(1 - p_i)^N$ and resampled 99 times from a normal distribution with mean $\hat{f}_o + S_o$

301   and standard deviation $SE(\hat{f}_o)\sqrt{n}$ using the *specpool* function of the *vegan* R package

302   (26,31).

303   We then analyzed the interactions of land management and species invasion with

304   biodiversity. To ensure we included all plant species in the ecosystem (i.e., both

305   observed and potentially unseen species) we used the estimated γ-diversity for this

306   analysis. This also allowed us to look at biodiversity resilience at the landscape scale. We

307   considered the following scenarios: 1) grazing and invader; 2) grazing without invader;

308   3) short-term grazing exclusion with invader; 4) short-term grazing exclusion without

309   invader; 5) long-term grazing exclusion with invader; 6) long-term grazing exclusion

310   without invader. We measured interactions between prickly burnet and γ-diversity

311   using the Relative Interaction Index (RII) (27). This RII was calculated as

312    $(\gamma\ intact - \gamma\ absent)/(\gamma\ intact + \gamma\ absent)$ and

313     $(\gamma\ intact - \gamma\ removed)/(\gamma\ intact + \gamma\ removed)$ to assess the effects of prickly burnet

314   presence and prickly burnet removal in each combination of grazing treatment,

315   respectively. In scenarios 1 and 2 we considered pastures, in scenarios 3 and 4 we

316   considered exclosures, in scenarios 5 and 6 we considered park lands. RII ranges from -1

317   to 1, with values smaller and higher than 0 indicating negative and positive interactions

318   between plants and prickly burnet, respectively. RII was tested in response to grazing

319   (presence/exclusion) and invader (presence/removal) with time scale (short- and long-

320   term effect) nested within grazing exclusion using hierarchical models (32); replicate

321   pairs were random effects. We ran comparison between specific levels using least-

322   square mean estimation (33).

323   We also quantified alpha (α) and beta (β) diversity. α-diversity refers to the observed

324   local diversity in each plot. It was quantified using the Shannon diversity index as

325     $H\ =\ -\ \sum_{i=1}^{S}\ p_i \ln\ p_i$, where p is the relative cover of plant species i occurring in the

326   community with S species. This index accounts for both abundance and evenness of

327   plant species. β-diversity refers to the dissimilarity (heterogeneity) in species

328   composition among communities, and indicates how many different and unique species

329   there are between each pair of plots. This was quantified using the Sørensen similarity

330   index (26,33) as β -diversity = b + /($2a+b+c$) , where a is the number of shared species

331   between two plots, b and c are the numbers of species unique to each plot.

332   We used hierarchical models (32,34) to test for differences among species invasion

333   treatments (open, prickly burnet, and removal) across land management types (pasture,

334   exclosure, and park), and their statistical interaction for indices of α- and β- diversity.

335   Site (parks) and block nested within site were considered as random effects. For each

336   fitted model, the significance of predictors was tested using type II Wald chi-square test

337   in terms of explained variance (33).

338   We then analyzed: (i) the response of aboveground biomass productivity (g m^{-2}), a

339   classic measure of ecosystem functioning (7), and (ii) the relationship between

340   biodiversity and productivity (BEF) over land management and species invasion. We

341   used a hierarchical model (32) to test for differences in productivity between land

342   management (pasture, exclosure, and park), species invasion (open, prickly burnet, and

343   removal), and their statistical interaction as a function of α-diversity. Site (parks) and

344   block nested within site were considered as random effects. We first reported the effects

345   of predictors considering the fitting of coefficient estimates. We then estimated the

346   diversity–productivity relationship (BEF) across treatments and land management

347   using marginal means of linear trends (35). Data analysis was performed in R ver. 3.5.0

348   (31).

349

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424

425 **Figures**
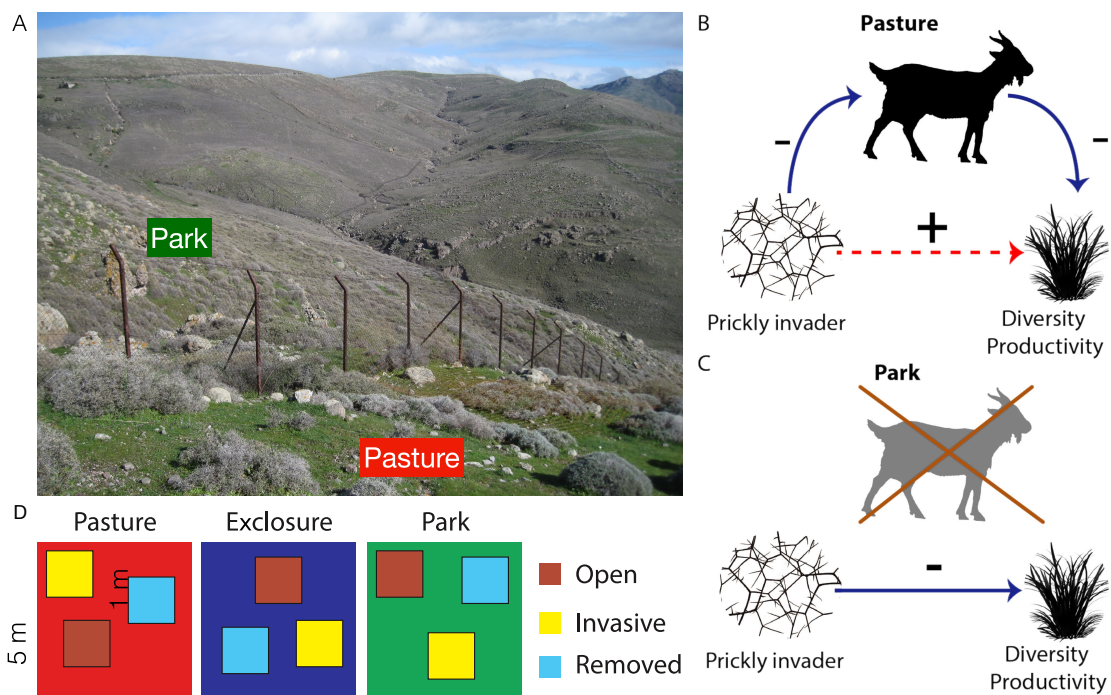
427 **Fig. 1** (A) Photograph of pasture and adjacent park land, separated by a fence, both

428 invaded by prickly burnet (the greyish shrub). (B) Under overgrazing, prickly burnet

429 protects otherwise vulnerable plants, ultimately increasing diversity. (C) Diversity–

430 prickly burnet interactions become negative once overgrazing ceases inside exclosures

431 and parks, limiting the resilience of biodiversity. (D) Scheme of the experimental design,

432 comprising plots (1 m x 1 m) of species invasion treatments within blocks (5 m x 5 m) in

433 each land management type (pasture, exclosure, park).

434
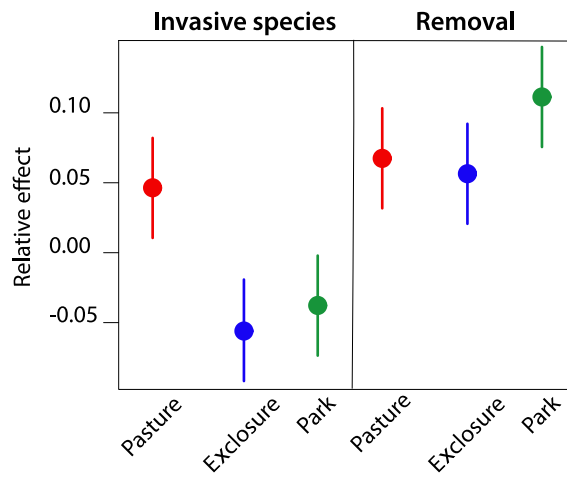
Fig. 2. Effects of an invasive plant (prickly burnet) and its removal on plant diversity
(species pool) in pasture (red), exclosure (blue) and park (green) lands. Invasive species
effect is relative to open communities (without prickly burnet). Removal effect is
relative to communities with prickly burnet. Dots represent estimated (marginal) means
with 95% CI of the Relative Interaction Index.
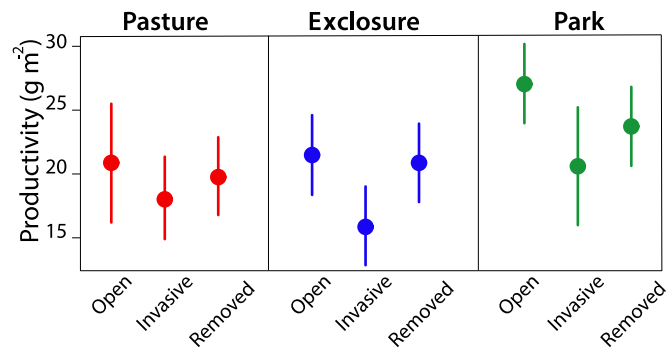
Fig. 3. Effects of land management (i.e., pasture, exclosure and park) on productivity (g

m^{-2}) across treatments (i.e., open, invasive species, and its removal). Dots represent

estimated (marginal) means with 95% CI.
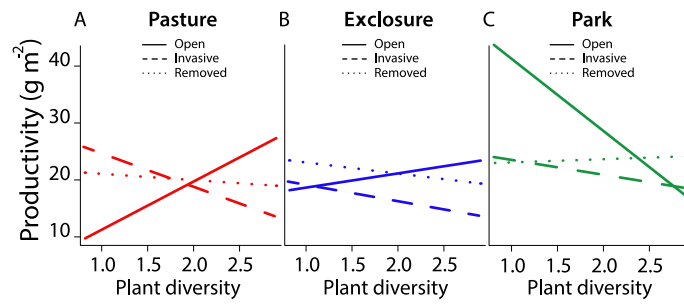
Fig. 4. Relationships between plant diversity and productivity across land-use management and treatments. (*A*) Pasture. (*B*) Exclosure. (*C*) Park. Solid lines represent open communities; dashed lines represent invasive species communities; dotted lines represent communities where invasive species was removed.

464

465   **Author contributions** G.L., T.T., and M.C.M. conceived the study; G.L., C.M.D.M., T.T., and

466   M.C.M designed the research; G.L. performed research, analyzed data and wrote the

467   paper with help from L.L.D, and M.C.M. All authors contributed to the interpretation of

468   results and provided input on the manuscript.

469   The authors declare no conflict of interest.

470

471   **Supplementary Information** is available in the online version of the paper.