1 **Historical context modifies plant diversity–community productivity relationships in**

2 **alpine grassland**

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4 Shan Luo[1,2*], Richard D. Bardgett[3*], Bernhard Schmid[4], David Johnson[3], Kenny Png[3], Urs

5 Schaffner[5], Huakun Zhou[6], Buqing Yao[6], Xiangyang Hou[7], Nicholas J. Ostle[1]

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7 [1]Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK.

8 [2]School of Agriculture and Food Science, University College Dublin, Belfield D04 V1W8,

9   Ireland.

10 [3]Department of Earth and Environmental Sciences, The University of Manchester, Oxford

11   Road, Manchester M13 PT, UK.

12 [4]Department of Geography, Remote Sensing Laboratories, University of Zürich,

13   Winterthurerstrasse 190, CH-8057 Zürich, Switzerland.

14 [5]Centre for Agriculture and Bioscience International, Rue des Grillons 1, CH-2800 Delémont,

15   Switzerland.

16 [6]Key laboratory of Restoration Ecology of Cold Area in Qinghai Province, Northwest Institute

17   of Plateau Biology, Chinese Academy of Science, Xining 810008, China.

18 [7]College of Grassland Science, Shanxi Agricultural University, Jinzhong 030801, China.

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20 [*]**Correspondence:** Shan Luo (luoshan.hi@gmail.com)

21   Richard D. Bardgett (richard.bardgett@manchester.ac.uk)

22

ABSTRACT

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24 1. While most studies yield positive relationships between biodiversity (B) and ecosystem

25 functioning (EF), awareness is growing that BEF relationships can vary with ecological context.

26 The awareness has led to increased efforts to understand how contemporary environmental

27 context modifies BEF relationships, but the role of historical context, and the mechanisms by

28 which it may influence biodiversity effects, remains poorly understood.

29 2. We examined how historical context alters plant diversity–community productivity

30 relationships via plant species interactions in alpine grassland. We also tested how historical

31 context modifies interactions between plants and arbuscular mycorrhizal (AM) fungi, which

32 can potentially mediate the above processes.

33 3. We studied biodiversity effects on plant community productivity at two grassland sites with

34 different histories related to grazing intensity — heavy versus light livestock grazing — but

35 similar current management. We assembled experimental communities of identical species

36 composition with plants from each of the two sites in disturbed soil from a contemporary

37 heavily grazed grassland, ranging in species richness from one to two, three and six species.

38 Moreover, we carried out a mycorrhizal hyphae-exclusion experiment to test how plant

39 interactions with AM fungi influence plant responses to historical context.

40 4. We detected a significantly positive diversity–productivity relationship that was driven by

41 complementarity effects in communities composed of plants from the site without heavy-

42 grazing history, but no such relationship in plant communities composed of plants from the site

43 with heavy-grazing history. Plants from the site with heavy-grazing history had increased

44 competitive ability and increased yields in low-diversity communities but disrupted

45 complementarity effects in high-diversity communities. Moreover, plants of one species from

46 the site with heavy-grazing history benefitted more from AM fungal communities than did

47 plants from the site without such history.

48 5. Synthesis: Using the same experimental design and species, communities assembled by

49 plants from two sites with different historical contexts showed different plant diversity–

50 community productivity relationships. Our results suggest that historical context can alter plant

51 diversity–community productivity relationships via plant species interactions and potentially

52 plant–soil interactions. Therefore, considering historical contexts of ecological communities is

53 of importance for advancing our understanding of long-term impacts of anthropogenic

54 disturbance on ecosystem functioning.

55

56 **KEYWORDS**

INTRODUCTION

Understanding how biodiversity (B) affects ecosystem functioning (EF) is essential for assessing the consequences of biodiversity changes under anthropogenic disturbances (Newbold et al., 2015; Tilman, May, Lehman, & Nowak, 1994). Many studies demonstrate that plant diversity can promote community productivity (Emmett Duffy, Godwin, & Cardinale, 2017; Grace et al., 2016; Tilman et al., 2001), which has been attributed to a variety of mechanisms relating to plant resource competition and plant–soil interactions (Loreau & Hector, 2001; Schnitzer et al., 2011). However, evidence is also mounting that the magnitude and sign of biodiversity effects vary with ecological context (Baert, Eisenhauer, Janssen, & De Laender, 2018; Fridley, 2001; Isbell et al., 2011). Moreover, biodiversity effects can increase over time due to the evolution of species interactions (Fiegna, Moreno-Letelier, Bell, & Barraclough, 2014; Schöb, Brooker, & Zuppinger-Dingley, 2018; Zuppinger-Dingley et al., 2014). Despite increased efforts testing the influence of contemporary environmental context on BEF relationships, the importance of historical context for biodiversity effects via plant species interactions and plant–soil interactions remains unclear. This lack of understanding hampers our ability to predict possible long-term anthropogenic impacts on ecosystem functioning.

Biodiversity effects on ecosystem functions depend on how species function differently in the presence of other species, which is mediated by species interactions (Fox, 2005; Loreau & Hector, 2001). Two classes of biodiversity effects have been proposed: complementarity and sampling effects (Fox, 2005; Loreau & Hector, 2001). The complementarity effect refers to niche complementarity and facilitation among species that increase species' functioning by reducing the intensity of competition individuals experience in diverse communities compared to monocultures. In contrast, the sampling effect is caused by an increased probability of diverse plant communities to contain competitive species with high functional contributions

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85 (Fox, 2005; Loreau & Hector, 2001). In addition to plant species interactions, there is growing

86 evidence that soil microbes contribute to positive plant diversity effects on community

87 productivity (Liang et al., 2019; Luo, Schmid, De Deyn, & Yu, 2018; Schnitzer et al., 2011),

88 for instance by promoting complementarity effects among plant species through soil nitrogen

89 partitioning (Luo et al., 2018).

90   The realized effects of mechanisms relating to plant species interactions and plant–soil

91 interactions on ecosystem functioning can be dependent upon ecological context. The nature

92 and intensity of species interactions usually change with contemporary environmental context

93 (Callaway et al., 2002; Maestre, Callaway, Valladares, & Lortie, 2009; Michalet, Le Bagousse-

94 Pinguet, Maalouf, & Lortie, 2014; A. Wright, Schnitzer, & Reich, 2014). For instance, a

95 theoretical study suggested that an intermediate level of environmental stress increases

96 interspecific competition that reduces positive complementarity effects among species, but

97 increases positive sampling effects (Baert et al., 2018). The context-dependency of species

98 interactions may thus drive varying BEF relationships under different environmental

99 conditions, including positive (Fridley, 2002; Steudel et al., 2012), non-significant (Fridley,

100 2002; Steudel et al., 2012), and even negative biodiversity effects on ecosystem functioning

101 (Wang et al., 2019). Plant–soil interactions also change with contemporary environmental

102 context. For example, high soil fertility can increase the negative effects of soil pathogens

103 (Walters & Bingham, 2007), but decrease the positive effects of mycorrhizal fungi on plants

104 (Hoeksema et al., 2010). As a result, changes in plant–microbe interactions under different soil

105 nutrient conditions can lead to different plant diversity–community productivity relationships

106 (Luo, De Deyn, Jiang, & Yu, 2017). Therefore, context-dependent plant species interactions

107 and plant–soil interactions may result in the context-dependency of BEF relationships (Baert

108 et al., 2018; Steudel et al., 2012; Wang et al., 2019).

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Plant species interactions and plant–soil interactions may not only respond to contemporary environmental context, but also to historical context. For example, plant species with 8 years of co-occurrence history in diverse community showed greater niche complementarity and facilitative interactions than did plant species with a history of growing in monoculture (Schöb et al., 2018; Zuppinger-Dingley et al., 2014). In contrast, plants with history in monoculture have been shown to benefit more from positive plant–soil interactions (Zuppinger-Dingley, Flynn, De Deyn, Petermann, & Schmid, 2016). Thus, plant responses to historical context may be contingent upon interactions with soil microbes. Because these plant interactions and plant–soil interactions underlie the functional response of ecosystems to varied levels of plant diversity, it is reasonable to expect that biodiversity effects on ecosystem functioning are also sensitive to historical context. However, it remains unclear how BEF relationships respond to historical context and how the ecological mechanisms underlying this response may vary depending on how historical context affects plant species interactions and plant–soil interactions.

Here, we investigated how historical context influences biodiversity effects on plant community productivity via plant species interactions. Arbuscular mycorrhizal (AM) fungi represent a major group of soil microbes known to influence the relationship between plant diversity and ecosystem functioning (Klironomos, McCune, Hart, & Neville, 2000; van der Heijden et al., 1998), so we also tested how historical context modifies interactions between plants and AM fungal communities to provide insights into potential belowground mechanisms underlying how historical context influences plant diversity–community relationships. We tested the effects of historical context in alpine grasslands on the Qinghai-Tibetan Plateau, using two sites with different disturbance histories related to grazing intensity — heavy versus light livestock grazing — but similar current management. We carried out an experiment of varying levels of diversity using the same six dominant species, but originating from the two

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134   sites with or without heavy-grazing histories, hereafter called "disturbed-" and "undisturbed-

135   plant types". We compared plant–plant interaction intensity and plant diversity–community

136   productivity relationships of the two plant types. Additionally, we carried out a mycorrhizal

137   hyphae-exclusion experiment (Johnson, Leake, & Read, 2001; Liang et al., 2020) to address

138   the roles of AM fungal communities in mediating plant responses to historical context.

139   Combined, the two experiments enabled us to test whether historical context modified

140   diversity–productivity relationships via plant species interactions and further plant–mycorrhiza

141   interactions.

142

143   **MATERIAL AND METHODS**

144   **Study sites and species**

145   We conducted our study at Haibei Alpine Meadow Ecosystem Research Station (latitude

146   37°29'N and longitude 101°12'E) in Qinghai Province, China. The research station lies at

147   3,200 m a.s.l. on the Qinghai-Tibetan Plateau, which is characterized by a high-elevation

148   continental climate with short cool summers and long cold winters. Mean annual temperature

149   is –1.7 °C. The annual precipitation ranges from 426 mm to 860 mm, 80% of which falls in the

150   growing season from May to September (Li et al., 2015).

151   We selected two sites (each > 4 km^2) of grassland at the Haibei Alpine Meadow

152   Ecosystem Research Station of similar topography, altitude, climate and soils, but with

153   different disturbance histories related to historic livestock grazing intensity (i.e., different

154   historical contexts). One of the two sites had a history of light livestock grazing (~ 1 ewe ha^{-1}

155   year^{-1}) from at least 1975 onwards, which we considered as a site without disturbance history

156   of heavy grazing; the other site was heavily grazed (2.5-3.5 ewe ha^{-1} year^{-1}) by livestock from

157   1981–2000, followed by 17 years of light grazing (~ 1 ewe ha^{-1} year^{-1}), which we considered

158   as a site with disturbance history of heavy grazing. Before 1975, there were no accurate records

159 of stocking rates, but both grassland sites were lightly grazed due to relatively low demand for

160 livestock products. In 2018, 18 years after heavy grazing had stopped, the two sites had reached

161 similar species composition (Figure S1a-b), but the site with disturbance history had lower soil

162 organic matter than the site without such history (Table S1).

163   We considered populations of the same plant species co-occurring at sites with and

164 without disturbance histories as two ecotypes, defining them as "disturbed-plant types" and

165 "undisturbed-plant types", respectively. We selected species that occurred at both sites and

166 with cover abundance larger than 5 %. Our six target species represented four functional groups:

167 grasses (*Elymus nutans* Griseb., *Poa annua* L.), sedges (*Kobresia humilis* (C. A. Mey ex

168 Trauvt.) Sergievskaya.), legumes (*Oxytropis kansuensis* Bunge) and herbs (*Potentilla anserina*

169 L., *Saussurea pulchra* Lipsch.). All species are perennial, except *P. annua*.

170

171 **Biodiversity experiment**

172   In May 2018, we collected disturbed soil from a contemporary heavily grazed grassland

173 located 10 km away from the two sites where we collected plants (Figure S1c-d). The soil had

174 low nitrogen availability and organic matter (Table S1), which is typical of heavily grazed

175 grasslands on the Qinghai-Tibetan Plateau (Dong et al., 2012). The disturbed soil was used to

176 mimic conditions associated with contemporary heavy grazing and was used in preference to

177 the heavily grazed grassland site where plants were collected, given that it had been under light

178 grazing since 2000. Further, by growing plant species taken from the two grasslands with

179 different disturbance histories in a single disturbed-soil type we were able to test how plant

180 diversity–community productivity relationships respond to heavy grazing depending on plant

181 disturbance histories (i.e., historical context), but independent of differences in soil conditions.

182   We conducted a biodiversity experiment in the field of the Haibei Alpine Meadow

183 Ecosystem Research Station. We collected disturbed- and undisturbed-plant types from the two

184 corresponding sites. We excavated single adult plants across flat areas of about 500×500 m at

185 each site to a depth of 10 cm and carefully washed the roots to remove most rhizosphere soil.

186 We chose plants with similar root sizes for the two plant types of the same species and

187 randomly assigned them to the different treatments described below. We filled pots of 20 cm

188 diameter and 25 cm height with 7 L of the disturbed soil. For each plant-type treatment, we

189 transplanted 12 plants of the same type and assembled plant communities into pots at four

190 species richness levels (one, two, three and six species; Figure 1). We grew 12 plants per pot

191 to ensure that the whole surface area of each pot was covered by adult plants. We planted the

192 six species in monocultures (richness level of one), seven two-species compositions, nine three-

193 species compositions and the six-species mixture with the species in equal proportions and the

194 same total density of 12 individuals per pot. We assembled communities of two and three

195 species by constrained random selection from the six-species pool to form partially crossed

196 gradients of species richness and functional group richness (Hector, Bazeley-White, Loreau,

197 Otway, & Schmid, 2002). The six-species mixtures were replicated nine times and all other

198 communities were replicated three times. In total, there were 150 pots and 1,800 plant

199 individuals (150 pots $\times$ 12 individuals). To quantify plant–plant interaction intensity in

200 monocultures and mixtures (Schöb et al., 2018), we additionally transplanted single plants into

201 pots (i.e. single-plant pots) for each plant type and species. Single-plant pots were replicated

202 10 times yielding a total of 120 pots (6 species $\times$ 2 plant types $\times$ 10 replicates). We placed all

203 270 pots into 3 blocks with random positions. To minimize transplantation-related issues we

204 transplanted plants after they had started sprouting, therefore they experienced experimental

205 conditions during most of their seasonal growth phase. We additionally clipped plants to 1 cm

206 above the soil surface to standardize their initial shoot sizes and reduce water stress during

207 transplantation and protected them with shade cloth for one week after transplantation. Plants

208 that died in the first two weeks were replaced. Note that transplants in contrast to plants raised

209 from seeds are genetically identical to the field-grown plants and they contain soil microbes

210 from the field, which made our experimental set-ups more realistic.

211 Plants were watered by hand twice a week, with ~1 L tap water each time, and were

212 grown for 20 weeks starting from May to September 2018. The experiment was not run longer

213 as we wanted to avoid changes in richness or evenness due to mortality under challenging

214 alpine conditions. Plant survival throughout the experiment was 96.3% and did not differ

215 between monocultures and species mixtures. We harvested the aboveground plant parts. We

216 determined the dry weight for each plant in single-plant pots and for each species in

217 monocultures and mixtures. Given the short duration of the experiment, our measures of plant

218 biomass reflect plant growth over 20 weeks.

219 At the time of harvest, we measured specific leaf area (SLA) for each plant type per

220 species in monocultures and mixtures to assess whether undisturbed- and disturbed-plant types

221 differed in phenotypes. SLA is associated with plant strategies to acquire resources such as

222 light and nutrients (Westoby, Falster, Moles, Vesk, & Wright, 2002; Wright et al., 2004), and

223 hence represents a key functional trait that can regulate plant growth and productivity. We

224 randomly selected three plants from different monocultures, two plants from each two- and

225 three-species composition, and seven plants from seven six-species mixtures per plant type per

226 species. We scanned 5–30 mature, fully expanded leaves per plant at 300 dpi to obtain fresh

227 leaf area using ImageJ software (NIH, Bethesda, MD, USA) within 5h after harvest. Before

228 scanning, all sampled leaves were wrapped in moist filter paper and packed into resealable

229 plastic bags. We determined the dry mass of scanned leaves to calculate SLA per plant.

230

231 **Mycorrhizal hyphae-exclusion experiment**

232 To test how historical context influences plant–mycorrhiza interactions, we conducted a

233 mycorrhizal hyphae-exclusion experiment (Johnson et al., 2001; Liang et al., 2020). We

234   assembled mesh-walled cores from 10 cm diameter × 15 cm deep PVC piping, perforated with

235   two 4-cm-diameter windows. The windows and the bottom were covered with 35-µm or 1-µm

236   nylon mesh (Plastok Associates Ltd, Birkenhead, UK). While nylon mesh with a pore size of

237   35-µm allows the formation of mycorrhizal networks between transplanted plants and

238   surrounding vegetation outside the cores, a mesh with a pore size of 1-µm has been shown to

239   be efficient in preventing hyphal penetration through mesh barriers since the typical diameter

240   of AM fungal hyphae is 2–20 µm (Johnson & Gilbert, 2015; van der Heijden & Horton, 2009).

241   Therefore, this hyphae-exclusion method is an effective means of preventing the formation of

242   mycorrhizal networks (Friese & Allen 1991; Johnson *et al.* 2001; Nottingham *et al.* 2010;

243   Liang *et al.* 2020).

244   In May 2018, we grew disturbed- and undisturbed-plant types in mesh-walled cores at

245   the site with a disturbance history of heavy grazing. This allowed us to test whether the two

246   plant types benefitted differently from being able to form mycorrhizal associations with

247   surrounding disturbed-type vegetation, and thus how historical context influenced plant–

248   mycorrhiza interactions. Being consistent with our biodiversity experiment that grew plants in

249   a single type of disturbed soil, this hyphae-exclusion experiment may provide insights into

250   potential belowground mechanisms underlying how historical context influenced plant

251   diversity–community productivity relationships. We used the two plant types of four species

252   representing our four functional groups: *E. nutans*, *K. humilis*, *O. kansuensis* and *P. anserina*.

253   We established 8 plots (1 × 1 m) within a 5 × 20 m area, with a distance of 1 m between plots.

254   Within each plot, we randomly allocated four cores (two with 35-µm mesh and two with 1-µm

255   mesh, which, respectively, allowed for and prevented the formation of mycorrhizal networks

256   between transplanted plants and surrounding vegetation outside the cores; Johnson *et al.* 2001;

257   Liang *et al.* 2020) into the centre of the four quadrants (0.5 × 0.5 m). We excavated holes in

258   the centre of quadrants by forcing a 10-cm-diameter tube into the soil and collected the top 15

259   cm of soil. The soil was thoroughly mixed and backfilled into cores at a similar bulk density to

260   the field soil. We transplanted eight plants of the same type into each core with the four species

261   in equal proportions. Plants were collected and transplanted as described in the biodiversity

262   experiment. We acknowledge that these plants could already have been colonized by AM fungi

263   but this should not have caused any confounding with the experimental treatment because it

264   should have been the same on average for both treatment groups. Again, we clipped plants to

265   1 cm above the soil surface to standardize their initial shoot sizes and reduce water stress during

266   transplantation. We protected plants with shade cloth for one week after transplantation and

267   replaced plants that died within the first two weeks. We fenced the experimental areas to

268   exclude grazing. Plants were watered by hand twice a week, with ~ 500 ml tap water each time,

269   and were grown for 20 weeks until September 2018. We harvested the aboveground part of

270   plants and determined the dry weight of each species.

271

272   **Plant interaction analyses**

273   To evaluate plant–plant interactions within pots, we calculated the cumulative neighbour-

274   effect intensity index (NIntC) for each monoculture and mixture in the biodiversity experiment

275   (Díaz-Sierra, Verwijmeren, Rietkerk, de Dios, & Baudena, 2017). We compared the

276   performance of plants in single-plant pots with that of plants growing with intraspecific or

277   interspecific neighbours in communities. For plants grown in single-plant pots, we calculated

278   the mean biomass per plant type per species. For each target species (i) biomass per individual

279   (b) was determined in single-plant pots (c) and communities (t) ($b_{(c,i)}$ and $b_{(t,i)}$, respectively).

280   The response of species i in community t was assessed as net neighbourhood effect:

281    $$NIntC_{(t,i)} = 2 \frac{b_{(t,i)} - b_{(c,i)}}{b_{(t,i)} + b_{(c,i)} + \left| b_{(t,i)} - b_{(c,i)} \right|}$$

282   which quantified relative change in individual biomass of a species in a community compared

283   with its biomass as a single plant. We set zero biomass for dead plants and the calculation was

284 based on planted density. The NIntC ranges from –1 to 1, with more negative values indicating

285 stronger competitive interactions (Díaz-Sierra et al., 2017). We did not partition net interactions

286 into facilitative and competitive interactions due to the rarity of facilitation in our case (20 of

287 369 plants; 5.4%). Comparisons of net neighbourhood effects among communities across plant

288 species richness levels and with different histories indicate differences in the net outcome of

289 plant–plant interactions on productivity among those communities.

290

291 **Statistical analysis**

292   We tested the response of aboveground community productivity, aboveground species

293 productivity and SLA to historical contexts and species richness. With regard to our specific

294 experiments we used "plant history" synonymous to "disturbance history". First, we tested how

295 plant history affected diversity–community productivity relationships using a linear mixed-

296 effects model. Community productivity and plant species richness were log-transformed. We

297 included plant history (disturbed- vs. undisturbed-plant types), the presence of *O. kansuensis*,

298 plant species richness and the two-way interactions among these variables as fixed terms.

299 Community composition and its interaction with plant history were included as random terms.

300 *Oxytropis kansuensis* was the only legume in our experiment and its presence was thus included

301 as a covariate to account for nitrogen-fixing effects (Schmid, Baruffol, Wang, & Niklaus, 2017;

302 Zuppinger-Dingley et al., 2014). Second, we analysed productivity of plant communities with

303 different histories separately using linear mixed-effects models. We included the presence of

304 *O. kansuensis* and log-transformed plant species richness as fixed terms and community

305 composition as a random term. For all linear mixed-effects models we used restricted

306 maximum likelihood estimation and assessed the significance of the fixed effects using type-I

307 ANOVA and *F* tests with adjusted error terms and the Satterthwaite approximation of

308 denominator degrees of freedom. We did not include blocks in the above models because

13

309 variation among blocks contributed little to the overall variation of community productivity.

310 Third, we analysed the response of individual species to the plant-history treatments. We used

311 log-ratios of biomass of disturbed- and undisturbed-plant types for each species averaged over

312 four species richness levels and species compositions within richness levels. We used t-test to

313 assess the significance of differences between log-ratios and zero. Fourth, we tested whether

314 plant history affected SLA of individual species. We used hierarchical analysis of variance

315 (ANOVA), which corresponds to mixed-model analysis but is more flexible in the case of

316 balanced data sets (Schmid et al., 2017). We fitted species identity, plant history, species

317 richness and the two-way interactions among these variables after block as explanatory

318 variables, and community composition as an error term in the model. The F values for species

319 richness were calculated with the mean square of community composition as denominator

320 (Schmid et al., 2017). Similar procedures were applied to each species by removing species

321 identity and its interaction terms from models.

322   To test how plant history affected biodiversity effects, we partitioned net biodiversity

323 effects (NEs) into complementarity effects (CEs) and sampling effects (SEs) following an

324 additive partitioning method (Loreau & Hector, 2001). Calculations were based on the

325 difference between the observed yield of each species in the mixture and mean monoculture

326 yield for that species for the specific plant history. Absolute values of SEs were square root-

327 transformed, with the transformed values preserving their original signs for analysis (Loreau

328 & Hector, 2001). We used hierarchical ANOVA by including plant history, the presence of *O.*

329 *kansuensis*, plant species richness and the two-way interactions among these variables as

330 explanatory variables, community composition as an error term and the NE, CE and SE as

331 response variables in separate models. We also tested whether the overall means of the NE, CE

332 and SE were different from zero, listing the significance of the intercept in the corresponding

333 ANOVA. The F values for species richness were calculated with the mean square of

334 community composition as denominator. Here, we did not include blocks in our final models

335 due to low variation among blocks.

336 We estimated how plant history affected plant–plant interactions. We analysed the net

337 neighbourhood effect (i.e. NIntC) on target species as a function of design variables using a

338 linear mixed-effects model. The fixed terms were log-transformed plant species richness, plant

339 history, target species is a legume (yes or no), neighbour species is a legume (yes or no) and

340 their interactions. The random terms were target species identity and neighbourhood species

341 composition.

342 For the mycorrhizal hyphae-exclusion experiment, we tested whether disturbed- and

343 undisturbed-plant types performed differently depending on access to mycorrhizal networks of

344 surrounding vegetation and species identity. We used ANOVA to detect differences in

345 aboveground biomass between species, plant history and AMF treatment (mesh sizes 1- vs. 35-

346 µm preventing or allowing the interaction between transplanted plants and surrounding

347 vegetation via AM fungal networks), with plot, species identity, plant history, AMF treatment

348 and their interactions fitted sequentially. We applied similar procedures to each species by

349 removing species identity and its interaction terms from models. We also applied t-tests to each

350 species to test the differences between the two plant types at each AMF treatment. All statistical

351 analyses were conducted in R version 4.0.3.

352

353 **RESULTS**

354 **Plant diversity–community productivity relationships vary with historical context**

355 Overall, aboveground community productivity increased with increasing plant species

356 richness (Figure 2; Model A in Table S2: $P = 0.043$ for log richness). However, the slope of

357 the plant species richness–community productivity relationship was steeper for undisturbed-

358 than disturbed-plant types (Model A in Table S2: $P = 0.019$ for interaction plant history $\times$ log

359   richness). When analysed separately, the species richness–community productivity relationship

360   was significantly positive for undisturbed-plant types originating from the site without heavy-

361   grazing history, but non-significant for disturbed-plant types originating from the site with

362   heavy-grazing history (Model B & Model C in Table S2). This suggests that different historical

363   contexts, represented by the same plant species originating from two grassland sites with

364   different disturbance histories, led to different plant diversity–community productivity

365   relationships. Furthermore, communities assembled with disturbed-plant types showed

366   significantly weaker biodiversity net effects and complementarity effects than communities

367   assembled with undisturbed-plant types (Figure 3; Table S3: $P = 0.007$ & $P < 0.001$ for plant-

368   history effect on NE and CE, respectively). Communities composed of disturbed-plant types

369   showed larger sampling effects than those of undisturbed-plant types, which was not

370   significantly different from zero (Figure 3; Table S3: $P < 0.001$ for plant-history effect on SE).

371   Therefore, the non-significant relationship between plant diversity and community productivity

372   was mainly attributed to the loss of complementarity effects for disturbed-plant types.

373   However, disturbed-plant types achieved higher aboveground productivity than did

374   undisturbed-plant types, both at the community and species levels. Productivity was 11.8%

375   higher on average for communities assembled with disturbed- than with undisturbed-plant

376   types (Figure 2; Model A in Table S2: $P = 0.007$ for plant history). In particular, legumes and

377   herbs of disturbed-plant types achieved higher productivity than did undisturbed-plant types of

378   these two functional groups (Figure S2). Moreover, SLA significantly differed between the two

379   plant types in herbs, with larger SLA of disturbed- than undisturbed-plant types in *Potentilla*

380   *anserina*, and the opposite difference between plant types in *Saussurea pulchra* (Model F and

381   G in Table S4: $P = 0.042$ and $P = 0.034$ for plant history, respectively). For the legume *O.*

382   *kansuensis*, SLA did not show significant differences between plant types.

383

Plant species interactions vary with historical context

The analysis of neighbourhood interaction intensities showed that across plant species-richness levels, disturbed-plant types competed more heavily than did undisturbed-plant types (Figure 4; Table S5: $P < 0.001$ for plant history). Consistently, for the legume *O. kansuensis*, competitive interaction was stronger in disturbed- than undisturbed-plant types [NIntC = –0.57 ± 0.04 (mean ± SE) and NIntC = –0.02 ± 0.08, respectively; Table S5: $P < 0.001$ for interaction plant history × target legume]. Therefore, differences in plant species interactions were related to differences in historical context from which plants derived.

Plant–soil interactions vary with historical context

Disturbed- and undisturbed-plant types responded differently to mycorrhizal hyphae exclusion depending on species identity (Figure 5; Model A in Table S6: $P = 0.011$ for interaction ID × plant history × AMF treatment). For the legume *O. kansuensis*, the disturbed-plant types had greater aboveground biomass than did undisturbed-plant types when they had access to mycorrhizal hyphae of surrounding disturbed-type vegetation, but not when access to surrounding mycorrhizal hyphae was prevented (Figure 5c; Model D in Table S6: $P = 0.026$ for interaction plant history × AMF treatment). Plant species of the other three functional groups did not show such a response (Figure 5; Table S6).

DISCUSSION

Our results demonstrate that communities assembled with undisturbed-plant types showed a positive plant diversity–productivity relationship, whereas communities assembled with disturbed-plant types displayed a non-significant plant diversity–productivity relationship and a lack of complementarity effects. We also found that competition was consistently stronger for disturbed- than undisturbed-plant types, and that, for one species, disturbed-plant

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409   types benefitted more from having access to mycorrhizal hyphae of surrounding disturbed-type

410   vegetation than did undisturbed-type plants. These results suggest that historical context can

411   alter biodiversity effects on plant community productivity by modifying plant species

412   interactions, and that historical context can mediate plant–mycorrhiza interactions.

413   Communities assembled by undisturbed-plant types showed a positive plant diversity–

414   community productivity relationship, which was driven by positive complementarity effects.

415   We note, however, that negative sampling effects of undisturbed-plant types may also suggest

416   pathogen control of dominant species (Mordecai, 2011; Morris et al., 2007). As such, it is

417   conceivable that complementarity effects in communities composed of undisturbed-plant types

418   may have included complementary pathogen niches (Petermann, Fergus, Turnbull, & Schmid,

419   2008; Turnbull, Isbell, Purves, Loreau, & Hector, 2016) and resource complementarity. We

420   acknowledge that our study used transplants that contained soil microbes from the field; while

421   making our experimental set-up more realistic, it is possible that those soil microbes have

422   influenced plant productivity. For example, it is possible that during transplantation

423   undisturbed-plant types harboured more beneficial soil microorganisms than did disturbed-

424   plant types, which may have been amplified in diverse plant communities and contributed to

425   the positive plant diversity effects on community productivity in undisturbed-plant types.

426   By analyzing neighbourhood interaction intensities, we found that disturbed-plant types

427   experienced more intense competition than undisturbed-plant types. This suggests that the

428   response of disturbed-plant types to historical disturbance may have involved an increase of

429   plant competition. Consistently, the sampling effects in communities composed of disturbed-

430   plant types indicate the importance of competitive hierarchies between species in these

431   communities (Luo et al., 2020). The lack of complementarity effects also indicates an increase

432   of interspecific competition that prevents niche partitioning among plant species (Baert et al.,

433   2018). As a result, the strong competition among disturbed-plant types may have led to the loss

434   of complementarity effects and a non-significant plant diversity–productivity relationship. This

435   is consistent with studies showing that certain levels of environmental stress can increase

436   species competition (Alba, Fahey, & Flory, 2019; De Boeck et al., 2007; Olsen, Töpper,

437   Skarpaas, Vandvik, & Klanderud, 2016; but see Callaway et al., 2002) and that species

438   competition reduces biodiversity effects on ecosystem functioning (Dimitrakopoulos &

439   Schmid, 2004; Paquette & Messier, 2011). Together, our biodiversity experiment indicates that

440   historical context can shape plant diversity–community productivity relationships by

441   modifying plant species interactions. This finding is consistent with studies showing that BEF

442   relationships can be contingent on the evolutionary history of species interactions (Aubree et

443   al., 2020; Gravel et al., 2011; van Moorsel et al., 2018, 2021) and points to the importance of

444   historical context in studies of BEF relationships.

445   Despite the lack of significant biodiversity effects, communities assembled by disturbed-

446   plant types had higher productivity than that of undisturbed plant types. Consistently, legumes

447   and herbs achieved higher productivity in their disturbed- than undisturbed-plant types. In

448   particular, for the legumes, disturbed-plant types showed more intense competitive interaction

449   than did undisturbed-plant types, suggesting a stronger competitive ability of disturbed-plant

450   types that can increase productivity (Mouquet, Moore, & Loreau, 2002; Tilman, Lehman, &

451   Thomson, 1997). Moreover, two herbs species showed opposite differences in SLA between

452   the two plant types, which can potentially increase SLA differences and complementarity

453   between herbs in response to heavy grazing (Zuppinger-Dingley *et al.* 2014), leading to

454   increased productivity of disturbed-type plants of herbs. These results suggest that disturbed-

455   plant types have responded to historical disturbance by increasing competitive ability and

456   productivity, which potentially depends on functional traits. This may partly explain the higher

457   community productivity of disturbed- than undisturbed-plant types.

458   The increased competitive ability and productivity of disturbed-plant types may result

459   from their adaptation to historical disturbance, including heavy grazing and the accompaying

460   changes of abiotic and biotic environmental conditions (Dong et al., 2012; Liu et al., 2020;

461   Wang et al., 2018; Yang et al., 2018). On the one hand, plants with high competitive ability

462   and productivity can increase community productivity via sampling effects (Loreau & Hector

463   2001), whereas on the other hand, they may exert strong competitive effects on co-occuring

464   species that can alter the evolutionay trajectory of plant species interactions (Terhorst et al.,

465   2018; Thompson, 1998; Whitham, Allan, Cooper, & Shuster, 2020), as many adaptations are

466   involving the means of acquiring resources in changing environments (Ackerly, 2003).

467   Consequently, the intense plant species competition can disrupt complementarity effects as

468   disscussed above. Consistent with this, other studies have shown the adaptation of plants to

469   changing environments, including grazing pressure (Davis, Shaw, & Etterson, 2005; Ren et al.,

470   2017), which could happen over a few years (Meilhac, Deschamps, Maire, Flajoulot, & Litrico,

471   2020). In particular, the potential adaptation of legumes to heavy grazing and associated

472   infertile soils may be related to their nitrogen-fixing ability. There is aslo the possibility of

473   priming (i.e., increased genetic disposition for plasticity) of disturbed-plant types in disturbed

474   soil (Conrath et al., 2006), and disturbed-plant types may have responded to historical

475   disturbance via epigenetic change. This latter possibility has been tested and rejected in a recent

476   biodiversity selection experiment in grassland, where epigenetic changes were largely due to

477   genetic changes (van Moorsel et al., 2019). Also, the observed responses of disturbed-plant

478   types could be due to maternal carry-over effects. However, both sites have experienced similar

479   histories over the last 17 years, which we considered as similar to growing plants under uniform

480   conditions for certain time that allowed carry-over effects to diminish (Weiner, Martinez, Stoll,

481   & Schmid, 1997). Therefore, the observed differences between disturbed- and undisturbed

482   plant types were most likely caused by the evolutionary responses of disturbed-plant types to

483 historical disturbance over a long period of time, which can lead to different plant diversity–

484 community productivity relationships via plant competitive processes.

485   When having access to mycorrhizal hyphae of surrounding disturbed-type vegetation,

486 disturbed-type *O. kansuensis* plants had higher aboveground biomass than undisturbed-type

487 plants. As the hyphae-exclusion method is an effective means of preventing the formation of

488 mycorrhizal associations (Johnson *et al.* 2001; Liang et al. 2020), it seems reasonable to

489 attribute the observed difference in biomass of the two plant types to associations with

490 mycorrhizal networks. In particular, it is possible that the disturbed-type *O. kansuensis* plants

491 could effectively integrate into the mycorrhizal networks of surrounding disturbed-type

492 vegetation from which they gained benefits in terms of enhanced growth (Johnson & Gilbert,

493 2015; Klein, Siegwolf, & Körner, 2016; van der Heijden & Horton, 2009). We acknowledge

494 that plant species from the other three functonal groups did not show such positive effects of

495 mycorrhizal fungi and that additional examination of the response of belowgound biomass

496 might have improved the possibility of detecting mycorrhizal effects. However, it is

497 conceivable that the response of disurbed-plant types to historcial heavy grazing may have

498 involved the enhancement of positive plant–mycorrhiza feedbacks, at least for the single

499 legume species (Zuppinger-Dingley et al., 2016). AM fungi can co-evolve with plants to

500 maximize mutualistic effects of symbioses under environmental stresses, such as resource

501 limitation (Johnson, Wilson, Bowker, Wilson, & Miller, 2010; Petipas, Geber, & Lau, 2021;

502 Rúa et al., 2016), so it is possible that heavy grazing and associated low soil nutrient availability

503 (Table S1) contributed to the enhancement of positive plant–mycorrhiza feedbacks. This is

504 consistent with the knowledge that plants depend more on AM fungi for nutrient acquisition in

505 less fertile soils (Hoeksema et al., 2010). As AM fungal communities in soils associated with

506 historical and contemporary heavy grazing were likely to be comparable, the above finding

507 may provide insights into potential belowground mechanisms underlying the different

508   responses of the two plant types to disturbed soil associated with contemporary heavy grazing

509   in our biodiversity experiments. It is conceivable that the two plant types might have interacted

510   differently with AM fungal communities contained in disturbed soil. Specifically, undisturbed-

511   plant types might be less effective when interacting with AM fungi in disturbed soil and thus

512   suffered more from pathogenic fungi than did disturbed-plant types, especially in low-diversity

513   communities (Schnitzer et al., 2011), which may have partly contributed to the positive

514   diversity–productivity relationship. In contrast, disturbed-plant types may have benefitted

515   more from interacting with AM fungi than did undisturbed-plant types in disturbed soil due to

516   the enhancement of positive plant–mycorrhiza feedbacks, which may have partly contributed

517   to the increased competitive ability and monoculture yields of disturbed-plant types, at least

518   for the legumes.

519

520   **CONCLUSIONS**

521   Our study shows that plant diversity–community productivity relationships depend on

522   historical context. In particular, we found a significantly positive diversity–productivity

523   relationship in communities composed of plants without heavy-grazing history, which was

524   driven by complementarity effects, but a non-significant diversity–productivity relationship

525   and a lack of complementarity effects in communities of plants with a history of heavy

526   livestock grazing. This finding may be attributed to plants responding to historical heavy

527   grazing with increased competitive ability that disrupted complementarity effects in high-

528   diversity communities, but increased yields in low-diversity communities. We also found that

529   plants of one legume species with heavy-grazing history responded more positively to

530   interactions with symbiotic soil fungal communities than did plants without such history.

531   Overall, our results indicate that historical context can alter plant diversity–community

532   productivity relationships via plant species interactions and potentially plant–soil interactions.

Thus, prolonged anthropogenic disturbance may have long-lasting impacts on biodiversity and ecosystem functioning (Macdougall, McCann, Gellner, & Turkington, 2013; Turner, 2010). We suggest that future studies of BEF relationships will need to incorporate historical perspectives that explicitly consider the historical context of ecological communities.

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768   **SUPPORTING INFORMATION**

769   Additional supporting information may be found online in the Supporting Information section

770   for this article.

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772   **DATA AVAILABILITY STATEMENT**

773   Data available from the Dryad Data Repository https://doi.org/10.5061/dryad.dv41ns21k (Luo

774   et al. 2022)

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782 with/key-donors/). We thank Walan Cuo and Lin Wang for assistance in the field. We are

783 grateful to Dr Yuxin Chen for providing comments on early versions of the manuscript.

784

785 **CONFLICT OF INTEREST**

786 There is no conflict of interest for any of the authors.
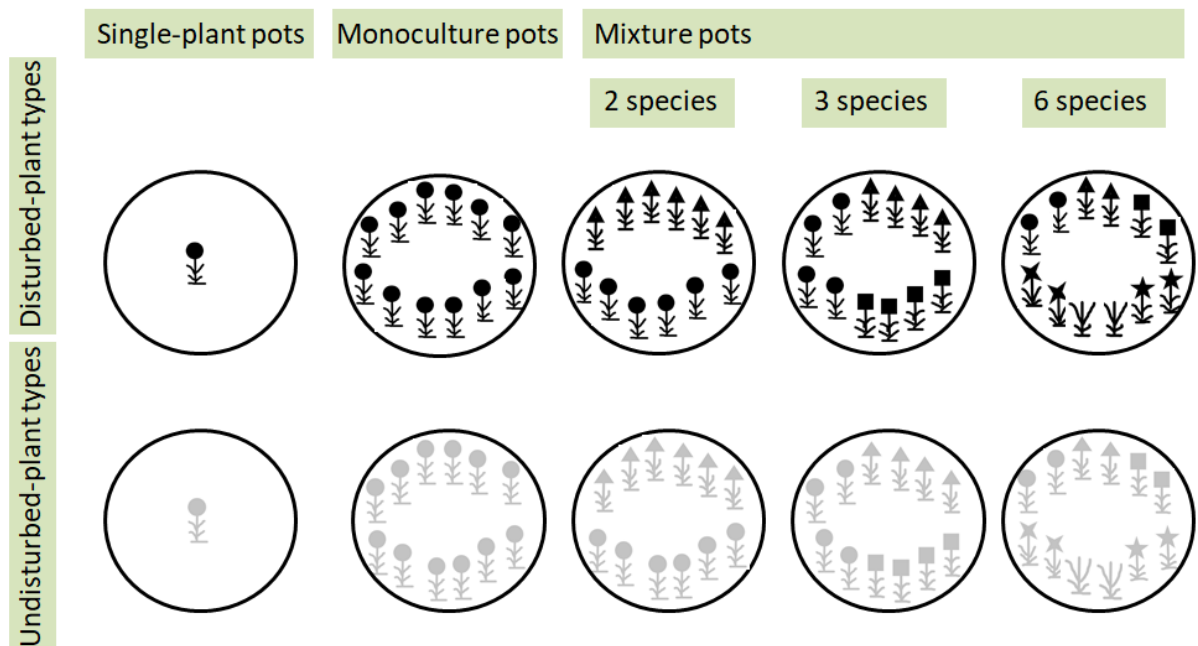
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788 **AUTHOR CONTRIBUTIONS**

789 RDB gained funding for the study with NJO. SL conceived the idea and designed the

790 experiment with input from NJO, RDB, BS and DJ. SL conducted the experiment and analysed

791 the data. SL wrote the manuscript in close consultation with RDB and BS. All authors

792 contributed to the final manuscript.

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FIGURES & TABLES

Figure 1 Design of the biodiversity experiment. Single-plant, monoculture and mixture pots were set up, separately for disturbed (black)- and undisturbed (grey)-plant types. Single-plant pots hosted one individual and were replicated 10 times per species per plant type (n = 120 pots). Monocultures hosted 12 individuals of one species and were replicated 3 times for each species and each plant type (n = 36 pots). Mixtures hosted 12 individuals of two, three, or six species (n = 42, 54, or 18 pots).

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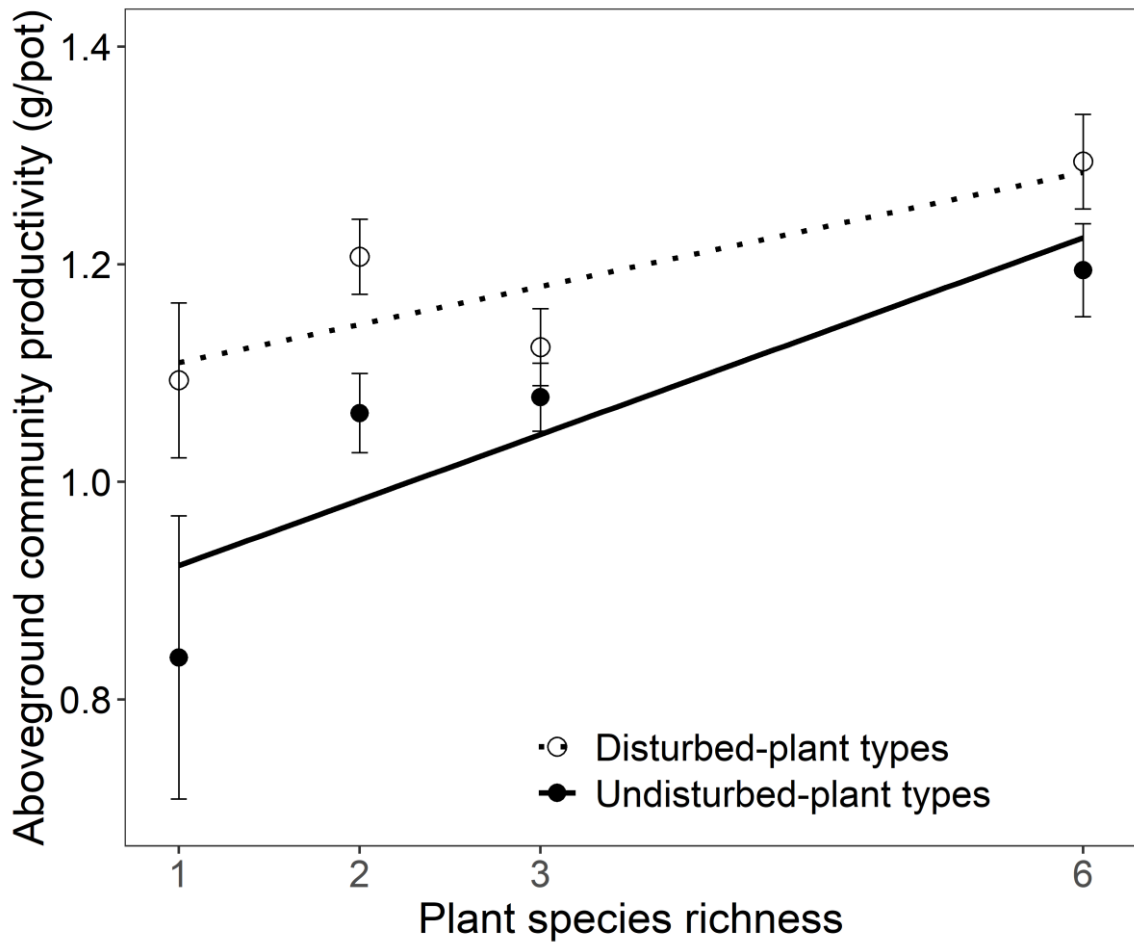
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807 **Figure 2** Species richness–productivity relationships for communities assembled with

808 undisturbed- and disturbed-plant types. Solid line indicates significant and dotted line indicates

809 insignificant relationships (the interaction term plant history × log richness was significant;

810 Table S2). Dots represent means (± SE) at each richness level, where values of aboveground

811 community productivity were adjusted by the variation explained by *Oxytropis kansuensis*.

812 Specifically, we fitted *O. kansuensis* first in the ANOVA and took the residuals. Then we added

813 those residuals to the overall mean value of community productivity (log10-scale) as adjusted

814 values of community productivity.
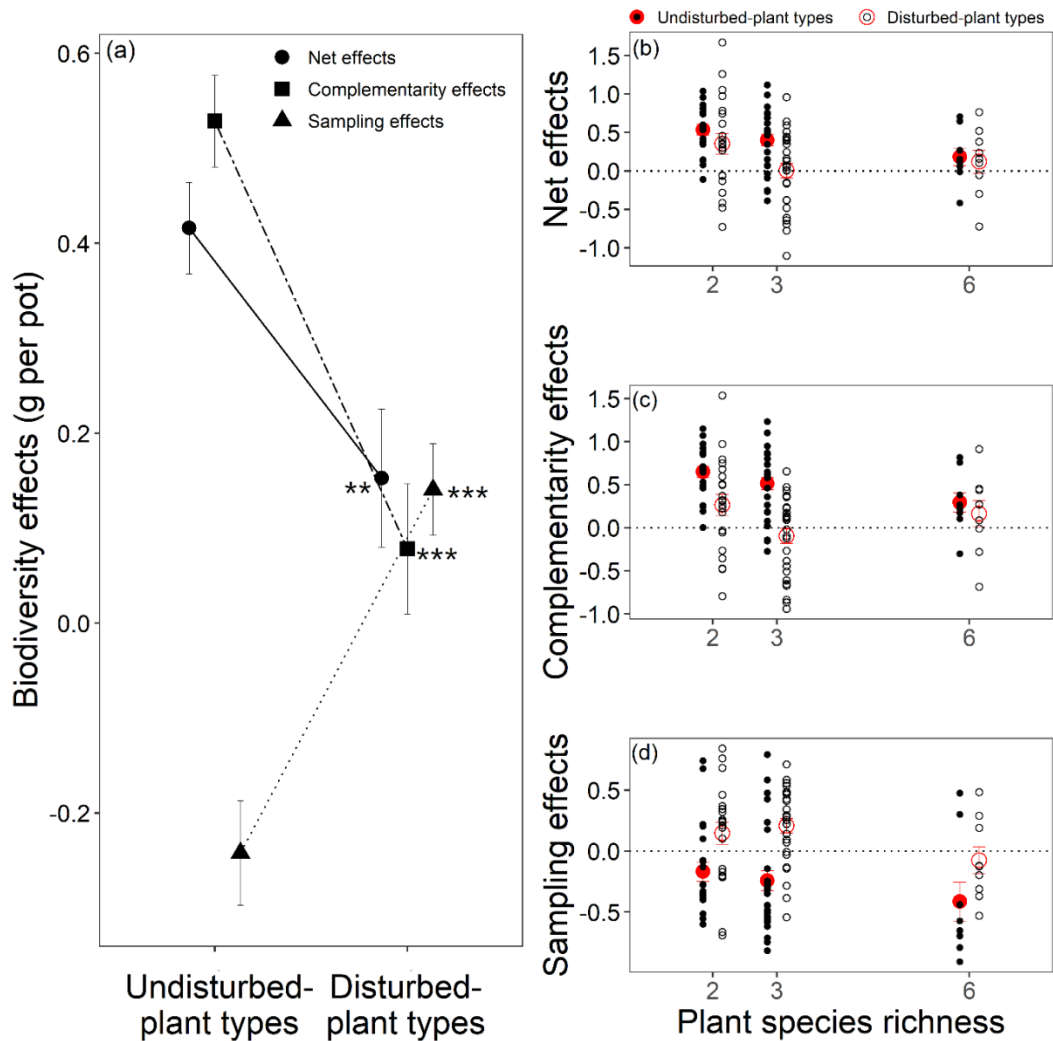
Figure 3 Biodiversity effects for communities assembled with undisturbed- and disturbed-plant types. (a) Biodiversity effects (net, complementarity and sampling effects) in the mixtures of disturbed- and undisturbed-plant types. Values are means (± SE). '**' and '***' indicate statistically significant differences between the two plant types ($P = 0.007$ and $P < 0.001$, respectively). (b–d) Biodiversity effects split into net, complementarity and sampling effects of disturbed- and undisturbed-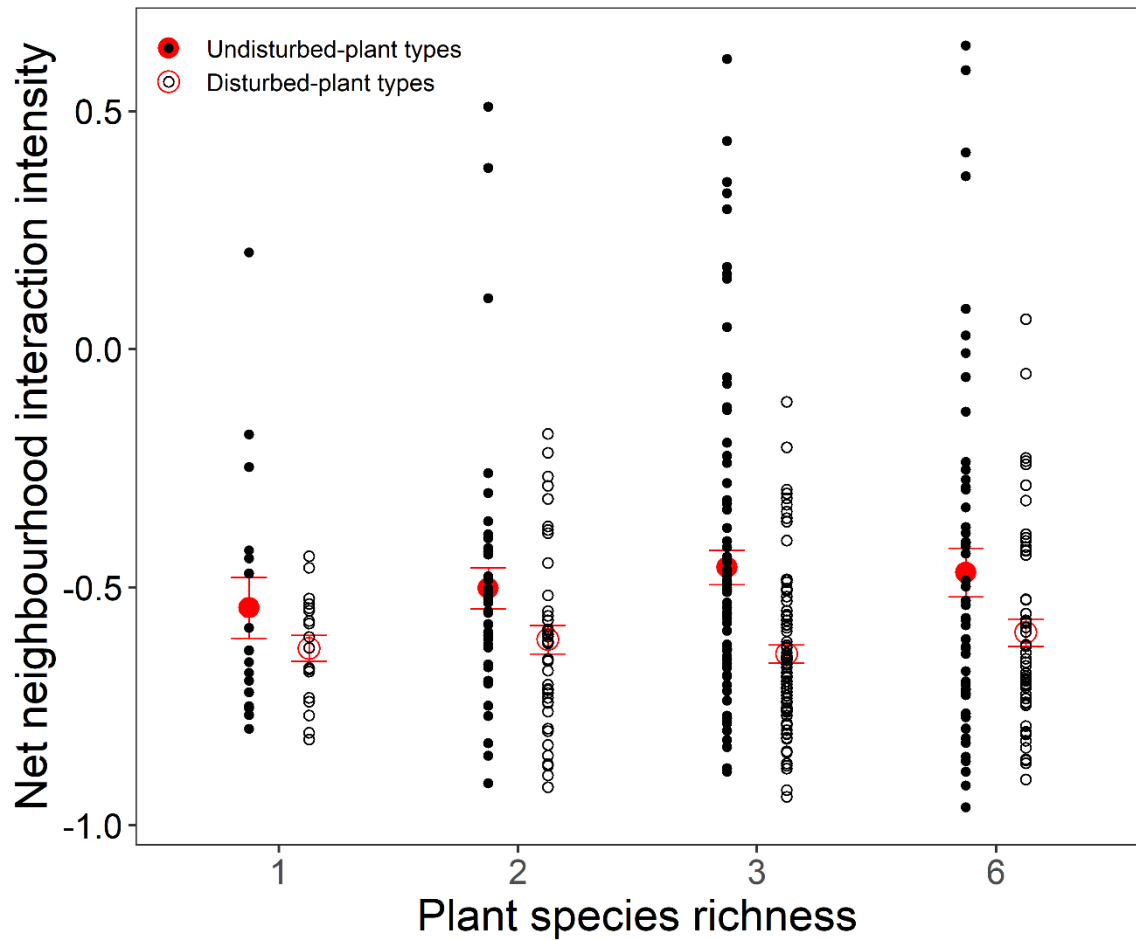plant types per species–richness level. Black dots represent observed values, whereas red dots represent means (± SE) calculated from observed values at each richness level. To make it consistent with the adjusted community productivity in Fig. 2, biodiversity effects were adjusted by the variation explained by *Oxytropis kansuensis*. For this, we fitted *O. kansuensis* first in the ANOVA separately for each biodiversity effect and took the

826   residuals. Then we added residuals to the overall mean values of corresponding biodiversity

827   effects as adjusted values of biodiversity effects.

Figure 4 Net neighbourhood interaction intensity in communities assembled with undisturbed- and disturbed-plant types. Black dots represent observed values, whereas red dots represent means (± SE) calculated from observed values at each richness level.
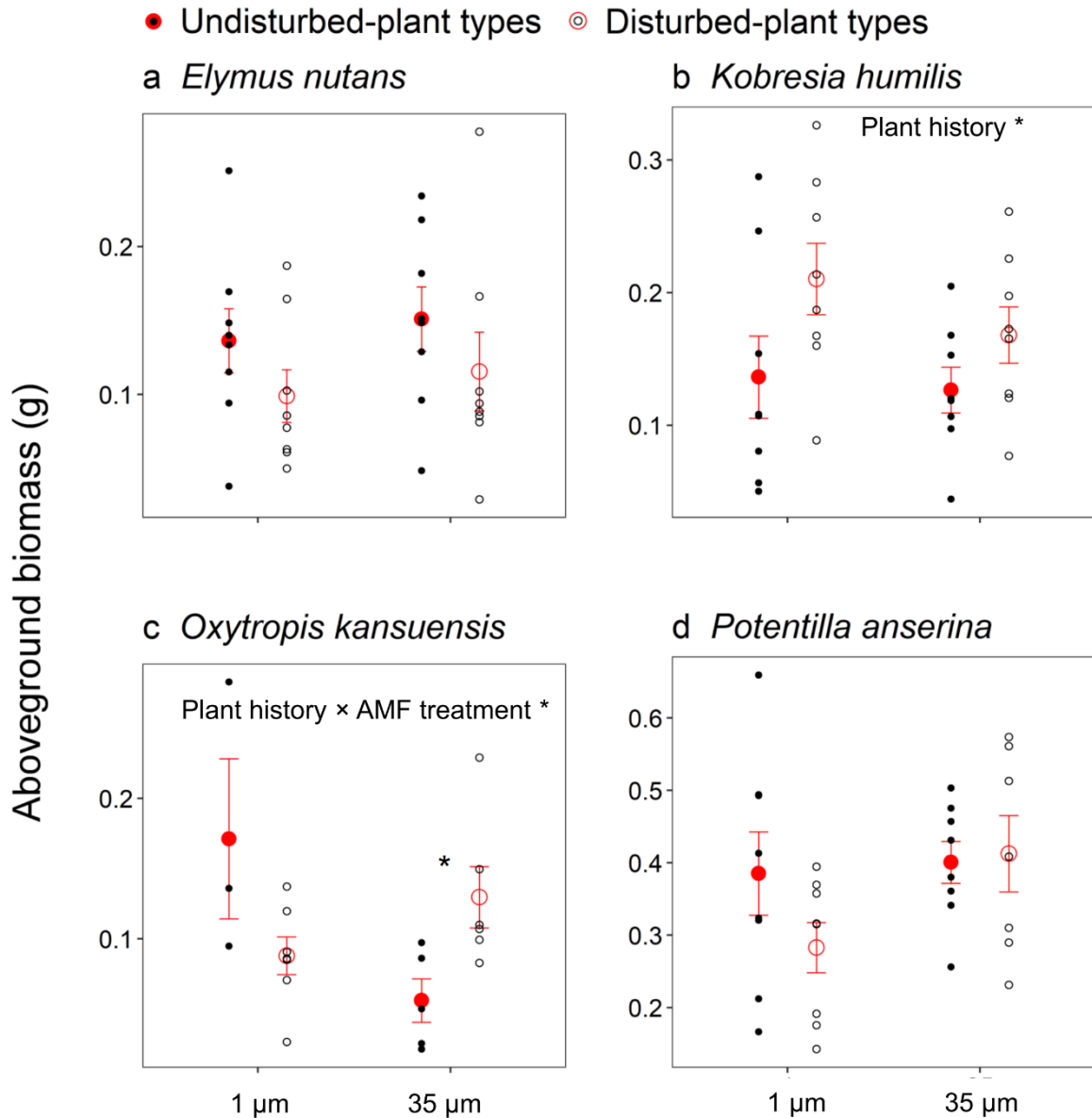
Figure 5 Aboveground biomass of plant species from the mycorrhizal hyphae-exclusion experiment. Variation in aboveground biomass within species indicated effects of plant history (undisturbed- vs. disturbed-plant types) and AMF treatment (mesh size 1- vs. 35-µm preventing or allowing the interaction between transplanted plants and surrounding vegetation via AM fungal networks). Black dots represent observed values, whereas red dots represent means ($\pm$ SE) calculated from observed values for each treatment. Statistically significant factors in ANOVA are marked with "*" ($P < 0.05$; see Table S6) and "*" between two groups of dots indicate significant difference between disturbed- and undisturbed-plant types of the same AMF treatment in *t*-test.

Species compositions

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	14	16	17	18	19	20	21	22	23
Elymus nutans	×						×		×	×	×			×	×	×			×	×		×	×
Poa annua		×					×							×	×	×							×
Potentilla anserina			×					×	×			×	×	×			×	×	×	×	×		×
Saussurea pulchra				×				×									×	×					×
Oxytropis kansuensis					×					×		×			×		×		×		×	×	×
Kobresia humilis						×					×		×			×		×		×	×	×	×
Functional group richness	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	3	3	3	3	4
Species richness	1	1	1	1	1	1	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	6
Replicates	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	9

843

844 **Table 1.** Design number of replicates for each combination of species. We chose disturbed- and undisturbed-plant types of six species from four
845 functional groups: grasses (*Elymus nutans*, *Poa annua*), herbs (*Potentilla anserina*, *Saussurea pulchra*), legumes (*Oxytropis kansuensis*) and
846 sedges (*Kobresia humilis*). In total, we had 23 different combinations of species for each plant type.
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