1   **Evolution increases ecosystem temporal stability and recovery from a flood in**

2   **grassland communities**

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Abstract

Understanding factors that increase ecosystem stability is critical in the face of environmental change. Biodiversity plays a key role in buffering ecosystems against disturbances such as extreme climatic events. The evolution of biological communities within their local environment may also increase ecosystem stability and resilience, but this has yet to be tested. Here, we provide evidence for such evolutionary effects using a long-term grassland biodiversity experiment. Communities of plants with a history of co-occurrence (co-selected communities) were temporally more stable at low diversity than the same communities of plants with no such history (naïve communities). Furthermore, co-selected communities exhibited greater recovery following a major flood, resulting in more stable post-flood productivity. These results demonstrate that community evolution can increase ecosystem stability under normal circumstances and in response to extreme disturbance, but also suggest that high diversity can in part compensate for evolutionary naïvety.

Introduction

It has long been recognized that greater biodiversity can stabilize ecosystem functioning[1–5]. Such findings emphasize the importance of biodiversity for maintaining ecosystem functioning under future anticipated extreme climatic events[6,7]. The positive effect of biodiversity on maintaining ecosystem productivity over many years can be attributed to greater temporal stability and improved resistance, recovery and resilience to environmental disturbances[4,8,9]. Greater resistance increases ecosystem stability by reducing the loss in productivity[10], while greater recovery increases the amount of productivity that the ecosystem can regain after the disturbance-induced loss[11]. Together resistance and recovery determine ecosystem resilience as we define it here, namely how ecosystem productivity differs between pre- and post-disturbance states[12]. Consequently, how plant diversity stabilizes ecosystem productivity through mediating ecosystem resistance, recovery and resilience has become a focal question in ecology[3,4,9,10,13,14].

Many of the underlying mechanisms by which diversity stabilizes ecosystem productivity are based on the inherent differences among species in their niche requirements and life strategies[15–19]. For instance, different plant species may exhibit high performance under different environmental conditions (termed response diversity). Consequently, a greater plant diversity may stabilize ecosystem productivity under normally fluctuating environmental conditions and especially under environmental disturbance, because there is a higher probability that some species may perform well at any given time point. Asynchrony of species performances, derived from interspecific differences in responses to environmental variation, can thus allow more diverse ecosystems to resist more or recover faster to maintain performance, often referred to as the insurance or portfolio effect[16–18].

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62   Species asynchrony has been conceptually and empirically demonstrated as a

63   mechanism by which biodiversity can stabilize ecosystem productivity[16,18,20–23].

64   There are a number of community and population attributes associated with

65   ecosystem stability. Ecosystem resistance, recovery and resilience that underlie

66   stability may be dependent upon plant diversity[4,13], plant density[24] and plant

67   functional traits[25]. However, we lack information about the importance of

68   evolutionary processes that may be occurring over the same temporal scales across

69   which ecosystem stability is measured[26]. So far, evolutionary mechanisms underlying

70   the biodiversity–stability relationship have been considered in terms of phylogenetic

71   relatedness that reflects evolutionary mechanisms over broad time scales[27,28]. It

72   remains unclear whether evolution over short time scales can increase the stability of

73   communities under normally fluctuating environmental conditions as well as in

74   response to extreme climatic events by potentially improving resistance, recovery or

75   resilience. Such evolution leading to changes at the community level is referred to as

76   community evolution[29], but so far has almost exclusively been studied in microbial

77   ecosystems[30–32].

78   Here we test the hypothesis that short-term community evolution in grassland

79   ecosystems will affect ecosystem stability and that this effect may depend on plant

80   diversity, which was experimentally manipulated. This hypothesis is based on

81   community evolution increasing niche differentiation[26], and niche differentiation

82   having the potential to affect community biomass[29], population variability, and

83   population synchrony, all of which contribute to ecosystem stability. We measured

84   ecosystem stability as temporal variation in primary productivity during normal

85   environmental fluctuations. Furthermore, we measured ecosystem responses to

86   disturbance by an extreme event, a naturally occurring major flood, as resistance,

87   recovery, resilience and post-disturbance stability of productivity[33]. We compared co-

88   selected communities with naïve communities of 1, 2, 4 or 8 plant species. Co-

89   selected communities were assembled with offspring from individuals that had co-

90   occurred in the same communities over 8 years. Naïve communities were assembled

91   with individuals that were obtained from the same supplier that provided the original

92   seeds at the beginning of the 8-year selection period of the co-selected

93   communities[26,29]. To take into account the importance of the local environment, plant

94   communities were planted in their home soil ("native") or a sterilized soil that was

95   inoculated with either their native soil biota ("inoculated") or with soil biota from a

96   different field ("neutral"). Co-selected and naïve communities were grown from

97   2012–2015 at the field site in Jena, Germany. Productivity was measured in May of

98   each year and in August of 2012–2014.

99

100   **Results**

101   *Temporal stability, asynchrony and population variation*

102   Community evolution significantly modified the diversity–stability

103   relationship and the diversity–population variation relationship (interaction plant

104   history x species richness in Table 1). Stability more strongly increased with diversity

105   in the naïve than in the co-selected communities (Fig. 1a). Conversely, population

106   variation increased more strongly with diversity in the co-selected than in the naïve

107   communities. Species asynchrony significantly increased with diversity (main effect

108   of species richness in Table 1). Different soil treatments did not alter the diversity–

109   stability relationship (Fig. 1b) and generally, the community-evolution treatments and

110   soil treatments did not affect stability, asynchrony and population variation (Table 1).

111   The different diversity–stability relationships between the two community-

5

112   evolution treatments were related to different asynchrony and stability relationships.

113   That is, asynchrony of species-level productivity fluctuations was less positively

114   correlated with ecosystem stability in co-selected than in naïve communities or, in

115   other words, community evolution significantly reduced the coupling between

116   species-level asynchrony and ecosystem stability (Fig. 1c). In contrast to the altered

117   relationship between asynchrony and stability, community evolution did not alter the

118   relationship between population variation and stability (Fig. 1d).

119

120   *Responses to an extreme flood event*

121   A naturally occurring flood in early summer 2013 had devastating effects on

122   the plant communities and reduced productivity in the corresponding time interval

123   (Fig. 2). Whereas diversity had no general effect on resistance to the flood, the

124   diversity–resistance relationships differed significantly between the two community-

125   evolution treatments (Table 2). This resulted from the co-selected communities

126   having a generally lower resistance at high diversity (Fig. 3a; Table 2). Native and

127   inoculated soil treatments resulted in highest resistance to the flood, in particular at

128   high diversity (Fig. 3b).

129   Ecosystem recovery following the flood was independently increased by

130   diversity and by community evolution, but soil treatments had no significant effects

131   (Fig. 3c, d; Table 2). At low (but not at high) diversity, co-selected communities were

132   more resilient (Fig. 3e). On the other hand, similar to temporal stability, high diversity

133   could compensate for the reduced resilience of naïve as compared with co-selected

134   communities (marginally significant interaction plant history x species richness in

135   Table 2). The effect of species richness on resilience was strongest on the soil that

136   was inoculated with native soil because of the very low resilience of the

6

137   corresponding monocultures (Fig. 3f; Table 2). Species turnover was not influenced

138   by community-evolution or soil treatments, but did increase with species richness

139   (Fig. S1; Table S1). Whereas before the flood, co-selected and naïve communities

140   were equally stable (Fig. 4a), the flood event significantly destabilized post-flood

141   productivity in the naïve compared with the co-selected communities (Fig. 4b; Table

142   S2).

143

144   **Discussion**

145   The potential for greater diversity to maintain a greater ecosystem functioning

146   over time has been well recognized[1–5]. Additionally, the positive effects of

147   biodiversity on ecosystem functioning have been shown to strengthen over time[34–36].

148   Such changes in the functioning of plant communities may reflect evolutionary

149   processes that occur over the same temporal scales across which ecosystem stability is

150   being measured. For instance, there is evidence that such temporal changes in the

151   functioning of communities may reflect rapid evolutionary increases in species

152   complementarity and community productivity[26,29,32]. Yet the importance of the

153   interactive effects of biodiversity and community evolution for ecosystem stability

154   has not been tested so far. Our study provides strong evidence that community

155   evolution maintained a more stable primary productivity at low diversity, which

156   consequently altered the diversity–stability relationship under normally fluctuating

157   environmental conditions. Furthermore, we found that co-selected communities had

158   an overall greater recovery and post-perturbation stability following a naturally

159   occurring extreme climatic event. In comparison to the plant diversity and

160   community-evolution treatments, treatments simulating co-selected vs. novel soil

161   microbial communities only had minor effects on ecosystem stability. Overall, our

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162 findings demonstrate the potential importance of community-wide evolutionary

163 processes for maintaining ecosystem functioning and highlights the need to further

164 consider the integration of evolutionary processes in understanding biodiversity–

165 ecosystem functioning relationships.

166 Several mechanisms could have led to the observed differences between co-

167 selected and naïve communities. First, the changes at community level could have

168 been due to altered species abundance distributions. However, this would have had to

169 be related to changed performances of species due to community evolution, because

170 co-selected and naïve communities only differed in regard to selection history but not

171 with regard to initial species composition or environment. Furthermore, we could not

172 detect any significant changes in species abundance distributions. This leaves a

173 second explanation for the observed community-level effects, phenotypic changes

174 within species. Such changes could have a genetic or other heritable basis such as

175 epigenetic or maternal carry-over effects[37]. The latter are unlikely because the

176 communities were started from seeds rather than cuttings and the effects were

177 observed over a 4-year time span. We tested in a separate study using a reduced-

178 representation bisulfate sequencing method[38] for five of the 60 species from the Jena

179 Experiment if selection on the field site led to genetic or epigenetic changes and found

180 evidence for genetic but not for epigenetic changes[39]. These genetic changes could

181 have been due to differential mortality, growth or reproduction among the initially

182 sown genotypes[40], recombination during sexual reproduction in the field or the

183 experimental garden or, presumably least likely, to mutation and selection, all

184 occurring before the start of the present experiment.

185

186   *Stability, synchrony and population variation*

187   Numerous studies have shown that biodiversity increases ecosystem stability

188   due to the effects of species asynchrony in diverse communities, allowing high

189   compensatory population variation to be combined with low community-level

190   variation over time[15,17,22,41]. Here we also observed such compensatory dynamics, but

191   this was significantly modified by community evolution. We found that the positive

192   diversity–stability relationship was stronger in naïve plant communities where species

193   did not share a common selection history. While this positive diversity–stability

194   relationship in these naïve plant communities provides further support for the notion

195   that diversity is a key component underlying ecosystem stability, it also indicates that

196   the effects of plant diversity on stability may be particularly strong in newly

197   assembled plant communities. The weaker effect of diversity on stability in the co-

198   selected communities was due to greater stability at lower diversity in comparison to

199   the naïve plant communities. These findings suggested that the evolutionary history of

200   co-occurring species compensated for lower biodiversity by exhibiting a more stable

201   productivity and, conversely, that biodiversity in naïve communities could partly

202   compensate for a lack of evolutionarily increased ecosystem stability.

203   The modified diversity–stability relationship between the co-selected and

204   naïve plant communities may at least in part have been due to the dampening effect of

205   community evolution on the positive relationship between species asynchrony and

206   stability. As expected, species asynchrony increased stability overall. However, in co-

207   selected communities, species asynchrony was less positively associated with

208   stability, indicating community evolution led to a partial decoupling of asynchrony

209   and stability and thus allowed for higher stability at low diversity compared with

210   naïve communities. More specifically, in communities where species synchrony was

211   high, such as in less diverse communities, co-selected plant communities were

212   generally more stable than naïve plant communities. At low diversity, species in co-

213   selected communities compared with species in naïve communities were also

214   generally less temporally variable in their productivity (see significant interaction

215   plant history x species richness in Table 1). Therefore, the co-selected plant

216   communities with low asynchrony were able to maintain greater community stability.

217   On the other hand, the stronger coupling between asynchrony and stability allowed

218   naïve compared with co-selected communities to have a more stable productivity at

219   high diversity, where species fluctuated more asynchronously through time.

220   The reduced temporal stability at low synchrony in our co-selected plant

221   communities (see Fig. 1c) may be due to the effect of community evolution on species

222   competitive interactions. For instance, it has been previously shown that more diverse

223   communities can result in the selection for characteristics by which individuals avoid

224   competition and exhibit greater complementarity[26,29]. Such changes in species

225   interactions can impact species dynamics and ultimately the stability of the net

226   community productivity. This is because species competing more strongly with one

227   another can exhibit greater asynchrony in their temporal performance since temporal

228   variations in the environment may temporarily favor the competitive advantage of one

229   species over another resulting in their negative temporal covariance[15,20,41]. Such

230   destabilizing effects of evolution have been demonstrated in microalgae communities

231   where a greater phylogenetic distance among community members results in weaker

232   competitive interactions, that in turn reduces the competition-driven temporal

233   asynchrony among species and the compensatory dynamics that are required to

234   stabilize the net productivity of the communities[28].

235   The interactions between plants and their soil communities are well known to

236   influence ecosystem functioning[43] and these interactions likely change over ecological

237   time-scales[44–46]. We therefore anticipated that soils would play an important role in

238   ecosystem stability. However, we found little evidence that our soil treatments

239   influenced the temporal performance of plant communities under field conditions and

240   did not have any interactive effects with the community-evolution treatments on the

241   temporal performance of the plant communities. However, we did observe that the

242   soils influenced the pre-flood productivity of the plant communities. In particular, we

243   found that the pre-flood productivity was generally lower in communities grown in

244   native soil, which might have been due to a greater density of antagonistic soil biota

245   or the inoculated soils may have had a greater pool of available soil resources

246   resulting from the soil sterilization process[47]. The difference between inoculated and

247   native soils was, perhaps literally, "washed away" by the flood event. The flood event

248   may thus have equalized the soil properties among soil treatments and consequently

249   dampened any potential plant–soil interactions that have been observed elsewhere to

250   influence ecosystem stability[48,49].

251

252   *Responses to an extreme flood event*

253   Our study system was exposed to a naturally occurring extreme flood event

254   that strongly reduced the productivity of the plant communities[50]. Here we took

255   advantage of this to further assess the hypothesis that community evolution may

256   enhance ecosystem stability in response to disturbance events, due to greater

257   resistance, recovery or resilience. Biodiversity decreased resistance, confirming

258   previous findings[11,24], but the relationship was context-dependent. Community

259   evolution reduced resistance to flooding at high diversity (see Fig. 3a). This lower

260   resistance can be attributed to greater pre-flood productivity of the co-selected

261   communities. In this sense, co-selected communities had "more to lose" when faced

262   with this extreme climate event, an observation reported also in other grassland

263   systems in response to drought[11]. Thus, overall the reduced productivity of naïve

264   communities resulted in less absolute loss in productivity due to the flood and their

265   greater resistance. It was previously shown that selection for niche differentiation

266   results in higher community productivity[26]. Our results indicate that the selection-

267   driven increase in productivity may consequently reduce the resistance to extreme

268   climate events at higher levels of diversity. However, the greater productivity of co-

269   selected plant communities may have also allowed them to recover back to their pre-

270   disturbed state and maintain a more stable post-flood productivity. This is supported

271   by our analysis using pre-flood productivity as a covariate (see Supporting

272   Information, Fig. S2, Table S3). Once we corrected for the pre-flood productivity,

273   species richness increased resilience in both co-selected and naïve communities, and

274   we observed a strong interactive effect of community evolution and species richness

275   for ecosystem resistance (Table 2).

276   Biodiversity had a strong positive effect on the recovery and, in the naïve

277   communities also on resilience of the plant communities, paralleling numerous other

278   studies emphasizing the importance of biodiversity for ecosystem recovery and

279   resilience[4,11,12,26]. In addition, community evolution further increased recovery and

280   resilience (see Fig. 3c, e). The positive effect of community evolution on post-flood

281   recovery suggests that the local environment may have acted as a selective filter on

282   these plant communities. The ancestral communities of the co-selected plants were

283   initially sown into the field site in 2002, which is a natural floodplain where the plant

284   communities were exposed to environmental conditions related to soil moisture

285   saturation at previous milder flood events in winter 2003 and winter 2005 (personal

286   communication with C. Roscher) than the one in 2013 and thus selection likely

287   favored individuals with traits that allowed them to perform well under such

288   conditions and recover more rapidly[51]. It has also been shown that community

289   evolution can result in increased plant species complementarity in this system[26]. In

290   line with this, the result that community evolution in these plant communities resulted

291   in greater recovery may be suggestive of selection for greater facilitative effects after

292   the perturbation as may be anticipated under the stress-gradient hypothesis[53].

293   The greater recovery in the co-selected communities also resulted in a greater

294   resilience up to a diversity level of 4 species and was followed by an increased post-

295   flood stability compared with naïve communities. This means that community

296   evolution aided the return of the functioning of these communities to their pre-

297   perturbed state and their pre-perturbation temporal performance. Our results

298   demonstrate that community evolution can have strong effects on altering the

299   population- and community-level mechanisms underpinning increased stability in

300   ecosystem productivity, specifically mechanisms relating synchrony, recovery, and

301   resilience. Finally, it is important to note that the greater post-flood stability in our

302   study was not due to compositional changes as indicated by the similar compositional

303   turnover between naïve and co-selected plant communities. Thus, the increased

304   resistance and post-flood stability can be attributed to the greater recovery and post-

305   flood performance of the individual species functioning in concert. We suggest that

306   genetic changes within the species comprising the co-selected communities were

307   responsible for the increased stability. In a study comparing plant individuals within

308   species from different selection backgrounds in the Jena Experiment (high vs. low

309   diversity), we did not find evidence for epigenetic divergence, but a strong genetic

13

310 signal[39]. Likely two different evolutionary processes — co-selection between the

311 species within each particular community composition and "diffuse" co-selection

312 among all species within the community — have improved the species' abilities to

313 function more complementarily with other species in the community[26,29].

314

315 *Conclusions*

316 Our findings show that ecosystem stability and recovery can not only be

317 promoted by biodiversity but also by evolutionary processes in plant communities

318 over the time scales at which stability is being measured. In particular, we found that

319 community evolution can enhance the stability of ecosystem productivity when

320 diversity is low, whereas in the absence of community evolution a greater diversity

321 was more critical for increasing stability. The community evolution-driven increase in

322 ecosystem stability and recovery was likely linked to the selection on individual plant

323 characteristics that facilitated greater recovery in these plant communities. If

324 evolution in grassland communities increases ecosystem resilience and stability,

325 maintaining co-selected plant communities could be a crucial precaution under global

326 change and increased frequency of extreme climatic events[6,7]. Furthermore,

327 integrating evolutionary processes into the temporal changes in biodiversity–

328 ecosystem functioning relationships is likely to be a promising future avenue for

329 predicting how ecosystems may respond to climatic extremes and biodiversity loss.

330

331 **Methods**

Field site. This study was conducted at the Jena Experiment field site (Jena, Thuringia, Germany, 51 ˚N, 11 ˚E, 135 m a.s.l.) from 2011 to 2015. The Jena Experiment is a long-term biodiversity field experiment located on the banks of the Saale River. In 78 experimental field plots of different diversity levels, 60 central European grassland species are grown in a number of species combinations since 2002[54].

Community-evolution treatments. This study included eleven monocultures, twelve 2-species mixtures, twelve 4-species mixtures and twelve 8-species mixtures for a total of 47 experimental plots. We used two community-evolution treatments: plants with eight years of shared community selection in these experimental plots (co-selected communities) and plants without a common selection history in the Jena Experiment (naïve communities). The naïve plant seeds without a common selection history were obtained from the same commercial seed supplier (Rieger Hofmann GmbH, in Blaufelden-Raboldshausen, Germany) who provided the seeds used for the establishment of the original Jena Experiment plant communities[54]. The supplied seeds originated from various field sites in Germany and have been cultivated by reseeding every year for at least five years in monoculture. Seeds of co-selected communities were produced in an experimental garden in Zurich, Switzerland, from cuttings that had been made in the Jena Experiment. The cuttings were planted in Zürich in the original species combination in plots fenced with plastic netting to reduce pollination between communities[26]. A small number of seeds were additionally collected directly in the plots of the Jena Experiment. The "selected" seeds were thus offspring of plant populations that had been sown in 2002 and grown until 2010 in plots of the Jena Experiment.

357   In January 2011, the seeds of co-selected and naïve communities were

358   germinated in potting soil (BF4, De Baat; Holland) in a glasshouse in Zurich.

359   Subsequently, the seedlings were transported back to the Jena Experiment field site

360   and transplanted into 2 x 2 m subplots of the original plots (in March 2011). There

361   were four 1 x 1 m quadrats with different soil treatments in each subplot (see next

362   section) and each quadrat was split into two 1 x 0.5 m halves ("half-quadrats"). We

363   planted seedlings of co-selected communities into one half and seedlings of naïve

364   communities into the other half of each quadrat in a hexagonal pattern at a density of

365   210 plants per m^2 with a 6-cm distance between individuals. We planted the species in

366   equal proportions, but five species were excluded from both co-selected and naïve

367   communities because they were no longer present in the original plot of the Jena

368   Experiment. After transplanting, the seedlings received water every second day for six

369   weeks.

370

371   **Soil treatments**. Within each 2 x 2 m subplot of the 47 plots of the Jena Experiment,

372   we removed the original plant cover in September 2010 and used it for the plant

373   propagation in the experimental garden in Zurich (see previous section).

374   Subsequently, we excavated the soil to a depth of 0.35 m, added a 10-cm layer of sand

375   to the bottom of the plots and covered it with a 0.5 mm mesh net. We separated the

376   borders of the subplots and the quadrats by plastic frames. The excavated native soil

377   from each of the plots was sieved and four soil treatments were prepared. Half of the

378   soil (approximately 600 kg per plot) was γ-irradiated to remove the original soil biota.

379   Half of this sterilized soil was then inoculated with 4% (by weight) of live sugar-beet

380   soil and 4% of sterilized native soil of the corresponding plot ("neutral soil" obtained

381   by inoculation). Live sugar-beet soil was added to create a neutral soil community and

16

382   was previously collected in an agricultural sugar-beet field not associated with the

383   Jena Experiment, but with comparable soil properties. The second half of the

384   sterilized soil was inoculated with 4% (by weight) of live sugar-beet soil and 4% of

385   live native soil of the corresponding plot ("native soil" obtained by inoculation). The

386   non-sterilized part of the excavated soil was used for the second two soil treatments.

387   Half of this soil was filled back into one quadrat of the corresponding plot ("native

388   soil"). The other half of the unsterilized soil was mixed among all plots and filled into

389   the remaining quadrats. However, this fourth soil treatment was abandoned after two

390   years, which is why this treatment is not included here.

391   The soils were left to rest in closed bags to allow for the soil chemistry to

392   equalize and to encourage soil biota of the inocula to colonize the sterilized soil

393   before planting. The soils were then added into the quadrats in December 2010 and all

394   quadrats were covered with a net and a water permeable black sheet to avoid spilling

395   between quadrats until seedling transplantation in March 2011.

396

397   **Sampling of aboveground biomass.** The test communities were weeded three times

398   a year and the plants were cut to three cm above ground twice a year at typical

399   grassland harvest times (late May and August) in central Europe. Plant material from

400   a 50 x 20 cm area in the centre of each half-quadrat was collected to measure

401   aboveground biomass. We sorted the biomass into species, dried it at 70°C and

402   weighed the dried biomass. There were four May harvests (2012–2015) and three

403   August harvest (2012–2015) because the experiment was terminated after the fourth

404   May harvest in 2015.

405

406   **Natural flood event.** In June 2013, the field site was flooded due to heavy rains in

407   central Europe[50,55]. The flood duration (maximum 25 days) and depth of water

408   (maximum of 40 cm) was variable among plots and quadrats due to small

409   topographical differences among the plots in the experiment[25]. The variation in

410   flooding severity was distributed across the diversity gradient and within subplots the

411   quadrats and half-quadrats experienced the same flooding severity. We tested whether

412   flood severity[50] influenced the diversity–stability relationship and any other of our

413   dependent variables (data not shown). This was not the case, which made us exclude

414   these indices in all analyses.

415

416   **Data analysis.** We first calculated the stability of ecosystem functioning as the

417   inverse coefficient of variation (CV_{com}^{-1}) in the net community biomass over six time

418   points. We excluded the flooding time point to avoid any confounding effects of the

419   dramatic biomass loss in response to the flood. The stability of a single community is

420   thus the mean net community biomass (μ_{com}) divided by its standard deviation (σ_{com}).

421   To explain the change in stability with biodiversity and between the community-

422   evolution treatments we split the community-level variation across the six harvests

423   (CV_{com}) into its two component parts, these being the weighted population variation

424   (CV_{pop}) and the species synchrony (θ) that are defined elsewhere[18,22]. Variation in

425   these indices of stability, synchrony and population stability was analyzed with linear

426   mixed-effects models. Fixed-effects terms were plant species richness (log scale),

427   community-evolution treatment (plant history co-selected vs. naïve) and soil treatment

428   (native, inoculated and neutral soil); subplots and quadrats were used as random-

429   effects terms to get appropriate errors for significance tests[56].

430   We calculated the resistance, recovery and resilience (see Fig. 2) to assess the

431   communities' responses to the flood event. Resistance is the change in productivity

432   between the average of the three harvests prior to the flood and the productivity

433   during the flood event, more negative values indicating lower resistance. Recovery is

434   the difference in the biomass produced post-flood (averaged over the three post-flood

435   harvests) from the biomass produced during the flood event, where positive values

436   indicate the amount of biomass recovered. Resilience is the difference between the

437   pre- and post-flood biomasses where positive values indicate communities that were

438   more productive after than before the flood event, whereas negative values indicate

439   that the post-flood productivity had not returned to its pre-flood state. Variation in

440   resistance, recovery and resilience was analyzed with linear mixed-effects models.

441   Fixed-effects terms were plant species richness (log scale), community-evolution

442   treatment (plant history co-selected vs. naïve) and soil treatment (native, inoculated

443   and neutral soil); subplots and quadrats were used as random-effects terms. Since the

444   measures of resistance, recovery and resilience can be dependent upon the magnitude

445   of the pre-flood productivity[24,57], we created additional models which included the

446   pre-flood productivity as a covariate (see Supporting Information).

447   We calculated the species compositional turnover between pre- and post-flood

448   conditions. Because it includes species abundances, we used the Bray-Curtis

449   dissimilarity between pre-flood abundances of species (averaged over the three pre-

450   flood harvests) and the post-flood abundances of species (averaged over the three

451   post-flood harvests). The analysis was the same as for the resistance, recovery and

452   resilience measures. We also analyzed pre-flood (three harvests before the flooding

453   event) and post-flood (three harvests after the flooding event) stability in the same

454   way as described at the beginning of this section.

455   All analyses were conducted using the software R, version 3.2.4[58]. Mixed

456   models using residual maximum likelihood (REML) were fitted using the package

457   ASReml for R[59] and the package 'Pascal' available at GitHub[56].

458

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460

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Additional information

Supplementary information is available for this paper online.

Data availability. Data for this study are available from the corresponding author and will be made publicly available upon acceptance on the Pangaea repository.

Code availability. All R scripts are available upon request from the corresponding author C.W.

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627 **Author contributions**

628 B.S. designed research, T.H. and S.J.V.M. performed research; S.J.V.M., C.W. and

629 B.S. analyzed data; S.J.V.M., B.S. and C.W. wrote the paper with substantial
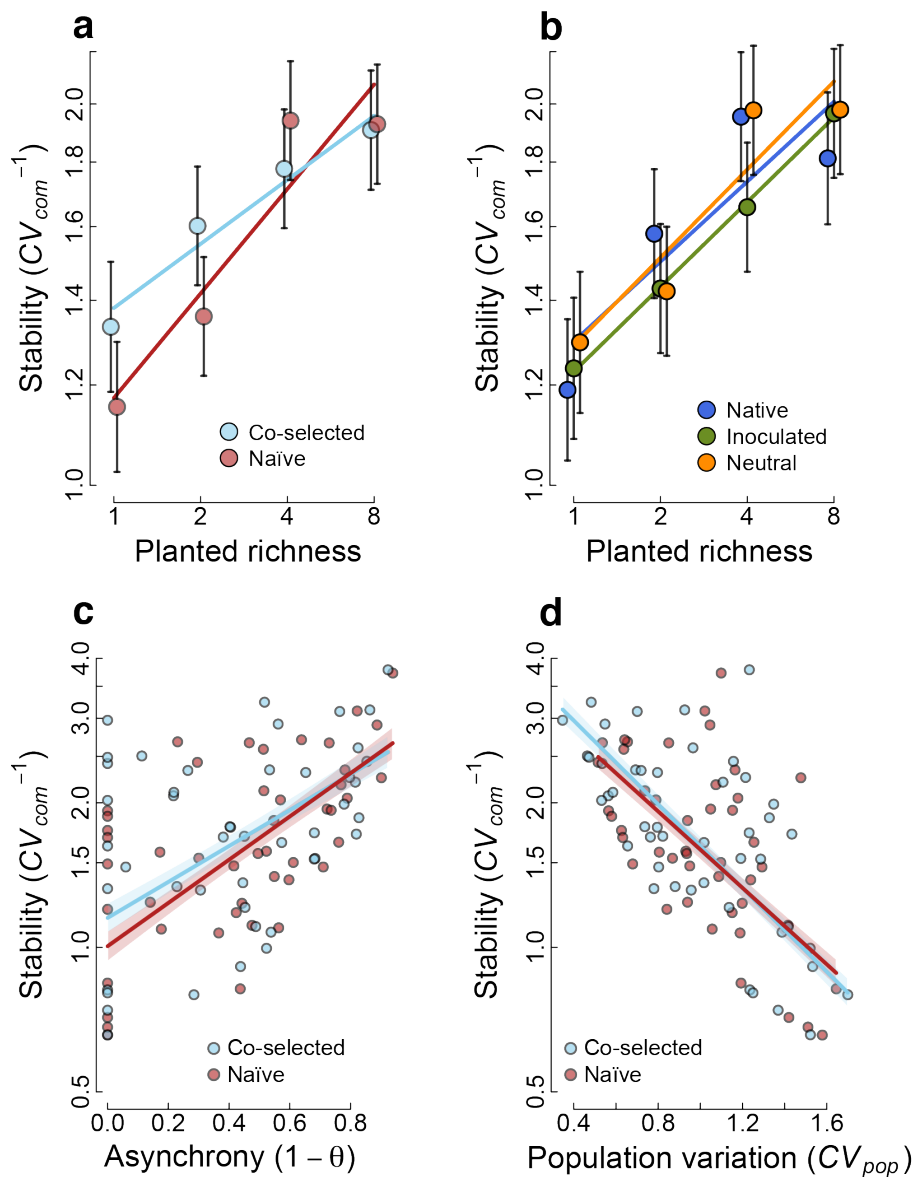
630 contributions of the other authors.

631

632 **Competing interests**

633 The authors declare no conflicts of interest.

634

635   **FIGURES & TABLES**

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638   **Fig. 1 | The biodiversity–stability relationship in response to community-**

639   **evolution and soil treatments. a,** Greater plant diversity is required for greater

640   stability, but more strongly so in naïve communities (plant history x species richness

641   (log-transformed): $F_{1,\ 135.0} = 4.794$, $P = 0.030$). **b,** Different soils did not alter the

642   overall biodiversity–stability relationship (soil treatment x species richness (log-

643   transformed): $F_{2,\ 87.1} = 0.048$, $P = 0.954$). The three soil treatments were: native soil,

644   sterilized soil inoculated with native soil (inoculated) and sterilized soil (neutral).

28

645   Means and standard errors are shown for each diversity level. **c,** Stability increased

646   with asynchrony strongly for both naïve and selected communities (main effect

647   asynchrony: $F_{1, 204.5} = 84.55$, $P =$ <0.001) but stability increased more steeply with

648   asynchrony in naïve plant communities than in co-selected communities (plant history

649   x asynchrony interaction: $F_{1, 145.8} = 3.93$, $P = 0.049$). **d,** The relationship between

650   stability and population variation was not altered by community evolution (plant

651   history x population CV: $F_{1, 160.3} = 1.348$, $P = 0.247$).

652
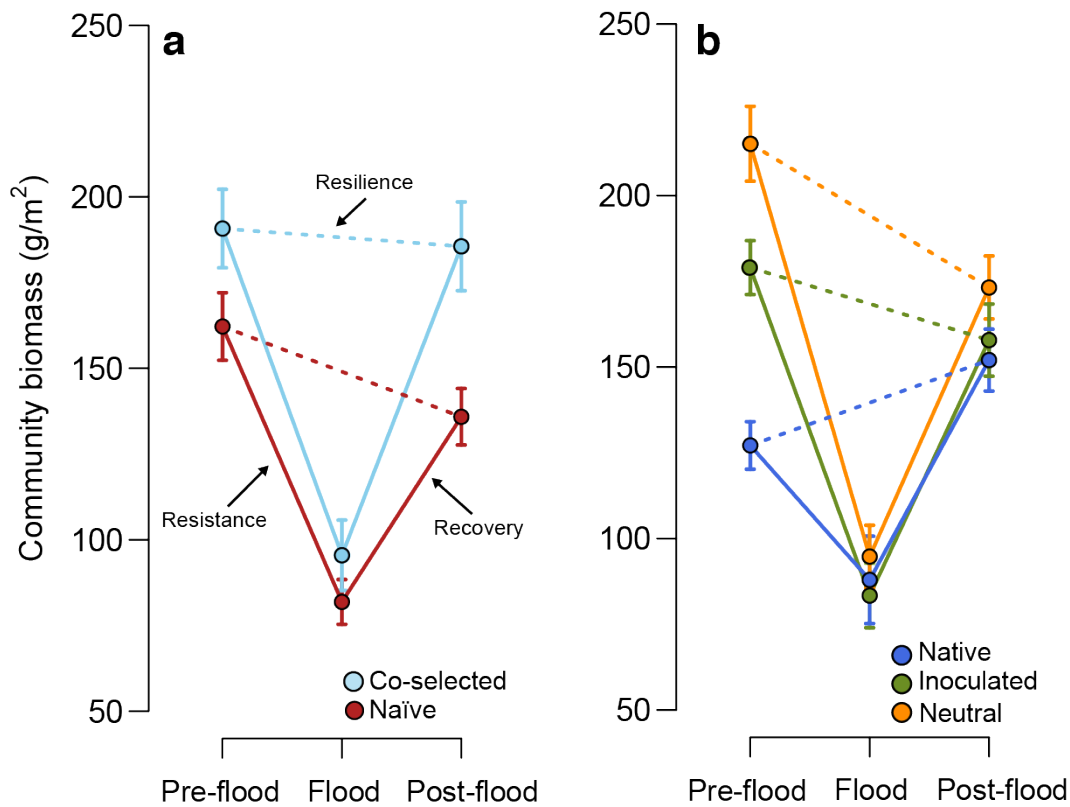
Fig. 2 | The flood event greatly reduced ecosystem productivity. Points indicate **a**, the average productivity for co-selected and naïve plant communities and **b**, the average productivity for the three soil treatments native soil, sterilized soil inoculated with native soil (inoculated) and sterilized soil (neutral). Resistance is the change in productivity between the average of the three harvests prior to the flood and the productivity during the flood event (label "Flood" on x-axis corresponding to August 2013). Recovery is the change in productivity from this level to the average of the three post-flood harvests. Resilience is the change from the average of the three pre-flood harvests to the average of the three post-flood harvests.
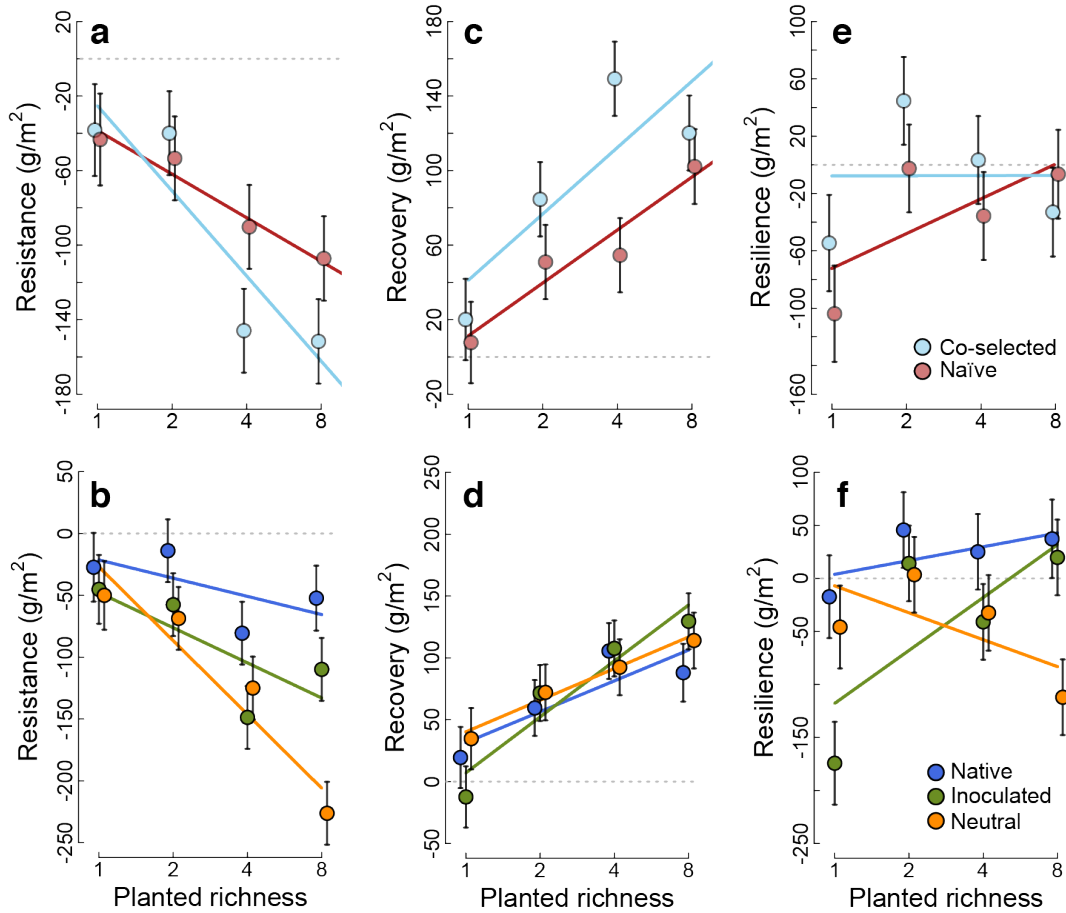
**Fig. 3 | Resistance, recovery and resilience responses to a major flood event.** Biodiversity–resistance relationships are shown in response to **a**, community-evolution and **b**, soil treatments. Biodiversity–recovery relationships are shown in response to **c**, community-evolution and **d**, soil treatments. Biodiversity–resilience relationships are shown in response to **e**, community-evolution and **f**, soil treatments. Means and standard errors are shown for each diversity level.
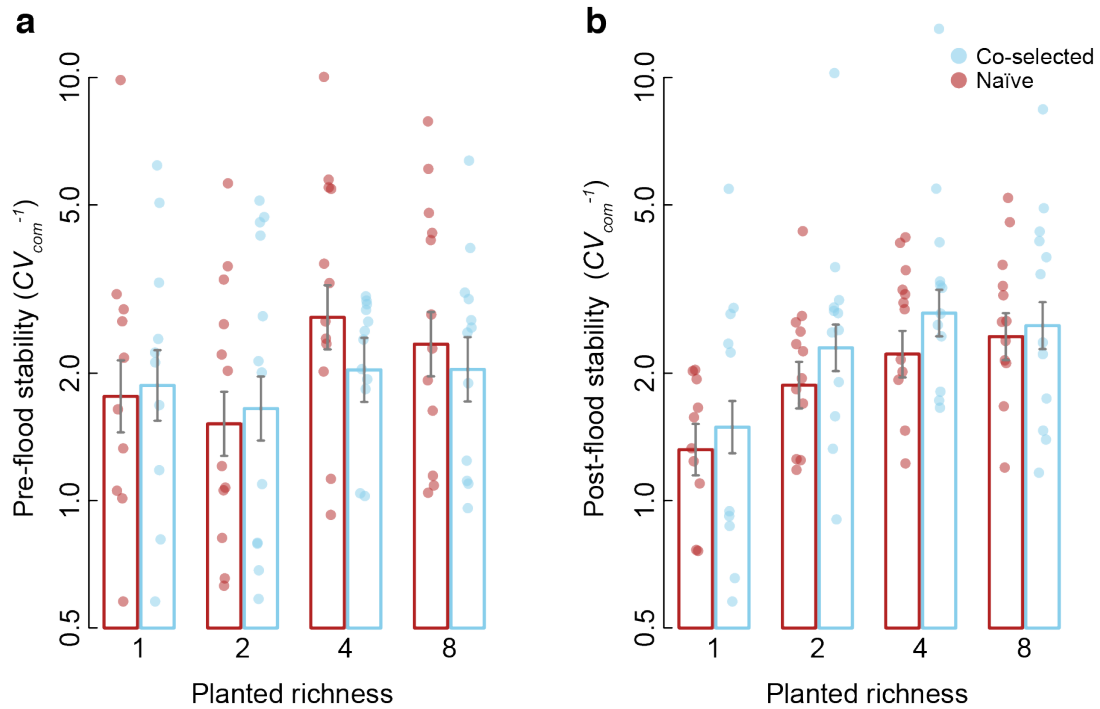
Fig. 4 | Influence of the community-evolution treatments on stability pre-flood vs. post-flood. Means for each diversity and community-evolution treatment with error bars indicating the model-estimated standard error are shown. **a,** naïve plant communities and co-selected communities were equally stable pre-flood ($F_{1,\,130.8}$ = 1.54, P = 0.217). **b,** co-selected plant communities were more stable than naïve plant communities post-flood ($F_{1,\,131.6}$ = 4.94, P = 0.028). Results are presented on a log-scale.

680 **Table 1 | Mixed-model ANOVA results for stability, population variance and**

681 **synchrony.** The effects of species richness (log-scale), community-evolution (plant

682 history) and soil treatments on the stability of community productivity, population

683 variance and synchrony across the entire experimental period form 2012–2015. The

684 time point of the flooding event was excluded in the calculations of stability,

685 population variance and asynchrony to prevent any confounding effects of the flood.

686 Bold italic text highlights significant effects.

		Stability			Population variance			Asynchrony		
Fixed terms	DF_{num}	DF_{den}	F	P	DF_{den}	F	P	DF_{den}	F	P
Log richness (R_{log})	1	***44.1***	***10.74***	***0.002***	***44.1***	***5.27***	***0.027***	***44.1***	***143***	***<0.001***
Plant history (PH)	1	135	1.805	0.181	135	3.79	0.054	135	0.5	0.479
Soil treatment (SH)	2	87.1	0.641	0.529	87.1	1.3	0.278	87.1	0.87	0.424
PH x R_{log}	1	***135***	***4.794***	***0.030***	***135***	***8.38***	***0.004***	135	0.05	0.830
SH x R_{log}	2	87.2	0.048	0.954	87.2	0.01	0.992	87.2	0.38	0.685
		Var.	*SE*		*Var.*			*Var.*	*SE*	
Random terms	N	10^{-3}	10^{-3}		10^{-3}	*SE* 10^{-3}		10^{-3}	10^{-3}	
Plot	46	100.1	25.9		95.6	23.5		17.9	4.57	
Plot x SH	137	15.5	10.9		13.9	7.4		-0.05	1.96	
Residual	274	92.3	11.23		58.4	7.1		20.02	2.46	

687 *Note*: DF_{num} = numerator degrees of freedom, DF_{den} = denominator degrees of freedom, F =
688 variance ratio, P = probability of type-I error.
689

690 **Table 2 | Mixed effect ANOVA results for resistance, recovery and resilience.** The

691 effects of species richness (log-scale), community-evolution (plant history) and soil

692 treatments are shown for the changes in productivity due to flooding. Bold italic text

693 highlights significant effects.

		Resistance			Recovery			Resilience		
Fixed terms	DF_{num}	DF_{den}	F	P	DF_{den}	F	P	DF_{den}	F	P
Log richness (R_{log})	1	*44.2*	*9.413*	*0.004*	*44.1*	*15.95*	*<0.001*	44.2	1.69	0.200
Plant history (PH)	1	*135*	*4.19*	*0.043*	*135*	*14.5*	*<0.001*	135	3.476	0.064
Soil treatment (SH)	2	*87.3*	*14.07*	*<0.001*	87.2	0.295	0.746	*87.3*	*6.116*	*0.003*
PH x R_{log}	1	*135*	*5.323*	*0.023*	135	0.484	0.488	135	2.65	0.106
SH x R_{log}	2	*87.5*	*5.949*	*0.004*	87.4	1.728	0.184	*87.5*	*6.97*	*0.002*
Random terms	N	Var.	SE		Var.	SE		Var.	SE	
Plot	46	3645.1	1073.9		2233.7	771.4		6909.8	2237.8	
Plot x SH	137	775.2	702.4		-157.6	744.9		1933.2	1784.5	
Residual	274	6245.8	760.2		7851.01	955.6		15913.8	1937	

694

695 *Note*: DF_{num} = numerator degrees of freedom, DF_{den} = denominator degrees of freedom, F =

696 variance ratio, P = probability of type-I error.