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## **Co-occurrence history increases ecosystem stability and resilience in experimental plant communities**

van Moorsel, Sofia J ; Hahl, Terhi ; Petchey, Owen L ; Ebeling, Anne ; Eisenhauer, Nico ; Schmid, Bernhard ; Wagg, Cameron

**Abstract:** Understanding factors that maintain ecosystem stability is critical in the face of environmental change. Experiments simulating species loss from grassland have shown that losing biodiversity decreases ecosystem stability. However, as the originally sown experimental communities with reduced biodiversity develop, plant evolutionary processes or the assembly of interacting soil organisms may allow ecosystems to increase stability over time. We explored such effects in a long-term grassland biodiversity experiment with plant communities with either a history of co-occurrence (selected communities) or no such history (naïve communities) over a 4-yr period in which a major flood disturbance occurred. Comparing communities of identical species composition, we found that selected communities had temporally more stable biomass than naïve communities, especially at low species richness. Furthermore, selected communities showed greater biomass recovery after flooding, resulting in more stable post-flood productivity. In contrast to a previous study, the positive diversity–stability relationship was maintained after the flooding. Our results were consistent across three soil treatments simulating the presence or absence of co-selected microbial communities. We suggest that prolonged exposure of plant populations to a particular community context and abiotic site conditions can increase ecosystem temporal stability and resilience due to short-term evolution. A history of co-occurrence can in part compensate for species loss, as can high plant diversity in part compensate for the missing opportunity of such adaptive adjustments.

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1 **Co-occurrence history increases ecosystem stability and resilience in**  
2 **experimental plant communities**  
3

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32 **Running head: Co-occurrence history boosts stability**

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## Abstract

Understanding factors that maintain ecosystem stability is critical in the face of environmental change. Experiments simulating species loss from grassland have shown that losing biodiversity decreases ecosystem stability. However, as the originally sown experimental communities with reduced biodiversity develop, plant evolutionary processes or the assembly of interacting soil organisms may allow ecosystems to increase stability over time. We explored such effects in a long-term grassland biodiversity experiment with plant communities with either a history of co-occurrence (selected communities) or no such history (naïve communities) over a four-year period in which a major flood disturbance occurred.

Comparing communities of identical species composition, we found that selected communities had temporally more stable biomass than naïve communities, especially at low species richness. Furthermore, selected communities showed greater biomass recovery after flooding, resulting in more stable post-flood productivity. In contrast to a previous study, the positive diversity–stability relationship was maintained after the flooding. Our results were consistent across three soil treatments simulating the presence or absence of co-selected microbial communities. We suggest that prolonged exposure of plant populations to a particular community context and abiotic site conditions can increase ecosystem temporal stability and resilience due to short-term evolution. A history of co-occurrence can in part compensate for species loss, as can high plant diversity in part compensate for the missing opportunity of such adaptive adjustments.

*Key words: asynchrony; co-occurrence history; disturbance; grassland biodiversity; recovery; resistance; flood; selection; diversity – stability relationship*

## INTRODUCTION

59

60 Biodiversity experiments simulating the loss of plant species from grassland  
61 communities have shown that less diverse communities have reduced mean  
62 (Balvanera et al. 2006, Cardinale et al. 2012) and increased temporal variation in  
63 aboveground biomass (Tilman et al. 1998, 2006, Hector et al. 2010). However, it is  
64 not clear whether these communities may regain functioning and stability over time  
65 while still being at low diversity. The few biodiversity experiments that lasted more  
66 than 10 years showed that functioning tended to decrease in low-diversity  
67 communities and to increase in high-diversity communities, leading to an increased  
68 slope of the biodiversity–biomass production relationship over time (Reich et al.  
69 2012, Meyer et al. 2016, Guerrero-Ramírez et al. 2017). In one of these experiments,  
70 the Jena Experiment in Germany (Weisser et al. 2017), it was shown that divergent  
71 evolutionary changes of plant species in monocultures vs. mixtures during the first 8  
72 years contributed to this strengthening of the biodiversity–functioning relationship  
73 (Zuppinger-Dingley et al. 2014, van Moorsel et al. 2018, 2019). Feedbacks between  
74 plants and soil organisms, however, had less explanatory power (van Moorsel et al.  
75 2018, Schmid et al. 2019, Hahl et al. 2020).

76 Ecosystem resistance, recovery, and resilience that underlie stability may  
77 depend on plant diversity (Pfisterer and Schmid 2002, Isbell et al. 2015, Fischer et al.  
78 2016). The mechanisms by which diversity stabilizes ecosystem biomass production  
79 are based on differences among genotypes or species in their responses to the abiotic  
80 or biotic environment (Schmid 1994, Tilman et al. 1998, Hector et al. 2010). This  
81 response diversity (Elmqvist et al. 2003, Isbell et al. 2011) could increase over time.  
82 Evolution in communities may lead to divergence in trait expression between species  
83 via selection for genetically fixed divergent phenotypes or via selection for genotypes

84 with increased trait plasticity (Zuppinge-Dingley et al. 2014, Meilhac et al. 2020). By  
85 extension, similar processes may also occur between genotypes within monocultures  
86 (Henn et al. 2018, van Moorsel et al. 2018). Such a greater trait diversity between  
87 species in mixtures (or within species in monocultures) may result in greater response  
88 diversity or temporal niche occupation and thus greater stability (de la Riva et al.  
89 2017, Hallett et al. 2017). These processes may even be more important in low-  
90 diversity communities because of closer interactions between the few remaining  
91 species and of the refilling of community niche space (Salles et al. 2009). In contrast,  
92 in more diverse communities, such opportunities for evolutionary adjustments may be  
93 more limited.

94         Asynchrony among species performances in terms of biomass production can  
95 allow diverse communities to resist disturbance or recover to maintain performance,  
96 often referred to as insurance or portfolio effect (Yachi and Loreau 1999, Hector et al.  
97 2010, Thibaut and Connolly 2013, de Mazancourt et al. 2013). The development of  
98 stability over time in long-term biodiversity experiments has not been analyzed so far,  
99 but in the Jena Experiment (Weigelt et al. 2010, Weisser et al. 2017) combined intra-  
100 and inter-annual biomass variation in experimental communities decreased over time  
101 for the first 8 years (i.e. ecosystem stability, measured as the inverse of the coefficient  
102 of variation of plant biomass, increased over time; Appendix S1: Fig. S1A). During  
103 this time, climatic stability did not increase but the stability of interannual  
104 precipitation did increase (Appendix S1: Fig. S1B, C, D). This correlation between  
105 precipitation and biomass stability demonstrates a fundamental problem of  
106 interpretation in studies that confound (community) age and physical time. Therefore,  
107 we designed an experiment that separated the two.

108           We hypothesize that the increase in biomass stability over time in the Jena  
109 Experiment can at least in part be attributed to community age. As communities  
110 develop following sowing, species abundance distributions and gene frequencies  
111 change, and such adjustments between and within species may increase stability  
112 (Strauss et al. 2006, Aubree et al. 2020). We addressed our overall hypothesis by  
113 comparing such “old” communities with “new” communities of the same species  
114 composition at the same time and under the same environmental conditions. We use  
115 “co-occurrence history” when we refer to plant species with a history of growing in  
116 the company of one another over a certain period of time, potentially developing  
117 stronger interactions or associations with both the plant and soil community partners  
118 over time.

119           A prolonged period of co-occurrence can increase “stabilizing differences”  
120 between phylogenetically distinct annual plant species in comparison with similar  
121 pairs of species without co-occurrence history over a long time span (Germain et al.  
122 2016) and, in theory, co-adaptation can modify biodiversity–productivity and  
123 biodiversity–stability relationships also over shorter time spans (Aubree et al. 2020).  
124 Here we ask if prolonged co-occurrence within a local community can result in  
125 changed species interactions and reduced competition in the short term, such as  
126 during the course of a biodiversity experiment, and not only for annual but also for  
127 perennial species. In addition, we applied different soil treatments to assess the  
128 potential contribution of soil organisms that over time associate with plant  
129 communities and may (de)stabilize plant communities by changing nutrient provision  
130 and the plant’s health (Eisenhauer et al. 2011, 2012). Our experimental communities  
131 ranged in richness from one, two and four to eight plant species. We refer to “old”  
132 communities as “*selected* communities” since they were assembled with offspring

133 from individuals that had co-occurred in the same plots of the Jena Experiment over 8  
134 years from 2002–2010. We refer to “new” communities as “*naïve* communities”  
135 because they were assembled with offspring from seeds that were obtained from the  
136 original seed supplier for the Jena Experiment. We grew these communities from  
137 2012–2015 within cleared space in the original plots of the Jena Experiment.

138 We previously found that selected communities were more productive than  
139 naïve communities in the same experiment at the 2- and 4-species richness levels but  
140 not at the 8-species richness level. We thus firstly hypothesized (1) that selected  
141 communities have more stable biomass than naïve communities and that differences  
142 in stability between selected and naïve communities are most pronounced at low to  
143 intermediate diversity (hypothesis 1). Secondly, we hypothesized that stability is  
144 further increased when plants grow with their native soil organisms (hypothesis 2).

145 A flood in summer 2013 (Blöschl et al. 2013) allowed us to analyze the  
146 resistance, recovery, and resilience (Ruijven and Berendse 2010, Lloret et al. 2011,  
147 Hillebrand et al. 2018) of our communities in response to this disturbance. Together,  
148 resistance and recovery determine ecosystem resilience as we define it here, namely  
149 how ecosystem biomass production differs between pre- and post-disturbance states  
150 (Lloret et al. 2011). We hypothesized that co-occurrence history should also increase  
151 stability towards perturbation, thus that selected communities show greater resistance,  
152 recovery, and resilience in response to the flood event (hypothesis 3).

153

154

## METHODS

155

### Field site

156

This study was conducted at the Jena Experiment field site (Jena, Thuringia,

157

Germany, 51 °N, 11 °E, 135 m a.s.l.) from 2011–2015. The Jena Experiment is a long-



158 term biodiversity field experiment located on the banks of the Saale River. In 78  
159 experimental field plots of different diversity levels, 60 mostly perennial species  
160 typically forming species-rich grassland ecosystems under low-intensity management  
161 are grown in a number of species combinations since 2002 (Roscher et al. 2004).

162

### 163 **Co-occurrence (selection) history**

164 This study included eleven monocultures, twelve 2-species mixtures, twelve 4-species  
165 mixtures and twelve 8-species mixtures for a total of 47 species compositions  
166 assembled from a pool of 49 species in the large plots of the Jena Experiment  
167 (Roscher et al. 2004). This subset of large plots excluded 16- and 60-species mixtures  
168 as well as monocultures and mixtures with very poor growth of some species to obtain  
169 nearly equal replication of communities at each diversity level (one initially chosen  
170 monoculture could not be used because it contained individuals of a different species  
171 from the one originally planted, van Moorsel et al. 2018). The 49 species were mostly  
172 outcrossing perennials and represented the functional groups grasses (including  
173 graminoids of families other than Poaceae; 16 species), legumes (Fabaceae; 12  
174 species) and herbs (21 species, Appendix S1: Table S5).

175 We used two co-occurrence-history treatments: communities assembled with  
176 offspring of plants that had grown together for 8 years in the 47 large plots of the Jena  
177 Experiment (“selected” communities, Appendix S1: Table S5) and communities  
178 assembled with plants without a common history of co-occurrence in the Jena  
179 Experiment (“naïve” communities). The naïve communities were naïve in the way  
180 that they had not experienced selection in communities in the Jena Experiment but  
181 have been exposed to selection in their original field sites and the monoculture  
182 gardens of the seed supplier.

183           In total, there were 219 selected populations from different diversity levels in  
184 the Jena Experiment for the 49 species. The plants of naïve communities were grown  
185 from seeds obtained in 2010 from the same commercial supplier (Rieger Hofmann  
186 GmbH, in Blaufelden-Raboldshausen, Germany) who provided the seeds used for the  
187 establishment of the Jena Experiment in 2002. The supplied seeds for both the  
188 original seed lots in 2002 and the new seed lots in 2010 originated from various field  
189 sites in Germany and had been cultivated by reseeded every year for up to five years  
190 in monoculture. We could not use seeds from the original lots for the naïve  
191 communities because there was not enough seed material left, some species had low  
192 germination rates and we were concerned that the long storage might have affected  
193 seed quality. The new seed lots from 2010 likely contained other genotypes than the  
194 original seeds lots from 2002, but we focused on the species- and community-level  
195 replication to test our evolutionary hypotheses. We assumed a random variation for  
196 potential biases between seed lots from 2002 and 2010 for each of the 49 species and  
197 each of the 141 assembled communities (47 species compositions x 3 soil treatments).  
198 These biases could have inflated the error terms used in the hypothesis tests of the  
199 mixed models described below and thus reduced observed effect sizes for the term co-  
200 occurrence history.

201           To reduce potential maternal carry-over effects from the field, seeds of  
202 selected communities were produced in an experimental garden in Zurich,  
203 Switzerland, from cuttings that had been made in the Jena Experiment in 2010.  
204 Cuttings from multiple individuals per species were planted in Zürich in the original  
205 species combination in plots fenced with plastic netting to minimize cross-pollination  
206 between the plots and surrounded by concrete walkways and frequently mowed lawns  
207 to avoid pollinations from outside plants. To allow pollinator access the plots in the

208 experimental garden were left open at the top (Zuppinger-Dingley et al. 2014). In a  
209 subset of experimental communities, seed production in Zürich was not sufficient. In  
210 those cases, additional seeds were collected directly in the plots of the Jena  
211 Experiment (see Appendix S1: Table S6). The “selected” seeds were thus offspring of  
212 plant populations that had been sown in 2002 and grown until 2010 in plots of the  
213 Jena Experiment plus – for most of the seeds – one season in the experimental garden  
214 in Zurich in the same species composition.

215         To make sure selected and naïve plants had similar starting conditions and to  
216 reduce differential maternal carry-over effects between the two co-occurrence  
217 histories, we germinated all seeds and propagated the resulting seedlings in a  
218 glasshouse at the same time and under the same environmental conditions. In January  
219 2011, the seeds were germinated in potting soil (BF4, De Baat; Holland) and in March  
220 2011 the seedlings were transported to the Jena Experiment field site and transplanted  
221 into 2 x 2 m smaller plots within the original large plots (see Fig. 1). There were four  
222 1 x 1 m quadrats with different soil treatments in each 2 x 2 m plot (see next section)  
223 and each quadrat was split into two 1 x 0.5 m halves. We planted seedlings of selected  
224 communities into one half and seedlings of naïve communities into the other half of  
225 each quadrat in a hexagonal pattern at a density of 210 plants per m<sup>2</sup> with a 6-cm  
226 distance between individuals. By planting seedlings instead of sowing seeds, we  
227 ensured equal abundances of species in the 141 pairs of 1 x 0.5 m subplots containing  
228 the 282 test communities of different co-occurrence history, species diversity, and soil  
229 treatments. After transplanting, the seedlings received water every second day for six  
230 weeks.

231

232

### Soil treatments

233 Within each 2 x 2 m plot of the 47 large plots of the Jena Experiment, we removed the  
234 original plant cover in September 2010 and used it for the plant propagation in the  
235 experimental garden in Zurich (see previous section). We excavated the soil to a depth  
236 of 0.35 m, added a 10-cm layer of sand to the bottom of the plots and covered it with  
237 a 0.5-mm mesh net. We separated the borders of the plots and the quadrats by plastic  
238 frames. The excavated native soil from each of the plots was sieved and four soil  
239 treatments were prepared. Half of the soil (approximately 600 kg per plot) was  $\gamma$ -  
240 irradiated to remove the original soil biota. Half of the sterilized soil was then  
241 inoculated with 4% (by weight) of live sugar-beet soil and 4% of sterilized native soil  
242 of the corresponding plot (“neutral soil” obtained by inoculation). We added live  
243 sugar-beet soil collected in an agricultural sugar-beet field not associated with the  
244 Jena Experiment, but with comparable soil properties to create a neutral soil  
245 community. The second half of the sterilized soil was inoculated with 4% (by weight)  
246 of live sugar-beet soil and 4% of live native soil of the corresponding plot (“native  
247 soil” obtained by inoculation). The non-sterilized part of the excavated soil was used  
248 for the second two soil treatments. Half of this soil was filled back into one quadrat of  
249 the corresponding plot (“native soil”). The other half of the unsterilized soil was  
250 mixed among all plots and filled into the remaining quadrats (“mixed soil”). However,  
251 this fourth soil treatment was destructively harvested for another experiment, which is  
252 why we excluded it from all analyses.

253         The soils were left to rest in closed bags to encourage soil biota of the inocula  
254 to colonize the sterilized soil before planting. The soils were then added into the  
255 quadrats in December 2010. We assessed whether the soil treatments remained  
256 distinct by taking samples in 2011 and 2012 (van Moorsel et al. 2018) and again in

257 2015. Differences in both soil chemistry and microbial composition between  
258 treatments were well maintained (Appendix S1: Table S4).

259

### 260 **Sampling of aboveground biomass**

261 The plant communities were weeded three times a year and the plants were cut to 3  
262 cm above ground twice a year. These harvests were conducted over an extended  
263 period of approximately two weeks at typical grassland harvest times (late May and  
264 August) in central Europe. Plant material from a 50 x 20 cm area in the center of each  
265 half-quadrat was collected to measure aboveground biomass. We sorted the biomass  
266 by species, dried it at 70°C and weighed the dried biomass. There were four May  
267 harvests (2012–2015) and three August harvests (2012–2014) because the experiment  
268 was terminated after the fourth May harvest in 2015.

269

### 270 **Flood event**

271 In June 2013, the field site was flooded because of sustained heavy rains in central  
272 Europe (Blöschl et al. 2013, Wright et al. 2015). Due to heavy rainfall, a dam  
273 upstream of the Saale river was opened on 31 May, which resulted in a very fast  
274 influx of water to the field site and consequently standing water in the experimental  
275 plots. The flood duration (maximum 25 days) and depth of water (maximum of 40  
276 cm) varied between 2 x 2 m plots but not between co-occurrence-history and soil  
277 treatments within plots (Fischer et al. 2016). Because flood severity (Wright et al.  
278 2015) did not differentially influence any of the dependent variables in the present  
279 study (data not shown), we excluded flood severity indices from all analyses. The  
280 biomass harvest in May 2013 took place before the flood event from 20–30 May and  
281 was terminated once the flooding of the field site began (31 May). Eight plots located

282 closest to the river (three 8-species communities, three 2-species communities and  
283 two 4-species communities) could not be harvested in time and the spring 2013  
284 harvest data from these plots were therefore excluded from all analyses.

285

## 286 **Data analysis**

### 287 *Temporal stability of community biomass and climate*

288 To address hypothesis 1, we first calculated the stability of community aboveground  
289 biomass as the inverse coefficient of combined intra- and inter-annual variation  
290 ( $CV_{com}^{-1}$ ) among sequential spring and summer harvests. The stability of a single  
291 community was thus the mean community aboveground biomass ( $\mu_{com}$ ) divided by its  
292 standard deviation ( $\sigma_{com}$ ). The basic sequence for this measure was spring year  $n$ ,  
293 summer year  $n$ , and spring year  $n+1$ , which had shown increasing stability during the  
294 8 selection years in the Jena Experiment (2003/4, 2005/6, 2007/8, 2009/10; see  
295 Appendix S1: Fig. S1A). This sequence allowed us to exclude the summer harvest  
296 2013, which was taken two months after the flood event in August 2013 and was used  
297 for the calculation of resistance and recovery (see below); and it increased the  
298 independence of the sequential measures from 2003–2010. We calculated interannual  
299 mean spring precipitation and temperature stability (Knapp 2001) for the same time  
300 intervals in Jena (see Appendix S1: Fig. S1B).

301 We also analyzed pre-flood (first three harvests) and post-flood (last three  
302 harvests) stability separately. Furthermore, we calculated the species compositional  
303 turnover between pre- and post-flood conditions. Because it includes species  
304 abundances, we used the Bray-Curtis dissimilarity between pre-flood (averaged over  
305 the first three harvests) and post-flood abundances of species (averaged over the last  
306 three harvests). Although the separate analyses of pre- and post-flood stabilities are

307 partly confounded with the analysis of overall stability across the three pre- and three  
308 post-flood harvests, we did both types of analyses to focus on different aspects of  
309 stability. Whereas the analysis of the overall stability as an integrative measure  
310 allowed us to better estimate contributions of asynchrony and population stability to  
311 community stability, the separate analyses of pre- and post-flood stabilities allowed us  
312 to test if the flooding event not only affected resistance, recovery, and resilience of  
313 communities (see below) but also the temporal stability over time in absence of  
314 further perturbations.

315

#### 316 *Population stability and species asynchrony*

317 We calculated average stability of biomass at the population level ( $CV_{pop}^{-1}$ ) and  
318 community-wise species biomass asynchrony ( $1-\theta$ ) over the same time span as  
319 overall stability. Stability of biomass at the population level was calculated as the  
320 average stability of biomass of individual species (Thibaut and Connolly 2013).  
321 Asynchrony was calculated as the “synchrony index” ( $\theta$ , Loreau and de Mazancourt  
322 2008), which ranges between 0 and 1, thus, asynchrony is  $1-\theta$ . For monocultures,  
323 population stability equals community stability, and asynchrony is zero ( $\theta$  is 1).  
324 Because community stability is the product of population stability and the square root  
325 of species synchrony (Thibaut and Connolly 2013, de Mazancourt et al. 2013), we  
326 could assess the two components separately.

327

#### 328 *Resistance, recovery, and resilience*

329 To address hypothesis 3, we calculated resistance, recovery, and resilience measures  
330 (Schläpfer and Schmid 1999, Ruijven and Berendse 2010, Hillebrand et al. 2018) in  
331 response to the flood event in 2013 (see Fig. 3). Resistance is the difference in

332 community biomass between the average of the three harvests before the flood and  
333 the community biomass two months after the flood (August 2013), more negative  
334 values indicating lower resistance. Recovery is the difference between the biomass  
335 produced after recovery from the flood (averaged over the three last harvests) and the  
336 biomass two months after the flood (August 2013), where positive values indicate the  
337 amount of biomass recovered. Resilience is the difference between the average  
338 biomass of the three harvests before the flood and the average biomass of the three  
339 harvests after recovery. Values close to zero or positive values indicate that  
340 communities had returned or overshot their pre-flood state, respectively, after the  
341 flood; and negative values indicate that post-flood biomass had not returned to its pre-  
342 flood state.

343

#### 344 *Statistical analysis*

345 Variation in community stability, synchrony, and population stability was analyzed  
346 with linear mixed-effects models. Stability measures were log-transformed to improve  
347 homoscedasticity and obtain normally distributed residuals in the analyses (Schmid et  
348 al. 2017). Fixed-effects terms were plant species richness (log scale, addressing  
349 hypothesis 1), co-occurrence history (selected vs. naïve communities, addressing  
350 hypothesis 1), and soil treatment (native, inoculated-native, or inoculated-neutral soil,  
351 addressing hypothesis 2). Plots and quadrats were used as random-effects terms to get  
352 appropriate errors for significance tests (Schmid et al. 2017). We added all significant  
353 interactions of the fixed-effects terms as additional fixed-effects terms to the models  
354 (see Table 1). For reasons of consistency and to allow the use of all data in analyses  
355 with covariates, we included monocultures in the analysis of asynchrony. For  
356 graphical displays of relationships between species richness and stability measures



357 and asynchrony, means across soil treatments were corrected for differences between  
358 plots within species-richness levels, which corresponds to using plots and quadrats in  
359 the mixed-model analyses. Because co-occurrence history was a split-plot/split-  
360 quadrat treatment applied within each quadrat, it was not affected by the correction.  
361 The corrections were obtained by fitting a model with plots and quadrats only and  
362 adding the residuals to the diversity-level means.

363 Variation in resistance, recovery, and resilience was also analyzed with the  
364 same linear mixed-effects models as described above. Since the measures of  
365 resistance, recovery, and resilience can depend on the magnitude of the pre-flood  
366 biomass (Pfisterer and Schmid 2002, Wright et al. 2015), we analyzed additional  
367 models, which included the average of the three harvests before the flood as covariate  
368 (see Appendix S1: Table S1).

369 To assess the magnitude of the plant community response to either  
370 biodiversity or co-occurrence, we calculated percentage sum of squares (%SS) as  
371 effect sizes using general linear models (Schmid et al. 2017). The total SS of all fixed-  
372 effects terms was defined as 100% SS (see Appendix S1: Fig. S3). All analyses were  
373 conducted using the software R, version 3.2.4 (R Development Core Team 2017).  
374 Mixed models using residual maximum likelihood (REML) were fitted using the  
375 package ASReml for R (Butler 2009) and the package ‘Pascal’ available at GitHub  
376 (Schmid et al. 2017).

377

378

## RESULTS

379

### **Co-occurrence history partially compensates the negative effects of**

380

### **biodiversity loss on biomass stability**

381

Community biomass stability across pre-flood and post-flood harvests increased with

382 species richness (Figure 2A, Table 1). Differences in community biomass stability  
383 between soil treatments were insignificant (Table1). Differences between selected and  
384 naïve communities (co-occurrence treatment) were small, however, at low diversity,  
385 selected communities were more stable than naïve communities, reflected by a  
386 significant co-occurrence history x species richness interaction (Table 1; Fig. 2A).

387 Population biomass stability decreased with species richness, but at low  
388 diversity, the population biomass stability was also greater in selected communities  
389 (Table 1; Fig. 2B). In contrast, species asynchrony in terms of biomass increased for  
390 both selected and naïve communities with increasing species richness (Table 1; Fig.  
391 2C). When we corrected community stability and species asynchrony for all model  
392 terms except co-occurrence history (i.e. taking residuals after fitting the plot x soil  
393 treatment interaction), stability residuals strongly increased with asynchrony residuals  
394 ( $P < 0.001$ ). Selected communities were consistently more stable than naïve  
395 communities ( $P < 0.01$ ; Fig. 2D). An analysis of effect sizes showed that log-  
396 transformed richness had the strongest effect (between 77 and 99%, Appendix S1:  
397 Fig. S3A) on community stability, population stability, and asynchrony.

398

### 399 **Diverse communities were less resistant to a flood event but recovered better**

400 A flood in early summer 2013 strongly reduced biomass in that summer (Fig. 3 and  
401 Appendix S1: Fig. S2). However, in contrast to the main plots in the Jena Experiment  
402 (Wright et al. 2015), the flood did not interfere with the positive diversity–community  
403 biomass stability relationship in our plots (Fig. 5). In the short term, diverse  
404 communities, especially selected ones, were the least resistant (Fig. 4A). At low  
405 diversity, selected communities tended to have greater resistance than naïve  
406 communities, especially when adjusting for community biomass before the flood (by

407 adding pre-flood biomass as a term in the model, see Appendix S1: Table S1; Fig.  
408 S4A).

409 Plant communities in the non-sterilized native soil had the lowest biomass  
410 prior to the flood, lost the smallest amount that summer, and were thus most resistant  
411 (Fig. 3B). In contrast, plant communities grown in neutral soil had the highest  
412 biomass prior to the flood and were the least resistant to the flood resulting in a  
413 significant effect of soil treatment on resistance (Table 2; Fig. 3B). However, after  
414 first accounting for the pre-flood biomass, there were no effects of soil treatments on  
415 resistance (Appendix S1: Table S1).

416 Recovery of community biomass after the flood increased with species  
417 richness and was greater in selected than in naïve communities across all diversity  
418 levels and soil treatments (Table 2 and Appendix S1: Table S1; Fig. 4B and Appendix  
419 S1: Fig. S2B). Selected communities were also more resilient than naïve  
420 communities, as shown by the comparison of community biomass before and after  
421 recovery (Fig. 3A), and particularly at low diversity (Fig. 4C). However, the effect of  
422 co-occurrence on resilience was only significant if adjusted for pre-flood community  
423 biomass (Table 2 and Appendix S1: Table S1; Fig. 4C and Appendix S1: Fig. S4C).  
424 The three soil treatments strongly differed in their resilience, which averaged out their  
425 pre-flood differences in community biomass (Table 2; Fig. 3B).

426 Effect sizes (%SS) showed that species richness had the strongest impact on  
427 resistance (42%), the interaction between soil history and species richness the  
428 strongest impact on recovery (37%) and species richness the strongest impact on  
429 resilience (70%, Appendix S1: Fig. S3B). Co-occurrence history contributed with  
430 23% to resilience.

431

### 432 Selected communities were more stable after the flood

433 We compared the combined intra- and interannual biomass stability over the first  
434 three harvests before the flood event (2012–2013, Fig. 5A) with the last three harvests  
435 after recovery (2014–2015, Fig. 5B). Before the flood, selected communities were not  
436 significantly more stable than naïve communities (Appendix S1: Table S2). After the  
437 flood event, the selected communities were consistently more stable than the naïve  
438 communities across all diversity levels (Appendix S1: Table S2). Lastly, species  
439 turnover rates (Bray-Curtis similarity) between pre-and post-flood species  
440 compositions were not influenced by co-occurrence history or soil treatments,  
441 although they increased with species richness (Appendix S1: Table S3 and Fig. S5).

442

### 443 DISCUSSION

444 We previously found that, in comparison with naïve communities, selected  
445 low-diversity mixtures were more productive but this was not the case for selected  
446 higher-diversity mixtures (van Moorsel et al. 2018). Here, we show that selected  
447 communities from the Jena Experiment also showed greater community biomass  
448 stability in comparison with naïve communities, particularly at low diversity.

449 Temporal stability in terms of biomass at the community level in grassland  
450 ecosystems can be driven by asynchronous population dynamics of species, allowing  
451 high compensatory population variation to be combined with low community-level  
452 variation over time (Flynn et al. 2008, Isbell et al. 2009, Hector et al. 2010, de  
453 Mazancourt et al. 2013, Gross et al. 2014). As shown before (e.g. Tilman et al. 2006),  
454 we found that community biomass stability increased but population biomass stability  
455 decreased with increasing species richness. However, this effect of species richness  
456 on population stability was weaker in naïve communities (see Fig. 2B), suggesting

457 that adaptation to the abiotic environment partially compensated for the reduced  
458 species richness over time, especially in monocultures and low-diversity mixtures. In  
459 low-diversity mixtures, population stability could also have been increased due to  
460 reduced competitive interactions between plant species, consistent with the findings  
461 of evolutionary niche differentiation (Zuppinge-Dingley et al. 2014) and increased  
462 facilitation (Schöb et al. 2018) among species in mixtures in the Jena Experiment. By  
463 extension, similar evolutionary processes may have occurred between genotypes  
464 within monocultures, again consistent with previous findings showing evolutionarily  
465 changed phenotypic variation within monocultures after eight years of selection in the  
466 Jena Experiment (van Moorsel et al. 2018). The evolution of reduced inter- and  
467 intraspecific competition and parallel adaptations among the multiple species to the  
468 local abiotic conditions are mutually non-exclusive explanations for the increased  
469 population stability at low diversity. Because community stability is the product of  
470 species stability and species synchrony (Thibaut & Connolly, 2013), yet asynchrony  
471 did not differ between selected and naïve communities (see Fig. 2C), we conclude that  
472 asynchrony did not contribute to the greater community stability of selected  
473 communities at low diversity.

474

475 **Selected communities at low diversity are more stable and recover better from**  
476 **disturbance**

477 Diverse communities are more stable in the face of disturbances (Isbell et al.  
478 2015), such as a flood as happened to our test communities halfway through the  
479 experiment in June 2013 (Wright et al. 2015). Considering predicted future climate  
480 scenarios with increased frequency of extreme events (Stocker et al. 2013), including  
481 floods (Hirabayashi et al. 2013), this aspect of stability may even be more relevant

482 than temporal stability under unperturbed conditions (Donohue et al. 2016).

483         In our experiment, diversity reduced ecosystem resistance in the short term, in  
484 line with previous findings for example in micro-ecosystems with ciliates responding  
485 to warming (Pennekamp et al. 2018). This was because 4- and 8-species communities  
486 had more biomass before the flood and lost more biomass (in absolute terms), a result  
487 found previously for community responses to drought (Pfisterer and Schmid 2002,  
488 Wang et al. 2007, Ruijven and Berendse 2010) and flood (Wright et al. 2015).  
489 Because selected communities were additionally more productive than naïve  
490 communities at the 8-species richness level, naïve communities were more resistant  
491 than selected communities as they had less to lose (see Fig. 4A). Diverse communities  
492 made up for their reduced resistance by increased recovery, as often found in  
493 biodiversity experiments (Ruijven and Berendse 2010, Lloret et al. 2011, but see  
494 Isbell et al. 2015). Remarkably, however, selected communities showed greater  
495 recovery than naïve communities along the entire species-richness gradient. In  
496 combination, the differential responses regarding resistance and recovery caused  
497 selected communities at low diversity to be more resilient than naïve communities,  
498 whereas no differences in resilience between selected and naïve communities were  
499 observed at higher diversity (see Fig. 4C).

500         Some communities, mostly selected 2- and 4-species communities and both  
501 selected and naïve 8-species communities, were more productive after the flood than  
502 ever before (reflected in the positive resilience values shown in Fig. 4C). This could  
503 have been due to several potential non-exclusive causes: 1) continued accumulation of  
504 belowground biomass potentially less affected by flooding (and greater in selected  
505 than in naïve communities), 2) relative accumulation of beneficial microbes in  
506 comparison to plant antagonistic microbes (especially in sterilized soil treatments), 3)

507 resource enrichment associated with the flood (as suggested by Wright et al. 2015).  
508 Accumulation of beneficial soil microbes seems to play a minor role though because  
509 soil treatments did not differentially affect selected vs. naïve communities. However,  
510 selected communities may have been able to benefit more from resource enrichment  
511 because they had evolved better division of labor (Zuppinger-Dingley et al. 2014).  
512 Such an evolutionary driven trait divergence would have increased functional  
513 diversity which has been shown to contribute to greater stability in response to  
514 extreme climatic events (de la Riva et al. 2017).

515         Whereas the differences in community temporal biomass stability between  
516 selected and naïve communities were only positive in monocultures before the flood  
517 (see Fig. 5A), the selected communities showed increased post-flood stability at all  
518 diversity levels (see Fig. 5B and Appendix S1: Table S2). This was driven by the  
519 improved recovery of the selected communities which resulted in a larger increase in  
520 mean biomass (van Moorsel et al. 2018) than in temporal variation of biomass and a  
521 consequently reduced CV of biomass. This improved stability of selected  
522 monocultures and mixtures after the flood event was likely due to local adaptation of  
523 plants to the abiotic conditions at the Jena field site, a natural floodplain. The plant  
524 communities were exposed to previous milder flood events in winter 2003 and winter  
525 2005 (personal communication with C. Roscher) which selected for individuals with  
526 traits that allowed them to recover more rapidly (Garssen et al. 2015, Wright et al.  
527 2017). The contribution of such parallel evolutionary responses among the multiple  
528 species of our experiment to their abiotic environment was reflected in their increased  
529 population stability at low diversity (see Fig. 2B) and the consistently greater stability  
530 of selected communities across the entire range of species asynchronies (see Fig. 2D).  
531 However, in mixtures, adaptation to the biotic environment, i.e. species interactions,

532 must also have been involved because the differences between selected and naïve  
533 communities depended on diversity.

534         Because we did not detect any altered species abundance distributions (Vogel  
535 et al. 2019), it seems likely that changes in genotype frequencies within species, i.e.  
536 evolution in the community context (Strauss et al. 2006), contributed to increased  
537 stability. Genetic analyses on a subset of five species from the Jena Experiment  
538 confirmed for one annual species and two perennial species the potential for such  
539 rapid evolutionary changes and their genetic basis, with consequential epigenetic and  
540 phenotypic changes (van Moorsel et al. 2019). Furthermore, we found quantitative-  
541 genetic divergence in eleven species (Zuppinge-Dingley et al. 2014). The changes in  
542 genotype frequencies within species in selected communities could be attributable to  
543 differential mortality, growth, or reproduction among the initially sown genotypes  
544 (Barrett and Schluter 2008), recombination during sexual reproduction or, least likely,  
545 to mutation. An additional explanation for the observed patterns could be a  
546 physiological process in perennial species, i.e. priming to abiotic stress (Conrath et al.  
547 2006). Perennial individuals may be more capable of producing flood-resistant  
548 structures due to priming earlier in their lives. However, even in this case there would  
549 have been a difference between selected and naïve communities in priming, again  
550 suggesting evolution in low-diversity communities after simulated species loss in the  
551 original field experiment.

552

### 553         **Diverse communities were more stable regardless of co-occurrence history**

554 At the highest diversity level, differences between selected and naïve communities  
555 were small and only visible in the more negative resistance, the more positive  
556 recovery, and in the greater post-flood stability. This result mirrors earlier findings for



557 productivity, where mean yearly biomass was similar for selected and naïve  
558 communities at the 8-species richness level (van Moorsel et al. 2018). Potential  
559 effects of co-evolution may be weaker at higher diversity with less consistent and  
560 stable interactions between particular species (Connell 1980, van Moorsel et al. 2018).  
561 Stronger selective pressure between particular species leading to co-evolution could  
562 explain why the differences between selected and naïve communities were stronger at  
563 lower diversity, especially in 2- and 4-species mixtures. The increased resilience of  
564 selected communities at the lower diversity levels may in part also have been driven  
565 by evolutionarily increased facilitation (Bronstein 2009), which has been  
566 demonstrated for these plants in the Jena Experiment (Schöb et al. 2018). This would  
567 be in line with predictions that environmental stress might select for more positive  
568 interactions between species in plant communities (Callaway et al. 2002).

569         Resilience was slightly overshooting at the 8-species richness level (Fig. 4C),  
570 which indicates that species richness *per se* is already beneficial in the way that at  
571 lower richness, communities, in general, were not fully resilient. The increased  
572 resilience in selected and naïve 8-species communities was driven by a high recovery  
573 that overshot pre-flood levels of biomass production, which may have been aided by  
574 the same causes as those mentioned in the previous section, namely higher  
575 belowground biomass or greater resource enrichment in more diverse communities.  
576 However, in contrast to Wright et al. (2015), we found that flooding did not decrease  
577 community stability and that after flooding diverse communities were still more stable  
578 than less diverse communities. Some of these dissimilarities between the two studies  
579 might have been due to different calculations of stability measures, species diversity  
580 gradients and managements of experimental plots.

581

## **Influence of associated soil organisms**

582  
583 Soil communities can strongly affect biodiversity effects in plant communities.  
584 Specifically, for the Jena Experiment, previous findings suggested differential  
585 evolution of plant–soil feedbacks in monocultures vs. mixtures (Zuppinger-Dingley et  
586 al. 2016). Therefore, we designed our experiment with three soil treatments to detect  
587 possible effects of associated microbial communities on community stability.  
588 However, we could not find any interactions between them and plant community co-  
589 occurrence history. Based on this “negative” result, we tentatively conclude that our  
590 above interpretations about plant evolutionary changes due to co-occurrence history  
591 were not confounded by a differential assembly of soil communities over time in the  
592 Jena Experiment. That the soil treatments did work in principle could be seen by the  
593 main effects. Pre-flood productivity was lower when native soil biota were present,  
594 which could have been due to a greater density of antagonistic soil biota in native and  
595 native-inoculated soils (Schnitzer et al. 2011), or a greater pool of available soil  
596 resources resulting from the soil sterilization process in the two inoculated soils  
597 (Gebremikael et al. 2015). Recovery and resilience were greater for communities  
598 growing in native soil (see Fig. 3B), suggesting that native soil organisms did have a  
599 beneficial effect on both selected and naïve plant communities after they had been  
600 affected by the flood event.

601

## **Conclusions**

602  
603 So far, evolutionary mechanisms underlying ecosystem stability in biodiversity  
604 experiments have only been studied in terms of phylogenetic relatedness that reflects  
605 evolutionary processes over long time scales, with conflicting results (e.g., Cadotte et  
606 al. 2012, Venail et al. 2015). Experimental evidence for short-term evolution leading

607 to changes at the community level, referred to as community evolution (van Moorsel  
608 et al. 2018), has been reported for microbial ecosystems (Gravel et al. 2011, Lawrence  
609 et al. 2012, Fiegna et al. 2014, 2015, Zhao et al. 2016). However, short-term  
610 evolutionary processes could be particularly relevant in plant communities facing  
611 rapid global change (Schmid et al. 1996, Davis et al. 2005) because plants are fixed in  
612 place and can only move by propagule dispersal. Here we show that evolution can  
613 affect biomass stability after only 8 years and a few generations of sexual  
614 reproduction in communities of perennial plant species, likely due to sufficient  
615 “standing genetic variation” (Fakheran et al. 2010) in the original seed populations  
616 (van Moorsel et al. 2019). At low diversity, communities could compensate with  
617 evolutionary adjustments resulting in a better occupation of the available niche space  
618 either via evolved (genetic) trait divergence or evolved trait plasticity (Zuppinge-  
619 Dingley et al. 2014, Meilhac et al. 2020). In more complex and diverse communities,  
620 opportunities for community evolution may be more restricted due to weaker  
621 interactions between particular species (Fox 1988) and because the community niche  
622 (Salles et al. 2009) is already large due to “random” differences between species. In  
623 this sense, we speculate that communities may either be stabilized by co-evolution  
624 between few species or diversity of many species, both leading to greater trait  
625 diversity. We encourage others with long-term biodiversity experiments to do similar  
626 follow-up experiments. Comparable results from biodiversity experiments around the  
627 globe will strengthen the hypothesis that selection in a community context can  
628 increase stability, which would have far-reaching consequences for the fields of  
629 conservation and restoration ecology.

630

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#### **Additional information**

904 **Supplementary information** is available for this paper online.

905 **Data and code availability.** Data and code (R scripts) are available from the  
906 corresponding author and will be made publicly available upon acceptance on the  
907 Pangaea repository.

908

909

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922

### **Author contributions**

923 B.S. designed research, T.H. and S.J.V.M. performed research; A.E. and N.E.  
924 maintained and coordinated the field site; S.J.V.M., C.W. and B.S. analyzed data;  
925 S.J.V.M., B.S., O.L.P. and C.W. wrote the paper. All co-authors contributed to  
926 subsequent versions of the paper.

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### **Competing interests**

929 The authors declare no conflicts of interest.

930 **TABLE 1. Mixed-model ANOVA results for log-transformed community stability, log-transformed mean population stability and**  
 931 **untransformed asynchrony.**

	Stability ( $CV^{-1}$ )				Population stability ( $CV_{pop}^{-1}$ )			Asynchrony ( $1-\theta$ )		
	$DF_n$									
Fixed terms	$um$	$DF_{den}$	$F$	$P$	$DF_{den}$	$F$	$P$	$DF_{den}$	$F$	$P$
Log richness ( $R_{log}$ )	1	<b>44.1</b>	<b>10.74</b>	<b>0.002</b>	44.1	5.27	0.027	44.1	<b>143.00</b>	<b>&lt;0.001</b>
Soil treatment (SH)	2	87.1	0.64	0.529	87.1	1.30	0.278	87.1	0.87	0.424
Co-occurrence history										
(CH)	1	135.0	1.80	0.181	135.0	3.79	0.054	135.0	0.50	0.479
SH x $R_{log}$	2	87.2	0.05	0.954	87.2	0.01	0.992	87.2	0.38	0.685
CH x $R_{log}$	1	<b>135.0</b>	<b>4.79</b>	<b>0.030</b>	<b>135.0</b>	<b>8.38</b>	<b>0.004</b>	135.0	0.05	0.830
Random terms	$N$	$Var. 10^{-3}$	$SE 10^{-3}$		$Var. 10^{-3}$	$SE 10^{-3}$		$Var. 10^{-3}$	$SE 10^{-3}$	
Plot	46	100.1	25.9		95.6	23.5		17.9	4.6	
Plot x SH	137	15.5	10.9		13.9	7.4		-0.1	2.0	
Residual	274	92.3	11.2		58.4	7.1		20.0	2.5	

932 *Notes:* The effects of species richness (log scale), soil treatments, and co-occurrence history on the stability of community and population  
 933 biomass and on asynchrony across the entire experimental period from 2012–2015 were analyzed (excluding the time point immediately after  
 934 the extreme event of a late spring flood in June 2013). Significant effects are highlighted in bold.  $DF_{num}$  = numerator degrees of freedom,  $DF_{den}$   
 935 = denominator degrees of freedom,  $F$  = variance ratio,  $P$  = probability of type-I error.



936 **TABLE 2. Mixed-model ANOVA results for resistance, recovery, and resilience of**  
937 **community biomass in response to the extreme event of a late spring flood in**  
938 **June 2013.**  
939

	Resistance				Recovery			Resilience		
Fixed terms	<i>DF<sub>num</sub></i>	<i>DF<sub>den</sub></i>	<i>F</i>	<i>P</i>	<i>DF<sub>den</sub></i>	<i>F</i>	<i>P</i>	<i>DF<sub>den</sub></i>	<i>F</i>	<i>P</i>
Log richness ( $R_{\log}$ )	1	<b>44.2</b>	<b>9.41</b>	<b>0.004</b>	44.1	<b>15.95</b>	<b>&lt;0.001</b>	44.2	1.69	0.200
Soil treatment (SH)	2	<b>87.3</b>	<b>14.07</b>	<b>&lt;0.001</b>	87.2	0.29	0.745	<b>87.3</b>	<b>6.12</b>	<b>0.003</b>
Co-occurrence										
history (CH)	1	<b>135</b>	<b>4.19</b>	<b>0.043</b>	<b>135</b>	<b>14.50</b>	<b>&lt;0.001</b>	135	3.48	0.064
SH x $R_{\log}$	2	<b>87.5</b>	<b>5.95</b>	<b>0.004</b>	87.4	1.73	0.184	<b>87.5</b>	<b>6.97</b>	<b>0.002</b>
CH x $R_{\log}$	1	<b>135</b>	<b>5.32</b>	<b>0.023</b>	135	0.48	0.488	135	2.65	0.106
Random terms	<i>N</i>	<i>Var.</i>	<i>SE</i>		<i>Var.</i>	<i>SE</i>		<i>Var.</i>	<i>SE</i>	
Plot	46	3645	1074		2234	771		6910	2238	
Plot x SH	137	775	702		-158	745		1933	1784	
Residual	274	6246	760		7851	956		15914	1937	

940

941 *Notes:* The effects of species richness (log scale), soil treatments, and co-occurrence  
942 history on responses of community biomass to flooding were analyzed. Bold italic  
943 text highlights significant effects. (Similar ANOVAs with pre-flood biomass as  
944 covariate are shown in Appendix S1: Table S3.)  $DF_{num}$  = numerator degrees of  
945 freedom,  $DF_{den}$  = denominator degrees of freedom,  $F$  = variance ratio,  $P$  = probability  
946 of type-I error.

947

948

## FIGURE CAPTIONS

949

950 **FIG. 1. Experimental set-up of plant communities in the field.** Seeds from plants  
951 that had been co-occurring for eight years in 47 plots of the Jena Experiment (selected  
952 plants) and seeds purchased from a seed supplier (naïve plants) were germinated at  
953 the same time in a glasshouse. These seedlings were then transplanted back to the  
954 Jena field site in March 2011 according to randomized planting schemes with equal  
955 species composition and abundances. Selected (light green) and of naïve communities  
956 (dark green) were grown, in the same 47 plots from which selected plants had been  
957 taken, in four quadrats separated by plastic frames with different soil treatments  
958 (unsterilized native or mixed soil or sterilized soil with native or neutral inoculum, see  
959 Methods). The mixed-soil treatment was not used in this paper because it was  
960 harvested early for a different experiment. Co-occurrence history (selected vs. naïve)  
961 was thus a split-split plot treatment replicated for 47 community compositions  
962 (including 11 monocultures) times three soil treatments. We ensured equal  
963 abundances and positions of species in the 141 pairs of 1 x 0.5 m subplots (see  
964 planting scheme).

965

966 **FIG. 2. The biodiversity–stability relationship for selected (blue) and naïve**  
967 **communities (red). (A) Community stability, (B) mean population stability, (C)**  
968 **asynchrony, (D) relationship between stability and asynchrony after correction for all**  
969 **other model terms except co-occurrence history. The corrections were obtained by**  
970 **fitting a model with plots and quadrats only and adding the residuals to the diversity-**  
971 **level means (see Methods). Colored bands show standard errors of predictions from**  
972 **mixed models as presented in Table 1. For significances see Table 1 (panels A–C);**  
973 **the slopes in panel D are significant at  $P < 0.001$ . In panels A–C points are means of**

974 the three soil treatments estimated from the model in Table 1. Points in D are residual  
975 values of each plant community after accounting for the variation due to soil  
976 treatments, planted richness, and plot identity.

977

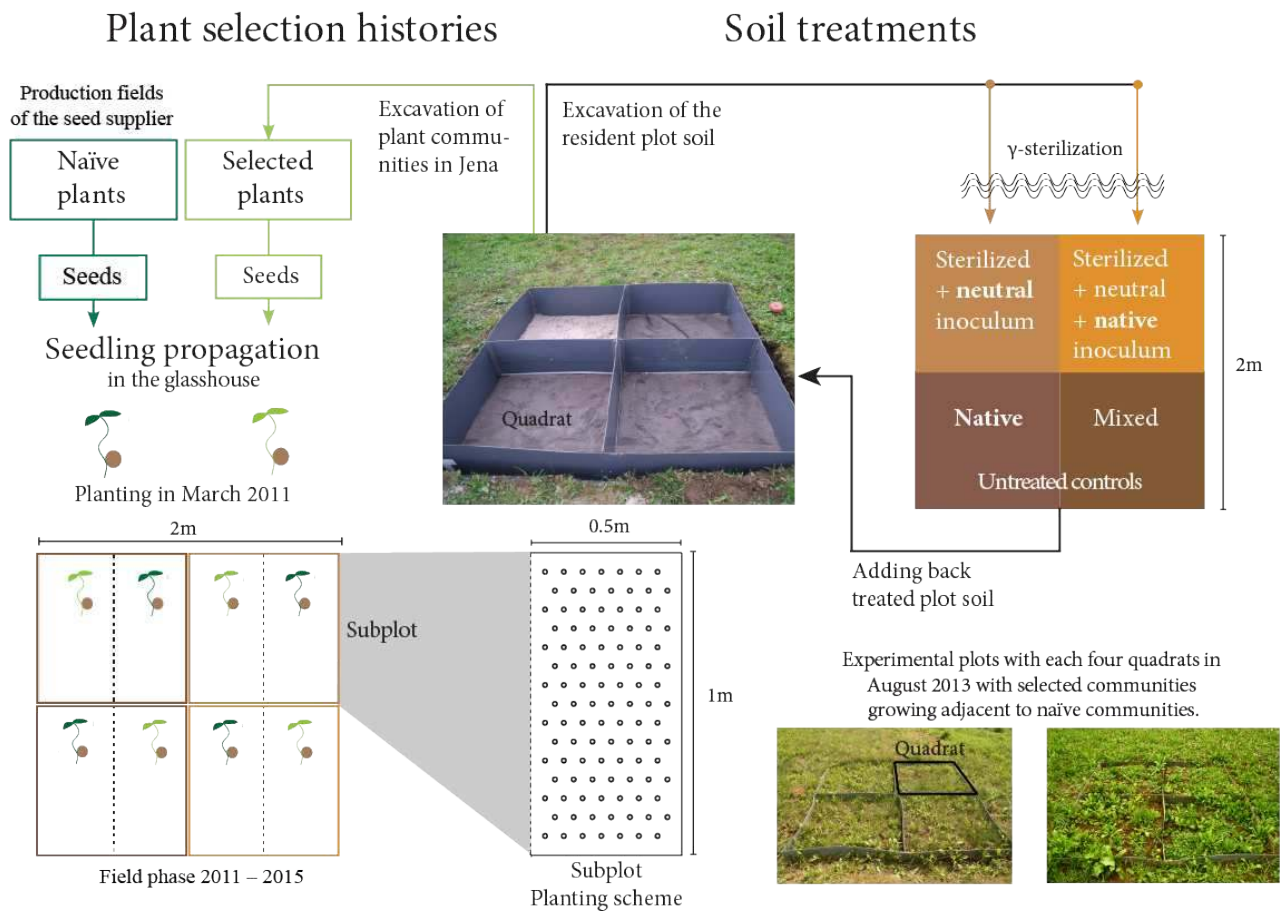
978 **FIG. 3. Plant community biomass before and after the flood event.** Points indicate  
979 the average community biomass across all diversity levels for **(A)** selected (blue) and  
980 naïve communities (red) and **(B)** native soil (blue), sterilized soil with native  
981 inoculum (“inoculated”, green) and sterilized soil with neutral inoculum (“neutral”,  
982 orange). Resistance is the difference in biomass between the average of the three  
983 harvests before the flood (May 2012, August 2012, and May 2013) and the biomass  
984 directly after the flood (label “Flood” on x-axis corresponding to summer harvest in  
985 August 2013). Recovery is the difference in biomass between the average of the three  
986 harvests after recovery from the flood (May 2014, August 2014, and May 2015) and  
987 the biomass directly after the flood (“Flood” label). Resilience is the difference in  
988 biomass between the average of the three harvests after recovery from the flood and  
989 the average of the three harvests before the flood. See also Appendix S1: Figure S2.  
990 Means and standard errors were calculated from raw data.

991

992 **FIG. 4. Resistance, recovery, and resilience to the flood event.** **(A)** Biodiversity–  
993 resistance relationships, **(B)** biodiversity–recovery relationships, and **(C)**  
994 biodiversity–resilience relationships for selected (blue) and naïve communities (red).  
995 Colored bands show standard errors of predictions from mixed models as presented in  
996 Table 2. For significances see Table 2. Points are means of the three soil treatments  
997 estimated from the model in Table 2. The dashed line at 0 indicates no change in  
998 biomass in response to the flood (resistance), after the flood (recovery), or between

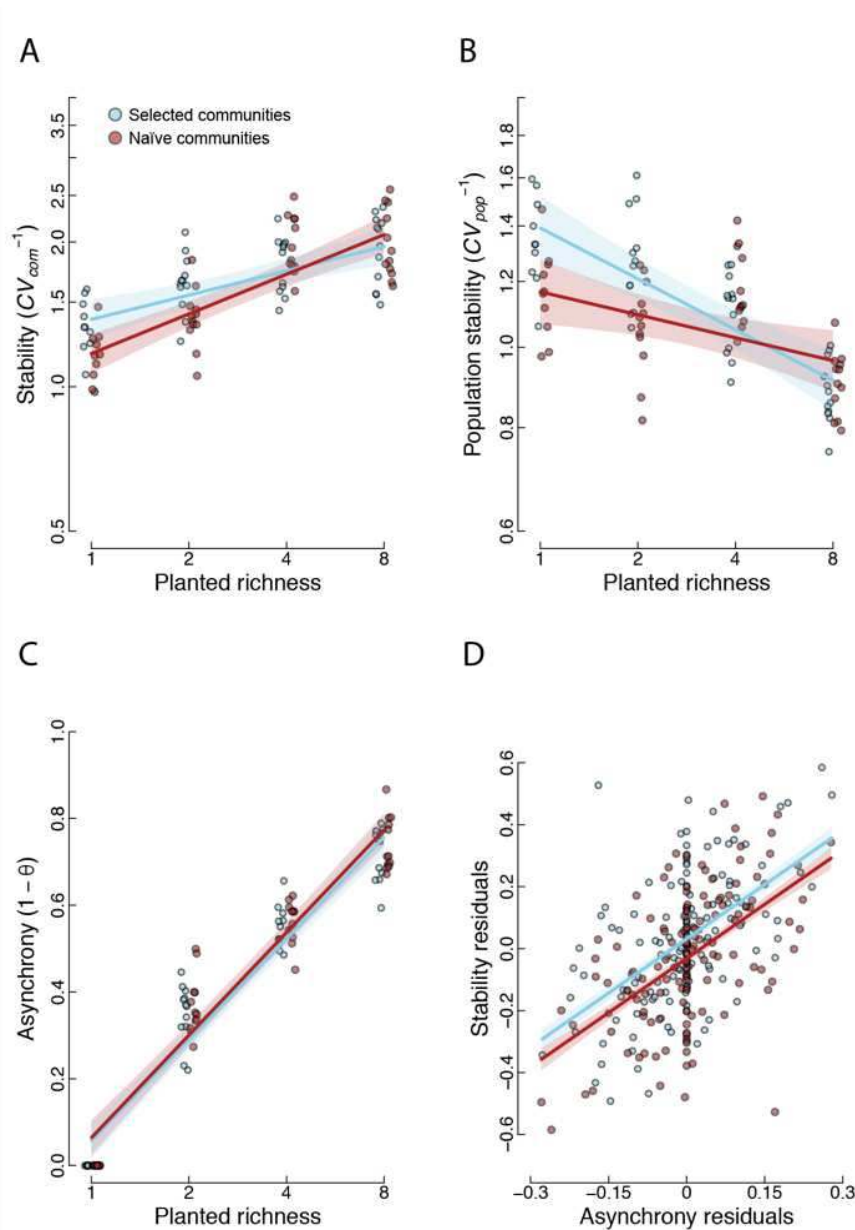
999 pre- and post-flood harvests (resilience). Similar plots with values corrected for  
1000 variation in pre-flood biomass as covariate are shown in Appendix S1: Fig. S3.  
1001  
1002 **FIG. 5. The biodiversity–stability relationship for selected (blue) and naïve**  
1003 **communities (red). (A)** The three harvests before the extreme event of a late spring  
1004 flood in June 2013 and **(B)** the three harvests after recovery from the flood. Colored  
1005 bands show standard errors of predictions from mixed models as presented in  
1006 Appendix S1: Table S2.  $P < 0.001$  for the effect of log richness in post-flood stability  
1007 and  $P = 0.027$  for the effect of co-occurrence history on post-flood stability. For other  
1008 test-statistics see Appendix S1: Table S2. Points are means of the three soil treatments  
1009 estimated from the model in Appendix S1: Table S2.  
1010

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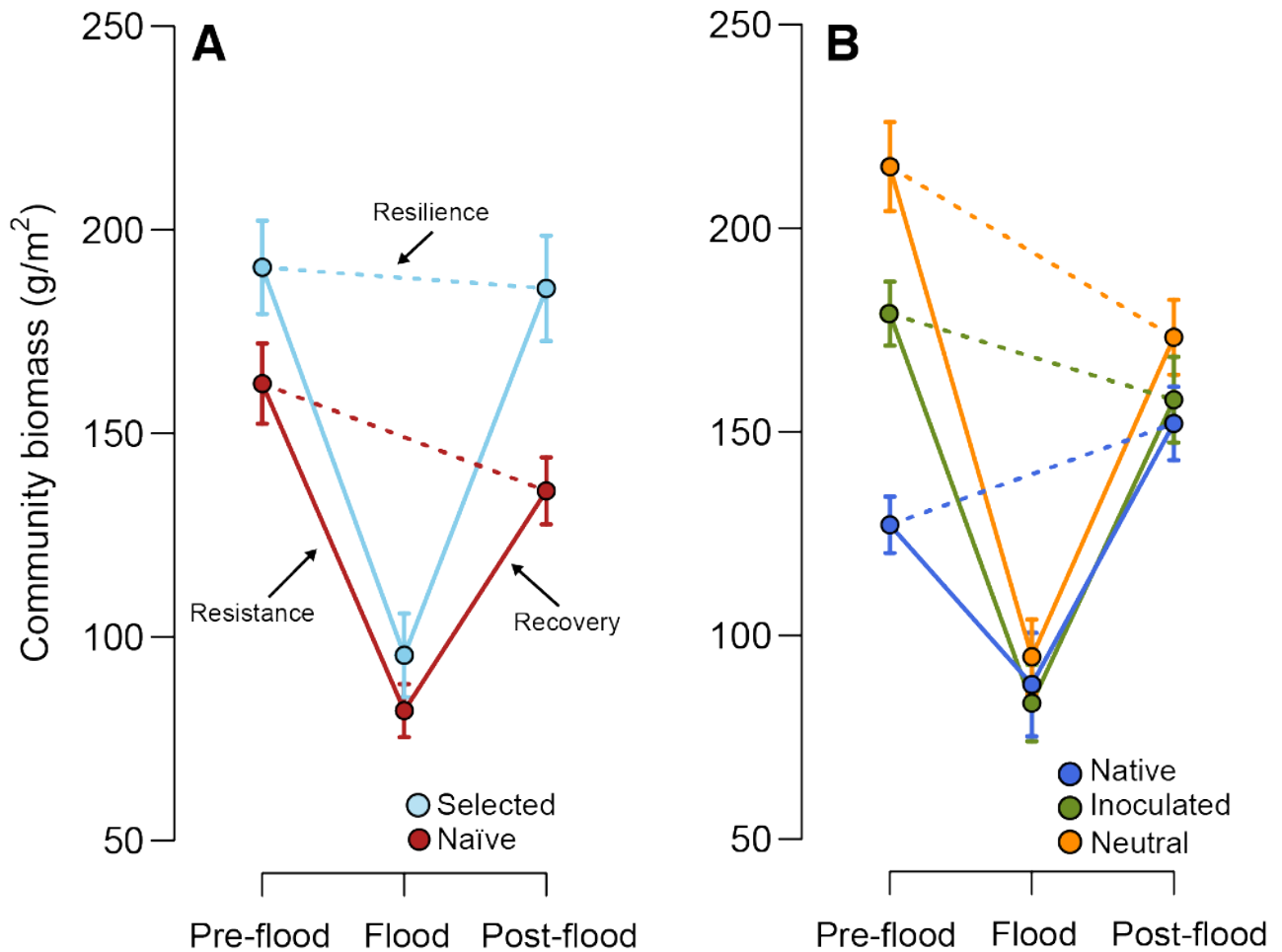
1013

1014 **FIG. 1. Experimental set-up of plant communities in the field.** Seeds from plants  
1015 that had been co-occurring for eight years in 47 plots of the Jena Experiment (selected  
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1017 the same time in a glasshouse. These seedlings were then transplanted back to the  
1018 Jena field site in March 2011 according to randomized planting schemes with equal  
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1021 taken, in four quadrats separated by plastic frames with different soil treatments  
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1027 abundances and positions of species in the 141 pairs of 1 x 0.5 m subplots (see  
1028 planting scheme).



1029  
1030

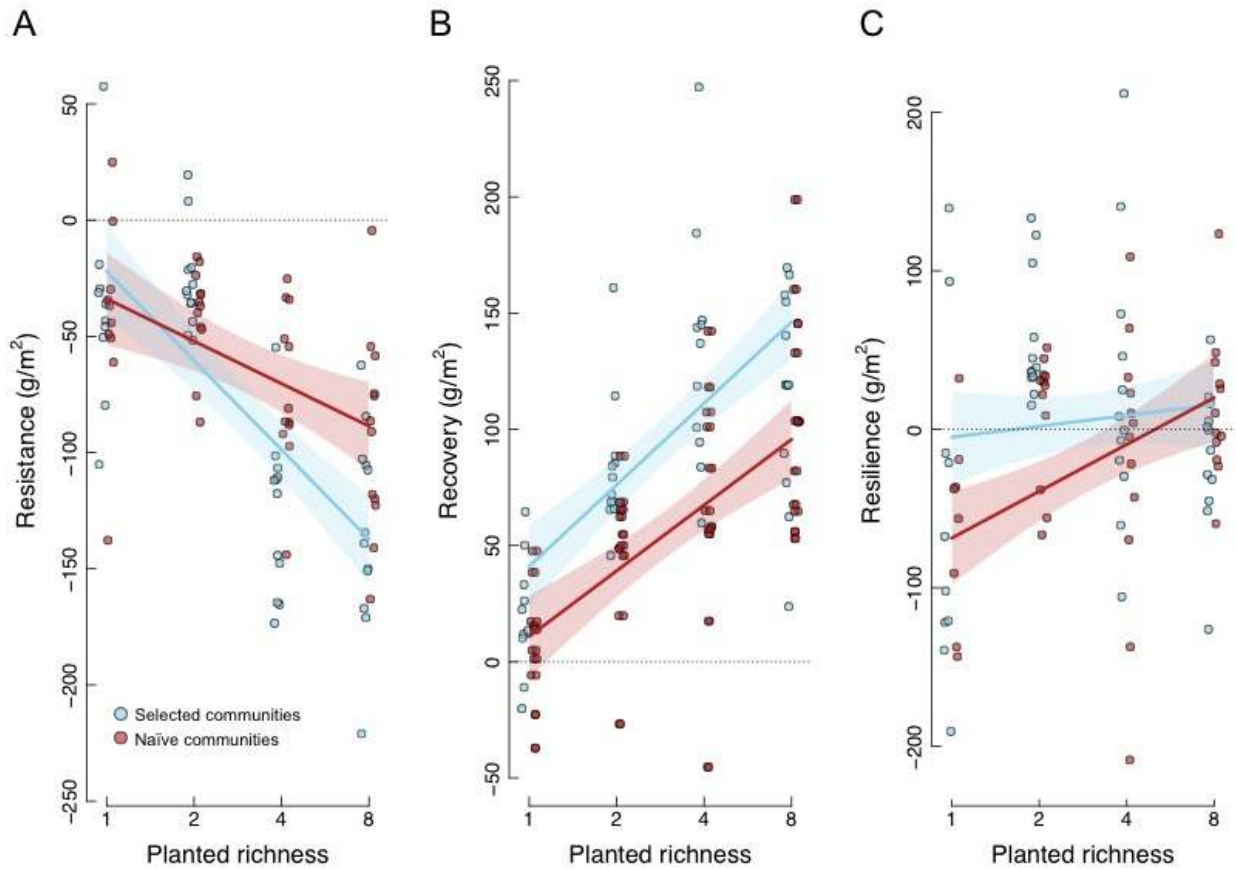
1031 **FIG. 2. The biodiversity–stability relationship for selected (blue) and naïve**  
 1032 **communities (red).** (A) Community stability, (B) mean population stability, (C)  
 1033 asynchrony, (D) relationship between stability and asynchrony after correction for all  
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 1036 level means (see Methods). Colored bands show standard errors of predictions from  
 1037 mixed models as presented in Table 1. For significances see Table 1 (panels A–C);  
 1038 the slopes in panel D are significant at  $P < 0.001$ . In panels A–C points are means of  
 1039 the three soil treatments estimated from the model in Table 1. Points in D are residual  
 1040 values of each plant community after accounting for the variation due to soil  
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1042

1043

1044 **FIG. 3. Plant community biomass before and after the flood event.** Points indicate  
 1045 the average community biomass across all diversity levels for (A) selected (blue) and  
 1046 naïve communities (red) and (B) native soil (blue), sterilized soil with native  
 1047 inoculum (“inoculated”, green) and sterilized soil with neutral inoculum (“neutral”,  
 1048 orange). Resistance is the difference in biomass between the average of the three  
 1049 harvests before the flood (May 2012, August 2012, and May 2013) and the biomass  
 1050 directly after the flood (label “Flood” on x-axis corresponding to summer harvest in  
 1051 August 2013). Recovery is the difference in biomass between the average of the three  
 1052 harvests after recovery from the flood (May 2014, August 2014, and May 2015) and  
 1053 the biomass directly after the flood (“Flood” label). Resilience is the difference in  
 1054 biomass between the average of the three harvests after recovery from the flood and  
 1055 the average of the three harvests before the flood. See also Figure Appendix S1: S2.  
 1056 Means and standard errors were calculated from raw data.

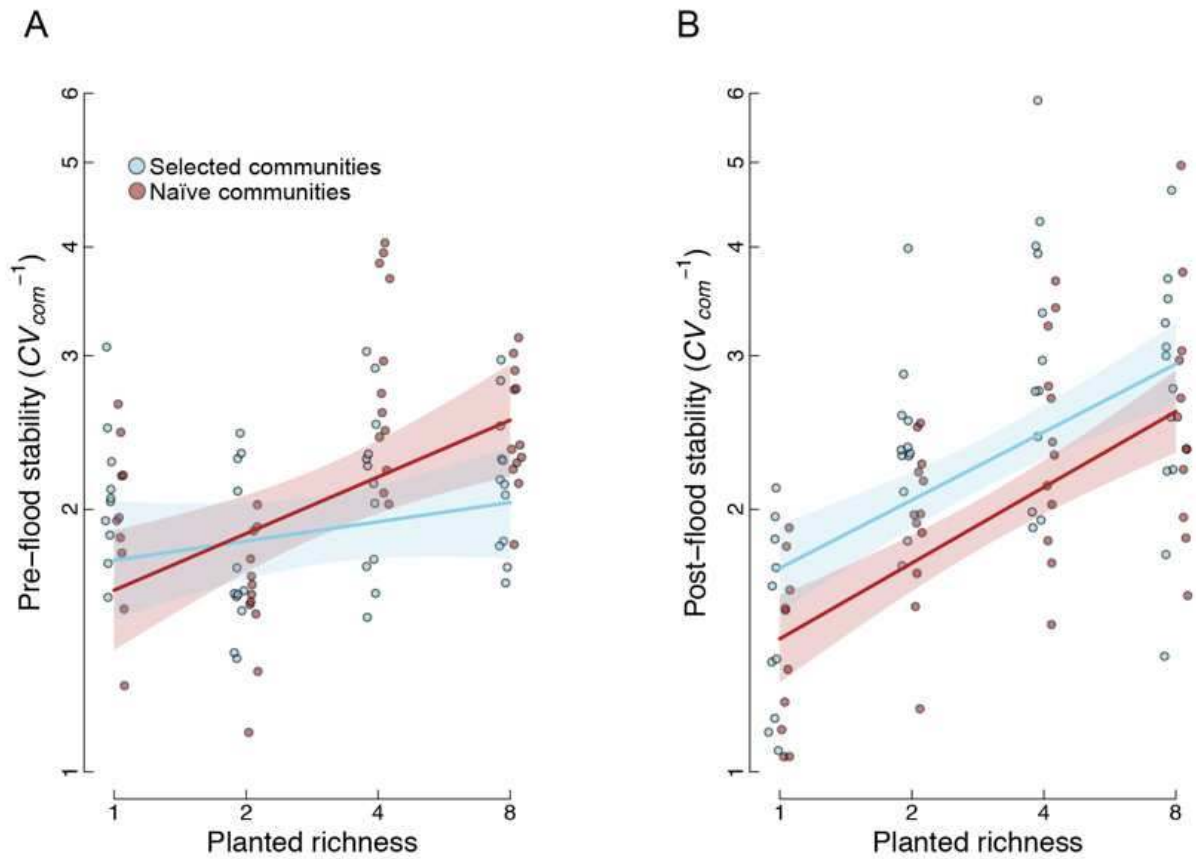


1057

1058

1059 **FIG. 4. Resistance, recovery, and resilience to the flood event.** (A) Biodiversity–  
 1060 resistance relationships, (B) biodiversity–recovery relationships, and (C)  
 1061 biodiversity–resilience relationships for selected (blue) and naïve communities (red).  
 1062 Colored bands show standard errors of predictions from mixed models as presented in  
 1063 Table 2. For significances see Table 2. Points are means of the three soil treatments  
 1064 estimated from the model in Table 2. The dashed line at 0 indicates no change in  
 1065 biomass in response to the flood (resistance), after the flood (recovery), or between  
 1066 pre- and post-flood harvests (resilience). Similar plots with values corrected for  
 1067 variation in pre-flood biomass as covariate are shown in Appendix S1: Fig. S3.





1068

1069 **FIG. 5. The biodiversity–stability relationship for selected (blue) and naïve**  
 1070 **communities (red).** (A) The three harvests before the extreme event of a late spring  
 1071 flood in June 2013 and (B) the three harvests after recovery from the flood. Colored  
 1072 bands show standard errors of predictions from mixed models as presented in  
 1073 Appendix S1: Table S2.  $P < 0.001$  for the effect of log richness in post-flood stability  
 1074 and  $P = 0.027$  for the effect of co-occurrence history on post-flood stability. For other  
 1075 test-statistics see Appendix S1: Table S2. Points are means of the three soil treatments  
 1076 estimated from the model in Appendix S1: Table S2.

1077

1078

## Ecology

### Appendix S1 for:

#### **Co-occurrence history increases ecosystem stability and resilience in experimental plant communities**

Sofia J. van Moorsel, Terhi Hahl, Owen L. Petchey, Anne Ebeling, Nico Eisenhauer, Bernhard Schmid, and Cameron Wagg

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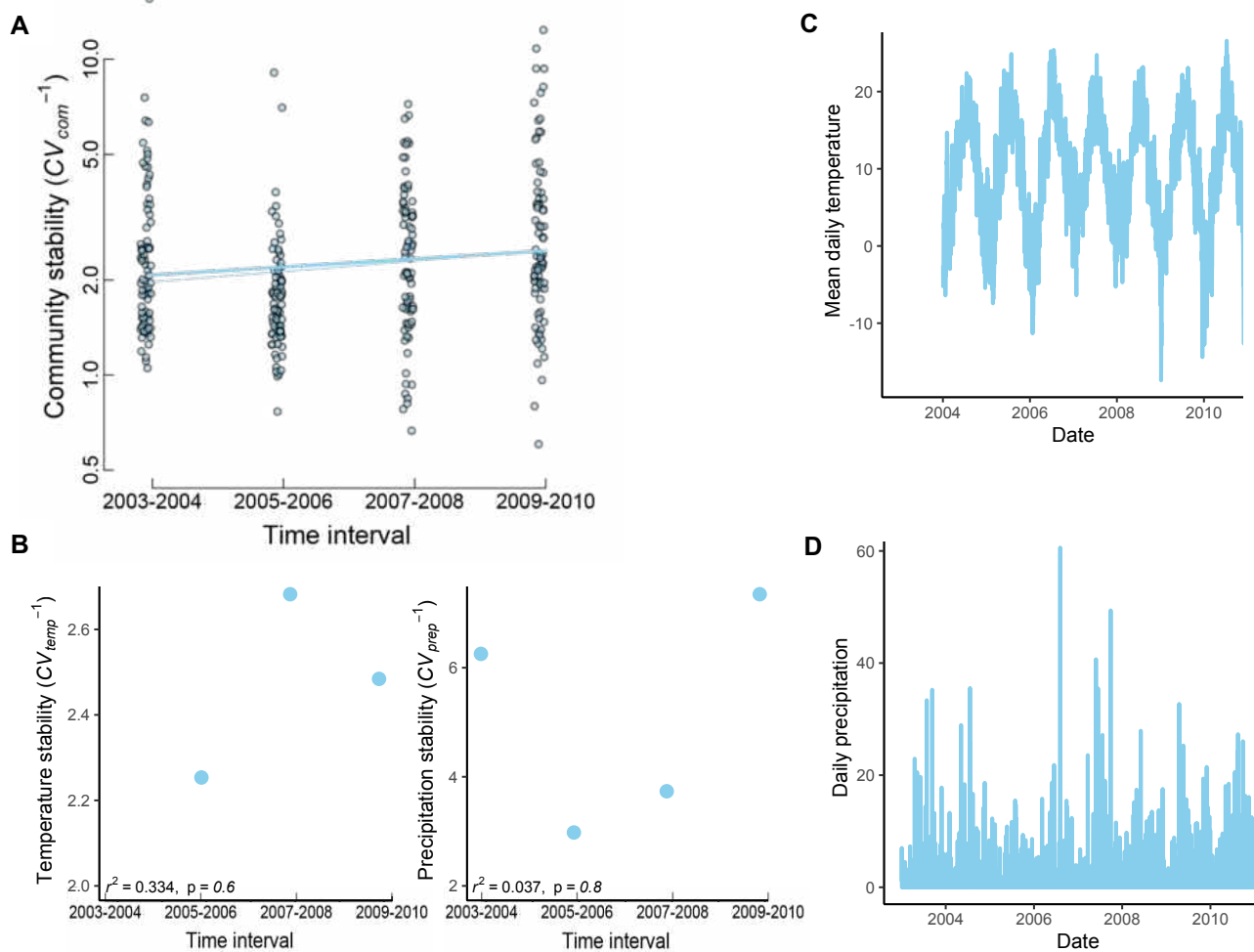
Page 9: **Appendix S1: TABLE S3.** ANOVA results for Bray-Curtis compositional turnover

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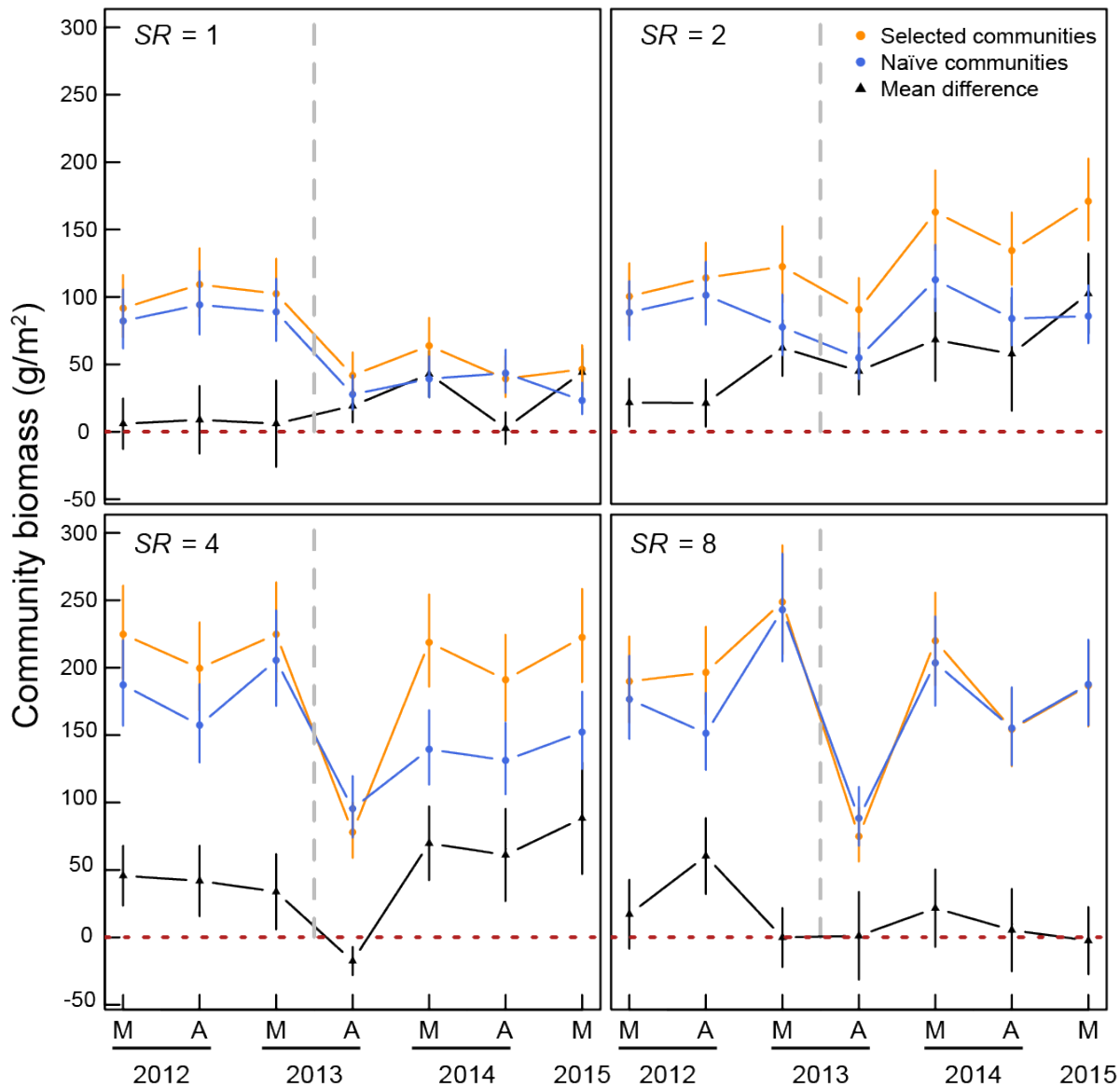
Page 11: **Appendix S1: TABLE S5.** Species list.

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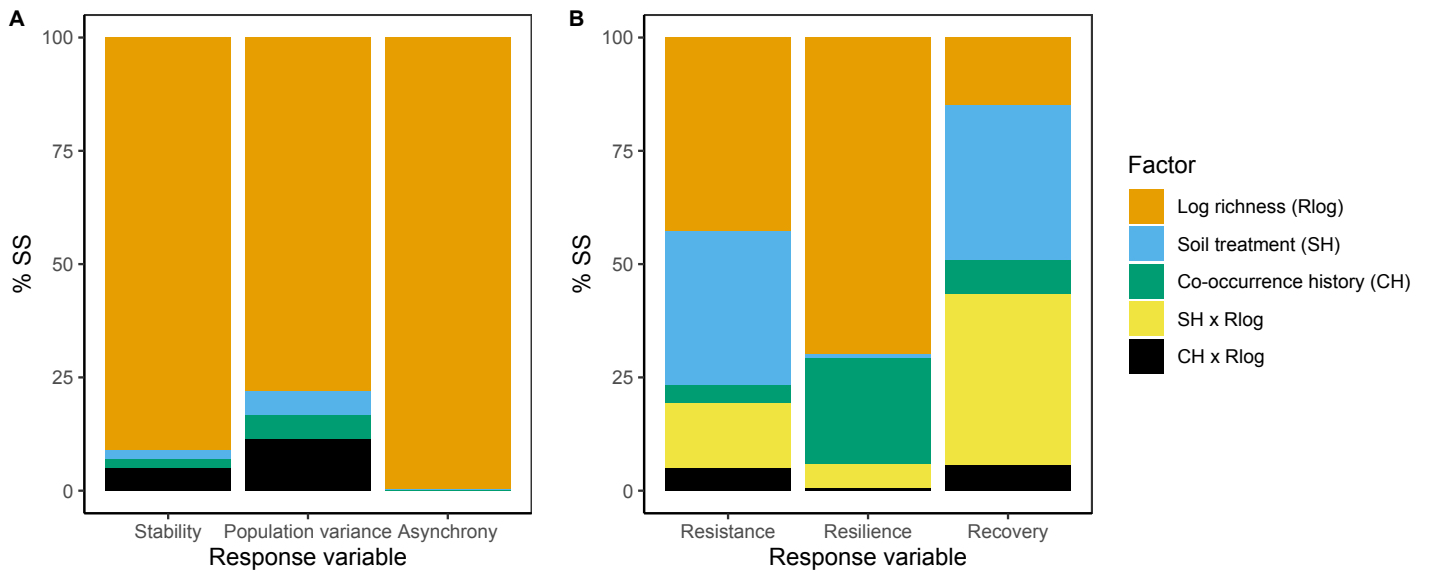
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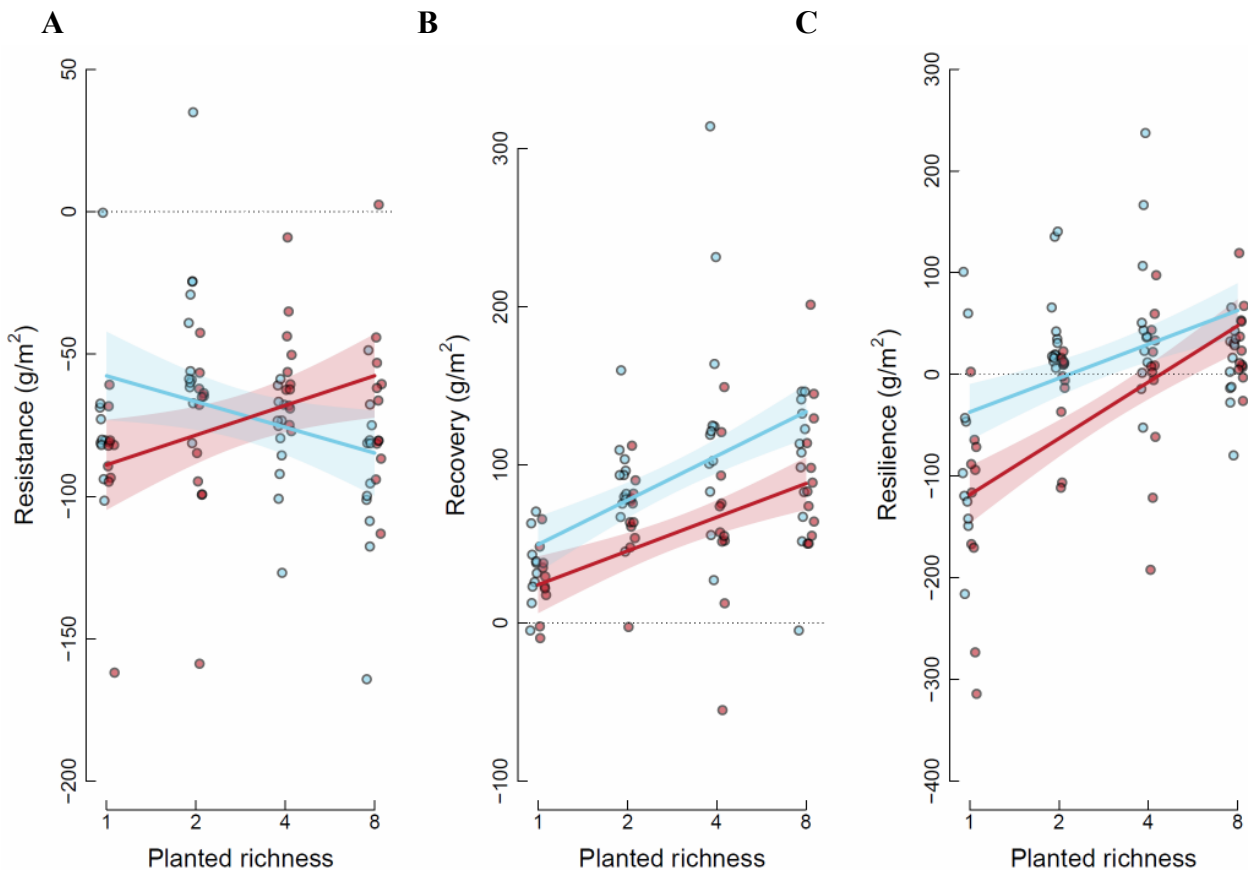
**Appendix S1: FIG. S1. Stability of community biomass and climate from 2003 to 2010.** (A) Combined intra- and inter-annual stability of experimental communities over the first 8 years in a grassland biodiversity experiment (Jena Experiment; species richness levels: 1, 2, 4, 8, 16, 60). The 8-year period was partitioned into four 2-year periods and within each stability was calculated for spring and summer harvests in year  $n$  and spring harvest in year  $n+1$ , corresponding to the same sequence of three harvests used in subsequent tests communities collected from the Jena Experiment in 2010 (selected communities) or re-established from seeds of the original supplier (naïve communities). Thick regression line includes three outliers outside the top margin of the plot ( $P = 0.037$ ), thin line excludes these outliers ( $P = 0.0018$ ). Changes in community biomass stability over time were also significantly correlated with precipitation stability ( $P < 0.001$  when “precipitation stability” is fitted in the model instead of the term “time”). (B) Stability (inverse of the CV) over time for mean temperatures and precipitation in spring (March-May) and summer (June-August), times that correspond to the growth of biomass. The CV was calculated across three time points (spring year  $n$ , summer year  $n$  and spring year  $n+1$ ). Temperature from the year 2003 is missing, which is why the first value appears in 2004. Note that the CV is the inverse of stability, thus lower values mean higher stability. Test statistics are shown in the figure. (C) Mean temperatures from 2003 to 2010. (D) Total daily precipitation from 2003 to 2010. Temperature and precipitation were measured with a weather station on site (see Appendix S1: Fig. S1C, D).



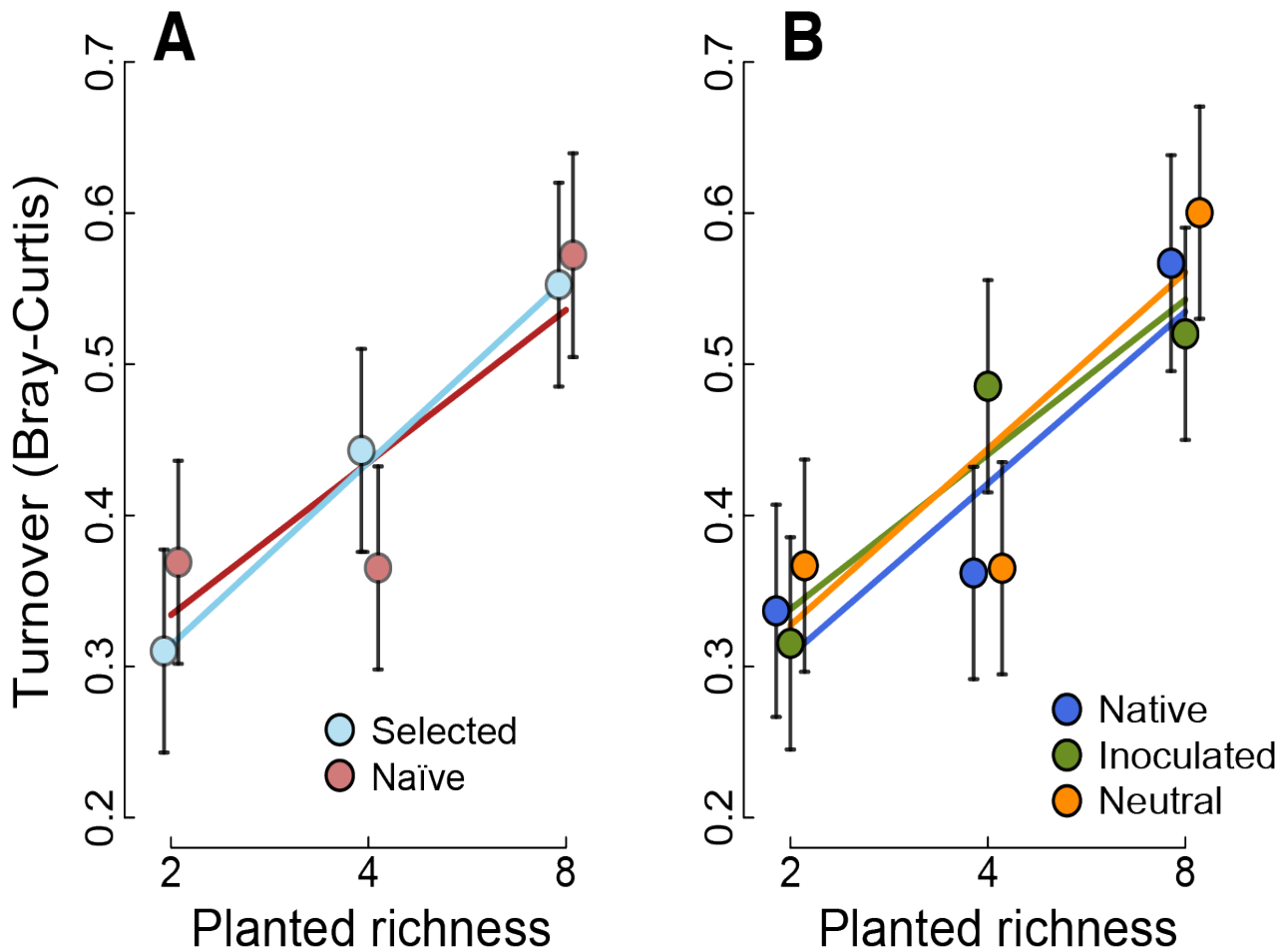
**Appendix S1: FIG. S2. Aboveground community biomass over time at four species richness levels (SR).** Selected and naïve plant communities and their mean difference are plotted with means and standard errors calculated from raw data. The dashed line indicates the flood event. M = May, A= August. For the calculation of resistance, resilience, and recovery, we averaged the community biomass in May 2012, August 2012, and May 2013 to obtain pre-flood biomass. We used the August 2013 biomass as our measure of biomass during the flood (even though we harvested several weeks after the water had receded). For post-flood biomass we averaged community biomasses from May 2014, August 2014, and May 2015.



**Appendix S1: FIG. S3. Effect sizes (% SS) for fixed factors from a linear model. (A)** Asynchrony, population variance and community stability. **(B)** Recovery, resilience, and resistance. We used linear models to get % SS as effect sizes to compare relative explanatory power of the different fixed effects tested in the mixed models as done in hierarchical partitioning (Grömping 2006). Note that, due to the almost fully orthogonal experimental design, % SS for different fitting sequences and results from linear and mixed models were nearly identical.



**Appendix S1: FIG. S4. Resistance, recovery, and resilience corrected for pre-flood biomass.** (A) Biodiversity–resistance relationships, (B) biodiversity–recovery relationships and (C) biodiversity–resilience relationships for selected (blue) and naïve communities (red). Colored bands indicate standard errors of predictions from mixed models as presented in Table S1. In contrast to Fig. 4 in the main text here the raw data were not only corrected for variation within diversity levels between plots and quadrats but also for variation in pre-flood biomass. Means across the three soil treatments are shown. The dashed line is drawn at 0 in each graph.



**Appendix S1: FIG. S5. The biodiversity–turnover relationship.** (A) Selected (blue) and naïve communities (red). (B) Home soil (blue), sterilized soil with native inoculum (“inoculated”, green) and sterilized soil with neutral inoculum (“neutral”, orange). Species compositional turnover was calculated between three pre- and three post-flood harvests. The species richness effect was significant but none of the other effects and none of the interactions were significant (see Appendix S1: Table S3). Shown are predicted means and standard errors.

**Appendix S1: TABLE S1.** Mixed-model ANOVA results for pre-flood biomass-corrected resistance, recovery, and resilience of community biomass. The effects of species richness (log scale), soil treatments and co-occurrence history on responses of community biomass to flooding were analyzed. In contrast to Table 2 (and the corresponding Fig. 4) in the main text, here the average of the three harvests before the flood (pre-flood productivity) was included as a covariate to account for the dependence of resistance, recovery, and resilience measures on the initial productivity. Bold italic text highlights significant effects.

Fixed terms	Resistance				Recovery			Resilience		
	<i>DF<sub>num</sub></i>	<i>DF<sub>den</sub></i>	<i>F</i>	<i>P</i>	<i>DF<sub>den</sub></i>	<i>F</i>	<i>P</i>	<i>DF<sub>den</sub></i>	<i>F</i>	<i>P</i>
Pre-flood productivity	1	<b>239.0</b>	<b>271.60</b>	<b>&lt;0.001</b>	<b>199.7</b>	<b>17.05</b>	<b>&lt;0.001</b>	<b>223.8</b>	<b>47.75</b>	<b>&lt;0.001</b>
Log richness ( $R_{\log}$ )	1	48.4	0.02	0.886	<b>49.6</b>	<b>9.53</b>	<b>0.003</b>	<b>49.2</b>	<b>11.50</b>	<b>0.001</b>
Soil treatment (SH)	2	96.2	0.41	0.668	95.2	0.13	0.877	96.4	1.50	0.229
Co-occurrence history (CH)	1	140.3	0.03	0.860	<b>140.0</b>	<b>11.65</b>	<b>&lt;0.001</b>	<b>140.7</b>	<b>10.95</b>	<b>0.001</b>
SH x $R_{\log}$	2	90.3	1.23	0.296	89.5	2.39	0.097	<b>90.5</b>	<b>3.75</b>	<b>0.027</b>
CH x $R_{\log}$	1	<b>133.9</b>	<b>8.77</b>	<b>0.004</b>	134.4	0.48	0.491	134.6	2.84	0.094
Random terms	<i>N</i>	<i>Var.</i>	<i>SE</i>		<i>Var.</i>	<i>SE</i>		<i>Var.</i>	<i>SE</i>	
Plot	46	2124	643		1887	717		5971	1920	
Plot x SH	137	669	429		112	756		1265	1521	
Residual	274	3534	432		7583	925		14035	1711	

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



**Appendix S1: TABLE S2.** Mixed-model ANOVA results for log-transformed community stability for the three harvests before the flood event in late spring of June 2013 (pre-flood stability) and the three harvests after recovery from the flood event (post-flood stability). The effects of species richness (log scale), soil treatments, and co-occurrence history on the pre- and post-flood stability of community biomass were analyzed. Bold italic text highlights significant effects.

Fixed terms	Pre-flood stability				Post-flood stability		
	$DF_{num}$	$DF_{den}$	$F$	$P$	$DF_{den}$	$F$	$P$
Log richness ( $R_{log}$ )	1	44.1	1.67	0.203	<b>43.9</b>	<b>13.89</b>	<b>&lt;0.001</b>
Soil treatment (SH)	2	86.2	1.04	0.356	86.3	0.99	0.377
Co-occurrence history (CH)	1	133.1	1.50	0.222	<b>133.6</b>	<b>5.03</b>	<b>0.027</b>
SH x $R_{log}$	2	87.9	2.26	0.110	87.1	0.28	0.754
CH x $R_{log}$	1	134.5	2.86	0.093	134.1	0.10	0.749
Random terms	$N$	$Var.$	$SE$		$Var.$	$SE$	
Plot	36	0.273	0.069		0.092	0.032	
Plot x SH	107	0.008	0.027		-0.013	0.030	
Residual	214	0.267	0.033		0.321	0.039	

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

**Appendix S1: TABLE S3.** Mixed-model ANOVA results for Bray-Curtis compositional turnover between three pre- and three post-flood harvests. The effects of species richness (log scale), soil treatments, and co-occurrence history on the compositional turnover were analyzed. Bold italic text highlights significant effects.

<b>Turnover</b>				
Fixed terms	<i>DF<sub>num</sub></i>	<i>DF<sub>den</sub></i>	<i>F</i>	<i>P</i>
Log richness ( $R_{\log}$ )	1	<b><i>34.0</i></b>	<b><i>6.25</i></b>	<b><i>0.017</i></b>
Soil treatment (SH)	2	67.1	0.30	0.744
Co-occurrence history (CH)	1	105.0	0.00	1.000
SH x $R_{\log}$	2	67.1	0.08	0.927
CH x $R_{\log}$	1	105.0	0.40	0.527
Random terms	<i>N</i>	<i>Var. 10<sup>-3</sup></i>	<i>SE 10<sup>-3</sup></i>	
Plot	36	41.29	11.55	
Plot x SH	107	0.00	4.00	
Residual	214	35.95	4.96	

**Appendix S1: TABLE S4. Analysis of soil-history treatments at the end of the experiment in October 2015.** Means and standard errors (SEMs) are given together with the *P*-values testing the significance of treatment effects in analyses of variance. SEMs were calculated with the raw data.

Soil characteristics	Native soil		Sterilized soil with native inoculum		Sterilized soil with neutral inoculum		Significance
	Mean	SEM	Mean	SEM	Mean	SEM	
Nitrate (ppm)	7	0.26	5.7	0.26	5.5	0.25	< 0.001
Phosphorous (ppm)	23.5	1.5	31.1	1.8	31	1.9	< 0.001
Microbial carbon	626.5	16.1	451.8	14.2	442.3	14.6	< 0.001
Microbial nitrogen	150.7	3.5	112.2	3.1	106.1	3.3	< 0.001
Bacterial richness (# 16S-OTUs)	5230.4	71.1	4919.9	82	4822.5	92.1	< 0.001
Bacterial evenness	0.889	8E-04	0.875	0.0007	0.864	0.00082	< 0.001
Fungal richness (# ITS-OTUs)	774.8	17.9	765.7	17.6	765.9	19	0.1
Fungal evenness	0.879	0.002	0.885	0.0013	0.888	0.00148	< 0.001

**Appendix S1: TABLE S5. Species list.** In the 47 experimental communities, a total of 49 species were grown in different community diversities and compositions. The eleven species occurring in monoculture are highlighted in bold. For species authorities and definition of functional groups see (Roscher et al. 2004). Biomass values are taken from small 3.5 x 3.5 m monoculture plots and represent yearly aboveground averages from 2003–2006 (Marquard et al. 2013).

<b>Species</b>	<b>Functional group</b>	<b>Life cycle</b>	<b>Self-incompatible (yes/no)</b>	<b>Biomass (g/m<sup>2</sup>)</b>
<i>Achillea millefolium</i>	herb	perennial	yes	338.0
<i>Ajuga reptans</i>	herb	perennial	no	10.1
<i>Alopecurus pratensis</i>	grass	perennial	no	433.9
<i>Anthoxanthum odoratum</i>	grass	perennial	no	259.6
<i>Arrhenatherum elatius</i>	grass	perennial	yes	616.4
<i>Avenula pubescens</i>	grass	perennial	yes	422.6
<i>Bromus erectus</i>	grass	perennial	yes	675.5
<i>Bromus hordeaceus</i>	grass	annual–biennial	no (mostly selfing)	251.6
<b><i>Crepis biennis</i></b>	herb	perennial	no	326.4
<i>Cynosurus cristatus</i>	grass	perennial	yes	78.2
<i>Dactylis glomerata</i>	grass	perennial	yes	462.5
<i>Daucus carota</i>	herb	biennial	yes	376.9
<i>Festuca pratensis</i>	grass	perennial	yes	329.9
<b><i>Festuca rubra</i></b>	grass	perennial	no	334.7
<b><i>Galium mollugo</i></b>	herb	annual	no	438.1
<b><i>Geranium pratense</i></b>	herb	perennial	no	262.1
<i>Glechoma hederacea</i>	herb	perennial	no	92.8
<i>Heracleum sphondylium</i>	herb	biennial–perennial	no	180.0
<i>Holcus lanatus</i>	grass	perennial	mostly yes	500.7
<i>Knautia arvensis</i>	herb	perennial	no	644.4
<b><i>Lathyrus pratensis</i></b>	legume	perennial	no	357.8
<i>Leontodon autumnalis</i>	herb	perennial	yes	290.8
<i>Leontodon hispidus</i>	herb	perennial	no	331.8
<i>Leucanthemum vulgare</i>	herb	perennial	yes	445.6
<i>Lotus corniculatus</i>	legume	perennial	mostly yes	388.0
<i>Luzula campestris</i>	grass	perennial	mostly yes	0.1
<i>Medicago lupulina</i>	legume	annual–perennial	no	52.4
<i>Medicago x varia</i>	legume	perennial	no	815.9
<b><i>Onobrychis viciifolia</i></b>	legume	perennial	no	1290.5
<i>Phleum pratense</i>	grass	perennial	mostly yes	417.8
<b><i>Plantago lanceolata</i></b>	herb	perennial	yes	224.6
<i>Plantago media</i>	herb	perennial	no	420.8
<b><i>Poa pratensis</i></b>	grass	perennial	no	235.0
<i>Poa trivialis</i>	grass	perennial	no	164.7
<i>Primula veris</i>	herb	perennial	yes	168.1

<i>Prunella vulgaris</i>	herb	perennial	no	222.3
<i>Ranunculus acris</i>	herb	perennial	yes	242.7
<i>Ranunculus repens</i>	herb	perennial	yes	132.4
<i>Sanguisorba officinalis</i>	herb	perennial	no	414.7
<i>Taraxacum officinale</i>	herb	perennial	yes	286.2
<i>Trifolium campestre</i>	legume	annual	no	8.9
<i>Trifolium dubium</i>	legume	annual	yes?	2.8
<i>Trisetum flavescens</i>	grass	perennial	yes?	422.6
<i>Trifolium fragiferum</i>	legume	perennial	mostly yes	143.1
<i>Trifolium hybridum</i>	legume	perennial	mostly yes	227.1
<i>Trifolium pratense</i>	legume	perennial	yes	353.1
<b><i>Trifolium repens</i></b>	legume	perennial	yes	361.4
<i>Veronica chamaedrys</i>	herb	perennial	yes	220.2
<i>Vicia cracca</i>	legume	perennial	no	93.2

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**Appendix S1: TABLE S6. Overview of seeds collected in the Jena plots.** For those species that did not produce enough seeds in the experimental garden in Zurich, some additional seeds were collected directly in the Jena experimental plots. Shown are percentages of total seed weight with an origin of the Jena plots for each species in each experimental community.

Plot	SR	Species	%seeds collected in Jena	Plot	SR	Species	%seeds collected in Jena	Plot	SR	Species	%seeds collected in Jena				
<b>B1A01</b>	16	Pla lan	21.4	<b>B2A01</b>	4	Ant odo	0.0	<b>B3A04</b>	8	Alo pra	0.0				
		Lat pra	0.0			Pru vul	0.0			Cyn cri	0.0				
		Poa pra	0.0			Kna arv	0.0			Fes rub	0.0				
		Ger pra	1.1			Tri pra	0.0			Poa tri	0.0				
<b>B1A02</b>	8	Alo pra	29.7	<b>B2A02</b>	2	Fes rub	0.0	<b>B3A05</b>	8	Arr ela	0.0				
		Bro ere	0.0			Tri fla	0.0			Dac glo	0.0				
		Car pra	0.0	<b>B2A03</b>	60	Fes pra	100.0			Hol lan	0.0				
		Her sph	0.0			Fes rub	0.0			Tri fla	0.0				
<b>B1A03</b>	8	Fes rub	0.0	<b>B2A04</b>	1	Pru vul	0.0	<b>B3A06</b>	1	Ant odo	0.0				
		Phl pra	0.0			Ver cha	100.0			Bro ere	0.0				
		Ran acr	63.0	<b>B2A05</b>	1	Poa pra	0.0			Poa tri	20.5				
		San off	0.0			Pla lan	100.0			Ant syl	100.0				
		few seed	8	Cyn cri	0.0	<b>B2A06</b>	4			Ger pra	0.0	<b>B3A07</b>	8	Leu vul	0.0
				Phl pra	0.0					Fes pra	0.0			Lot cor	5.0
				Gle hed	0.0	<b>B2A08</b>	2			Pla lan	10.3			Ono vic	99.9
				Pri ver	0.0					Tar off	0.0			Tri hyb	0.0
				Tri fla	0.0	<b>B2A09</b>	4			Lat pra	73.7			Fes rub	53.0
				Ver cha	0.0					Med lup	0.0			Bro hor	0.0
<b>B1A04</b>	4	Lot cor	0.0	<b>B2A12</b>	8	Ran acr	20.4	<b>B3A08</b>	2	Hol lan	0.0				
		Med lup	0.0			Tri cam	0.0			Pri ver	0.0				
		Fes pra	0.0			<b>B2A10</b>	4			Aju rep	0.0	Ran rep	100.0		
		Pla lan	33.0							Pla lan	4.6	Her sph	0.0		
<b>B1A05</b>	2	Cam pat	0.0	<b>B2A11</b>	8	Pri ver	0.0	<b>B3A09</b>	16	Leu vul	0.0				
		Ono vic	0.0			Pru vul	3.6			Med lup	0.0				
<b>B1A07</b>	2	Ono vic	0.0	<b>B2A13</b>	1	Ant syl	0.0	<b>B3A11</b>	4	Ono vic	82.7				
		Med lup	0.0			Ger pra	0.0			Dac glo	0.0				
<b>B1A11</b>	16	Ono vic	0.0	<b>B2A14</b>	8	Kna arv	52.6	<b>B3A12</b>	1	Fes pra	0.0				
		Ran acr	17.2			Ran acr	4.3			Fes pra	94.0				
<b>B1A12</b>	8	San off	0.0	<b>B2A15</b>	1	Ran acr	4.3	<b>B3A13</b>	4	Fes rub	0.0				
		Ger pra	0.0			Gal mol	0.0			Poa pra	0.0				
		Cre bie	10.1			Her sph	0.0			Bro ere	0.0				
		Gal mol	0.0			Leu vul	0.0			Poa tri	0.0				
few seed	8	San off	0.0	<b>B2A16</b>	4	San off	0.0	<b>B3A17</b>	1	Pla lan	6.7				
		Lat pra	0.0			Pla lan	1.2			Pru vul	2.1				
		Med var	0.0	<b>B2A17</b>	8	Luz cam	0.0			<b>B3A19</b>	2	Lat pra	30.1		
		Tri cam	0.0			Phl pra	0.0					Alo pra	0.0		
		Tri hyb	0.0	<b>B2A18</b>	1	Leo his	0.0			<b>B3A21</b>	2	Bro ere	96.3		
		Med lup	0.0			Ver cha	0.0					Ant odo	0.0		
<b>B1A13</b>	4	Ono vic	81.2	<b>B2A19</b>	4	Kna arv	79.9	<b>B3A20</b>	4	Poa tri	0.0				
		Tri dub	0.0			San off	0.0			Ver cha	30.0				
		Tri pra	0.0			Tri dub	0.0			Tri fla	0.0				
		Tri pra	0.0			Tri hyb	5.5			Tar off	0.0				
<b>B1A13</b>	4	Lot cor	0.0	<b>B2A20</b>	1	Ono vic	48.1	<b>B3A21</b>	2	Lot cor	0.5				
		Med var	0.0			<b>B2A21</b>	4			Leo aut	0.0				
		Ono vic	0.0												
		Med lup	0.0												

<b>B1A14</b>	<b>8</b>	Luz cam	0.0			Pla med	9.6			Tri pra	0.0
		Tri fla	0.0			Kna arv	80.4	<b>B3A22</b>	<b>16</b>	Fes rub	0.0
		Leo his	0.0			Vic cra	0.0			Ver cha	0.0
		Pla lan	28.4	<b>B2A17</b>	<b>8</b>	Gle hed	0.0			Cre bie	0.7
		Ant syl	0.0			Pla med	25.2			Ger pra	41.6
		Dau car	0.0			Leo aut	0.0			Gal mol	99.7
		Tri cam	8.4			Tar off	0.0			Pla lan	100.0
		Tri fra	0.0			Lat pra	0.0			Ono vic	0.0
<b>B1A15</b>	<b>1</b>	Cre bie	0.0			Vic cra	47.9	<b>B4A06</b>	<b>8</b>	Pru vul	0.0
<b>B1A16</b>	<b>2</b>	Poa pra	0.0			Tri cam	0.0			Ver cha	0.0
		Pla lan	6.0			Tri fra	0.0	<b>B4A08</b>	<b>8</b>	Ant odo	0.0
<b>B1A17</b>	<b>2</b>	Alo pra	46.6	<b>B2A18</b>	<b>16</b>	Poa pra	0.0			Bro hor	0.0
		Dau car	0.0			Ger pra	0.0			Ave pub	0.0
<b>B1A18</b>	<b>1</b>	Pru vul	2.4			Tri rep	18.5			Fes rub	0.0
<b>B1A19</b>	<b>4</b>	Arr ela	31.8	<b>B2A19</b>	<b>2</b>	Pla med	23.9			Aju rep	0.0
		Luz cam	0.0			Tar off	0.0			Tar off	0.0
		Pru vul	0.0	<b>B2A20</b>	<b>2</b>	Pla lan	8.0			Pla lan	22.1
		Cam pat	0.0			Tri dub	0.0			Ver cha	100.0
<b>B1A21</b>	<b>4</b>	Fes pra	0.0	<b>B2A21</b>	<b>8</b>	Leo his	23.0	<b>B4A09</b>	<b>1</b>	Tri rep	0.0
		Luz cam	0.0			Pla med	49.7	<b>B4A12</b>	<b>1</b>	Poa pra	45.1
		Ach mil	0.0			Cre bie	0.0	<b>B4A18</b>	<b>16</b>	Ver cha	78.1
		Cre bie	0.0			Gal mol	0.0			Cre bie	0.0
<b>B1A22</b>	<b>60</b>	Fes pra	0.0			Lot cor	69.9			Lat pra	83.8
		Fes rub	0.0			Med lup	0.0			Ono vic	97.5
		Pru vul	0.0			San off	65.1	<b>B4A22</b>	<b>4</b>	Cam pat	0.0
		Ver cha	0.0			Ono vic	92.1			Ger pra	0.0
		Ger pra	0.0	<b>B3A01</b>	<b>1</b>	Gal mol	92.5			Car pra	0.0
		Poa pra	0.0	<b>B3A02</b>	<b>2</b>	Fes pra	0.0			Kna arv	0.0
		Pla lan	8.1			Car car	0.0				
				<b>B3A03</b>	<b>4</b>	Phl pra	0.0				
						Pla med	55.3				
						Tri hyb	0.0				
						Vic cra	25.1				

## Appendix S1: LITERATURE CITED

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