Evolution increases ecosystem temporal stability and recovery from a flood in grassland communities

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Keywords: community evolution | compensatory dynamics | environmental perturbation | flood | grassland biodiversity | recovery | resilience | resistance | stability

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].

Species asynchrony has been conceptually and empirically demonstrated as a mechanism by which biodiversity can stabilize ecosystem productivity[16,18,20–23].

There are a number of community and population attributes associated with ecosystem stability. Ecosystem resistance, recovery and resilience that underlie stability may be dependent upon plant diversity[4,13], plant density[24] and plant functional traits[25]. However, we lack information about the importance of evolutionary processes that may be occurring over the same temporal scales across which ecosystem stability is measured[26]. So far, evolutionary mechanisms underlying the biodiversity–stability relationship have been considered in terms of phylogenetic relatedness that reflects evolutionary mechanisms over broad time scales[27,28]. It remains unclear whether evolution over short time scales can increase the stability of communities under normally fluctuating environmental conditions as well as in response to extreme climatic events by potentially improving resistance, recovery or resilience. Such evolution leading to changes at the community level is referred to as community evolution[29], but so far has almost exclusively been studied in microbial ecosystems[30–32].

Here we test the hypothesis that short-term community evolution in grassland ecosystems will affect ecosystem stability and that this effect may depend on plant diversity, which was experimentally manipulated. This hypothesis is based on community evolution increasing niche differentiation[26], and niche differentiation having the potential to affect community biomass[29], population variability, and population synchrony, all of which contribute to ecosystem stability. We measured ecosystem stability as temporal variation in primary productivity during normal environmental fluctuations. Furthermore, we measured ecosystem responses to 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-

evolution treatments were related to different asynchrony and stability relationships. That is, asynchrony of species-level productivity fluctuations was less positively correlated with ecosystem stability in co-selected than in naïve communities or, in other words, community evolution significantly reduced the coupling between species-level asynchrony and ecosystem stability (Fig. 1c). In contrast to the altered relationship between asynchrony and stability, community evolution did not alter the relationship between population variation and stability (Fig. 1d).

Responses to an extreme flood event

A naturally occurring flood in early summer 2013 had devastating effects on the plant communities and reduced productivity in the corresponding time interval (Fig. 2). Whereas diversity had no general effect on resistance to the flood, the diversity–resistance relationships differed significantly between the two community-evolution treatments (Table 2). This resulted from the co-selected communities having a generally lower resistance at high diversity (Fig. 3a; Table 2). Native and inoculated soil treatments resulted in highest resistance to the flood, in particular at high diversity (Fig. 3b).

Ecosystem recovery following the flood was independently increased by diversity and by community evolution, but soil treatments had no significant effects (Fig. 3c, d; Table 2). At low (but not at high) diversity, co-selected communities were more resilient (Fig. 3e). On the other hand, similar to temporal stability, high diversity could compensate for the reduced resilience of naïve as compared with co-selected communities (marginally significant interaction plant history x species richness in Table 2). The effect of species richness on resilience was strongest on the soil that was inoculated with native soil because of the very low resilience of the

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

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

high, such as in less diverse communities, co-selected plant communities were generally more stable than naïve plant communities. At low diversity, species in co-selected communities compared with species in naïve communities were also generally less temporally variable in their productivity (see significant interaction plant history x species richness in Table 1). Therefore, the co-selected plant communities with low asynchrony were able to maintain greater community stability. On the other hand, the stronger coupling between asynchrony and stability allowed naïve compared with co-selected communities to have a more stable productivity at high diversity, where species fluctuated more asynchronously through time.

The reduced temporal stability at low synchrony in our co-selected plant communities (see Fig. 1c) may be due to the effect of community evolution on species competitive interactions. For instance, it has been previously shown that more diverse communities can result in the selection for characteristics by which individuals avoid competition and exhibit greater complementarity[26,29]. Such changes in species interactions can impact species dynamics and ultimately the stability of the net community productivity. This is because species competing more strongly with one another can exhibit greater asynchrony in their temporal performance since temporal variations in the environment may temporarily favor the competitive advantage of one species over another resulting in their negative temporal covariance[15,20,41]. Such destabilizing effects of evolution have been demonstrated in microalgae communities where a greater phylogenetic distance among community members results in weaker competitive interactions, that in turn reduces the competition-driven temporal asynchrony among species and the compensatory dynamics that are required to 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

resistance can be attributed to greater pre-flood productivity of the co-selected communities. In this sense, co-selected communities had "more to lose" when faced with this extreme climate event, an observation reported also in other grassland systems in response to drought[11]. Thus, overall the reduced productivity of naïve communities resulted in less absolute loss in productivity due to the flood and their greater resistance. It was previously shown that selection for niche differentiation results in higher community productivity[26]. Our results indicate that the selection-driven increase in productivity may consequently reduce the resistance to extreme climate events at higher levels of diversity. However, the greater productivity of co-selected plant communities may have also allowed them to recover back to their pre-disturbed state and maintain a more stable post-flood productivity. This is supported by our analysis using pre-flood productivity as a covariate (see Supporting Information, Fig. S2, Table S3). Once we corrected for the pre-flood productivity, species richness increased resilience in both co-selected and naïve communities, and we observed a strong interactive effect of community evolution and species richness for ecosystem resistance (Table 2).

Biodiversity had a strong positive effect on the recovery and, in the naïve communities also on resilience of the plant communities, paralleling numerous other studies emphasizing the importance of biodiversity for ecosystem recovery and resilience[4,11,12,26]. In addition, community evolution further increased recovery and resilience (see Fig. 3c, e). The positive effect of community evolution on post-flood recovery suggests that the local environment may have acted as a selective filter on these plant communities. The ancestral communities of the co-selected plants were initially sown into the field site in 2002, which is a natural floodplain where the plant 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

signal[39]. Likely two different evolutionary processes — co-selection between the species within each particular community composition and "diffuse" co-selection among all species within the community — have improved the species' abilities to function more complementarily with other species in the community[26,29].

Conclusions

Our findings show that ecosystem stability and recovery can not only be promoted by biodiversity but also by evolutionary processes in plant communities over the time scales at which stability is being measured. In particular, we found that community evolution can enhance the stability of ecosystem productivity when diversity is low, whereas in the absence of community evolution a greater diversity was more critical for increasing stability. The community evolution-driven increase in ecosystem stability and recovery was likely linked to the selection on individual plant characteristics that facilitated greater recovery in these plant communities. If evolution in grassland communities increases ecosystem resilience and stability, maintaining co-selected plant communities could be a crucial precaution under global change and increased frequency of extreme climatic events[6,7]. Furthermore, integrating evolutionary processes into the temporal changes in biodiversity–ecosystem functioning relationships is likely to be a promising future avenue for predicting how ecosystems may respond to climatic extremes and biodiversity loss.

Methods

332 **Field site.** This study was conducted at the Jena Experiment field site (Jena,
333 Thuringia, Germany, 51 ˚N, 11 ˚E, 135 m a.s.l.) from 2011 to 2015. The Jena
334 Experiment is a long-term biodiversity field experiment located on the banks of the
335 Saale River. In 78 experimental field plots of different diversity levels, 60 central
336 European grassland species are grown in a number of species combinations since
337 2002[54].
338
339 **Community-evolution treatments.** This study included eleven monocultures, twelve
340 2-species mixtures, twelve 4-species mixtures and twelve 8-species mixtures for a
341 total of 47 experimental plots. We used two community-evolution treatments: plants
342 with eight years of shared community selection in these experimental plots (co-
343 selected communities) and plants without a common selection history in the Jena
344 Experiment (naïve communities). The naïve plant seeds without a common selection
345 history were obtained from the same commercial seed supplier (Rieger Hofmann
346 GmbH, in Blaufelden-Raboldshausen, Germany) who provided the seeds used for the
347 establishment of the original Jena Experiment plant communities[54]. The supplied
348 seeds originated from various field sites in Germany and have been cultivated by
349 reseeding every year for at least five years in monoculture. Seeds of co-selected
350 communities were produced in an experimental garden in Zurich, Switzerland, from
351 cuttings that had been made in the Jena Experiment. The cuttings were planted in
352 Zürich in the original species combination in plots fenced with plastic netting to
353 reduce pollination between communities[26]. A small number of seeds were additionally
354 collected directly in the plots of the Jena Experiment. The "selected" seeds were thus
355 offspring of plant populations that had been sown in 2002 and grown until 2010 in
356 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

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.

All analyses were conducted using the software R, version 3.2.4[58]. Mixed models using residual maximum likelihood (REML) were fitted using the package ASReml for R[59] and the package 'Pascal' available at GitHub[56].

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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.

Acknowledgements

Thanks to Debra Zuppinger-Dingley, Dan Flynn and Varuna Yadav for the establishment of the experimental plots. Thanks to the Jena Experiment for providing infrastructure and help and to D. Trujillo and M. Furler for technical assistance. This study was supported by the Swiss National Science Foundation (grant numbers 130720, 147092 and 166457 to B.S.) and the University Research Priority Program Global Change and Biodiversity of the University of Zurich. The Jena Experiment is funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation, FOR1451).

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

FIGURES & TABLES

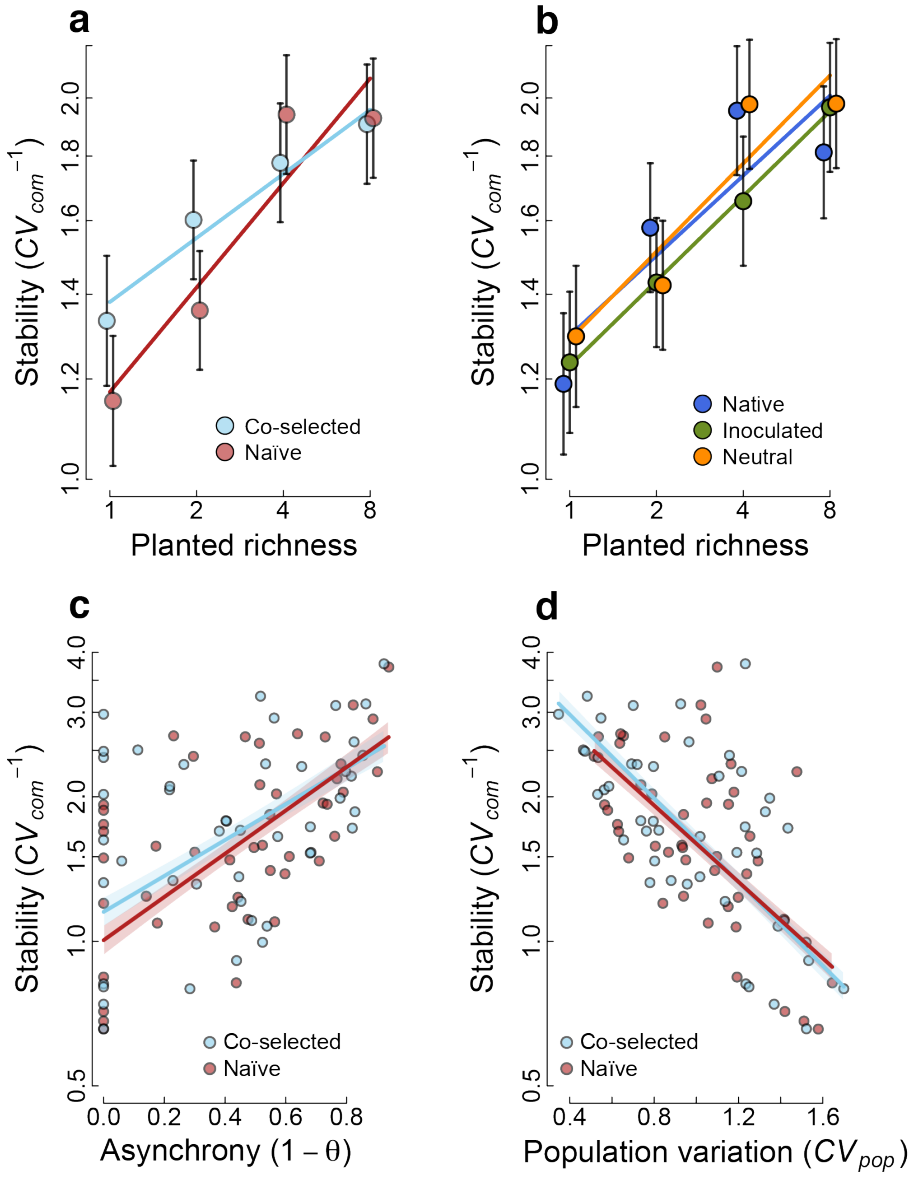

Fig. 1 | The biodiversity–stability relationship in response to community-evolution and soil treatments. a, Greater plant diversity is required for greater stability, but more strongly so in naïve communities (plant history x species richness (log-transformed): $F_{1,\ 135.0} = 4.794$, $P = 0.030$). **b,** Different soils did not alter the overall biodiversity–stability relationship (soil treatment x species richness (log-transformed): $F_{2,\ 87.1} = 0.048$, $P = 0.954$). The three soil treatments were: native soil, sterilized soil inoculated with native soil (inoculated) and sterilized soil (neutral).

Means and standard errors are shown for each diversity level. **c,** Stability increased with asynchrony strongly for both naïve and selected communities (main effect asynchrony: $F_{1, 204.5} = 84.55$, $P = <0.001$) but stability increased more steeply with asynchrony in naïve plant communities than in co-selected communities (plant history x asynchrony interaction: $F_{1, 145.8} = 3.93$, $P = 0.049$). **d,** The relationship between stability and population variation was not altered by community evolution (plant history x population CV: $F_{1, 160.3} = 1.348$, $P = 0.247$).

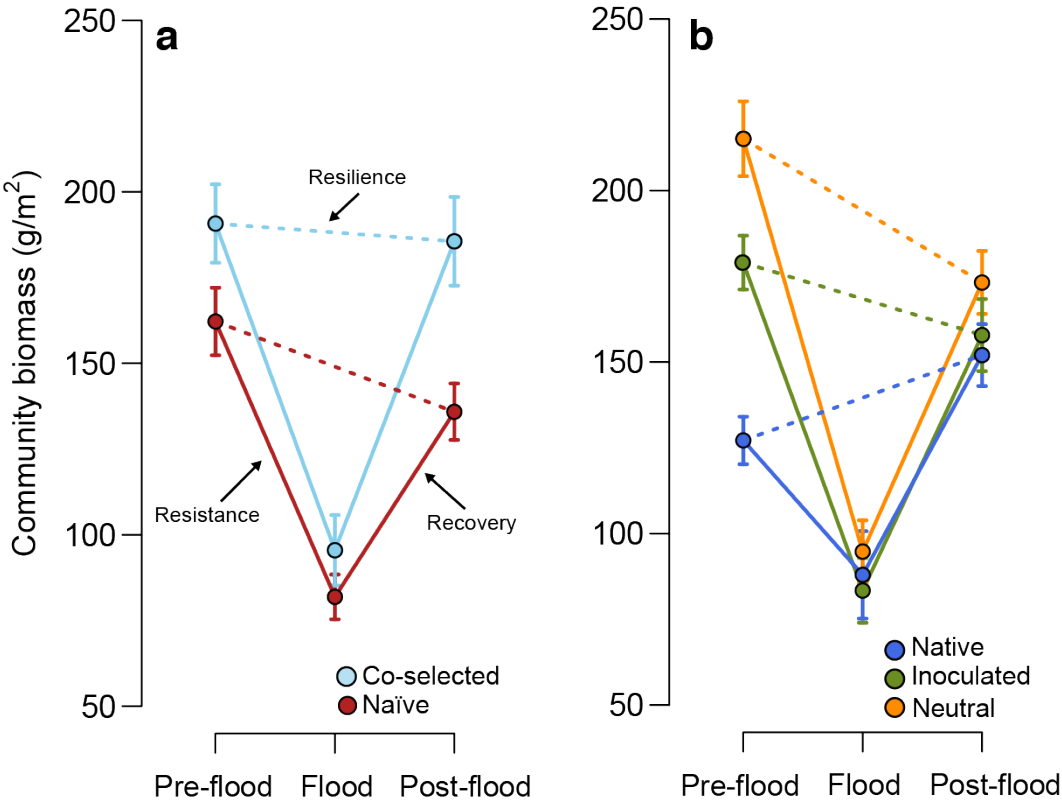

Fig. 2 | The flood event greatly reduced ecosystem productivity. Points indicate **a**, the average productivity for co-selected and naïve plant communities and **b**, the average productivity for the three soil treatments native soil, sterilized soil inoculated with native soil (inoculated) and sterilized 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.

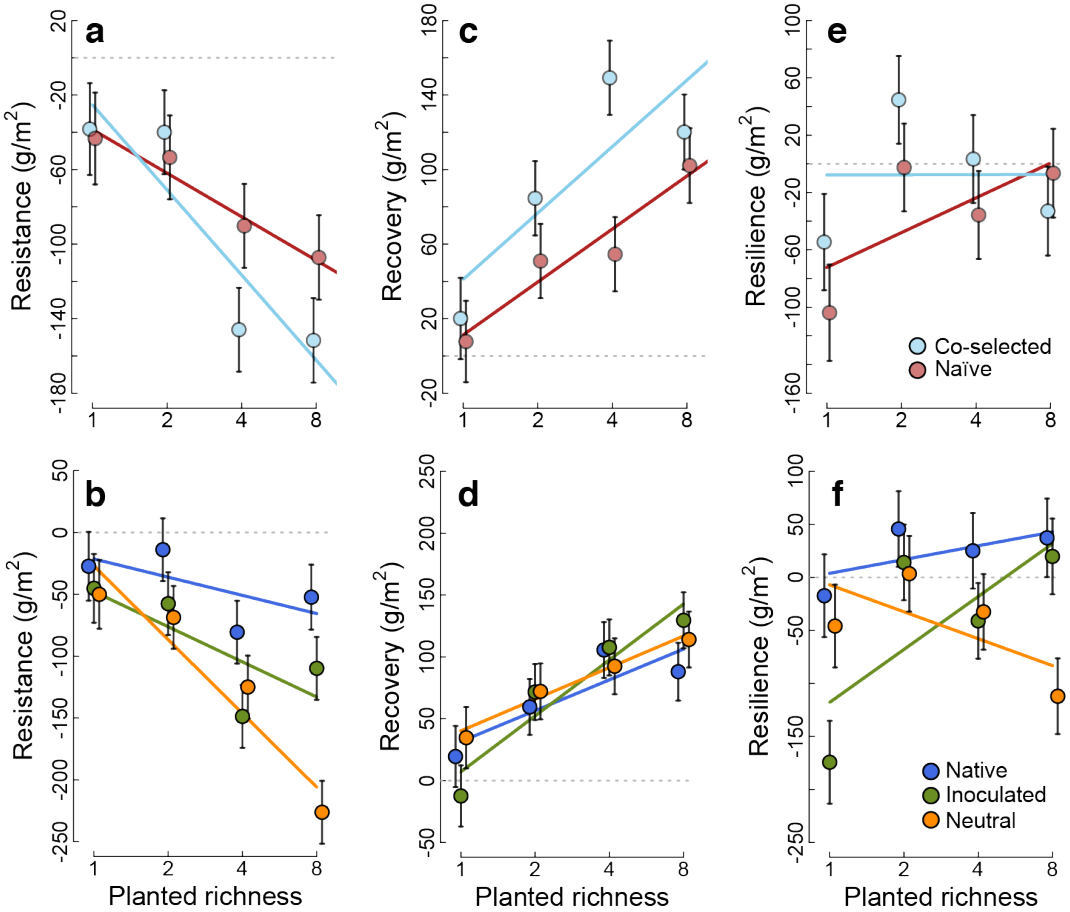

Fig. 3 | Resistance, recovery and resilience responses to a major flood event. Biodiversity–resistance relationships are shown in response to **a**, community-evolution and **b**, soil treatments. Biodiversity–recovery relationships are shown in response to **c**, community-evolution and **d**, soil 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.

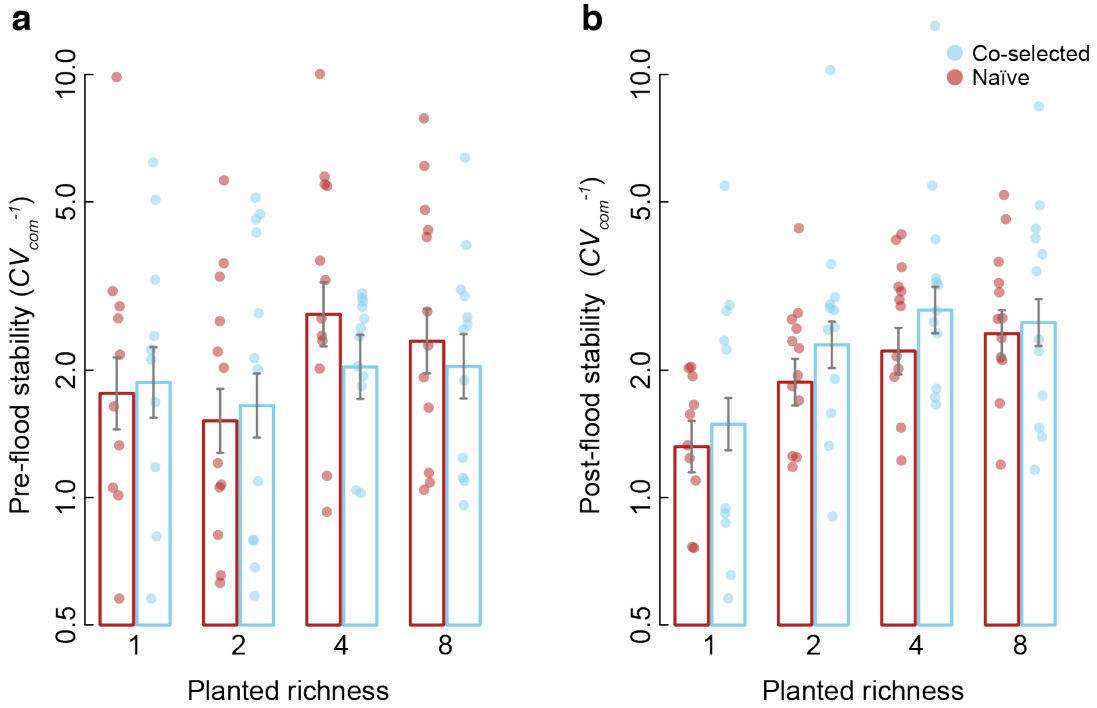

Fig. 4 | Influence of the community-evolution treatments on stability pre-flood vs. post-flood. Means for each diversity and community-evolution treatment with error bars indicating the model-estimated standard error are shown. **a,** naïve plant communities and co-selected communities were equally stable 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.

Table 1 | Mixed-model ANOVA results for stability, population variance and synchrony. The effects of species richness (log-scale), community-evolution (plant history) and soil treatments on the stability of community productivity, population variance and synchrony across the entire experimental period form 2012–2015. The time point of the flooding event was excluded in the calculations of stability, population variance and asynchrony to prevent any confounding effects of the flood. 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
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	4.57	
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	

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

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.