Rapid evolution allows plant communities to regain stability after simulated species loss

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Abstract

Experiments simulating species loss from grassland ecosystems have shown that losing biodiversity decreases the ability of ecosystems to buffer disturbances. However, plant or plant-soil evolutionary processes may allow ecosystems to regain stability and resilience over time. We explored such effects in a long-term grassland biodiversity experiment. Low diversity communities of plants with a history of co-occurrence (selected communities) were temporally more stable than the same communities of plants with no such history (naïve communities). Furthermore, selected communities showed greater recovery following a major flood, resulting in more stable post-flood productivity. These results were consistent across soil treatments simulating the presence or absence of co-selected microbial communities. We suggest that plant evolution in a community context can increase ecosystem temporal stability and resistance to disturbances. Evolution can thus in part compensate for extreme species loss as can high plant diversity in part compensate for the missing opportunity of evolutionary adjustments.

Biodiversity experiments simulating the loss of plant species from grassland communities have shown that less diverse communities have reduced mean [1,2] and increased variation of aboveground biomass [3–5]. However, it is not clear whether these communities may regain functioning and stability over time while still being at low diversity. The few biodiversity experiments that lasted more than 10 years showed that functioning tended to decrease in low-diversity communities and to increase in high-diversity communities, leading to an increased slope of the biodiversity–productivity relationship over time [6,7]. In one of these experiments, the Jena Experiment in Germany [7], it was shown that divergent evolutionary changes of plant species in monocultures vs. mixtures during the first 8 years contributed to this strengthening of the biodiversity–functioning relationship [8–10]. Feedbacks between plants and soil organisms, however, had less explanatory power [9,11].

Ecosystem resistance, recovery and resilience that underlie stability may depend on plant diversity [12–14]. The mechanisms by which diversity stabilizes ecosystem productivity are based on differences between genotypes or species in their responses to the abiotic or biotic environment [3,5,15,16]. For instance, different plant species may exhibit high performance under different environmental conditions (termed response diversity [17]). Asynchrony of species performances, derived from interspecific differences in responses to environmental variation, can thus allow diverse communities to resist disturbance or recover to maintain performance, often referred to as insurance or portfolio effect [5,16,18,19].

The development of stability over time in the long-term biodiversity experiments had not been analyzed so far, but using data from the Jena Experiment [20,21], we found that combined intra- and inter-annual variation in experimental communities decreased over time for the first 8 years (i.e. ecosystem stability, measured as inverse of coefficient of variation of total biomass, increased over time; Fig. 1), suggesting that temporal stability could be regained. As new communities develop following sowing, species abundance distributions and gene frequencies can change, and such adjustments between and within species may explain increased stability [22]. For example, a prolonged period of co-occurrence increased "stabilizing differences" between phylogenetically distinct annual plant species in comparison with similar pairs of species without co-occurrence history [23]. However, it has not been tested yet if similar effects of co-occurrence history might already appear during the course of biodiversity experiments. This is because in such experiments,

individual plants age and take up nutrients which may also affect stability besides effects of co-occurrence history. In addition, it has proven difficult to disentangle the contribution of soil organisms that over time associate with the plant communities. The interplay between mutualistic and pathogenic soil organisms (bacteria, fungi, invertebrates) and their impact on plant communities could have (de)stabilizing effects by changing nutrient provision and the plant's health [24,25].

To test specifically for the importance of co-occurrence history we therefore compared communities of plants of the same age but with or without co-occurrence history on soils with or without soil organisms that had become associated with the plants with co-occurrence history (Fig. 2). *Selected* communities were assembled with offspring from individuals that had co-occurred in the same plots of the Jena Experiment over 8 years. *Naïve* communities were assembled with offspring from seeds that were obtained from the same supplier that had provided the original seeds for the Jena Experiment. We then asked whether (1) selected plant communities had more stable productivity than naïve plant communities, (2) potential differences in stability between naïve and selected communities depended on plant diversity and (3) stability was further increased when plants were growing with their native soil organisms. Test communities ranged in species richness from one to two (low diversity) to four and eight species (medium diversity). We assessed the combined intra- and inter-annual variation in the test communities across seven seasonal biomass harvests from 2012–2015 (Fig. S1).

A natural flood event [26] after the third harvest gave us the opportunity to additionally analyze the resistance, recovery and resilience [27–29] of test communities in response to the flood and compare the pre- with the post-flood stability using the first three and the last three harvests, respectively. Together, resistance and recovery determine ecosystem resilience as we define it here, namely how ecosystem productivity differs between pre- and post-disturbance states [30].

Finding a more stable productivity for selected communities (question (1)) would provide evidence for short-term plant evolutionary processes increasing ecosystem stability. So far, evolutionary mechanisms underlying ecosystem stability in biodiversity experiments have only been studied in terms of phylogenetic relatedness that reflects evolutionary processes over long time scales with conflicting results [31,32]. Short-term evolution leading to changes at the community level, referred to as community evolution ([9], have almost exclusively been studied in microbial

ecosystems [33–36]. However, short-term evolutionary processes could be particularly relevant in plant communities facing rapid global change [37,38], including increased extreme climatic events, and for conservation and restoration approaches [39], because plants are fixed in place and can only move by propagule dispersal.

Question (2) is based on the observation that evolution in a community context in the Jena Experiment increased niche differentiation between species in mixtures [8]. This could potentially affect species asynchrony and average population variability, which in turn contribute to ecosystem stability. The increasing slope of biodiversity–productivity relationships in long-term biodiversity experiments could suggest that biodiversity–stability relationships also increase and thus differences between plant communities with and without co-occurrence history should be larger at higher species richness levels. Alternatively, it could be argued that such differences reflecting the regaining of functioning and stability after species loss should be more pronounced in plant communities that lost more species, i.e. communities of low diversity.

Question (3) addresses the possibility that plant–soil feedback dynamics, including both mutualistic and pathogenic effects [40,41], contributed to the increased stability of experimental plant communities during the 8 years of the Jena Experiment [42]. Soil microbial communities with a shared history of the respective plant community may be more efficient in using plant-derived substrates, providing nutrients to plant growth and protect plants against soil-borne pathogens [25]. Moreover, a higher soil biodiversity is likely to provide nutrients at a higher and more stable level [e.g. 43].

Given our experimental design, question (1) relates to main effects of plant co-occurrence history, question (2) to the interaction between co-occurrence history and plant species richness and question (3) to main effects of soil organisms (native vs. neutral). Potential interactions between effects of soil organisms and plant co-occurrence history were also tested but never significant. We first present the results for the overall temporal stability of test communities and then those for the response to the flood event.

Results

Community and population stability and species asynchrony

We used the inverse of the combined intra- and interannual variation over six

biomass harvests from spring 2012–spring 2015 (excluding the harvest taken directly after the flood event in summer 2013) as stability measure of test communities. Whereas the test communities showed the usual strong increase of stability with species richness, overall differences between co-occurrence history and especially soil treatments were small and insignificant (Table 1). However, at low diversity, selected communities were more stable than naïve communities, reflected by a significant co-occurrence history x species richness interaction (Table 1; Fig. 3A). This shows that communities of low diversity regained more stability 8 years after simulated species loss in the Jena Experiment. Population stability decreased with species richness but at low diversity population stability was also higher in selected communities (Table 1; Fig. 3B). In contrast, species asynchrony increased for both selected and naïve communities in parallel with increasing species richness (Table 1; Fig. 3C). When we corrected community stability and species asynchrony for all model terms except co-occurrence history (i.e. taking residuals after fitting the plot x soil treatment interaction), selected communities were more stable than naïve communities for any given level of asynchrony (Fig. 3D).

Responses to 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 [44]; Fig. 4). Diverse test communities, especially selected communities, lost the greatest amount of biomass, i.e. showed the least resistance to the flood. When we adjusted for community biomass before the flood, selected communities showed higher resistance at low diversity and lower resistance at high diversity compared with the naïve communities (Table S1; Fig. S2A). As for temporal stability, selected communities simulated to have lost more species (monocultures) again regained more resistance.

Communities were most resistant in non-sterilized native soil. Comparing the two other soil treatments, the plant communities were more resistant in sterilized soil inoculated with native soil organisms than in sterilized soil inoculated with neutral organisms (Table 2; Fig. 4, 5A). Here, an adjustment for pre-flood biomass made soil treatments insignificant (Table S1; Fig. S2A).

Recovery of community biomass after the flood increased with species richness and was higher in selected than in naïve communities across all diversity levels and soil treatments (Table 2 and S1; Fig. 5B and S2B). Selected communities

had regained more resilience than the naïve communities, particularly at low diversity, as shown by the comparison of community biomass before and after recovery. However, the effect of co-occurrence was only significant if adjusted for pre-flood community biomass (Table 2 and S1; Fig. 5C and S2C). The three soil treatments strongly differed in their resilience, which averaged out their pre-flood differences in community biomass (Table 2; Fig. 3B). The water moving across plot borders during the flood may also have transported soil organisms between different soil treatments, further diluting soil treatment effects (see Fig. 2).

We then compared the combined intra- and interannual stability over the first three harvests before the flood event (2012–2013, Fig. 6A) with the last three harvests after recovery (2014–2015, Fig. 6B). The increased stability of selected communities was mainly due to higher stability after the flood. Furthermore, the greater regain of overall stability in selected communities of low diversity was due to the time before the flood, when selected communities of high richness had even lower stability than naïve communities of high richness (Fig. 6A). After the flood, when test communities had already been developing for more than two years, there was still a consistent difference across all diversity levels with selected communities being more stable than naïve communities. This suggests that these differences may have a heritable basis or, alternatively, that initial differences between selected and naïve test communities were accentuated by species abundance shifts within them. We therefore assessed species turnover rates with the Bray-Curtis similarity measure between pre- and post-flood species compositions but found that it was not influenced by co-occurrence history or soil treatments, although it increased with species richness (Table S3; Fig. S3).

Discussion

Biodiversity experiments test how simulated species loss affects ecosystem functioning and stability and, if run over longer time periods, can address the question whether both functioning and stability can be regained over time. In the Jena Experiment [45], a typical central European grassland ecosystem of 60 plant species was reduced to experimental communities containing 16, 8, 4, 2 or 1 species, which led to decreases in aboveground biomass production and its stability over time [21]. Strengthening biodiversity–productivity relationships observed in long-term biodiversity experiments [e.g. 6,46] indicate a deterioration of monocultures and low-

228 diversity mixtures and regaining of functioning in more diverse mixtures [7,46]. We
229 previously found that, in comparison with naïve communities, selected low-diversity
230 mixtures regained more functioning than mixtures with higher diversity [9]. Here, we
231 show that selected communities from the Jena Experiment also regained stability in
232 comparison with naïve communities, particularly the experimental communities
233 reflecting more extreme species loss.
234
235 *Species-poor selected communities regained temporal stability*
236 Selected communities had increased temporal stability of aboveground
237 biomass production but only at the lower levels of diversity up to four species. At the
238 eight-species richness level, we did not detect any differences as all communities
239 showed the highest stability values. This mirrors earlier findings for productivity
240 where biomass was similar for naïve and selected communities at the eight-species
241 richness level [9].
242 Several mechanisms could have led to the increased stability of selected
243 communities. For mixtures, the changes at the community level could have been
244 solely caused by altered species abundance distributions [47], driven by changed
245 performances of species due to evolution in their particular communities (Zuppinger-
246 Dingley et al. 2014). However, we did not detect any changes in species abundance
247 distributions between selected and naïve communities. A more likely explanation
248 therefore is that changes in genotype frequencies within species, i.e. evolution in the
249 community context (Strauss et al. 2006), led to increased temporal stability, which
250 could also explain the increased stability of selected monocultures. For five of the 60
251 species from the Jena Experiment the potential for such rapid evolutionary changes
252 and their genetic basis, with consequential epigenetic and phenotypic changes has
253 been confirmed [10]. The changes in genotype frequencies within species in selected
254 communities could be attributable to differential mortality, growth or reproduction
255 among the initially sown genotypes [48], recombination during sexual reproduction or,
256 least likely, to mutation. Rapid evolutionary changes in systems of interacting species,
257 referred to as community evolution [9], have so far mainly been observed in microbial
258 communities [33–36,49], but are here shown to also occur in communities of perennial
259 plant species.
260 Temporal stability at the community level in grassland ecosystems can be
261 driven by asynchronous population dynamics of species, allowing high compensatory

population variation to be combined with low community-level variation over time [5,18,50–52]. As shown before [e.g. 4], we found that population stability decreased with increasing diversity.

We further observed that, for any given level of asynchrony, selected communities were more stable than naïve communities (see Fig. 3D). The greater community stability at the same level of asynchrony suggests that evolution in communities reduced competitive interactions between plant species, consistent with the findings of evolutionary niche differentiation [8] and increased facilitation [53] among species in mixtures in the Jena Experiment. By extension, similar evolutionary processes may have occurred between genotypes within monocultures, again consistent with previous findings showing evolutionarily changed phenotypic variation within monocultures after eight years of selection in the Jena Experiment [9].

The increased stability over the first eight years of ecosystem development in the Jena Experiment (see Fig. 1) could also have been due to the selection of soil communities associated with the plants [41,54–56]. Therefore, we grew the selected and naïve plant communities in three soil treatments: native soil of the selected communities, sterilized soil inoculated with native soil organisms or sterilized soil inoculated with neutral soil organisms collected outside the Jena Experiment. Previously, highly significant differences between these soil treatments regarding microbial community composition have been demonstrated [9,11], Marc W. Schmid pers. comm. June 2019). However, contrary to our expectation, there were no differences in plant community temporal stability between the three soil treatments and no interactions of these with plant co-occurrence history. Thus, we conclude that the changes in ecosystem stability observed in the Jena Experiment were not primarily driven by plant–soil feedbacks but more likely due to plant evolution. Still, we cannot rule out the possibility that the greater stability of selected communities was also in part because of more stable associations with both native and neutral soil organisms. Indeed, plants selected for eight years in monocultures in the Jena Experiment developed positive plant–soil feedbacks [56], which may in part have contributed to their increased stability in the present study.

Selected communities recover better from an extreme event than naïve communities

Diverse communities are more stable in the face of disturbance [13], for example when they are hit by an extreme climatic event, such as a flood as happened to our test

296 communities halfway through the experiment in June 2013 [44]. Considering predicted
297 future climate scenarios with increased frequency of extreme events [57], including
298 floods [58], this aspect of stability may be even more relevant than temporal stability
299 under unperturbed conditions [59]. Further, both temporal stability and resistance to
300 perturbations need to be considered because they may not always be positively
301 correlated [60].

302 There are several ways in which a community may retain stability through
303 perturbations. Greater resistance increases ecosystem stability by reducing the loss in
304 productivity [61], while greater recovery increases the amount of productivity that the
305 ecosystem can regain after the disturbance-induced loss [28]. Together, resistance and
306 recovery then determine ecosystem resilience [30]. Consequently, how plant diversity
307 stabilizes ecosystem productivity through mediating ecosystem resistance, recovery
308 and resilience has become a focal question in ecology [13,51,62,63].

309 In our experiment, diversity reduced ecosystem resistance, in line with
310 previous findings for example in micro-ecosystems with ciliates responding to
311 warming [60]. This was because diverse communities had more biomass before the
312 flood and thus could also lose more, a result found previously for community
313 responses to drought [12,28,64]. For example, Wang et al. (2007) showed that at the same
314 diversity level, communities with higher productivity were more susceptible to an
315 experimental drought treatment. Here, when correcting for differences in pre-flood
316 biomass, selected communities were more resistant than naïve communities at low
317 diversity. At 8-species richness, the opposite pattern was found and naïve
318 communities were more resistant than selected communities (see Fig. S2A). Diverse
319 communities made up for their reduced resistance by increased recovery, as typically
320 found in biodiversity experiments [28,30], but, remarkably, selected communities showed
321 greater recovery than naïve communities along the entire species-richness gradient.
322 Consequently, at low diversity selected communities regained resilience, which was
323 not the case at higher diversity (see Fig. 4C). Changes in genotype frequencies during
324 community development in the first eight years of the Jena Experiment may not only
325 have led to increased community productivity [9] and temporal stability (see above) but
326 also to increased ecosystem stability in the face of disturbance, i.e. the flood event.
327 Key here is the adaptation to the abiotic conditions at the Jena field site, which is a
328 natural floodplain, where the plant communities were exposed to soil moisture
329 saturation at previous milder flood events in winter 2003 and winter 2005 (personal

communication with C. Roscher). Selection thus likely favored individuals with traits that allowed them to perform well under such conditions and to recover more rapidly [65,66].

However, species interactions may also have played a role for adaptation to flooding, as selected communities were more resilient at lower compared with higher diversity. Evolutionarily increased facilitation, demonstrated for these plants in the Jena Experiment [53], may in part have caused the increased resilience. This would be in line with predictions that environmental stress might select for greater facilitative effects in plant communities (stress-gradient hypothesis; [67]. Furthermore, such effects, which could be interpreted as diffuse co-evolution [68], are more likely to occur in communities of few interacting species [9,69]. This could additionally explain why selected communities regained more temporal stability and resilience at lower than at higher diversity.

Further, we tested if the association with native soil organisms over time might have affected the stability of plant communities in response to the flood. We found that pre-flood productivity was lowest in communities grown in native soil, higher in soil with native inoculum, and highest in soil with neutral inoculum (see Fig. 4B). This could have two reasons: first, a greater density of antagonistic soil biota in native and native-inoculated soils [70], or, second, a greater pool of available soil resources resulting from the soil sterilization process in the two inoculated soils [71]. Consequently, resistance was lowest for communities growing in native soil. In contrast, it seems that native soil organisms did increase recovery and resilience of plant communities to the flood event. First, by reducing pre-flood community biomass and thus cutting losses. However, previous studies showed that plants evolving under drought can select for a different set of microbial organisms than when evolving under wet conditions [55], which offers an alternative mechanism that selected communities may have associated with a better suited native soil community over time.

After the flood, the effect of soil treatments on plant community biomass was insignificant. In part, this might have been caused by an exchange of soil organisms during the flood event. However, differences between the soil treatments in terms of microbial community composition remained highly significant [11], Marc Schmid pers. comm. June 2019), which makes it more likely that the flood had an equalizing effect due to the differential resistance, recovery and resilience among the soil treatments.

After disturbance selected communities are more stable than naïve communities

As a third aspect of stability, we compared the combined intra- and inter-annual ecosystem stability for the three harvests before and after recovery from the flood separately [65]. Whereas the differences between selected and naïve communities were not significant before the flood, selected communities showed increased post-flood stability (see Table S2 and Fig. 6). This shows first that the effect of co-occurrence history was long-lasting, i.e. at least for two years after re-establishment of the test communities, and second that naïve communities could not make up for the lack of co-occurrence history from spring 2011 to summer 2013. Furthermore, the finding suggests that genotype frequencies need time to change and potential sorting out does not happen immediately after sowing genetically diverse species collections. Finally, selected communities of all diversity levels showed increased post-flood stability, but selected communities at lower diversity levels regained more overall temporal stability. This suggests that in the longer term also the more diverse communities will regain stability.

It is important to note that the greater post-flood stability of selected communities in our study was not driven by compositional changes as shown by the similar compositional turnover between selected and naïve communities. We suggest that genetic changes within the species populations comprising the selected communities were responsible for the increased stability [10]. Independent of the underlying mechanism, our study demonstrates that experimental plant communities with simulated species loss over time can regain some of the temporal stability and capacity to buffer extreme events, and this is likely due to plant evolutionary changes in a community context [22], with few additional effects of assembling soil communities. Our results can be viewed from two different angles. First, the greater level of regained stability in communities of lower diversity still can only partly make up for the stability lost because of simulated species loss in the first place. The more optimistic view in terms of restoration approaches for plant communities is that our findings imply that even though naïve communities may not provide the same level of functioning as those with a history of co-occurrence, this disadvantage can be partly compensated by sowing or planting diverse mixtures.

Methods

398 **Field site.** This study was conducted at the Jena Experiment field site (Jena,
399 Thuringia, Germany, 51 ˚N, 11 ˚E, 135 m a.s.l.) from 2011–2015. The Jena
400 Experiment is a long-term biodiversity field experiment located on the banks of the
401 Saale River. In 78 experimental field plots of different diversity levels, 60 mostly
402 perennial species typically forming species-rich grassland ecosystems under low-
403 intensity management are grown in a number of species combinations since 2002 [45].
404
405 **Co-occurrence history.** This study included eleven monocultures, twelve 2-species
406 mixtures, twelve 4-species mixtures and twelve 8-species mixtures for a total of 47
407 experimental plots. The original design of the Jena Experiment [45] dictated the types of
408 monocultures and species combinations we used. We used two co-occurrence-history
409 treatments: communities assembled with offspring of plants that had grown together
410 for 8 years in the 47 plots of the Jena Experiment (selected communities) and
411 communities assembled with plants without a common history of co-occurrence in the
412 Jena Experiment (naïve communities). The plants of naïve communities were grown
413 from seeds obtained in 2010 from the same commercial supplier (Rieger Hofmann
414 GmbH, in Blaufelden-Raboldshausen, Germany) who provided the seeds used for the
415 establishment of the Jena Experiment in 2002. The supplied seeds originated from
416 various field sites in Germany and had been cultivated by reseeding every year for up
417 to five years in monoculture. Seeds of selected communities were produced in an
418 experimental garden in Zurich, Switzerland, from cuttings that had been made in the
419 Jena Experiment in 2010. The cuttings were planted in Zürich in the original species
420 combination in plots fenced with plastic netting to reduce pollination between
421 communities [8]. A small number of seeds were additionally collected directly in the
422 plots of the Jena Experiment. The "selected" seeds were thus offspring of plant
423 populations that had been sown in 2002 and grown until 2010 in plots of the Jena
424 Experiment.
425 For this study we wanted to exclude potential maternal carry-over effects and
426 therefore used for both selection histories seedlings propagated in a glasshouse. To
427 this aim, in January 2011, the seeds of selected and naïve communities were
428 germinated in potting soil (BF4, De Baat; Holland) in a glasshouse in Zurich.
429 Subsequently, the seedlings were transported back to the Jena Experiment field site
430 and transplanted into 2 x 2 m smaller plots within the original large plots (in March
431 2011). There were four 1 x 1 m quadrats with different soil treatments in each 2 x 2 m

432 plot (see next section) and each quadrat was split into two 1 x 0.5 m halves ("half-
433 quadrats"). We planted seedlings of selected communities into one half and seedlings
434 of naïve communities into the other half of each quadrat in a hexagonal pattern at a
435 density of 210 plants per m^2 with a 6-cm distance between individuals. We planted
436 the species in equal proportions, but five species were excluded from both selected
437 and naïve communities because they were no longer present in the original plot of the
438 Jena Experiment. After transplanting, the seedlings received water every second day
439 for six weeks. The experimental set up is shown in Fig. 2.
440
441 **Soil treatments**. Within each 2 x 2 m plot of the 47 plots of the Jena Experiment, we
442 removed the original plant cover in September 2010 and used it for the plant
443 propagation in the experimental garden in Zurich (see previous section).
444 Subsequently, we excavated the soil to a depth of 0.35 m, added a 10-cm layer of sand
445 to the bottom of the plots and covered it with a 0.5-mm mesh net. We separated the
446 borders of the plots and the quadrats by plastic frames. The excavated native soil from
447 each of the plots was sieved and four soil treatments were prepared. Half of the soil
448 (approximately 600 kg per plot) was γ-irradiated to remove the original soil biota.
449 Half of this sterilized soil was then inoculated with 4% (by weight) of live sugar-beet
450 soil and 4% of sterilized native soil of the corresponding plot ("neutral soil" obtained
451 by inoculation). Live sugar-beet soil was added to create a neutral soil community and
452 was previously collected in an agricultural sugar-beet field not associated with the
453 Jena Experiment, but with comparable soil properties. The second half of the
454 sterilized soil was inoculated with 4% (by weight) of live sugar-beet soil and 4% of
455 live native soil of the corresponding plot ("native soil" obtained by inoculation). The
456 non-sterilized part of the excavated soil was used for the second two soil treatments.
457 Half of this soil was filled back into one quadrat of the corresponding plot ("native
458 soil"). The other half of the unsterilized soil was mixed among all plots and filled into
459 the remaining quadrats ("mixed soil"). However, this fourth soil treatment was
460 abandoned after two years, which is why this treatment is not included here.
461 The soils were left to rest in closed bags to allow for the soil chemistry to
462 equalize and to encourage soil biota of the inocula to colonize the sterilized soil
463 before planting. The soils were then added into the quadrats in December 2010 and all

464 quadrats were covered with a net and a water permeable black sheet to avoid spilling
465 between quadrats until seedling transplantation in March 2011.
466
467 **Sampling of aboveground biomass.** The test communities were weeded three times
468 a year and the plants were cut to three cm above ground twice a year at typical
469 grassland harvest times (late May and August) in central Europe. Plant material from
470 a 50 x 20 cm area in the center of each half-quadrat was collected to measure
471 aboveground biomass. We sorted the biomass into species, dried it at 70° C and
472 weighed the dried biomass. There were four May harvests (2012–2015) and three
473 August harvests (2012–2014) because the experiment was terminated after the fourth
474 May harvest in 2015.
475
476 **Natural flood event.** In June 2013, the field site was flooded because of heavy rains
477 in central Europe [26,44]. The flood duration (maximum 25 days) and depth of water
478 (maximum of 40 cm) was variable among plots due to small topographical differences
479 among the plots in the experiment [14]. The variation in flooding severity was
480 distributed across the diversity gradient and within plots the quadrats and half-
481 quadrats experienced the same flooding severity. We tested whether flood severity [44]
482 influenced the diversity–stability relationship and any other of the dependent variables
483 (data not shown). This was not the case, which made us exclude these indices in all
484 analyses.
485
486 **Data analysis.** We first calculated the stability of community aboveground biomass
487 as the inverse coefficient of combined intra- and inter-annual variation (CV_{com}^{-1})
488 among sequential spring and summer harvests. We deliberately combined seasonal
489 and annual variation in the stability measure to encompass both aspects of temporal
490 variation in a single measure. The basic sequence for this measure was spring year n,
491 summer year n and spring year n+1, which had shown increasing stability during the 8
492 selection years in the Jena Experiment (2003/4, 2005/6, 2007/8, 2009/10; see Fig. 1).
493 This sequence allowed us to exclude the summer harvest 2013, which was taken
494 shortly after the flood event and was used for the calculation of resistance and
495 recovery (see below); and it increased the independence of the sequential measures
496 from 2003–2010. We also calculated overall temporal stability for test communities
497 combining the three harvests before the flood with the three after recovery (i.e.

excluding the summer harvest 2013, see Fig. S1). The stability of a single community was thus the mean community aboveground biomass (μ_{com}) divided by its standard deviation (σ_{com}). We also calculated average population stabilities (CV_{pop}^{-1}) and species asynchrony ($1-\theta$, where θ is synchrony) over the same time spans as stability [18,19]. For monocultures population stability equals community stability and asynchrony is zero. Variation in community stability, synchrony and population stability was analyzed with linear mixed-effects models. Stability measures were log-transformed to improve homoscedasticity and obtain normally distributed residuals in the analyses [72]. Fixed-effects terms were plant species richness (log scale), community-history treatment (selected vs. naïve) and soil treatment (native, inoculated-native or inoculated-neutral soil); plots and quadrats were used as random-effects terms to get appropriate errors for significance tests [72]. For reasons of consistency and to allow the use of all data in analyses with covariates we included monocultures in the analysis of asynchrony. For graphical displays of relationships between species richness and stability measures and asynchrony means across soil treatments were corrected for differences between plots within species-richness levels, which corresponds to using plots and quadrats in the mixed-model analyses. Because co-occurrence history was a split-plot/split-quadrat treatment applied within each quadrat it was not affected by the correction. The corrections were obtained by fitting a model with plots and quadrats only and adding the residuals to the diversity-level means. This correction corresponds for example to that used in metabolic ecology when metabolic rate corrected for temperature is plotted against body size [73].

To analyze community responses to the flood event in 2013, we calculated resistance, recovery and resilience measures [27–29]; see Fig. 4). Resistance is the difference in community biomass between the average of the three harvests before the flood and the community biomass directly after the flood (summer 2013), more negative values indicating lower resistance. Recovery is the difference between the biomass produced after recovery from the flood (averaged over the three last harvests) and the biomass directly after the flood (summer 2013), where positive values indicate the amount of biomass recovered. Resilience is the difference between the average biomass of the three harvests before the flood and the average biomass of the three harvests after recovery. Positive values indicate communities were more productive after the flood and negative values indicate that post-flood biomass had not

returned to its pre-flood state. Variation in resistance, recovery and resilience was analyzed with linear mixed-effects models. Fixed-effects terms were plant species richness (log scale), co-occurrence-history treatment (selected vs. naïve) and soil treatment (native, inoculated-native, or inoculated-neutral soil); plots and quadrats were used as random-effects terms. Since the measures of resistance, recovery and resilience can be dependent upon the magnitude of the pre-flood biomass [12], we analyzed additional models, which included the average of the three harvests before the flood as covariate (see Table S1). It should be noted that summer biomass was generally lower than spring biomass and that because the biomass directly after the flood was measured in summer, absolute values for resistance and recovery were overestimated. However, because we were only interested in the comparison of measures between treatments, and these had the same conditions, we did not consider this overestimation in absolute values as a problem.

We also analyzed pre-flood (first three harvests) and post-flood (last three harvests) stability in the same way as described at the beginning of this section. Furthermore, we calculated the species compositional turnover between pre- and post-flood conditions. Because it includes species abundances, we used the Bray-Curtis dissimilarity between pre-flood abundances of species (averaged over the first three harvests) and the post-flood abundances of species (averaged over the last three harvests). The analysis was the same as for the resistance, recovery, and resilience measures.

All analyses were conducted using the software R, version 3.2.4 [74]. Mixed models using residual maximum likelihood (REML) were fitted using the package ASReml for R [75] and the package 'Pascal' available at GitHub [72].

557 **References**

558 1. Balvanera, P. *et al.* Quantifying the evidence for biodiversity effects on ecosystem
559 functioning and services: Biodiversity and ecosystem functioning/services. *Ecol.*
560 *Lett.* **9**, 1146–1156 (2006).
561 2. Cardinale, B. J. *et al.* The functional role of producer diversity in ecosystems. *Am.*
562 *J. Bot.* **98**, 572–592 (2011).
563 3. Tilman, D., Lehman, C. L. & Bristow, C. E. Diversity-Stability Relationships:
564 Statistical Inevitability or Ecological Consequence? *Am. Nat.* **151**, 277–282
565 (1998).
566 4. Tilman, D., Reich, P. B. & Knops, J. M. H. Biodiversity and ecosystem stability
567 in a decade-long grassland experiment. *Nature* **441**, 629–632 (2006).
568 5. Hector, A. *et al.* General stabilizing effects of plant diversity on grassland
569 productivity through population asynchrony and overyielding. *Ecology* **91**, 2213–
570 2220 (2010).
571 6. Reich, P. B. *et al.* Impacts of biodiversity loss escalate through time as
572 redundancy fades. *Science* **336**, 589–592 (2012).
573 7. Meyer, S. T. *et al.* Effects of biodiversity strengthen over time as ecosystem
574 functioning declines at low and increases at high biodiversity. *Ecosphere* **7**,
575 e01619 (2016).
576 8. Zuppinger-Dingley, D. *et al.* Selection for niche differentiation in plant
577 communities increases biodiversity effects. *Nature* **515**, 108–111 (2014).
578 9. van Moorsel, S. J. *et al.* Community evolution increases plant productivity at low
579 diversity. *Ecol. Lett.* **21**, 128–137 (2018).
580 10. van Moorsel, S. J. *et al.* Evidence for rapid evolution in a grassland biodiversity
581 experiment. *Mol. Ecol.* **in press**, (2019).
582 11. Schmid, M. W. *et al.* Feedbacks of plant identity and diversity on the diversity
583 and community composition of rhizosphere microbiomes from a long-term
584 biodiversity experiment. *Mol. Ecol.* **28**, 863–878 (2019).
585 12. Pfisterer, A. B. & Schmid, B. Diversity-dependent production can decrease the
586 stability of ecosystem functioning. *Nature* **416**, 84–86 (2002).
587 13. Isbell, F. *et al.* Biodiversity increases the resistance of ecosystem productivity to
588 climate extremes. *Nature* **526**, 574–577 (2015).

14. Fischer, F. M. *et al.* Plant species richness and functional traits affect community stability after a flood event. *Philos. Trans. R. Soc. B Biol. Sci.* **371**, 20150276 (2016).
15. Schmid, B. Effects of Genetic Diversity in Experimental Stands of Solidago Altissima -- Evidence for the Potential Role of Pathogens as Selective Agents in Plant Populations. *J. Ecol.* **82**, 165 (1994).
16. Yachi, S. & Loreau, M. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Natl. Acad. Sci.* **96**, 1463–1468 (1999).
17. Elmqvist, T. *et al.* Response diversity, ecosystem change, and resilience. *Front. Ecol. Environ.* **1**, 488–494 (2003).
18. de Mazancourt, C. *et al.* Predicting ecosystem stability from community composition and biodiversity. *Ecol. Lett.* **16**, 617–625 (2013).
19. Thibaut, L. M. & Connolly, S. R. Understanding diversity-stability relationships: towards a unified model of portfolio effects. *Ecol. Lett.* **16**, 140–150 (2013).
20. Weigelt, A. *et al.* The Jena Experiment: six years of data from a grassland biodiversity experiment. *Ecology* **91**, 930–931 (2010).
21. Weisser, W. W. *et al.* Biodiversity effects on ecosystem functioning in a 15-year grassland experiment: Patterns, mechanisms, and open questions. *Basic Appl. Ecol.* **23**, 1–73 (2017).
22. Strauss, S. Y., Lau, J. A. & Carroll, S. P. Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? *Ecol. Lett.* **9**, 357–374 (2006).
23. Germain, R. M., Weir, J. T. & Gilbert, B. Species coexistence: macroevolutionary relationships and the contingency of historical interactions. *Proc. R. Soc. B Biol. Sci.* **283**, 20160047 (2016).
24. Eisenhauer, N. *et al.* Plant Diversity Surpasses Plant Functional Groups and Plant Productivity as Driver of Soil Biota in the Long Term. *PLoS ONE* **6**, e16055 (2011).
25. Eisenhauer, N., Reich, P. B. & Scheu, S. Increasing plant diversity effects on productivity with time due to delayed soil biota effects on plants. *Basic Appl. Ecol.* **13**, 571–578 (2012).

26. Blöschl, G., Nester, T., Komma, J., Parajka, J. & Perdigão, R. A. P. The June 2013 flood in the Upper Danube Basin, and comparisons with the 2002, 1954 and 1899 floods. *Hydrol. Earth Syst. Sci.* **17**, 5197–5212 (2013).
27. Schläpfer, F. & Schmid, B. Ecosystem effects of biodiversity: a classification of hypotheses and exploration of empirical results. *Ecol. Appl.* **9**, 893–912 (1999).
28. Van Ruijven, J. & Berendse, F. Diversity enhances community recovery, but not resistance, after drought. *J. Ecol.* **98**, 81–86 (2010).
29. Hillebrand, H. *et al.* Decomposing multiple dimensions of stability in global change experiments. *Ecol. Lett.* **21**, 21–30 (2018).
30. Lloret, F., Keeling, E. G. & Sala, A. Components of tree resilience: effects of successive low-growth episodes in old ponderosa pine forests. *Oikos* **120**, 1909–1920 (2011).
31. Cadotte, M. W., Dinnage, R. & Tilman, D. Phylogenetic diversity promotes ecosystem stability. *Ecology* **93**, (2012).
32. Venail, P. *et al.* Species richness, but not phylogenetic diversity, influences community biomass production and temporal stability in a re-examination of 16 grassland biodiversity studies. *Funct. Ecol.* **29**, 615–626 (2015).
33. Gravel, D. *et al.* Experimental niche evolution alters the strength of the diversity–productivity relationship. *Nature* **469**, 89–92 (2011).
34. Lawrence, D. *et al.* Species interactions alter evolutionary responses to a novel environment. *PLoS Biol.* **10**, e1001330 (2012).
35. Fiegna, F., Moreno-Letelier, A., Bell, T. & Barraclough, T. G. Evolution of species interactions determines microbial community productivity in new environments. *ISME J.* **9**, 1235–1245 (2014).
36. Fiegna, F., Scheuerl, T., Moreno-Letelier, A., Bell, T. & Barraclough, T. G. Saturating effects of species diversity on life-history evolution in bacteria. *Proc. R. Soc. B Biol. Sci.* **282**, 20151794 (2015).
37. Schmid, B., Birrer, A. & Lavigne, C. Genetic Variation in the Response of Plant Populations to Elevated CO2 in a Nutrient-Poor, Calcareous Grassland. in *Körner, C., Bazzaz, F.A. (Eds.), Carbon Dioxide, Populations, and Communities* 31–50 (Academic Press, San Diego, California, 1996).
38. Davis, M. B., Shaw, R. G. & Etterson, J. R. Evolutionary responses to changing climate. *Ecology* **86**, 1704–1714 (2005).

39. Nagel, R., Durka, W., Bossdorf, O. & Bucharova, A. Rapid evolution in native plants cultivated for ecological restoration: not a general pattern. *Plant Biol.* **21**, 551–558 (2019).
40. Bever, J. D. Soil community feedback and the coexistence of competitors: conceptual frameworks and empirical tests. *New Phytol.* **157**, 465–473 (2003).
41. van der Putten, W. H. *et al.* Plant-soil feedbacks: the past, the present and future challenges. *J. Ecol.* **101**, 265–276 (2013).
42. Pellkofer, S., van der Heijden, M. G. A., Schmid, B. & Wagg, C. Soil Communities Promote Temporal Stability and Species Asynchrony in Experimental Grassland Communities. *PLOS ONE* **11**, e0148015 (2016).
43. Eisenhauer, N. Aboveground–belowground interactions as a source of complementarity effects in biodiversity experiments. *Plant Soil* **351**, 1–22 (2012).
44. Wright, A. J. *et al.* Flooding disturbances increase resource availability and productivity but reduce stability in diverse plant communities. *Nat. Commun.* **6**, 6092 (2015).
45. Roscher, C. *et al.* The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community. *Basic Appl. Ecol.* **5**, 107–121 (2004).
46. Guerrero-Ramírez, N. R. *et al.* Diversity-dependent temporal divergence of ecosystem functioning in experimental ecosystems. *Nat. Ecol. Evol.* **1**, 1639–1642 (2017).
47. Vogel, A. *et al.* A new experimental approach to test why biodiversity effects strengthen as ecosystems age. in *Advances in Ecological Research* (Academic Press, 2019). doi:10.1016/bs.aecr.2019.06.006
48. Barrett, R. & Schluter, D. Adaptation from standing genetic variation. *Trends Ecol. Evol.* **23**, 38–44 (2008).
49. Zhao, L., Zhang, Q.-G. & Zhang, D.-Y. Evolution alters ecological mechanisms of coexistence in experimental microcosms. *Funct. Ecol.* **30**, 1440–1446 (2016).
50. Isbell, F., Polley, H. W. & Wilsey, B. J. Species interaction mechanisms maintain grassland plant species diversity. *Ecology* **90**, 1821–1830 (2009).
51. Gross, K. *et al.* Species richness and the temporal stability of biomass production: a new analysis of recent biodiversity experiments. *Am. Nat.* **183**, 1–12 (2014).

52. Flynn, D. F. B., Schmid, B., He, J.-S., Wolfe-Bellin, K. S. & Bazzaz, F. A. Hierarchical reliability in experimental plant assemblages. *J. Plant Ecol.* **1**, 59–65 (2008).
53. Schöb, C., Brooker, R. W. & Zuppinger-Dingley, D. Evolution of facilitation requires diverse communities. *Nat. Ecol. Evol.* **2**, 1381–1385 (2018).
54. Lau, J. A. & Lennon, J. T. Rapid responses of soil microorganisms improve plant fitness in novel environments. *Proc. Natl. Acad. Sci.* **109**, 14058–14062 (2012).
55. terHorst, C. P., Lennon, J. T. & Lau, J. A. The relative importance of rapid evolution for plant-microbe interactions depends on ecological context. *Proc. R. Soc. B Biol. Sci.* **281**, 20140028–20140028 (2014).
56. Zuppinger-Dingley, D., Flynn, D. F. B., De Deyn, G. B., Petermann, J. S. & Schmid, B. Plant selection and soil legacy enhance long-term biodiversity effects. *Ecology* **97**, 918–928 (2016).
57. Stocker, T. F. *et al.* Technical summary IPCC 2013. in *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* 33–115 (Cambridge University Press, 2013).
58. Hirabayashi, Y. *et al.* Global flood risk under climate change. *Nat. Clim Change* **3**, 816–821 (2013).
59. Donohue, I. *et al.* Navigating the complexity of ecological stability. *Ecol. Lett.* **19**, 1172–1185 (2016).
60. Pennekamp, F. *et al.* Biodiversity increases and decreases ecosystem stability. *Nature* **563**, 109–112 (2018).
61. Caldeira, M. C., Hector, A., Loreau, M. & Pereira, J. S. Species richness, temporal variability and resistance of biomass production in a Mediterranean grassland. *Oikos* **110**, 115–123 (2005).
62. Tilman, D. & Downing, J. A. Biodiversity and stability in grasslands. *Nature* **367**, 363–365 (1994).
63. Wagg, C. *et al.* Plant diversity maintains long-term ecosystem productivity under frequent drought by increasing short-term variation. *Ecology* **98**, 2952–2961 (2017).
64. Wang, Y., Yu, S. & Wang, J. Biomass-dependent susceptibility to drought in experimental grassland communities. *Ecol. Lett.* **10**, 401–410 (2007).

65. Garssen, A. G., Baattrup-Pedersen, A., Voesenek, L. A. C. J., Verhoeven, J. T. A. & Soons, M. B. Riparian plant community responses to increased flooding: a meta-analysis. *Glob. Change Biol.* **21**, 2881–2890 (2015).
66. Wright, A. J. *et al.* Plants are less negatively affected by flooding when growing in species-rich plant communities. *New Phytol.* **213**, 645–656 (2017).
67. Callaway, R. M. *et al.* Positive interactions among alpine plants increase with stress. *Nature* **417**, 844 (2002).
68. Fox, L. R. Diffuse Coevolution Within Complex Communities. *Ecology* **69**, 906–907 (1988).
69. Connell, J. H. Diversity and the Coevolution of Competitors, or the Ghost of Competition Past. *Oikos* **35**, 131 (1980).
70. Schnitzer, S. A. *et al.* Soil microbes drive the classic plant diversity–productivity pattern. *Ecology* **92**, 296–303 (2011).
71. Gebremikael, M. T., De Waele, J., Buchan, D., Soboksa, G. E. & De Neve, S. The effect of varying gamma irradiation doses and soil moisture content on nematodes, the microbial communities and mineral nitrogen. *Appl. Soil Ecol.* **92**, 1–13 (2015).
72. Schmid, B., Baruffol, M., Wang, Z. & Niklaus, P. A. A guide to analyzing biodiversity experiments. *J. Plant Ecol.* **10**, 91–110 (2017).
73. Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. & West, G. B. Toward a Metabolic Theory of Ecology. *Ecology* **85**, 1771–1789 (2004).
74. R Development Core Team. *R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.* (2017).
75. Butler, D. *asreml: asmrel() fits the linear mixed model.* (VSNI International, 2009).

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 first author.

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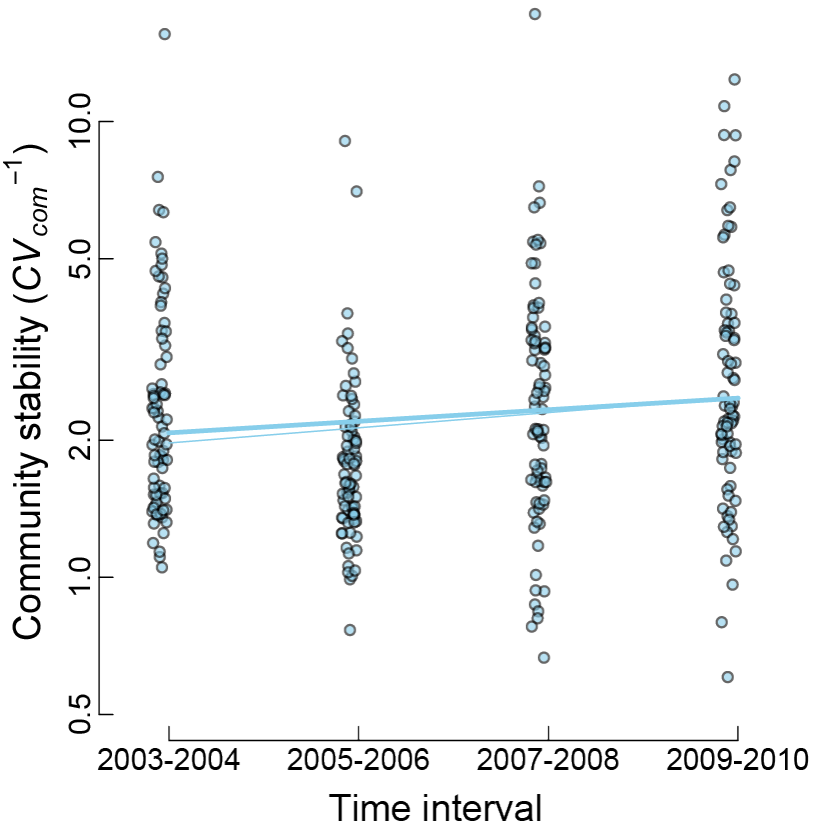
Author contributions

B.S. designed research, T.H. and S.J.V.M. performed research; A.E. and N.E. maintained and coordinated the field site; S.J.V.M., C.W. and B.S. analyzed data; S.J.V.M., B.S., O.L.P. and C.W. wrote the paper.

Competing interests

The authors declare no conflicts of interest.

771 **FIGURES & TABLES**



772

773 **Figure 1 | Combined intra- and inter-annual stability of experimental**
774 **communities over the first 8 years in a grassland biodiversity experiment (Jena**
775 **Experiment; species richness levels: 1, 2, 4, 8, 16, 60).** The 8-year period was
776 partitioned into four 2-year periods and within each stability was calculated for spring
777 and summer harvests in year n and spring harvest in year n+1, corresponding to the
778 same sequence of three harvests used in subsequent tests communities collected from
779 the Jena Experiment in 2010 (selected communities) or re-established from seeds of
780 the original supplier (naïve communities). Based on this figure we tested whether
781 selected communities have higher temporal stability than naïve communities if tested
782 under equal conditions and at the same age and time. Thick regression line includes
783 three outliers outside the top margin of the plot (P = 0.037), thin line excludes these
784 outliers (P = 0.0018).
785

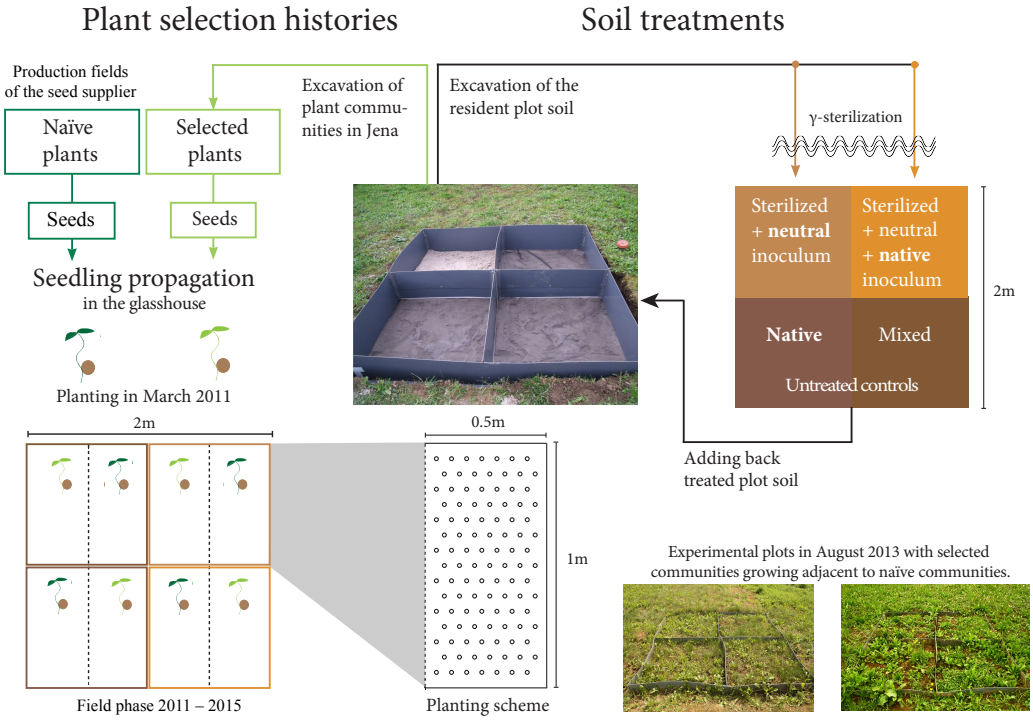


Figure 2 | Experimental set-up of test communities in the field. Seeds of cuttings made from plants that had been co-occurring for eight years in 47 plots of the Jena Experiment (selected plants) and seeds purchased from a seed supplier (naïve plants) were germinated at the same time in a glasshouse. These seedlings were then planted in the field in March 2011 according to randomized planting schemes with equal species composition and abundances. Selected (light green) and of naïve communities (dark green) were grown, in the same 47 plots from which co-selected plants had been taken, in four different soil treatments (unsterilized native or mixed soil or sterilized soil with native or neutral inoculum, see Methods). The mixed-soil treatment was not used in this paper because it was harvested early for a different experiment. Co-occurrence history (selected vs. naïve) was thus a split-split plot treatment replicated for 47 community compositions (including 11 monocultures) times three soil treatments.

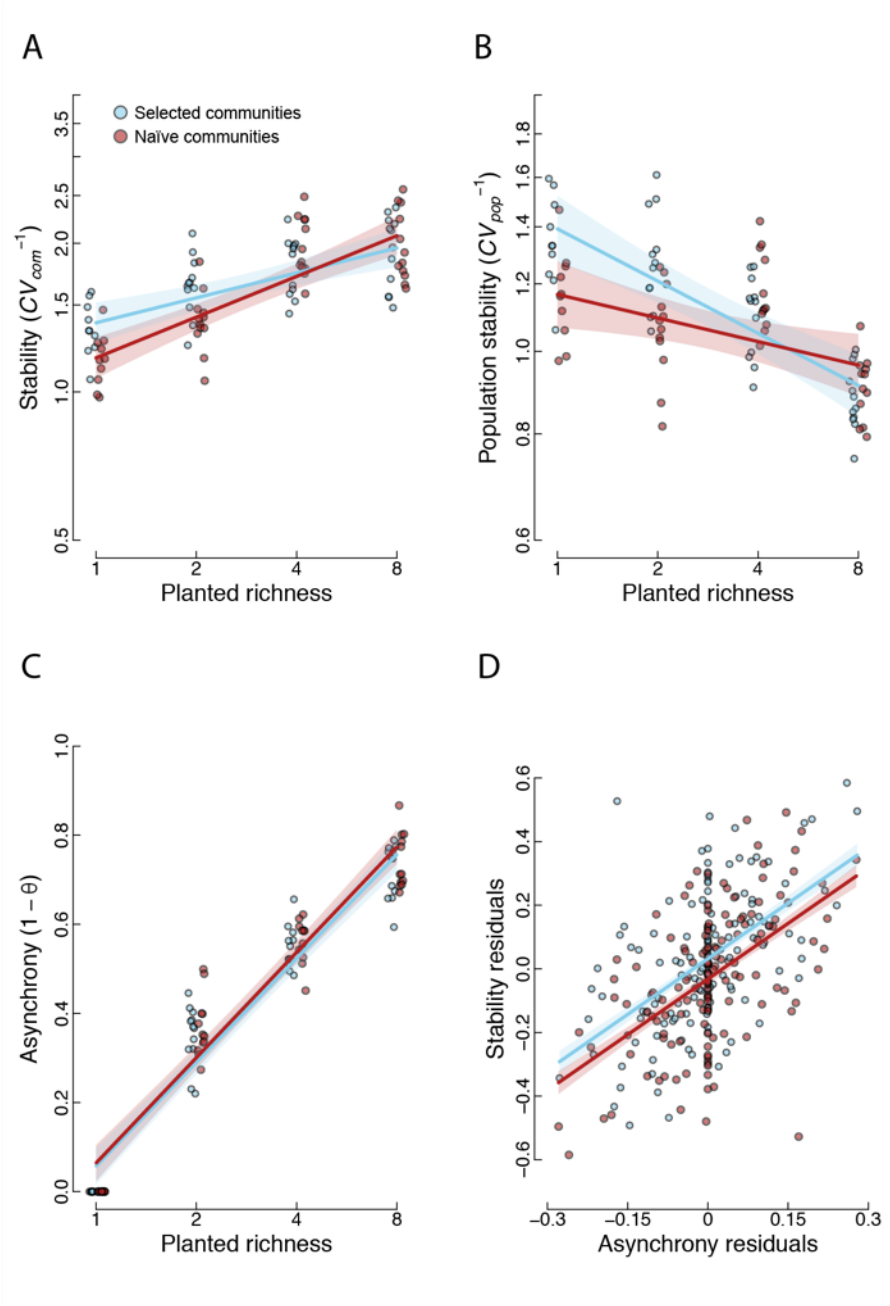


Figure 3 | The biodiversity–stability relationship for selected (blue) and naïve communities (red). (A) Community stability, (**B)** mean population stability, **(C)** asynchrony, **(D)** relationship between stability and asynchrony after correction for all other model terms except co-occurrence history. Colored bands show standard errors of predictions from mixed models as presented in Table 1. For significances see Table 1 (panels A–C); the slopes in panel D are significant at $P < 0.001$ and the difference between the two parallel lines is significant at $P = 0.005$. Means across the three soil treatments of values corrected for variation within diversity levels between plots and quadrats are shown in panels A–C and individual residual values are shown in panel D.

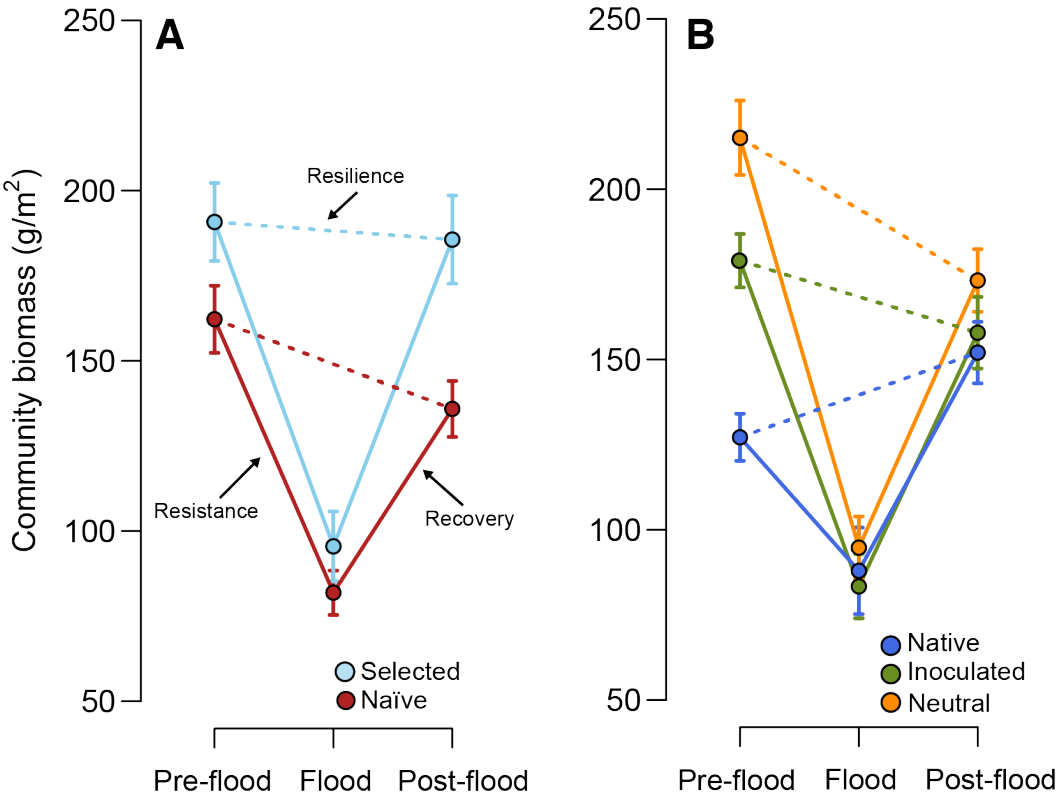


Figure 4 | Plant community biomass before and after the extreme event of a late spring flood in June 2013. Points indicate the average community biomass for **(A)** selected (blue) and naïve communities (red) and **(B)** native soil (blue), sterilized soil with native inoculum ("inoculated", green) and sterilized soil with neutral inoculum ("neutral", orange). Resistance is the difference in biomass between the average of the three harvests before the flood and the biomass directly after the flood (label "Flood" on x-axis corresponding to summer harvest 2013). Recovery is the difference in biomass between the average of the three harvests after recovery from the flood and the biomass directly after the flood. Resilience is the difference in biomass between the average of the three harvests after recovery from the flood and the average of the three harvests before the flood. Means and standard errors calculated from raw data.

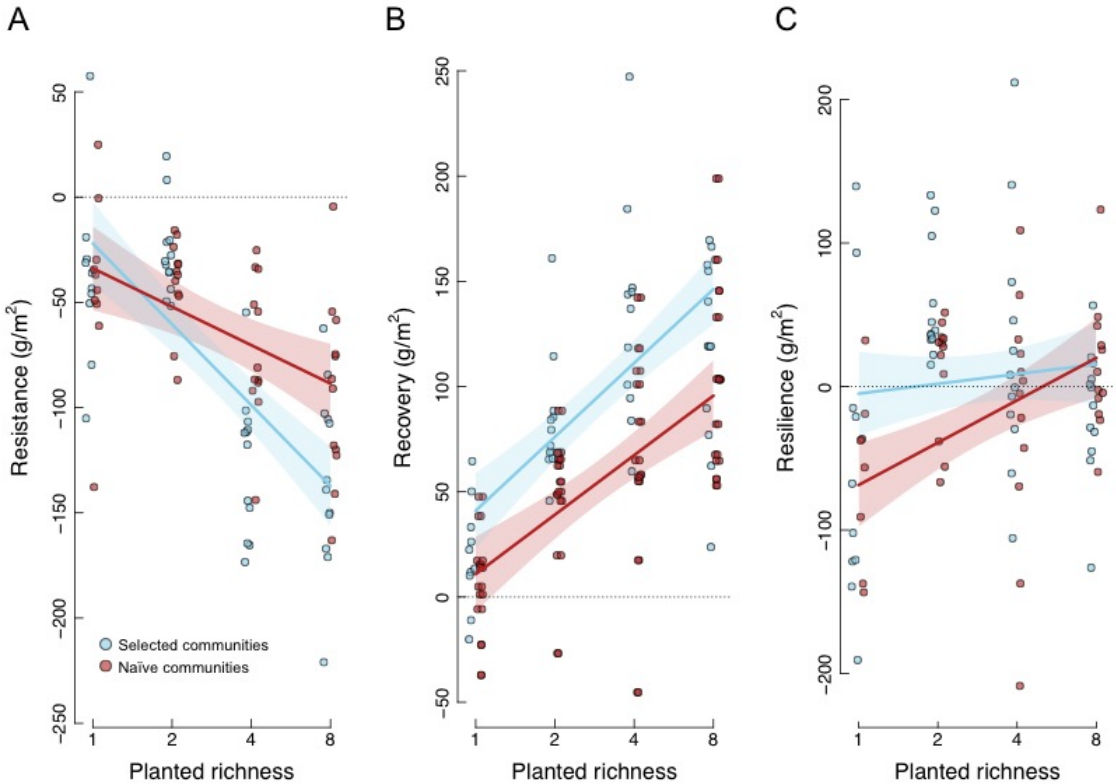


Figure 5 | Resistance, recovery, and resilience responses in terms of changes in community biomass caused by the extreme event of a late spring flood in June 2013. (A) Biodiversity–resistance relationships, **(B)** biodiversity–recovery relationships and **(C)** biodiversity–resilience relationships for selected (blue) and naïve communities (red). Colored bands show standard errors of predictions from mixed models as presented in Table 2. For significances see Table 2. Means across the three soil treatments of values corrected for variation within diversity levels between plots and quadrats are shown. The dashed line is drawn at 0 in each graph. (Similar plots with values corrected for variation in pre-flood biomass as covariate are shown in Fig. S3.)

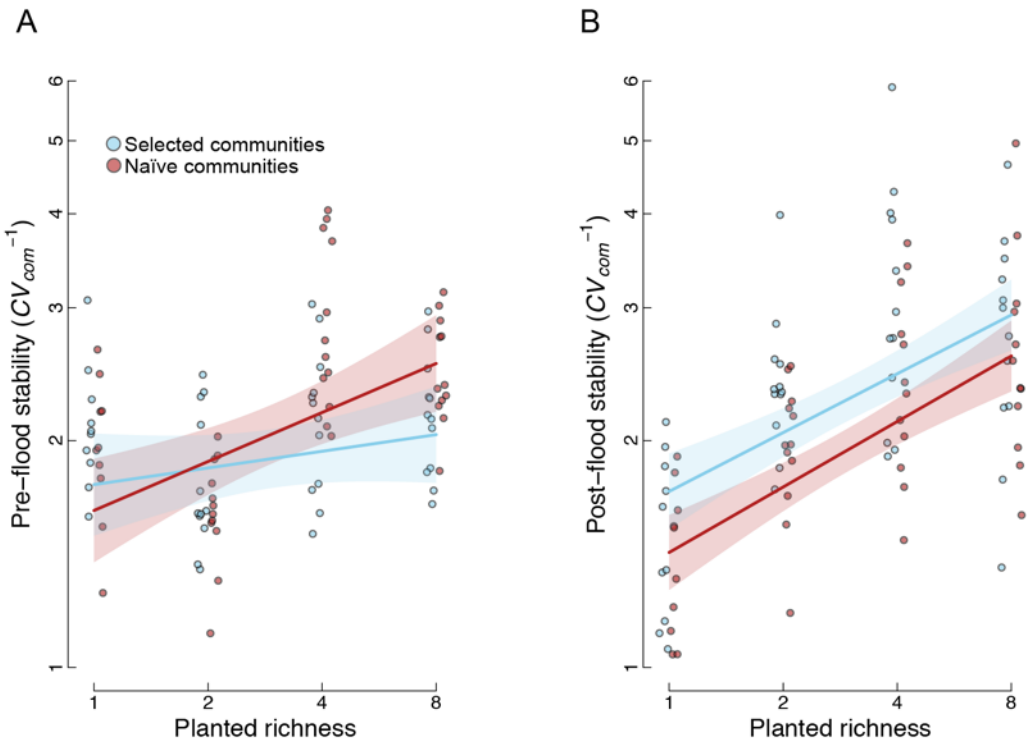


Figure 6 | The biodiversity–stability relationship for selected (blue) and naïve communities (red). (A) The three harvests before the extreme event of a late spring flood in June 2013 and **(B)** the three harvests after recovery from the flood. Colored bands show standard errors of predictions from mixed models as presented in Table S2. $P < 0.001$ for the effect of log richness in post-flood stability and $P = 0.027$ for the effect of co-occurrence history on post-flood stability. For other test-statistics see Table S2. Means across the three soil treatments of values corrected for variation within diversity levels between plots and quadrats are shown.

Table 1 | Mixed-model ANOVA results for log-transformed community stability, log-transformed mean population stability and untransformed asynchrony. The effects of species richness (log scale), soil treatments and co-occurrence history on the stability of community and population biomass and on asynchrony across the entire experimental period from 2012–2015 were analyzed (excluding the time point immediately after the extreme event of a late spring flood in June 2013). 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***	***143.00***	***<0.001***
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
CH x R_{log}	2	87.2	0.05	0.954	87.2	0.01	0.992	87.2	0.38	0.685
PH x R_{log}	1	***135.0***	***4.79***	***0.030***	***135.0***	***8.38***	***0.004***	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	

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

854 **Table 2 | Mixed-model ANOVA results for resistance, recovery, and resilience of**
855 **community biomass in response to the extreme event of a late spring flood in**
856 **June 2013.** The effects of species richness (log scale), soil treatments and co-
857 occurrence history on responses of community biomass to flooding were analyzed.
858 Bold italic text highlights significant effects. (Similar ANOVAs with pre-flood
859 biomass as covariate are shown in Table S3.)
860

		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***	***9.41***	***0.004***	***44.1***	***15.95***	***<0.001***	44.2	1.69	0.200
Soil treatment (SH)	2	***87.3***	***14.07***	***<0.001***	87.2	0.29	0.745	***87.3***	***6.12***	***0.003***
Co-occurrence history (CH)	1	***135***	***4.19***	***0.043***	***135***	***14.50***	***<0.001***	135	3.48	0.064
SH x R_{log}	2	***87.5***	***5.95***	***0.004***	87.4	1.73	0.184	***87.5***	***6.97***	***0.002***
CH x R_{log}	1	***135***	***5.32***	***0.023***	135	0.48	0.488	135	2.65	0.106
Random terms	*N*	*Var.*	*SE*		*Var.*	*SE*		*Var.*	*SE*	
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	

861

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