Community evolution increases plant productivity at low diversity

Sofia J. van Moorsel†, Terhi Hahl†, Cameron Wagg†, Gerlinde B. De Deyn, Dan F.B. Flynn†, Debra Zuppinger-Dingley† and Bernhard Schmid†*

† Department of Evolutionary Biology and Environmental Studies, University of Zürich, Winterthurerstrasse 190, 8057 Zürich, Switzerland

‡ Department of Environmental Sciences, Wageningen University, Droevendaalsesteeg 4, 6708 PB Wageningen, the Netherlands

*Email: bernhard.schmid@ieu.uzh.ch

† Shared first authorship

Emails of other authors (in order):

sofia.vanmoorsel@ieu.uzh.ch
terhi.hahl@ieu.uzh.ch
cameron.wagg@ieu.uzh.ch
gerlinde.dedeyn@wur.nl
danfbflynn@gmail.com
debra.zuppinger@ieu.uzh.ch

Type of contribution: Article
Species extinctions from local communities can negatively affect ecosystem functioning\textsuperscript{1}. Ecological mechanisms underlying these impacts are well studied\textsuperscript{2–4} but the role of evolutionary processes is rarely assessed\textsuperscript{5,6}. Using a long-term field experiment, we tested whether natural selection in plant communities increased the effects of biodiversity on productivity. We re-assembled communities with 8-year co-selection history adjacent to naïve communities with identical species composition but no history of co-selection. Mixtures of two to four co-selected species were more productive than their corresponding naïve communities over four years in soils with or without co-selected microbial communities. At the highest diversity level of eight plant species, no such differences were observed. Our findings suggest that plant community evolution can lead to rapid increases in ecosystem functioning at low diversity but may take longer at high diversity. This effect was not modified by treatments that simulated additional co-evolutionary processes between plants and soil organisms.

A large number of experiments have shown that species richness positively influences ecosystem functioning, in particular plant biomass production\textsuperscript{1,3,4,7–10}. These biodiversity effects have been explained by sampling effects that increase the chance of including productive species in diverse communities\textsuperscript{2,3} or by complementary effects between species, which allow mixtures to extract resources from the environment more efficiently\textsuperscript{11,12}. Furthermore, diversity-dependent reductions in soil fertility\textsuperscript{13} or density-dependent accumulations of specialist pathogens over time\textsuperscript{14} have been shown to contribute to decreasing productivity at low plant diversity and in plant monocultures.

Complementarity effects between co-occurring species increase over time\textsuperscript{8–10,15}. Evidence that this might be due to evolutionary processes in plant communities has been found in a glasshouse experiment comparing the performance of populations selected in monocultures vs. diverse plant communities in newly assembled test monocultures and two-
species mixtures. This suggests that community evolution may shape diversity–productivity relationship more generally, which could be tested if entire communities of co-selected plant species would be compared with communities of the same plant species but without co-selection history. Community evolution has been defined as genetically based changes among species constituting the community, which alter species performances and interactions. Such changes may occur via genetic recombination, mutations, or a sorting-out from standing genetic variation through differential survival and growth of individuals. Natural selection can lead not only to changes in gene frequencies in populations within species, but selection at the level of communities can in addition lead to correlated changes in gene frequencies in multiple species in response to one another or to co-varying environmental conditions. But empirical evidence for community evolution so far has only been demonstrated in planktonic and bacterial communities and not yet in higher plants. Here we report results from a field experiment where we tested whether plant community evolution influences plant community productivity.

Recent evidence suggests selection of particular genotypes from the total genetic pool of a species may affect ecosystem functioning in field experiments. We propose that selection of genotypes from the gene pool of entire communities may affect ecosystem functioning if non-random niche or trait changes in response to other phenotypes in the community result in reduced niche overlap and a more complete use of biotope space, thus leading to increased plant community productivity. We therefore compared the productivity of plant communities assembled from plants which have co-occurred for eight years in a long-term grassland biodiversity experiment (the Jena Experiment) with the productivity of plant communities of identical species composition, but without any co-occurrence history ("naïve communities"). The naïve species were obtained from the seed supplier of the original seeds used to establish the Jena Experiment. We used experimental
plant monocultures and 2-, 4- or 8-species mixtures with twelve different species compositions for each diversity level.

Plant community evolution in the field may also depend on the local environment, such as the soils in which co-evolution with soil microorganisms occurred. For instance, plant–soil feedback experiments have shown that soil biota change in response to different plant species, which can in turn modify the composition and productivity of plant communities. To assess whether additional co-evolutionary processes between plants and soil organisms modified plant community evolution, we grew the selected and naïve plant communities in soils with co-selected soil organisms (native soil) and with external soil organisms (neutral soil; see Methods and Extended Data Fig. 1). Community-level plant productivity was measured each year from 2012 to 2015 by collecting species-specific aboveground biomass at the time of peak biomass in spring (see Methods).

Results

Overall, for each doubling of species richness community aboveground biomass increased by 100 g·m⁻²·y⁻¹, a typical value for grassland biodiversity experiments. In general, communities of co-selected plants were more productive than naïve communities of the same species composition. The significant interaction between species richness and community-evolution treatment or in short plant history ($F_{3,191,2} = 2.77, P = 0.043$; Extended Data Table 1a) indicated that this was mainly due to increased productivity of 2- and 4-species mixtures and a smaller increase in monocultures of co-selected plants. In contrast, 8-species mixtures of co-selected or naïve plants were equally productive (Fig. 1a). The calculated relative productivity (percentage of the mean productivity of 8-species mixtures for each plant history-by-soil treatment-by-year combination) confirmed that especially 2- and 4-species mixtures of co-selected plants increased productivity relative to 8-species
mixtures ($F_{3,191.0} = 2.90, P = 0.036$; Fig. 1b; Extended Data Table 1b). The positive effect of community evolution on relative productivity was significantly larger in 2- and 4-species mixtures than in monocultures ($F_{1,43.7} = 6.37, P = 0.015$ for the interaction between plant history and the contrast of “2- or 4- species mixtures vs. others”). The differences in relative productivity between communities of co-selected plants and naïve communities increased over time for these low-diversity mixtures as well as for monocultures in all three soils (Fig. 2). For monocultures, this was due to the deteriorating performance of naïve plants, possibly due to the accumulation of soil pathogens, whereas for 2- and 4-species mixtures it was due to an increasing relative performance of communities of co-selected plants.

To test whether the communities of co-selected plants were particularly productive in 2- and 4-species mixtures at the beginning of the Jena Experiment (i.e. when they were “ naïve” communities themselves), we compared the productivity data of 2003–2006 with the data of 2012–2015. To standardize for differences in overall productivity between time periods we again used relative productivity (percentage of mean of 8-species mixtures per year). The plant communities were established in neutral soil in 2002 at the beginning of the experiment. We therefore used only data from neutral soil from 2012 to 2015. The communities of co-selected plants were significantly different in their response compared to the two types of naïve communities because of their increased relative productivity in 2- and 4- species mixtures ($F_{1,46.5} = 5.73, P = 0.021$ for the interaction of plant history with the contrast “2- or 4- species mixtures vs. others”; Extended Data Fig. 2). Differences between the communities of the naïve ancestors of the co-selected plants and our current re-assembled naïve plant communities were small and not significant ($F_{1,46.1} = 0.23, P = 0.637$ for the interaction of the contrast “naïve ancestors vs. current naïve communities” with the contrast “2- or 4- species mixtures vs. others”).
Plant community productivity was initially greater in inoculated soils, in particular at high diversity, which was reflected in an overall main effect of soil treatment and significant interactions with year, and with year and species richness (Extended Data Table 1). This was probably caused by the nutrient flush associated with gamma-sterilization of the soil\textsuperscript{35}. But we found no evidence that our soil treatments modified the differences in biodiversity effects between communities of co-selected plants and naïve communities ($F_{1,183} = 0.27$, $P = 0.847$ and $F_{1,183,8} = 1.401$ $P = 0.244$ for the three-way interactions of plant history with species richness and the soil-treatment contrasts neutral vs. native and sterilized native vs. unsterilized native, respectively).

To explore potential mechanisms for the increased biodiversity effects in 2- and 4-species mixtures of co-selected plants, we calculated the proportional increase (decrease) in plant productivity for each community composition and soil treatment as the log ratio between communities of co-selected plants and naïve communities (Fig. 3). As expected, there was no increase in productivity in 8-species mixtures, but a strong increase in 2-species mixtures followed by 4-species mixtures (which had a higher absolute increase than 2-species mixtures, see Fig. 1a) and monocultures. Using contrasts between the different diversity levels, we could confirm that the three low diversity levels were significantly different form the 8-species mixtures ($F_{1,37,1} = 5.34$ and $P = 0.026$). Among the three low diversity levels, the 2-species mixtures had significantly greater log ratios than 4-species mixtures and monocultures ($F_{1,39,2} = 4.44$, $P = 0.042$).

Next, we tested whether the presence of particular plant functional groups influenced the increase in productivity in communities of co-selected plants at the 2- and 4-species richness levels; especially as legumes are known to drive over-yielding in grasslands\textsuperscript{36}. The presence of legumes and other plant functional groups, however, did not provide any further explanation for our results. Species-level productivity within communities was higher for the
majority of plant species with a co-selection history, irrespective of functional-group identity (Fig. 4). Naïve communities showed more even species abundance distributions ($F_{1,132.2} = 4.28, P = 0.041$; Extended Data Table 2), mainly due to the lower evenness of communities of co-selected plants in the unsterilized native soil treatment (Extended Data Fig. 3). Over the course of the experiment, evenness decreased similarly in communities of co-selected plants and naïve communities (Extended Data Table 2).

Finally, we analysed changes in within-species trait variation along the species richness gradient as a potential mechanism contributing to the difference in productivity between communities of co-selected plants and naïve communities. Within-species variation in specific leaf area (SLA) decreased for communities of co-selected plants and increased for naïve communities with increasing species richness (Fig. 5; $F_{1,69.2} = 4.87, P = 0.031$ for interaction of log species richness with plant history).

**Discussion**

Our results show that eight years of community evolution in a biodiversity experiment can increase biodiversity effects on community productivity, suggesting that this may at least in part explain why biodiversity effects commonly increase over time in such experiments. The greater productivity in communities consisting of co-selected plants compared to communities consisting of naïve plants was particularly evident in communities comprised of two or four species. One might claim that these effects were because we purchased the plant material of co-selected and naïve plants at two different points in time. We argue that this is not the case for the following reasons. First, co-selected and naïve plants were obtained for 52 different species and for each of them there were different community-specific co-selection histories. Second, 8-species mixtures with and without co-selection history showed the same productivity. In other words, because the positive effect of the community-evolution
treatment was not statistically evident in the 8-species mixtures but strong in 2- and 4-
species mixtures, this effect was unlikely simply due to initial differences in plant material.

Why was the community-evolution treatment not effective at the highest richness
level tested? It is conceivable that selection pressure was dampened in communities where
more than four species co-occurred. For instance, during initial establishment in a diverse
community, each individual can have a very different set of immediate neighbours that could
constrain the consistency in the selection pressure on individuals within a community. With
fewer species in a mixture, the potential for the evolution of increased complementarity
between plant species should be greater, given the relative constancy of the neighbours any
given plant experiences. The greater proportional (but not absolute) increase of productivity
in communities of co-selected plant species at the 2-species level than at the 4-species
richness level, and the absence of such an increase at the 8-species richness level, are
compatible with the idea that evolution for co-adaptation is stronger at low than at high
diversity. At low diversity, intraspecific densities are higher and thus the chance for a
uniform selection pressure across all intraspecific individuals is greater. As a consequence,
there might be an upper limit of species richness beyond which selection is unlikely to
strengthen biodiversity effects\(^1\). Additionally, community evolution leading to increased plant
growth and productivity in diverse mixtures may be at the expense of reduced pathogen
defence\(^3\). This may explain why 8-species mixtures were initially much more productive in
neutral than in native soil.

The performance of the naïve communities in the current study over the four years
was comparable to the initial performance of the ancestral community of the co-selected
plants (2003–2006). This similarity supports the view that the observed results at 2- and 4-
species richness levels in communities of co-selected compared with communities of naïve
plants are likely due to diversity-dependent community evolution. Indeed, the naïve
communities did not catch up with the communities of co-selected plants during the course of the current experiment and differences in productivity from 2012 to 2015 even increased between the two community-evolution treatments (Fig. 2). With regard to underlying evolutionary mechanisms, this suggests that in our study community evolution was not or at least not solely due to an immediate sorting out of genotypes from standing variation\(^{17}\) during seedling establishment and initial growth.

The driving force behind community evolution for greater productivity at low diversity could have been related to particular species compositions\(^{6}\). There was, however, no evidence for any plant functional-group specific effect typically found in other contexts of biodiversity–ecosystem functioning research\(^{36,39}\). In fact, the majority of species produced greater biomass in communities of co-selected plants and evenness was only slightly reduced in these communities compared with communities of naïve plants.

Intraspecific variation in SLA decreased in communities of co-selected plants and increased in naïve communities with increasing species richness (Fig. 5), a result in line with previous findings for SLA in grassland species\(^{40}\). The increased within-species variation in monocultures suggests an evolutionary broadening of niches to benefit from a wider range of light conditions. In contrast, within-species trait variation may be less important in mixtures, due to the inherently lower intraspecific density at greater richness. The narrowing of within-species variation with increasing diversity in communities of co-selected plants could be an expected consequence of character displacement between species\(^{6}\). In relative terms, it seemed that species in naïve communities had not yet responded to different diversity treatments with an adjustment of within-species variation in the four years of this study. A more heterogeneous biotic environment may have caused their higher variation at high diversity.
Selected plants also had greater productivity than naïve plants in monoculture. The adaptation of selected plants to monoculture environments could have been due to the evolution of increased (belowground) pathogen defence\textsuperscript{41} or greater niche width\textsuperscript{42}. Assuming soil-borne plant pathogens accumulated over time\textsuperscript{14}, in particular in the initially sterilized treatments, the decrease in monoculture productivity in naïve communities (Fig. 2) would be consistent with the hypothesis of increased pathogen defence in selected communities\textsuperscript{41}. Assuming a correlation between resource-uptake and trait-based niches\textsuperscript{43}, the increase in within-species variation in SLA in monocultures of selected plants (Fig. 5) would be consistent with the second explanation related to niche width.

Positive plant diversity–productivity relationships may not only be driven by complementary resource use, and thus increased performance at high diversity\textsuperscript{11,12}, but also by pathogen accumulation in the soil and thus reduced performance at low diversity\textsuperscript{14}. Previous studies in the context of biodiversity–ecosystem functioning research have reported negative plant–soil feedbacks in native as opposed to neutral soils\textsuperscript{32,44,45}. Consequently, an increase of biodiversity effects during community evolution could also be due to the presence of co-selected soil biota. In our study, however, the outcome of the community-evolution treatment in mixtures was largely independent of the presence of co-selected soil biota. The generally lower productivity for both communities of co-selected plants and naïve communities in native soil, and with time in neutral soil, may have occurred through nutrient depletion or pathogen accumulation in all soil treatments. It is conceivable that co-evolution of plants with soil biota in our experimental systems was not effective because the large population sizes and short generation times of most soil organisms contributed to the re-assembly and fast evolution of soil communities\textsuperscript{24}. Another explanation could be that microbes were dispersed via wind-blown particles to adjacent plots thereby potentially
making the microbial communities less different in composition than if the plots would have been separated more in space.

Changes in the performance of individual species selected in different species diversity levels and tested under experimental abiotic or biotic conditions have been observed in previous studies\textsuperscript{6,25–27}. In our study, we demonstrated for the first time that changes in the performance of entire plant communities over time depend on a history of co-selection among the plants species of the assembled mixtures. We suggest that these changes are the result of community evolution because they were maintained through seed production in an experimental garden and propagation of seedlings in a glasshouse to the replanting of communities in the field. However, we cannot exclude maternal carry-over and epigenetic changes\textsuperscript{46} as additional potential evolutionary mechanisms. Independent of the mechanism, an ecosystem with individuals adapted to optimize the use of the local resources by reducing interspecific competition will be a well-functioning and sustainable system. Our new findings suggest that it is not sufficient to preserve species outside a community context for the conservation of biodiversity and its beneficial influence on ecosystem functioning and services. To protect species interactions and ecosystem functioning more efficiently, novel strategies should consider the conservation of entire communities or at least subsets of these. Our results emphasize that this is especially critical for less diverse communities, which may already suffer from the loss of some of their constituents.

**Methods**

**Study site.** The present study was conducted at the Jena Experiment field site (Jena, Thuringia, Germany, 51°N, 11°E, 135 m a.s.l.) from 2011 to 2015. The Jena Experiment is a long-term biodiversity field experiment located in the floodplain of the river Saale where 60
Central European grassland species have been grown in a number of species combinations since 2002\textsuperscript{25}.

**Community-evolution treatment.** The 48 experimental plant communities of this study included twelve monocultures (of which one had to be removed from all analyses because it was planted with the wrong species), twelve 2-species mixtures, twelve 4-species mixtures and twelve 8-species mixtures. We used two community-evolution treatments; plants with eight years of co-selection history in 48 different plant communities in the Jena Experiment (communities of co-selected plants) and plants without such co-selection history in the Jena Experiment (naïve communities). The plant seeds of naïve communities were obtained from the same commercial seed supplier (Rieger Hofmann GmbH, in Blaufelden-Raboldshausen, Germany) as the seeds used for the establishment of the original communities of the Jena Experiment. This supplier collected plants of the different species at field sites in Germany and propagated them for at least five years in monoculture, reseeding them every year. Seeds of communities of co-selected plants were produced in an experimental garden in Zurich, Switzerland, from cuttings that had been made in the Jena Experiment and were then planted in Zurich in the original species combination in plots fenced with plastic netting to reduce pollination between communities. To obtain sufficient numbers of seeds from communities of co-selected plants, a small number was additionally collected directly in the plots of the Jena Experiment. All these seeds were thus offspring of plant populations that had been sown in 2002 and grown until 2010 in plots of the Jena Experiment.

The seeds of communities of co-selected plants and naïve communities were germinated in potting soil (BF4, De Baat; Holland) in mid-January 2011 in a glasshouse in Zurich. In March 2011, the seedlings were transported back to the field site of the Jena Experiment and planted within 2 x 2 m subplots of the original plots (Extended Data Fig. 1). There were four 1 x 1 m quadrats with different soil treatments in each (see next section).
Each quadrat was further divided into two 1 x 0.5 m halves. The seedlings of communities of co-selected plants were transplanted into one half and seedlings of naïve communities into the other half of each quadrat at a density of 210 plants per m² with a 6-cm distance between individuals in a hexagonal pattern (Extended Data Fig. 1). Species were planted in equal proportions, but if a species was no longer present in an original plot of the Jena Experiment it was excluded from both communities of co-selected plants and naïve communities. Five plant species were excluded in total. The seedlings received water every second day for six weeks after transplanting to ensure the plants established.

**Soil treatment.** Within each 2 x 2 m subplot of the 48 plots of the Jena Experiment used for the present study, the original plant cover was removed in September 2010 (and used for the plant propagation in the experimental garden in Zurich, see previous section), and the soil was excavated to a depth of 0.35 m and sieved. To minimize exchange of soil components between quadrats within subplots and with the surrounding soil, two 5-cm layers of sand were added to the bottom of the plots and separated with a 0.5 mm mesh net. The borders of the quadrats and the subplots were separated by plastic frames (Extended Data Fig. 1). Using the excavated original soil from each of the plots, four soil treatments were prepared. First, half of the soil (approximately 600 kg per plot) was gamma-sterilized to remove the original soil community. Half of the gamma-sterilized soil was then inoculated with 4 % (by weight) of live sugar-beet soil and 4 % of sterilized original soil of the corresponding plot (“neutral soil” obtained by inoculation). Live sugar-beet soil was added to create a natural, but neutral soil community and was previously collected in an agricultural sugar-beet field not associated with the Jena Experiment, but with comparable soil properties. The other half of the gamma-sterilized soil was inoculated with 4 % (by weight) of live sugar-beet soil and 4 % of live original soil of the corresponding plot (“native soil” obtained by inoculation). The other half of the soil was unsterilized and used for the other two soil treatments. Half of this soil was...
filled back into one quadrat of the corresponding plot (“native soil”). The other half of the 
unsterilized soil was mixed among all plots and filled into the remaining quadrats. This fourth 
soil treatment was abandoned after two years because the plant community was excavated for 
another experiment. Therefore, this treatment is not included in the present study.

Before the soils were added into the quadrats in December 2010, they were rested in 
the field in closed bags to allow for the soil chemistry to equalize and to encourage soil biota 
of the inocula to colonize the sterilized soil before planting. After the soil was added, all 
quadrats were covered with a net and a water permeable black sheet to avoid spilling between 
quadrats until the seedlings were transplanted in March 2011.

**Maintenance and data collection.** We maintained the test communities by weeding three 
times a year and by cutting the plants twice a year at typical grassland harvest times (late 
May and August) in central Europe. To measure productivity, we harvested plant material 3 
cm aboveground from a 50 x 20 cm area in the centre of each half-quadrat, sorted it into 
especies, dried it at 70°C and weighed the dry biomass.

**SLA measurements.** At the end of the experiment, in May 2015, we measured specific leaf 
area (SLA) for 30 species in neutral soil. For each species, we collected up to 20 
representative leaves (depending on the leaf size of the species) from four individuals and 
measured the leaf area by scanning fresh leaves with a Li-3100 Area Meter (Li-cor Inc., 
Lincoln, Nebraska, USA) immediately after harvest and determining the mass of the same 
leaves after drying.

**T-RFLP assay.** Terminal restricted fragment length polymorphism (T-RFLP) targeting the 
16S RNA was used to characterize the composition of the soil bacterial communities\(^\text{47}\). In 
April 2011, four soil samples per quadrat were extracted and pooled to assess the 
establishment of soil microbial communities and to test whether soil treatments were distinct.
In 2012, a further set of soil samples was taken and analysed to confirm the establishment of different soil biotic treatments. T-RFLP soil analyses revealed that bacterial communities of the soil treatments remained distinct: each soil treatment had a characteristic bacterial composition both one and two years after planting, with some overlap (Extended Data Table 3).

**Statistical analysis.** We analysed the data from the four spring harvests 2012, 2013, 2014 and 2015, which corresponded to peak aboveground plant biomass values. We analysed plant biomass (g/m²) as a function of the design variables using mixed models and summarized results in analyses of variance (ANOVA) tables (e.g. Extended Data Table 1). Significance tests were based on approximate F-tests using appropriate error terms and denominator degrees of freedom.

The fixed terms in the model were species richness of the original plots of the Jena Experiment (factor with 4 levels: facSR), year of harvest (factor with 4 levels: Har), soil treatment (factor with 3 levels: SH), community-evolution treatment (communities of co-selected plants vs. naïve communities: PH) and interactions of these. The random terms were plot, quadrat, half-quadrat and their interactions with year of harvest. Statistical analyses were conducted using the software R, version 3.2.3. Mixed models using residual maximum likelihood (REML) were fitted using the package ASReml for R. Within-species variation in SLA was calculated as the within-species variance component for each community (residual mean square after fitting species). We had insufficient trait data to test for increased between-species variation in communities of co-selected plants containing a mixture of species.

The calculation of operational taxonomic units (OTUs) from the T-RFLP raw data (restriction enzyme products) was done using the T-RFLP processing software T-REX for
each soil treatment and year separately and the soil-specific outputs were then compared with an analysis of similarities (anosim() function of the vegan package\(^{51}\)).

### References


467 Plant selection and soil legacy enhance long-term biodiversity effects. Ecology 97, 918–
468 928 (2016).
469 42. Bazzaz, F. A. Plants in Changing Environments: Linking Physiological, Population, and
471 43. Roscher, C., Schumacher, J., Schmid, B. & Schulze, E.-D. Contrasting effects of
472 intraspecific trait variation on trait-based niches and performance of legumes in plant
474 44. Petermann, J. S., Fergus, A. J., Turnbull, L. A. & Schmid, B. Janzen-Connell effects are
475 widespread and strong enough to maintain diversity in grasslands. Ecology 89, 2399–
476 2406 (2008).
479 1617 (2016).
480 46. Verhoeven, K. J. F., vonHoldt, B. M. & Sork, V. L. Epigenetics in ecology and evolution:
481 what we know and what we need to know. Mol. Ecol. 25, 1631–1638 (2016).
482 47. Liu, W. T., Marsh, T. L., Cheng, H. & Forney, L. J. Characterization of microbial
483 diversity by determining terminal restriction fragment length polymorphisms of genes
488 www.vsni.co.uk (2009).
489 50. Culman, S.W., Bukowski, R., Gauch, H.G., Cadillo-Quiroz, H. & Buckley, D.H. T-REX:

**Online content** Methods, along with additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

**Supplementary Information** is available in the online version of the paper.

**Acknowledgements**

Thanks to the Jena Experiment for providing infrastructure and help, to D. Trujillo and M. Furler for technical assistance and to H. Martens for the lab work for the T-RFLP analyses. Thanks to V. Yadav for the establishment of the plots. We thank Tim Paine, Marc Cadotte and Mark van Kleunen for helpful comments on an earlier draft. 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).

**Author contributions**

B.S., D.B.F. and G.B.D.D. conceived the project; D.Z.-D. set up the experiment; S.J.V.M., T.H. and D.Z.-D. carried out the experiment; B.S., C.W., S.J.V.M. and T.H. analysed the data; D.B.F. analysed the TRFLP data; B.S., S.J.V.M., T.H. and C.W. wrote the first draft of the manuscript. All authors contributed to the final manuscript.
Author information

The authors declare no competing financial interests. Correspondence and requests for materials should be addressed to S.J.V.M. (sofia.vanmoorsel@ieu.uzh.ch) or B.S. (bernhard.schmid@ieu.uzh.ch).
**Figure 1 | Community productivity for naïve communities and communities of co-selected plants at different species-richness levels.** a, Peak community aboveground biomass (g/m²). Communities of co-selected plants (right panel) had slightly increased productivity in monocultures, more strongly increased productivity in 2- and 4-species mixtures, but similar productivity in 8-species mixtures as naïve communities (left panel). b, as in (a) but showing relative productivity (% of mean productivity of 8-species mixtures per plant history-by-soil treatment-by-year combination). Means and standard errors are shown. Raw data plotted as points.
Figure 2 | Relative productivity (% of mean of 8-species mixture) for naïve communities and communities of co-selected plants in neutral soil without or in native soil with co-selected soil biota.

Relative productivity of communities of co-selected plants (dashed lines, open circles) and naïve communities (solid lines, closed circles) in monocultures and 2- and 4-species mixtures in a, neutral soil (sterilized soil with neutral inoculum) b, native soil obtained by inoculation (sterilized soil with neutral inoculum and inoculum of co-selected soil biota from original plots) and c, native soil (unsterilized soil with co-selected soil biota from original plots). Raw means and standard errors are shown (for significances see Extended Data Table 1b).
Figure 3 | Log ratio of productivity in communities of co-selected plants (bm_{selected}) and productivity in naïve communities (bm_{naive}) across years and soil treatments. In 8-species mixtures, productivity did not differ between communities of co-selected and naïve plants (ratio=0). Especially in 2- and 4-species mixtures, but also in monocultures, communities of co-selected plants produced more biomass than naïve communities. Means and standard errors are shown. Raw data are plotted in the background.
Figure 4 | Log-transformed species biomass ratios between co-selected and naïve plants.

The majority of plant species attained greater aboveground biomass in communities of co-selected plants compared with naïve communities. The studied plant species belong to three different functional groups: grasses (white bars), herbs (light grey bars) and legumes (dark grey bars). Data are for each species across the four experimental years, across soil treatments and across species richness levels and species compositions of communities ($n = 32–352$). Three species with $n < 32$ were excluded from the analysis ($Anthriscus sylvestris$, $Campanula patula$ and $Cardamine pratensis$). The stars represent $P$-values $< 0.05$ for species tested separately.
Figure 5 | Within-species variation in specific leaf area (SLA) for communities of co-selected plants and naïve communities at the end of the experiment in 2015 in neutral soil. In monocultures within-species variation in SLA (measured as the within-species variance component in analysis of variance) was greater for co-selected than for naïve plants and this difference decreased with increasing species richness. Open circles and dashed line refer to communities of co-selected plants, closed circles and solid line refer to naïve communities. The interaction of log(species richness) and plant history was significant ($F_{1,69.2} = 4.87, P = 0.031$).