

Selection for niche differentiation in plant communities increases biodiversity effects

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In experimental plant communities, relationships between biodiversity and ecosystem functioning have been found to strengthen over time^{1,2}, a fact often attributed to increased resource complementarity between species in mixtures³ and negative plant–soil feedbacks in monocultures⁴. Here we show that selection for niche differentiation between species can drive this increasing biodiversity effect. Growing 12 grassland species in test monocultures and mixtures, we found character displacement between species and increased biodiversity effects when plants had been selected over 8 years in species mixtures rather than in monocultures. When grown in mixtures, relative differences in height and specific leaf area between plant species selected in mixtures (mixture types) were greater than between species selected in monocultures (monoculture types). Furthermore, net biodiversity and complementarity effects^{1,2} were greater in mixtures of mixture types than in mixtures of monoculture types. Our study demonstrates a novel mechanism for the increase in biodiversity effects: selection for increased niche differentiation through character displacement. Selection in diverse mixtures may therefore increase species coexistence and ecosystem functioning in natural communities and may also allow increased mixture yields in agriculture or forestry. However, loss of biodiversity and prolonged selection of crops in monoculture may compromise this potential for selection in the longer term.

Higher biodiversity promotes stability and productivity, with an increasing effect over time^{1,2}. These positive biodiversity effects on stability and productivity can arise from complementarity between species in resource use, such as partitioning of soil resources^{5,6} or, in some cases, accumulation of greater resources at high diversity⁷. Concurrently, the accumulation of natural enemies in low diversity, the Janzen–Connell effect^{8,9}, both promotes species coexistence through density-dependent mortality and limits productivity owing to the high pressure of species-specific pathogens⁴. Increasing biodiversity effects could therefore arise from increasingly complementary resource use and nutrient accumulation in mixtures or pathogen accumulation over time in monocultures. Here we propose a distinct, novel mechanism—that increased biodiversity effects over time result from selection for increased niche differentiation^{5,6} between plant species in diverse plant communities, reducing competition between species. Character displacement¹⁰, as reflected in functional trait differences, may drive such increasing niche differentiation between species¹¹. Our hypothesis predicts larger functional trait differences between species in mixtures and, associated with such divergence in traits, stronger positive biodiversity effects on productivity. Selection for increased niche differentiation could thus explain the experimentally observed^{1,2} increasing biodiversity effects over time, and may have implications for the effect of biodiversity on agricultural and forestry production, in which genetic diversity is known to promote production¹² and biodiversity may be essential in maintaining the pace of production gains¹³.

According to our hypothesis, mixture communities composed of the progeny of plants grown in conditions of high diversity ('mixture types') should have greater complementarity than mixture communities

composed of the progeny of plants grown in monocultures ('monoculture types'). We hypothesize that heritable phenotypes resulting from distinct genotypic or epigenetic features, including maternal effects, can arise from selection pressures in diverse communities. Our hypothesis of selection for niche differentiation through character displacement predicts adaptation to local diversity, with mixture types selected for niche differentiation and high performance in mixtures. We tested our hypothesis by growing mixture and monoculture types of 12 plant species—collected from selection communities of monocultures, mixtures of four or more species of a single functional group, and mixtures of four or more species of four functional groups (grasses, small herbs, tall herbs and legumes)—in pots containing four individuals of one or two species in a glasshouse (Extended Data Fig. 1). Our selection communities (selection history) were experimental plots of an 8-year biodiversity field experiment in Jena, Germany¹⁴, and our test communities (planted diversity) were the pots containing four individuals each (Fig. 1). We assessed above-ground plant biomass in mixtures versus monocultures to calculate biodiversity effects, partitioned into complementarity and sampling effects¹⁵ (which are usually called selection effects¹⁵, a phrase we will not use here to avoid confusion). We consider higher net biodiversity and complementarity effects for mixture types as an indication of niche differentiation,

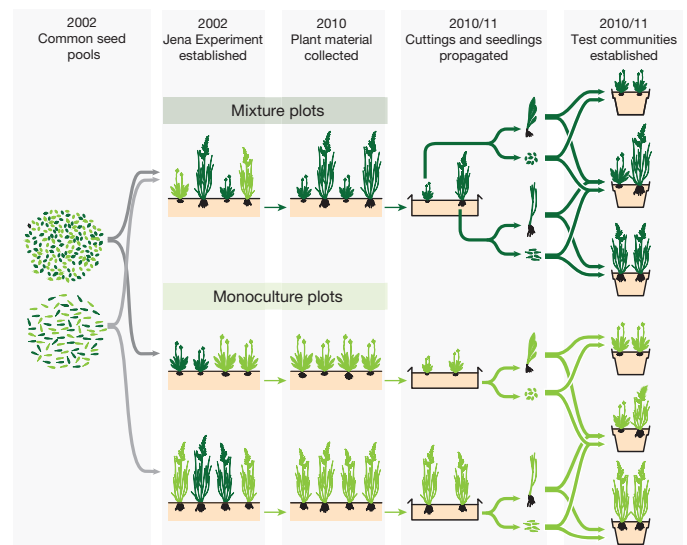


Figure 1 | Experimental design. Plant material, shoots and roots ($n = 4,900$) from experimental field monoculture versus mixture selection communities established in Jena, Germany in 2002, were collected in 2010 and assembled in new experimental glasshouse monoculture versus mixture test communities in 2010/11 ($n = 855$). We expected that mixture test communities would have higher productivity if assembled from plants collected from mixture selection communities in the field and vice versa for monocultures. Different shades of green represent the hypothesized selection for monoculture or mixture types from 2002 to 2010.

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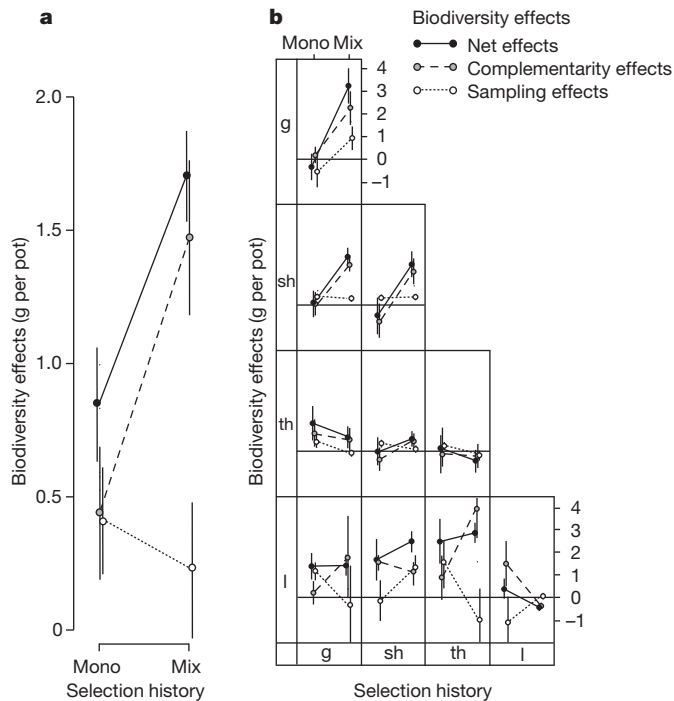


Figure 2 | Stronger biodiversity effects for plants selected in mixtures compared with plants selected in monocultures. **a, b**, Plants selected in mixture plots in the Jena Experiment over 8 years showed stronger biodiversity effects than plants selected in monoculture plots over the same time period. Mix, mixture types; Mono, monoculture types. **a**, Biodiversity effects were assessed by additive partitioning¹⁵ of net effects into complementarity and sampling effects ($n = 545$). **b**, The plots are ordered by functional group combinations: grasses (g); small herbs (sh); tall herbs (th); legumes (l). Symbols are means ± 1 standard error of the mean (s.e.m.) calculated from raw data.

and also tested whether such niche differentiation was greater for multi-functional group mixture types than for monofunctional group mixture types. Furthermore, we tested for character displacement by measuring relative differences in functional traits that reflect plant growth strategies¹⁶, height and specific leaf area (SLA) between species in mixtures (absolute difference between two species divided by the mean of the two).

Mixtures of mixture types had higher biomass than mixtures of monoculture types (Extended Data Table 1, $P = 0.024$), and this pattern was consistent across functional group combinations. Net biodiversity effects and complementarity effects were larger for mixture types than for monoculture types (Fig. 2a, b, $P = 0.017$ and $P = 0.005$, respectively; Table 1), indicating increased niche differentiation, with consistent results across the majority of functional group combinations, as illustrated in Fig. 2b. The positive effect of mixture types on net effects was strongest in grass mixtures, short-herb mixtures and mixtures of grasses with short herbs. Strong complementarity effects in response to selection history were found in these same mixtures, as well as in mixtures of legumes with

grasses or tall herbs. Positive sampling effects in response to selection history were found for grass mixtures, legume mixtures and mixtures of legumes with short herbs, but in general the response of sampling effects to selection history was slightly negative (Fig. 2a).

The stronger biodiversity effects obtained with mixture types in contrast to monoculture types were mirrored by larger functional trait differences between species in mixtures of mixture types rather than monoculture types. This was the case for relative height differences between species (Fig. 3a; Extended Data Table 2, $P = 0.011$) and for relative differences in SLA (Fig. 3b, $P < 0.001$). Mixture test communities with legumes showed particularly large SLA differences between mixture types (Extended Data Table 2, $P < 0.001$). Functional diversity, calculated from height, SLA and additionally reproductive biomass, was greater in test communities of mixture types than of monoculture types (Fig. 3c and Extended Data Table 2). We found a trend of increased intraspecific functional diversity when monocultures were planted with monoculture types as compared with mixture types (mean difference = -0.202 , paired t -test, $P = 0.101$), indicating a broader spread of phenotypes within the monoculture type populations.

The association between increased biodiversity effects and increased functional trait differences of mixture types was reflected in marginally significant correlations across selection history treatments: complementarity effects rose with greater relative differences in SLA ($P = 0.073$) and selection effects rose with greater relative differences in height ($P = 0.074$). We expect the functional traits measured here to be representative of relevant niche dimensions. However, niche differentiation is probably multivariate, and additional traits such as rooting depth could be included in future experiments. Furthermore, such experiments should assess potential changes of traits during the course of an experiment; here we only measured them at the end.

We demonstrate increased mixture performance and biodiversity effects in test communities of mixture types and provide evidence that these increases were driven by increased niche differentiation due to character displacement of functional traits between species. Our results were obtained with 12 typical grassland species of four different functional groups, supporting our hypothesis that increased biodiversity effects can result from selection for increased mixture performance and suggesting that these results may apply more generally. In a field-based extension of the current work, we found increased biodiversity effects across a wider range of species ($n = 52$) and species richness levels (1, 2, 4, 8) for communities sharing a common selection history (Extended Data Fig. 2, interaction of selection history and species richness, $P < 0.001$). Whereas mixtures may select for increased complementarity and character displacement between species, it is conceivable that selection pressures in monocultures select for greater defence against species-specific pathogens known to accumulate in monocultures⁸. We observed increased monoculture performance and reduced biodiversity effects in mixtures planted with monoculture types. Because mixture and monoculture types experienced selection environments for only 8 years, the standing variation at the beginning of the experiment may have already included genotypes or epigenetic variants pre-adapted for monoculture or mixture environments^{17,18}.

Table 1 | Net effect, complementarity effect and sampling effect on community biomass

Source of variation	numDF	NE			CE			SE		
		denDF	F	P	denDF	F	P	denDF	F	P
Selection history										
Monoculture versus mixture	1	62.9	6.04	0.017	64.4	8.49	0.005	66.7	0.01	0.921
Functional group combination	9	61.4	2.4	0.021	61.1	1.05	0.410	64.7	1.91	0.067
Monoculture versus mixture \times functional group combination	9	66.2	1.43	0.193	69.0	1.32	0.242	70.5	0.90	0.527
Random terms										
Monoculture versus mixture \times species combination	86	0.942	0.415		0.123	0.086		0.117	0.056	
Residual	545	8.314	0.547		2.254	0.148		1.245	0.082	

Results of mixed-effects analysis of variance (ANOVA) for net effects (NE; untransformed), complementarity effects (CE; square-root transformed) and sampling effects (SE; square-root transformed). denDF, degrees of freedom of error term (which can be fractional in residual maximum likelihood analysis); numDF, degrees of freedom of term. F, variance ratio; n, number of replicates for random effects; P, error probability; s.e., standard error of variance component; VC, variance component.

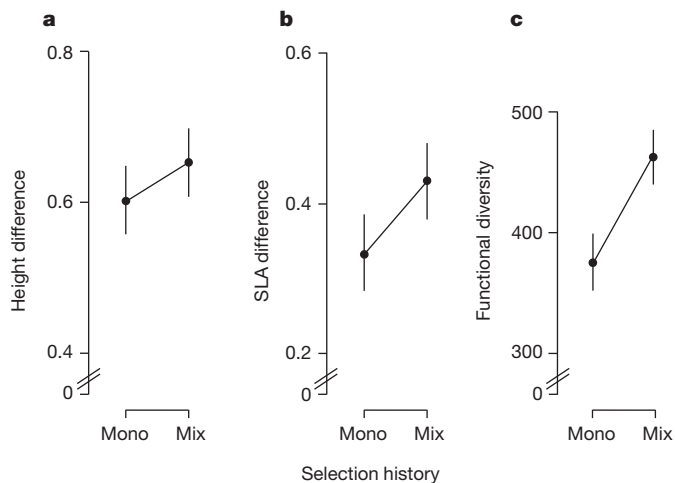


Figure 3 | Plants selected in mixtures show character displacement between species when grown in mixture. a–c, After 8 years of selection in the Jena Experiment, mixture types (Mix) in comparison with monoculture types (Mono) showed character displacement between species. a, b, Relative differences between the two species in mixture for plant height ($n = 219$ aggregated differences) (a) and SLA ($n = 208$ aggregated differences) (b). c, Functional diversity³⁰ (calculated from height, SLA and reproductive biomass) of the two species in mixture (unit-less functional diversity index, $n = 219$ aggregated values). Symbols are means ± 1 s.e.m. calculated from raw data. Means are averages over all 50 species combinations.

Niche differences between species decrease the strength of interspecific competition relative to intraspecific competition¹⁹. Thus, selection in high-diversity communities with high interspecific competition can be expected to favour genotypes with more distinct niches, reducing niche overlap and competition between species. Reduced interspecific competition could also result from the extension of the total community niche²⁰ in addition to, or instead of, finer division of currently used resources. The notion of diversity as a driver of plant population differentiation has been suggested in theory²¹ and a field study has demonstrated that differential selection for monoculture and mixture types in grassland species can occur²², supporting the idea that local evolutionary changes arise from selection through competition²³ over short time scales²⁴. In addition, species diversity has been shown to influence plant traits associated with light and resource uptake such as shoot, leaf and stem length^{25,26}, with increasing functional diversity within communities²⁷. In our study, mixture types across all functional groups showed greater relative differences in height and SLA between species in mixtures. These between-species differences may have resulted from directional selection or selection for increased plasticity in mixture types. Finally, infrared spectral fingerprints obtained for 8 of the 12 species showed significant differences in metabolic profiles between monoculture- and mixture-type individuals (Extended Data Fig. 3), reflecting differential chemistry.

We demonstrated an interaction between selection community and test community diversity, with increased community performance of mixture types. Furthermore, mixture types exhibited interspecific trait divergence, which potentially explains the increased biodiversity effects for mixtures of mixture types in our study. The consequences of selection in long-term field experiments have previously been considered in theory²⁸, and selection has been shown to drive community dynamics in microcosms²⁹; our results demonstrate that such evolutionary processes can cause the emergence of stronger biodiversity effects over time in plant biodiversity experiments. Capturing the potential of this production-enhancing niche differentiation in diverse communities may have profound impacts for agricultural and forestry applications, for example by achieving increased productivity in crop mixtures using varieties that have been selected in diverse planting regimes. This novel mechanism also implies that species losses can affect not only ecosystem

functioning in the short term, but also the long-term trajectory of biological communities.

Online Content Methods, along with any 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.

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Author Contributions B.S. and J.S.P. conceptualized the study; D.Z.-D. designed the experimental procedure and carried out the experiment with the help of B.S., D.F.B.F. and V.Y.; B.S., D.Z.-D. and D.F.B.F. analysed the data; D.Z.-D., B.S. and D.F.B.F. wrote the

paper with input from J.S.P., V.Y. and G.B.D.D. All authors discussed study design, field and glasshouse work, and analysis.

Author Information Data have been deposited at the Dryad Data Repository (<http://dx.doi.org/10.5061/dryad.750df>). Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to B.S. (bernhard.schmid@ieu.uzh.ch) or D.F.B.F. (dan.flynn@ieu.uzh.ch).

METHODS

Experimental setup. To test whether plant types selected over 8 years in mixtures outperform those types selected in monocultures when assembled in mixture test communities, and vice versa for types selected in monocultures, we first selected 12 of 16 species grown in large monoculture and mixture plots in the Jena Experiment, Germany (50°55' N, 11°35' E, 130 m above sea level) (<http://www.the-jena-experiment.de>; see ref. 14 for experimental details). Altogether there are 60 species in the Jena Experiment, but 44 of them do not occur in large monoculture plots. Three species from each of the following four functional groups of plant species used in the Jena Experiment were selected (a fourth species in each functional group was omitted because of poor growth in monoculture): grasses (*Festuca pratensis*, *Festuca rubra*, *Poa pratensis*), small herbs (*Plantago lanceolata*, *Prunella vulgaris*, *Veronica chamaedrys*), tall herbs (*Crepis biennis*, *Galium mollugo*, *Geranium pratense*) and legumes (*Lathyrus pratensis*, *Onobrychis viciifolia*, *Trifolium repens*) (Extended Data Fig. 1). These species had an 8-year community history growing in monocultures or mixtures consisting of plants belonging to a single functional group or to all four functional groups. In April 2010, we collected 4,900 plant cuttings from 48 of the 82 plots in the Jena Experiment.

We used these plant cuttings to establish plots in an experimental garden in slug enclosure compartments at the University of Zurich, Switzerland (47°23' N, 8°33' E, 534 m above sea level) with an identical plant composition to the plots in Jena from which the cuttings were collected. We added a layer of potting soil (BF 4, De Baat; Extended Data Table 3) to the soil in each plot to make sure the plants established. Netting around each plot minimized the possibility of cross-pollination between the same species from different community histories. The cuttings were used for the propagation of further cuttings or to produce seeds for our study.

Using 25 of the plant cuttings of each species from the three field community histories, we generated further cuttings, from April 2010 until September 2010, in pots in the experimental glasshouse to set up the first block of the experiment. Finally, the cuttings used in the experiment were the result of six rounds of propagation. This was done to reduce potential carry-over effects. Each set of cuttings was timed according to the slowest growing species, every 3 to 4 weeks.

During the summer of 2010, we collected seed material from the experimental garden plots for the second block of this experiment. The seed material was dried in a glasshouse compartment. We cleaned the seeds from the husks/pods and stored them at 10–15 °C, 50% humidity in a climate chamber. Once all the seeds were cleaned, they were treated with cold stratification at 5 °C for 2 months. Seeds were germinated in a 10.5-h day regime with 14–19 °C day and 10–16 °C night temperature.

In November 2010 we transplanted randomly selected individuals that were cuttings from the 25 original cuttings. We planted monocultures of four plants or two-species mixtures of two plus two plants into pots (4,275 cm³) filled with neutral agricultural soil (Extended Data Table 3) according to a diallel design containing all possible combinations of species within and among functional groups according to available plant material (Extended Data Fig. 1). Cuttings of the legume *Onobrychis viciifolia* were not successfully propagated and were therefore excluded from the first block. In October 2011, we transplanted seedlings into pots following the same procedure and design. In total we planted 12 monoculture and 50 two-species combinations as test communities with plants of three types of selection history: monoculture types and mixture types taken from mixtures of a single functional group (monofunctional group mixture types) and from mixtures of four different plant functional groups (multifunctional group mixture types), replicated, if possible, three times for cuttings and three times for seedlings ($n = 855$ pots; Extended Data Fig. 1). Single pots always contained four plants of a single selection history. Plant traits and biomass were measured 20 weeks after planting for the block established with cuttings and the block established with seedlings. To exclude effects of plant–soil feedbacks, we used a neutral growth substrate (50% agricultural sugarbeet soil, 25% sand, 25% Perlite; Ricoter AG; Extended Data Table 3) throughout the experiment.

Once the plants were transplanted into the pots, glasshouse conditions were set to natural summer day length and day temperatures of 20 °C and night temperatures

of 17 °C. To supplement sunlight, additional light was provided at a maximum of 30 kLux (Metallhalogenlamps 400 W, Iwasaki MT 400 DL/BH). Shading was at 20 kLux. To compensate for overheating, an adiabatic cooling system (Airwatech) was used. The plants were watered in the trays to make sure that each individual received equal water volume. Seedlings that died in the first 2 weeks were replaced with seedlings of the same age. Pot locations were randomized in the glasshouse without reference to history or species combination.

Measurements and harvest. Height and leaf number were measured at planting to ensure that the cuttings and seedlings were standardized. After 20 weeks of growth in the pots, plant height was measured again and the aboveground biomass of each individual was harvested at ground level. The inflorescence, if present at harvest, was collected separately and the dry biomass weighed as an indication of reproductive effort. SLA of representative leaves of each species in a pot was measured by scanning fresh leaves (Licor LI-3100) immediately after harvest and determining the mass of the same leaves after drying. Research assistants assisted in the regular measurements and harvesting of plants at the end of the experiment, and these assistants were not informed of the specific experimental treatments.

Statistical analysis. We compared the performance of plants in monoculture versus mixture test communities after being selected in either monoculture or mixture communities for 8 years using the mean aboveground dry biomass of our test communities as the response variable. We used general mixed models using residual maximum likelihood (REML) and summarized results in ANOVA tables. Significance tests were based on approximate F -tests using appropriate error terms and denominator degrees of freedom. The fixed terms in the models were: block (cuttings versus seedlings); planted diversity (monoculture versus mixture); planted functional group diversity (monoculture versus monofunctional group mixture versus multifunctional group mixture); selection history (monoculture selection versus mixture selection, resulting in monoculture versus mixture types); functional group diversity of the selection history (monoculture selection versus monofunctional group selection versus multifunctional group selection); presence or absence of legumes in the test community; functional group combination within a test community; and interactions among these. Glasshouse table, pot within table, and species combination were used as random terms. No outliers were excluded from this analysis; the full model is presented in Extended Data Table 1.

To assess biodiversity effects we followed the additive partitioning method previously described¹⁵, and partitioned the net effect (NE) into complementarity effects (CE) and sampling effects (SE). Calculations were based on the difference between the observed yield of each species in the mixture and mean monoculture yield for that species in the corresponding block and for that specific selection history. Absolute values of CE and SE were square-root transformed and the original signs put back on the transformed values for analysis¹⁵. There were 545 pots with mixture test communities for which NE, CE and SE could be calculated. For the analysis of the biodiversity effects we could simplify the full mixed model described earlier to a concise model presented in Table 1.

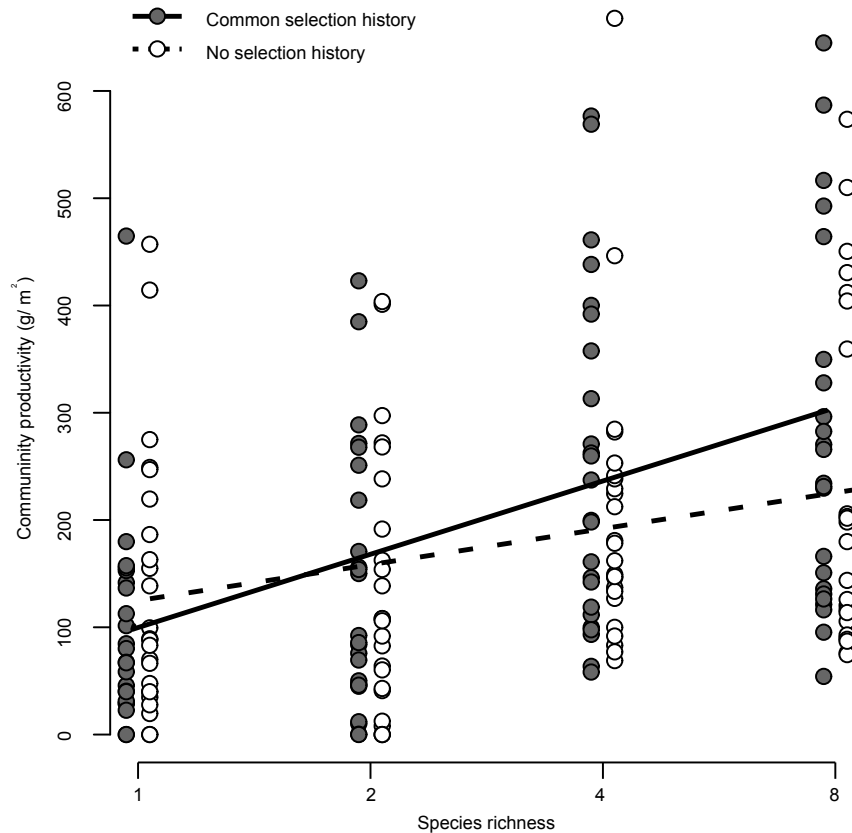
Relative differences in height and SLA (absolute difference between two species divided by the mean of the two), as well as functional diversity (FD), were calculated between species in mixtures. Differences in these measures between mixtures of monoculture versus mixture types might be associated with the differences in biodiversity effects between mixtures of monoculture versus mixture type; this would identify character displacement as a potential mechanism underlying positive biodiversity effects. FD was calculated following ref. 30 using height, SLA and reproductive biomass as functional traits. Relative differences and FD values between species means in mixture test communities were aggregated at the level of species combination by selection history by block ($n = 219$), using means calculated for each species by selection history by block combination. Statistical analysis was done with the full model described earlier and is presented in Extended Data Table 2.

Statistical analyses were conducted using the software products R, version 2.15.3 (R Development Core Team), and GenStat, version 16 (VSN International).

Planted diversity	Monoculture												Selection history												Mix-functional group														
	Grass			Short Herb			Tall Herb			Legume			Grass			Short Herb			Tall Herb			Legume			Grass			Short Herb			Tall Herb			Legume					
	g1	g2	g3	sh1	sh2	sh3	th1	th2	th3	l1	l2	l3	g1	g2	g3	sh1	sh2	sh3	th1	th2	th3	l1	l2	l3	g1	g2	g3	sh1	sh2	sh3	th1	th2	th3	l1	l2	l3			
Monoculture	Grass	g1	3									g1	3											g1	3														
		g2		3								g2		3										g2		3													
		g3			3							g3			3									g3			3												
	Short Herb	sh1			3							sh1			3									sh1			3												
		sh2				3						sh2				3								sh2				3											
		sh3					3					sh3					3							sh3					3										
	Tall Herb	th1					3					th1						3						th1						3									
		th2						3				th2							3					th2							3								
		th3							3			th3								3				th3								3							
Legumes	l1								3			l1									3			l1									3						
	l2									3		l2										3		l2										3					
	l3										3	l3											3	l3											3				
Monofunctional mixture	Grass	g1		3								g1		3										g1		3													
		g2			3							g2			3									g2			3												
		g3				3						g3				3								g3				3											
	Short Herb	sh1				3						sh1					3							sh1					3										
		sh2					3					sh2						3						sh2						3									
		sh3						3				sh3							3					sh3							3								
	Tall Herb	th1						3				th1								3				th1								3							
		th2							3			th2									3			th2									3						
		th3								3		th3										3		th3										3					
Legumes	l1									3		l1											3	l1											3				
	l2										3	l2												3	l2											3			
	l3											3	l3												3	l3												3	
Mix-functional mixture	Grass	g1		3		3			3			g1		3		3			3			3		g1		3		3			3			3					
		g2			3		3			3		g2			3		3			3			3	g2			3		3			3			3				
		g3				3		3			3	g3				3		3			3			3	g3				3		3			3			3		
	Short Herb	sh1			3			3			3	sh1				3			3				3	sh1				3			3				3				
		sh2				3				3		sh2					3				3				3	sh2					3				3			3	
		sh3					3				3	sh3						3					3	sh3						3					3				
	Tall Herb	th1					3				3	th1							3					3	th1								3				3		
		th2						3				th2								3					3	th2									3			3	
		th3							3			th3										3				3	th3										3		3
Legumes	l1								3			l1												3	l1												3		
	l2									3	l2													3	l2												3		
	l3										3	l3													3	l3													3

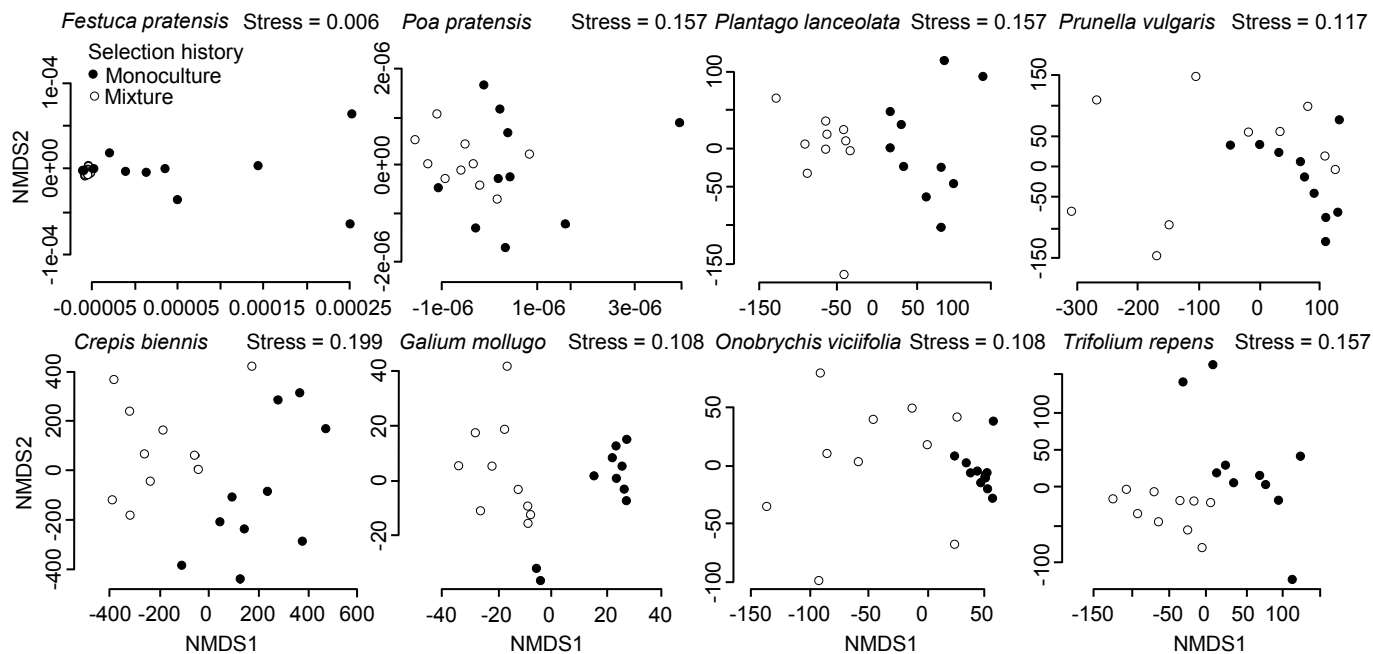
Extended Data Figure 1 | Designed number of pots planted for each combination of species. Plants from three different selection histories (monoculture, plot containing one species; monofunctional group, plot containing at least four species of the same functional group of plants; mixed-functional group, plot containing at least four species of four different functional groups) were grown in three different types of test communities (monoculture, monofunctional mixture, mixed-functional mixture). Twelve species in the Jena Experiment were chosen from all four functional groups: grass (g) (*Festuca pratensis*, *Festuca rubra*, *Poa pratensis*), small herb (sh) (*Plantago lanceolata*, *Prunella vulgaris*, *Veronica chamaedrys*), tall herb (th) (*Crepis biennis*, *Galium mollugo*, *Geranium pratense*), legume (l) (*Lathyrus pratensis*, *Onobrychis viciifolia*, *Trifolium repens*); numbers after the letter abbreviations refer to the different species. This design was used once with plants raised from cuttings (Block 1) and once with plants raised from seedlings

(Block 2). Overall we aimed to obtain the same 12 monocultures and 48 two-species combinations as test communities for each block. Availability of species precluded some of the two-species combinations in each block, such that they had to be replaced by other combinations. This yielded a total of 50 combinations across the two blocks, with several that were unique within a block. Each monoculture and each two-species combination was assembled three times for each of the three types of selection histories in each block. Some monocultures and some two-species combinations could not be realized with all types of selection histories in both blocks. Overall, there were 855 pots, 168 monocultures and 687 two-species mixtures; for 545 of the latter, the net biodiversity effect could be partitioned into complementarity and sampling effects. Some missing monocultures precluded the calculation of biodiversity effects in certain mixtures.



Extended Data Figure 2 | Biodiversity–productivity relationship is stronger for plants with a common selection history. Aboveground net primary productivity of communities in an experimental manipulation of plant species richness and selection history (common history versus no common history). In this experiment, species represented an expanded set from the present experiment (52 species), and were planted within a large-scale field experiment in Jena, Germany, on mixed soil from 48 plots from which plants had been selected, thus equalizing potential effects of soil legacy among treatments. Plants without selection history were grown from seed from a seed company,

while plants with selection history were seed progeny from plots of exactly the same species composition as the one in which they were replanted (same propagation procedure as for the 12 species used in the test communities of the present study). The slope of the biodiversity–productivity relationship was steeper for plants with a common selection history (significance of slope differences tested with interaction term $\log(\text{species richness}) \times \text{selection history}$ in mixed model with random-effects factor for 48 specific plant communities; $P < 0.001$, $n = 96$).



Extended Data Figure 3 | Selection for different biochemical features in monocultures and mixtures. Ordinations (non-metric multidimensional scaling (NMDS)) of second derivative of spectral wavenumbers of 8 of the 12 species used in the present study, showing effects of 8-year selection history on plant individuals derived from monoculture and mixture communities (Jena

Experiment). This can be an indication of selection for different biochemical features over 8 years in monoculture and mixtures. Stress values reflect a measure of goodness of fit for NMDS, with lower values showing better representation of the original data.

Extended Data Table 1 | Results of mixed-effects ANOVA for the aboveground biomass of test communities 20 weeks after transplanting plants into pots

Source of variation	numDf	denDf	<i>F</i>	<i>P</i>
Seedlings versus cuttings	1	65.2	5.89	0.018
Selection history: monoculture versus mixture	1	717.4	0.55	0.457
Selection history: monofunctional group versus multi-functional group mixture	1	707.1	0.11	0.735
Planted diversity: monoculture versus mixture	1	41.2	4.84	0.034
Planted diversity: monofunctional group versus multi-functional group mixture	1	41.9	0.09	0.767
Selection history: monoculture versus mixture × planted diversity: monoculture versus mixture	1	714.3	5.15	0.024
Selection history: monofunctional group versus multi-functional group mixture × planted diversity: monofunctional group versus multi-functional group mixture	3	713.4	1.30	0.274
Legumes	1	44.5	38.02	<0.001
Functional group combination	7	43.8	2.51	0.029
Selection history: monoculture versus mixture × legumes	1	727.7	4.04	0.045
Planted diversity: monoculture versus mixture × legumes	1	46.3	0.14	0.712
Selection history: monoculture versus mixture × functional group combination	7	729.2	1.17	0.318
Planted diversity: monoculture versus mixture × functional group combination	2	42.4	0.41	0.664
Selection history: monoculture versus mixture × planted diversity: monoculture versus mixture × legumes	1	704.0	1.27	0.260
Selection history: monoculture versus mixture × planted diversity: monoculture versus mixture × functional group combination	2	731.1	1.58	0.207
Selection history : monofunctional group versus multi-functional group mixture × planted diversity: monofunctional group versus multi-functional group mixture × legumes	3	725.8	0.45	0.719
Selection history : monofunctional group versus multi-functional group mixture × planted diversity: monofunctional group versus multi-functional group mixture × functional group combination	8	719.6	2.23	0.023
Block × selection history: monoculture versus mixture	1	729.9	2.9	0.089
Block × planted diversity: monoculture versus mixture	1	50.5	0.00	0.986
Block × selection history: monoculture versus mixture × planted diversity: monoculture versus mixture	1	722.1	2.08	0.149
Block × selection history: monofunctional group versus multi-functional group mixture × planted diversity: monofunctional group versus multi-functional group mixture	5	361.9	0.68	0.642
Random terms	<i>n</i>	VC	s.e.	
Block × glasshouse table	44	0.662	0.235	
Species combination	62	0.772	0.764	
Block × species combination	109	2.905	0.822	
Residual	855	6.708	0.367	

denDf, degrees of freedom of error term (which can be fractional in residual maximum likelihood analysis); numDf, degrees of freedom of term. *F*, variance ratio; *n*, number of replicates for random effects; *P*, error probability; s.e., standard error of variance component; VC: variance component.

Extended Data Table 2 | Results of mixed-effects ANOVA for relative height difference, relative SLA difference and for functional diversity

Source of variation	Height difference				SLA difference				Functional diversity			
	numDf	denDf	F	P	numDf	denDf	F	P	numDf	denDf	F	P
Seedlings versus cuttings	1	36.1	0.10	0.757	1	28.6	26.21	<0.001	1	33.7	3.07	0.089
Selection history: monoculture versus mixture	1	30.7	7.25	0.011	1	27.2	20.62	<0.001	1	32.3	17.42	<0.001
Planted diversity: monofunctional group versus multi-functional group mixture	-	-	-	-	1	38.0	1.24	0.272	1	37.8	4.23	0.047
Functional group combinations with legumes	1	37.1	8.20	0.007	1	38.7	0.28	0.602	1	39.2	3.69	0.062
Functional group combinations rest	8	36.8	0.90	0.525	7	38.5	3.25	0.008	7	38.2	4.64	<0.001
Seedlings versus cuttings x selection history: monoculture versus mixture	1	83.4	37.24	<0.001	1	82.3	91.76	<0.001	1	85.3	36.41	<0.001
Seedlings versus cuttings x planted diversity: monofunctional group versus multi-functional group mixture	-	-	-	-	1	27.7	4.34	0.047	1	33.3	2.84	0.101
Seedlings versus cuttings x functional group combinations with legumes	1	36.4	0.43	0.517	-	-	-	-	1	34.6	5.97	0.02
Seedlings versus cuttings x functional group combinations rest	8	36.1	0.55	0.809	-	-	-	-	-	-	-	-
Seedlings versus cuttings x functional group combinations all	-	-	-	-	8	29.2	1.20	0.334	-	-	-	-
Selection history: monoculture versus mixture x planted diversity: monofunctional group versus multi-functional group mixture	-	-	-	-	-	-	-	-	1	32.3	1.37	0.251
Selection history: monoculture versus mixture x functional group combinations with legumes	1	31.1	2.11	0.156	1	27.6	18.13	<0.001	1	32.7	13.00	0.001
Selection history: monoculture versus mixture x functional group combinations rest	8	30.7	2.48	0.034	8	27.2	0.60	0.773	-	-	-	-
Seedlings versus cuttings x selection history: monoculture versus mixture x planted diversity: monofunctional group versus multi-functional group mixture	-	-	-	-	-	-	-	-	1	88	12.08	<0.001
Seedlings versus cuttings x selection history: monoculture versus mixture x functional group combinations all	-	-	-	-	9	83.7	8.96	<0.001	-	-	-	-
Seedlings versus cuttings x selection history: monoculture versus mixture x functional group combinations with legumes	1	84.9	20.11	<0.001	-	-	-	-	1	85.8	5.41	0.022
Seedlings versus cuttings x selection history: monoculture versus mixture x functional group combinations rest	8	84.6	3.22	0.003	-	-	-	-	21	92.3	2.51	0.001
Random terms	<i>n</i>	VC	s.e.		<i>n</i>	VC	s.e.		<i>n</i>	VC	s.e.	
Species combination	50	0.006	0.031		50	0.040	0.015		50	4139	4449	
Selection history: monoculture versus mixture x species combination	93	0.005	0.002		89	0.007	0.003		93	6784	2010	
Seedlings versus cuttings x species combination	88	0.160	0.041		85	0.025	0.008		88	14483	4023	
Residual	219	0.002	0.003		208	0.005	0.001		219	2152	350	

denDf, degrees of freedom of error term (which can be fractional in residual maximum likelihood analysis); numDf, degrees of freedom of term. *F*, variance ratio; *n*, number of replicates for random effects; *P*, error probability; s.e., standard error of variance component; VC: variance component.

Extended Data Table 3 | Composition of the experimental substrate

Parameter	Unit	GVZ	AGR
Carbon*	µg/g	411.5	34.60
Hydrogen*	µg/g	47.7	4.6
Nitrogen*	µg/g	8.0	2.1
pH [†]		5.4	7.9
Organic matter [†]	%(mass)	55	3.5
Clay [†]	%(mass)	1.0	1.0
Silt [†]	%(mass)	1.0	1.0
Nitrate [†]	mg/l	439	730
Ammonium [†]	mg/l	0.7	2.5
Phosphorus [†]	mg/l	20	0.3
Potassium [†]	mg/l	54	127
Calcium [†]	mg/l	119	187
Magnesium [†]	mg/l	43	40

Composition of 1 g of substrate GVZ Tref GO PP 7000 (BF4: black peat; white peat; clay; mineral fertilizer, 1.3 kg m⁻³) and neutral agricultural soil (50% sugarbeet soil, sieved; 25% washed river sand, 0–2 mm; 25% perlite, 2–6 mm; AGR; RicoterAG). All units in mg l⁻¹ are per litre extract solution.

* Composition determined using elemental analysis.

† Composition determined by Ibu (Laboratory for Soil Analysis, Thun, Switzerland), program 40 analysis.