Evolution of species complementarity in response to drought in a grassland biodiversity experiment

Yuxin Chen (✉ yuxin.chen@xmu.edu.cn)

Xiamen University <https://orcid.org/0000-0003-0658-7562>

Anja Vogel

Leipzig University

Cameron Wagg

University of Zürich <https://orcid.org/0000-0002-9738-6901>

Tianyang Xu

University of Zürich

Maitane Iturrate-Garcia

University of Zurich

Michael Scherer-Lorenzen

University of Freiburg <https://orcid.org/0000-0001-9566-590X>

Alexandra Weigelt

University of Leipzig <https://orcid.org/0000-0001-6242-603X>

Nico Eisenhauer

German Center for Integrative Biodiversity Research <https://orcid.org/0000-0002-0371-6720>

Bernhard Schmid

University of Zurich

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1 **Title: Evolution of species complementarity in response to drought in a grassland**
2 **biodiversity experiment**

3 **Short title: Drought-induced selection for species complementarity**

4 **Authors**

5 Yuxin Chen^{1,2,3,*}, Anja Vogel^{4,5,6}, Cameron Wagg^{2,7}, Tianyang Xu², Maitane Iturrate
6 Garcia^{2,8}, Michael Scherer-Lorenzen⁹, Alexandra Weigelt^{4,10}, Nico Eisenhauer^{4,5},
7 Bernhard Schmid^{11,12,*}

8 **Affiliations:**

9 ¹Key Laboratory of the Ministry of Education for Coastal and Wetland Ecosystems,
10 College of the Environment & Ecology, Xiamen University, 361102 Xiamen, China.

11 ²Department of Evolutionary Biology and Environmental Studies, University of
12 Zürich, Winterthurerstrasse 190, 8057 Zürich, Switzerland.

13 ³School of Life Sciences/State Key Laboratory of Biocontrol, Sun Yat-sen University,
14 510275 Guangzhou, China.

15 ⁴German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig,
16 Puschstraße 4, 04103 Leipzig, Germany.

17 ⁵Institute of Biology, Leipzig University, Puschstraße 4, 04103 Leipzig,
18 Germany

19 ⁶Institute of Ecology and Evolution, Friedrich Schiller University Jena, 07743 Jena,
20 Germany.

21 ⁷Fredericton Research and Development Center, Agriculture and Agri-Food Canada,
22 850 Lincoln Road, Fredericton, New Brunswick, E3B 4Z7, Canada.

23 ⁸Department of Chemical and Biological Metrology, Federal Institute of Metrology
24 METAS, Lindenweg 50, 3003 Bern-Wabern, Switzerland

25 ⁹Geobotany, Faculty of Biology, University of Freiburg, 79106 Freiburg, Germany.

26 ¹⁰Institute of Biology, Leipzig University, Johannisallee 21-23, 04103 Leipzig,

27 Germany

28 ¹¹Department of Geography, Remote Sensing Laboratories, University of Zürich,

29 Winterthurerstrasse 190, 8057 Zürich, Switzerland.

30 ¹²Institute of Ecology, College of Urban and Environmental Sciences, Peking

31 University, 100871 Beijing, China.

32 ***Correspondence:** yuxin.chen@xmu.edu.cn and bernhard.schmid@uzh.ch

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Abstract

Growing threats from extreme climatic events and biodiversity loss have raised concerns about their interactive consequences for ecosystem functioning. Evidence suggests that biodiversity is crucial to buffer ecosystem functioning facing climatic extremes. However, whether evolutionary processes in species mixtures underpin such biodiversity-dependent stabilizing effects remains elusive. We tested this hypothesis by exposing experimental mixtures of grassland species to eight recurrent summer droughts vs. control in the field. Seed offspring of 12 species were subsequently grown individually, in monocultures or in 2-species mixtures and subjected to a novel drought event in the glasshouse. Comparing mixtures with monocultures, drought-selected plants showed greater between-species complementarity than ambient-selected plants when recovering from the drought event, which led to greater biodiversity effects on community productivity and better recovery of drought-selected mixtures after the drought. These findings suggest biodiversity can buffer the impacts of extreme climatic events through evolution of species complementarity.

Main text

Extreme climatic events such as droughts are predicted to be more frequent in the future ^{1,2}, with potentially negative effects on the functioning of ecosystems and the provision of ecosystem services for human well-being ³⁻⁷. Ecosystems may adjust to climatic extremes by changes in species abundances ⁸⁻¹⁰ or evolutionary responses of populations ¹¹⁻¹⁹. Both experimental and observational studies have shown that higher biodiversity buffers temporal variation in ecosystem functioning against extreme climatic events ²⁰⁻²⁴. Stabilizing effects can arise from various ecological mechanisms,

such as portfolio effects due to the scaling relationship between the mean and the variance²⁵, complementarity among species in responses to environmental fluctuations²⁶, and compensatory recovery in which increased recovery after extreme climatic events compensates for the event-driven loss of ecosystem functioning²³. However, large gaps remain in our empirical understanding of whether and how evolution may underpin such stabilizing effects of biodiversity on ecosystem functioning in the face of extreme climatic events. Rapid evolutionary change under such climatic perturbations may arise from a filtering of pre-existing genetic variation via differential demographic processes^{27,28}.

Extreme climatic events may select for specific plant traits with the consequence of higher tolerance under future climatic extreme events or faster recovery after such events. For example, drought may select for higher tolerance of water deficits (e.g., shorter height, greater leaf mass per area, higher turgor loss point, or higher root-shoot biomass ratio)²⁹⁻³², which may reduce plant mortality rates and increase community resistance to drought. Alternatively, drought may select for faster recovery after drought^{13,17}. Nutrient availability such as soil nitrogen may increase after drought and favor the growth of acquisitive individuals (e.g., with lower leaf mass per area, or higher leaf and root nitrogen content) that survived post drought³²⁻³⁴. As a consequence, community productivity may also be increased after drought²³.

Extreme climatic events may also induce the evolution of species interactions within communities in complex ways^{12,35-37}, affecting biodiversity effects on ecosystem functioning. First, selection for specific traits may change the average dissimilarity and niche difference between species within communities (Supplementary Fig. 1). For example, drought may exclude intolerant genotypes from intolerant species, which may increase the niche overlap and competition intensity

between intolerant and tolerant species ³⁸ (Supplementary Fig. 1a). Alternatively, drought may exclude intolerant genotypes from both intolerant and tolerant species, which may reduce the niche overlap and competition intensity between the two species (Supplementary Fig. 1b). Second, trait expression in one species may influence trait expression in another interacting species, leading to heritable changes in species interactions ³⁷. That is, selection may occur at the community level and not be inferred from the sum or average of trait variation of individual species ³⁷. Selection for reduced species competition and niche overlap could strengthen positive biodiversity effects ^{39,40}.

Experiments have shown that evolved species interactions strengthened the positive biodiversity effects on productivity in microbial communities ^{41,42} and in grassland communities under benign environments ⁴³⁻⁴⁵. But whether and how extreme climatic events will lead to evolutionary changes in species interactions, and further change the biodiversity effects in plant communities remains elusive.

In the present study, we assessed how an 8-year selection treatment of summer droughts affected plant diversity effects on ecosystem functioning and species interactions before, during and after a novel drought event. We exposed experimental mixtures of grassland species to eight recurrent summer droughts vs. control in a long-term biodiversity experiment in the field (the Jena Experiment ^{23,46,47}). Seed offspring of 12 species were subsequently grown individually, in monocultures or in 2-species mixtures and subjected to a novel drought event in the glasshouse (Fig. 1; Supplementary Table 1). In the glasshouse experiment, both monocultures and mixtures contained four individuals per pot. We harvested aboveground biomass (a proxy for productivity) of every pot three times: (1) after a first phase of three months with regular watering (ambient conditions, “before drought”); (2) after a second phase

of two weeks without watering (drought conditions, “during drought”) and (3) after a third phase of seven weeks with regular watering (ambient conditions for recovery, “after drought”).

We used the harvested aboveground biomass in four sets of analyses. First, we assessed how drought selection affected biodiversity effects on productivity before, during and after the drought event in the glasshouse. We used the biomass difference between 2-species mixtures vs. monocultures to calculate the net biodiversity effects, which we further partitioned into complementarity effects (indicating niche differentiation or facilitation) and sampling effects (indicating a disproportionate contribution to community productivity of one or the two species; which is also referred as “selection effect” elsewhere, a term we did not use in this study to avoid confusion)⁴⁸. Second, we assessed the effects of drought selection on resistance (biomass ratio during vs. before the drought), recovery (biomass ratio after vs. during the drought) and resilience (biomass ratio after vs. before the drought) of productivity^{19,20}. Third, we tested whether altered plant interactions drove the above differences between the two selection treatments. We calculated the intensities of neighbor interactions for mixtures (i.e., heterospecific interactions) and monocultures (i.e., conspecific interactions) separately, and then calculated their difference as a proxy for niche difference. Fourth, we assessed how drought selection influenced trait values on plants in pots with one individual and trait dissimilarities between interacting species in mixtures.

The objectives of this study were to (1), assess how drought selection affected biodiversity effects on productivity and stability over different phases of an experimental drought event; and to (2), investigate the roles of species interactions in driving the evolutionary changes in biodiversity effects on productivity and stability.

RESULTS

Effects of drought selection on biodiversity effects on productivity

We found that the net biodiversity effects for different species pairs were higher when plants had been selected under repeated summer droughts in the field, but this only became visible when their productivity was assessed after the drought event in the glasshouse (Figs. 2 & 3, Supplementary Tables 2 & 3). The positive net biodiversity effects in mixtures of drought-selected plants were mostly due to positive complementarity effects (Fig. 2). Of twelve drought-selected species pairs with sufficient replication for separate statistical tests per pair, eleven had positive complementarity effects and five of these were significant ($P < 0.05$; Fig. 2p); whereas ten had negative sampling effects, and six of these were statistically significant ($P < 0.05$; Fig. 2r). In contrast, of eleven ambient-selected species pairs with sufficient replication for separate statistical analyses, six had negative complementarity effects and one of these was significant ($P < 0.05$; Fig. 2o); whereas only two pairs had significantly negative sampling effects ($P < 0.05$; Fig. 2q).

When we used all species pairs in a combined statistical analysis, testing the overall drought selection effect against the variation among species pairs as error term, we found that drought selection had increased post-drought net biodiversity effects in mixtures independent of the particular species pair considered and could thus be generalized across the entire experiment (Fig. 3; Supplementary Table 3). Furthermore, drought-selected species pairs consistently had more positive complementarity and more negative sampling effects than ambient-selected species pairs after the drought event (Fig. 3f, i; Supplementary Table 3). These results suggest that drought-selected plants are more complementary between species than ambient-

selected plants in mixtures. However, before and during the drought, the effects of drought selection were not statistically significant (Fig. 3; Supplementary Table 3). Initially, the positive biodiversity effect was mainly due to positive sampling effect (Fig. 3a, d, g; Supplementary Table 2).

Effects of drought selection on stability

Drought-selected plants recovered faster from the drought event in the glasshouse than those of ambient-selected plant; however, this was only evident when plants were grown in mixtures but not in monocultures (Supplementary Fig. 2; Supplementary Table 4). These results suggest that species interactions in mixtures may play important roles in promoting the recovery of drought-selected plants. Plants with different selection treatments did not differ significantly in their resistance or resilience to the drought event neither in mixtures nor in monocultures (Supplementary Fig. 2; Supplementary Table 4).

The difference in recovery rates between mixtures and monocultures (i.e., biodiversity effects on recovery) for drought-selected plants were more positive than those for ambient-selected plants (Fig. 4b; Supplementary Table 5). This is consistent with the more positive biodiversity effects on productivity for drought-selected than ambient-selected plants after the drought event described in the previous section. However, biodiversity effects on resistance were more negative for drought-selected than for ambient-selected plants, thus leading to similar biodiversity effects on resilience between the two selection treatments (Fig. 4a, c).

Effects of drought selection on plant interactions

The neighbor interaction index $NInt_M^{49}$, which measures interaction intensity among

neighboring plants, was mostly negative (Supplementary Fig. 3), indicating that individual plants in pots with four individuals had less biomass than individual plants in pots with one individual. Nevertheless, in most cases average individuals in pots of four individuals had more than 25% of the biomass of individuals in pots with one individual, that is $NInt_M > -0.75$, the value expected under the reciprocal yield law⁵⁰. An exception were monocultures after the drought event, which produced the same amount of biomass per pot independent of the number of plants ($NInt_M \approx -0.75$; Supplementary Fig. 3f). Indications of facilitation, i.e., cases where individual plants in pots with four individuals had more biomass than individual plants in pots with one individual and $NInt_M > 0$, were very rare.

During the drought phase in the glasshouse, drought-selected plants competed more strongly in mixtures than ambient-selected plants (Supplementary Fig. 3c; Supplementary Table 6), which was also the time when drought-selected plants tended to have lower complementarity than ambient-selected plants (Fig. 3e). After the drought event, drought-selected plants showed weaker heterospecific than conspecific competition, which was less pronounced for ambient-selected plants (Figs. 5 & 6; Supplementary Tables 7 & 8), consistent with the positive net biodiversity effects on productivity and recovery reported above for drought-selected plants after the drought event. These results suggest that drought-selected plants compared with ambient-selected plants had evolved reduced interspecific relative to intraspecific competition (i.e., increased niche differentiation), at least when growing in mixtures and after a novel drought event.

Effects of drought selection on plant traits

We measured six traits that were closely related to plant water or carbon use on plants

from pots with one individual. Drought- and ambient-selected plants had similar average values of leaf relative chlorophyll content, leaf area (LA), leaf mass per area (LMA) and leaf osmotic potential before the drought event in the glasshouse (Supplementary Fig. 4). Species varied in their responses of LMA to the selection treatments (Supplementary Table 9). The drought event in the glasshouse reduced leaf stomatal conductance (Supplementary Fig. 5). However, leaf stomatal conductance did not vary significantly between the two selection treatments, neither before nor during the drought event (Supplementary Fig. 5). These results suggest that the drought selection treatments did not lead to significant changes in average values of leaf traits on plants grown alone, at least before the drought event. After the drought phase in the glasshouse, the time window for the biomass harvest after the drought did not allow us to take additional trait measurements. However, drought- and ambient-selected plants developed similar root-shoot biomass ratios after the drought (Supplementary Fig. 6).

We also measured leaf relative chlorophyll content, LA and LMA on plants in mixtures before the drought event in the glasshouse. Drought-selected plants diverged in LA between species pairs in mixtures when compared with the same species pairs of ambient-selected plants, although this difference was only marginally significant (Supplementary Fig. 7, Supplementary Table 10). However, species dissimilarities in LMA, leaf relative chlorophyll content or the three traits jointly did not vary significantly between the two selection treatments (Supplementary Fig. 7, Supplementary Table 10).

DISCUSSION

Increasing threats from extreme climatic events such as droughts have raised the

importance of predicting ecosystem responses and adaptation to climate change both in short and long terms, based on ecological and evolutionary theory^{3-6,12-14}. In this study, we tested whether recurrent summer droughts caused evolutionary adaptations and assessed the effects of drought selection on biodiversity effects for 21 pairs of plant species over the time course of an experimental drought event (before, during and after drought). We found that an 8-year treatment of recurrent droughts had selected for increased niche differentiation in mixtures during the recovery phase after the drought event, which led to more positive biodiversity effects on community productivity and recovery after the drought event. These findings suggest that mixed-species grassland communities bear the potential of evolutionary adaptations at the community level to extreme climatic events.

We found that drought selection caused a significant difference (relative to ambient selection) in biodiversity effects on productivity only after the drought event in the glasshouse. The selection for more positive biodiversity effects after the drought event was primarily due to the selection for more positive complementarity effects, whereas sampling effects were more negative than those of species pairs selected under ambient conditions. This selection for increased complementarity effects after the drought event was primarily the results of reduced interspecific relative to intraspecific competition (i.e., increased niche differentiation). In contrast to a previous grassland experiment with plants from the Jena Experiment selected under ambient conditions⁴⁴ and in contrast to predictions of the stress-gradient-hypothesis (SGH)⁵¹, we did not find evidence for facilitation underpinning complementarity effects. According to the SGH, interactions among plants are more facilitative in stressful environments where resources are harder to access, but more competitive in environments with a low stress level and a high supply of nutrients⁵¹.

However, facilitation, both within and between species, was very rare over the time course of the drought event in our case. During the most stressful phase of the drought event, drought-selected plants competed more strongly between species than did ambient-selected plants. This suggests that evolutionary processes of species interactions can differ between environmental conditions, and observations under ambient climates may not serve to make appropriate predictions for evolutionary responses of communities to extreme climatic events.

The selection for niche differentiation after the drought event could be related to effects of drought on soil nutrients. For example, droughts can increase leaf litter⁵² and reduce the mobility of soil nutrients, the activity of soil microbes and the rate of litter decomposition⁵³⁻⁵⁵. These constrained resources can be released after droughts^{33,34,54}, which increases the potential for niche partitioning among species.

We did not test the relative importance of genetic vs. epigenetic variation in explaining our results, but know from a previous study that adaptive changes that had taken place during the course of an 8-year community selection in the Jena Experiment were almost exclusively genetic, with epigenetic variation closely following genetic variation⁵⁶. We also could not determine which traits¹⁸ drove the observed selection for niche differentiation after the drought event. For the traits that we measured and analyzed, we did not find significant differences between plants selected under recurrent droughts vs. plants selected under ambient conditions. But we should note that this does not necessarily mean that the recurrent droughts did not select for specific traits or trait variation in response to being grown in mixtures, because most of the traits were measured before the drought event in the glasshouse and for single plants, while the primary effects of drought selection were detected after the drought event and in mixtures compared with monocultures. The effects of

selection on traits may be more evident in mixed-species communities, if the selection primarily induces evolution of species interactions at the level of the community^{37,43,45}. This is partially reflected by the findings that competing species composed of drought-selected plants diverged (relative to ambient-selected plants) in their leaf area before the drought event when they were growing together in mixtures. It is also possible that the drought-induced selection may be more apparent on root traits (e.g., root cortical thickness and hydraulic conductance) with close linkages to plant water acquisition but were not measured in this study³².

In line with the findings of drought selection for stronger species complementarity during the recovery phase after the drought event, mixtures of drought-selected plants recovered faster than those of ambient-selected plants, which led to a more pronounced positive biodiversity effect on recovery for drought-selected plants. A previous field experiment²³, where we collected the seeds for the present study, showed that more diverse communities were better able to compensate for drought-driven productivity loss, which led to stabilizing effects of biodiversity. The results from this study suggest that biodiversity-dependent evolutionary adaptation may be an important mechanism driving the above compensatory recovery observed in the field. Biodiversity effects on resistance were more negative for drought-selected than for ambient-selected plants, thus leading to similar biodiversity effects on resilience between the two selection treatments. These findings suggest that drought-selected plants competed more strongly between species than did ambient-selected plants during the drought event, which might have impeded the resistance of mixtures relative to monocultures. Plants of the two selection treatments had similar resistance both in monocultures and mixtures. One explanation for this result could be that the recurrent summer droughts in the field did not cause severe mortality immediately

during the droughts⁵⁷; thus, the importance of selection for fast recovery from droughts may overwhelm that of selection for high tolerance to droughts. The selection of acquisitive traits for fast recovery after droughts may have side effects on the processes during droughts, for example, intensifying species competition during droughts. Alternatively, the selection processes during droughts may have primarily played out below ground, which we only assessed by measuring biomass allocation to belowground organs in monocultures post drought. We expected it to be increased in drought-selected plants but could not statistically confirm it. A more thorough test of this possibility would require assessing root traits that have strong linkages with plant water acquisition³².

Predicting the evolution of species interactions and their consequences for ecosystems is challenging due to the prevalent and complex correlations between traits, and trade-offs between survival during extreme events and growth after events^{13,33,35,37,58,59}. These complexities imply that a big picture over the time course of an extreme climatic event, integrating both resistance and recovery processes, is necessary for predicting the responses and adaptations of ecosystems to extreme climatic events^{10,20,23}.

Drought- and ambient-selected plants had similar biodiversity effects on productivity before the drought event in the glasshouse. Drought-induced selection for niche differentiation after the drought event was not correlated with more positive biodiversity effects before the drought event, although both phases were under ambient conditions with regular watering. This difference may arise from at least the following two reasons. First, drought-induced selection may involve components of plasticity^{17,60}. In this case, the effects of selected niche differentiation were only visible when plants were stressed by water deficits, but weak or absent without water

stress. Second, the resource conditions may have differed between the two phases, which might have affected the available niche axes for partitioning^{17,61}. The productivity of mixtures before the drought event (quarter quantiles: [0.148 g/pot/week, 0.308 g/pot/week]) were about two times higher than that after the drought event ([0.048 g/pot/week, 0.100 g/pot/week]). Partitioning along axes associated with light and aboveground space may have been more important before the drought event, while partitioning along axes associated with belowground resources may have been more important after the drought event.

We demonstrated that biodiversity could buffer the impacts of an extreme drought event on ecosystem functioning through selected niche differentiation during the recovery phase post drought. Together with previous findings focusing on ecological processes²⁰⁻²⁴, we add an important mechanism, the evolution of species complementarity, to explain the stability of productivity in mixed-species grassland communities facing climate change. The selection of phenotypes with high recovery after recurrent droughts causes compensatory recovery after drought-related biomass loss. Our results suggest that biodiversity can buffer the impacts of extreme climatic events through evolution of species complementarity and that preserving or restoring biodiversity may increase the potential of evolutionary adaptations to climatic extremes at the community level.

METHODS

Experimental design

To test whether an 8-year selection treatment of recurrent summer droughts would change biodiversity effects and species interactions of grassland plants when facing a novel drought event, we grew ambient- vs. drought-selected plants of 12 species in a

glasshouse. The plants were grown from seeds collected from mixed-species communities under 8-year treatments of yearly summer droughts vs. ambient precipitation in a biodiversity field experiment in Jena, Germany^{23,47}.

The Jena Experiment was established in 2002 using a common seed pool of 60 grassland species, with 80 20 × 20m large plots of species richness levels of 1, 2, 4, 8, 16 and 60 species⁴⁶. Most of the species are perennial and capable of outcrossing. The Jena Drought Experiment^{23,47} was initiated in 2008. Two 1 × 1m subplots were set within each large plot, designated as either drought treatment or ambient control. For the drought treatment, rainout shelters were set up to exclude natural rainfall in mid-summer for six weeks. The ambient control treatment got the same shelter construction but rain water was reapplied to not confound the results with artifacts from the shelter⁶². We collected seeds from drought and control subplots throughout the 2016 growing season (Fig. 1). Seeds were collected from mixtures in order to test in the glasshouse the effects of drought-induced selection on species interactions, and because seeds of only two species were available from monocultures. Although we obtained seeds of 17 species, we only used 12 of them, because the other five species had either few seeds or low germination rates. The 12 plant species represented four functional groups (grass, small herb, tall herb, and legume) (Supplementary Table 1)⁴⁶.

We planted the seedlings in February 2017 in a glasshouse (day temperature range 20–25°C, night temperature range 15–21°C, and humidity range 60–80%) at the University of Zurich, Switzerland. Seeds from drought and ambient subplots of the same large plot in Jena were sown individually, in monocultures or in 2-species mixtures in the glasshouse (Fig. 1). Plants of the three community treatments (individual, monoculture and mixture) were from the same seed families as far as

possible. For those without perfect matches in seed families, plants at least originated from Jena subplots with the same plant functional group composition and selection treatment. In the glasshouse experiment, both monocultures and mixtures contained four plants within a pot. The pots were $11 \times 11 \times 11.5$ cm in size and filled with soil composed of 50% collected from a sugar-beet field, 25% sand and 25% perlite. We randomly assigned the pots into four blocks in the glasshouse. To test the effects of drought-induced selection on plant traits, we sowed individual plants of the 12 species in a fifth block. Within the first two weeks, dead individuals were replaced, thereafter dead individuals were not replaced anymore. In total, we established 958 pots: 257 pots of mixtures, 217 pots of monocultures and 484 pots of individual plants (244 pots of individuals in blocks 1–4, and 240 pots of individuals in block 5). For mixtures, there were 21 species pairs (Supplementary Table 1). Species pairs including *Crepis biennis* or *Lotus corniculatus* as one partner had low numbers of replicates (Supplementary Table 1). However, including or excluding these communities produced qualitatively similar results. Thus, we present the results including these two species in this paper (Figs. 3, 4 and 6).

During a first phase of three month in the glasshouse (Fig. 1), pots were watered regularly (“before drought”). After 14–18 weeks, when most of the species had reached peak aboveground biomass, we harvested them (first harvest). This was followed by a second phase of two weeks without watering (“during drought”). Soil moisture decreased from more than 40% to less than 10% after 10 days since the drought initiation. During a third phase of seven weeks, pots were watered regularly again for recovery until most plants reached a new aboveground biomass peak again (“after drought”). We conducted three harvests: 14–18 weeks (before the drought event), 20 weeks (at the end of the drought event) and 27 weeks (after complete

recovery from the drought event) after establishment of the experiment in the glasshouse. At each harvest, we cut the plants at about 3 cm above soil and dried the harvested plant material at 70°C for 48 hours to obtain the dry biomass. We refer to the three harvests as before, during and after drought, and use the aboveground biomass as a proxy for productivity.

Additive partitioning

We used the additive partitioning approach⁴⁸ to decompose the net biodiversity effect (NE) on aboveground biomass into complementarity effect (CE) and sampling effect (SE), separately for each harvest, selection treatment and block. We did not perform the partitioning for mixtures with zero biomass⁶³. For monocultures with zero biomass, we kept the ones which had alive plants in the previous harvest but excluded the ones which had already lost all of them. For example, when we did the partitioning for the second harvest, we kept the monocultures that had zero biomass in the second harvest but non-zero biomass in the first harvest; we excluded the monocultures that had zero biomass already in the first harvest. This was to assure that communities that died before the drought could not reappear during or after the drought, and communities that had died during the drought could not reappear after the drought.

We used mixed-effects models to assess the influences of drought vs. ambient selection treatments on biodiversity effects separately for each harvest (Fig. 3, Supplementary Table 3). Block and selection treatment were set as fixed-effects terms, while species composition (identity of species pair) and its interaction with selection treatment were set as random-effects terms. This conservative approach was used to allow for generalizations across all possible species compositions, although a more

liberal approach with species composition and its interactions as fixed-effects terms could also been applied (see Schmid *et al.* 2017⁶⁴ for a discussion of defining terms as fixed- vs. random-effects terms, including a justification of preference for treating block as fixed-effects term). We square-root transformed the CEs and SEs with sign reconstruction ($sign(y)\sqrt{y}$) prior to analysis to improve the normality of residuals⁴⁸. The mixed-effects model did not converge in the analysis with CE after the drought event. In this case, we used a general linear model, in which we fitted block, species composition, selection treatment, and species composition by selection treatment interaction in this order. Then we tested the significance of selection treatment using its interaction with species composition as error term. This procedure is an alternative to mixed-effects models that estimate variance components for random-effects terms with maximum likelihood⁶⁴.

We additionally tested the significance of biodiversity effects on productivity separately for each selection treatment and harvest (Supplementary Table 2). We set block and species composition as fixed- and random-effects terms, respectively. The model corresponding to CE for ambient-selected plants during the drought event did not converge so that we fitted it with a general linear model, in which we tested the significance of overall mean (intercept) using species composition as error term. All statistical analyses were conducted in R 3.6.3⁶⁵. The mixed-effects models were conducted with asreml-R package 4.1.0.110⁶⁶.

Finally, we also tested whether effects of drought selection on biodiversity effects in the glasshouse depended on the functional group richness (number of functional groups: 1, 2, 3 or 4) in the Jena field plots, but could not detect any significant trend (Supplementary Table 11). Therefore, we excluded the history of functional group richness from further analyses and presentation in this paper.

Biomass stability to the drought event in the glasshouse

To assess the temporal responses of community aboveground biomass to the drought event, we calculated three indices representing different facets of stability: biomass resistance, recovery and resilience (see van Moorsel *et al.* 2021¹⁹ for an example). We calculated resistance as the biomass ratio during vs. before the drought, recovery as the ratio after vs. during the drought and resilience as the ratio after vs. before the drought (see also Isbell *et al.* 2015²⁰). We log-transformed the indices (plus a half of the minimum positive value to allow taking logs of indices that were originally zero) prior to statistical analyses to improve the normality of residuals. Excluding index values that were originally zero produced qualitatively similar results.

To assess the effects of drought selection on biomass stability, we fitted mixed-effects models with block and selection treatment as fixed-effects terms, and species composition and its interaction with selection treatment as random-effects terms (Supplementary Fig. 2, Supplementary Table 4). We fitted the models separately for mixtures and monocultures. We included the log-transformed biomass at the first harvest as a covariate because biomass stability in response to droughts often depends on plant performance under ambient conditions.

In the same way as net biodiversity effects on productivity were calculated for additive partitioning, we calculated biodiversity effects on biomass stability as the difference between each mixture and its corresponding monocultures. Then, we tested the influence of selection treatment on the biodiversity effects on biomass stability. Block and selection treatment were set as fixed-effects terms; species composition and its interaction with selection treatment were set as random-effects terms (Fig. 4, Supplementary Table 5). The log-transformed biomass at the first harvest was also

included as a covariate ¹⁹. To assess the significance of biodiversity effects on biomass stability for each selection treatment, we fitted another set of simplified models, with block and log-transformed biomass as fixed-effects terms, and species composition as random-effects term (Fig. 4).

Neighbor interactions

We assessed interactions between neighboring plants within pots using the metrics of neighbor interaction intensity with multiplicative symmetry (NInt_M) ⁴⁹:

$$NInt_M = 2 \frac{\Delta P}{P_{-N} + P_{+N} + |\Delta P|} \quad (1),$$

where P_{-N} and P_{+N} are the productivities without (individual plant) and with neighbors (monocultures or mixtures), respectively; $\Delta P = P_{+N} - P_{-N}$. Negative values of NInt_M indicate competition and positive values indicate facilitation. NInt_M is bounded between -1 (competitive exclusion) and 1 (“obligate” facilitation). For monocultures, we first calculated the per-plant biomass as the ratio between total biomass and planting density, and then used the per-plant value to compare with the corresponding individuals (without neighbor) of the same species with the same selection treatment in the same block. Note that under the reciprocal yield law ⁵⁰, an individual grown alone in a pot should be four times larger than an individual grown with three others in a pot, resulting in a NInt_M of -0.75 . For 2-species mixtures, we calculated the per-plant biomass separately for each species and took the average NInt_M of the two species to measure the interaction intensity of the mixture. We set zero biomass for dead plants in the calculation. Again, if mixtures would also follow the reciprocal yield law independent of species identity, then NInt_M = -0.75 would be expected. Values greater than -0.75 indicate some sort of overyielding due to higher density or higher density and higher diversity.

To assess how selection treatment modified interactions between plants, we tested the effects of selection treatments on neighbor interaction intensity separately for monocultures and mixtures. We included block and selection treatment as fixed-effects terms, species composition and its interaction with selection treatment as random-effects terms (Supplementary Fig. 3, Supplementary Table 6).

We calculated the difference between heterospecific interaction in a mixture and conspecific interactions in its two corresponding monocultures. A positive value of this difference indicates a weaker heterospecific than conspecific competition (i.e., niche differentiation) or stronger heterospecific than conspecific facilitation, which may lead to a positive complementarity effect. We tested the effects of selection treatments on interaction difference for each harvest by fitting block and selection treatment as fixed-effects terms, and species composition and its interaction with selection treatment as random-effects terms (Fig. 6, Supplementary Table 8). We also tested the significance of the interaction difference for each selection treatment by fitting block and species composition as fixed- and random-effects term, respectively (Fig. 6, Supplementary Table 7).

Plant traits

To assess whether drought selection would change plant traits, we measured six traits (Supplementary Table 9), which are closely related to plant usages of water or carbon, on plants in pots with one individual from blocks 1–5. We focused on the traits on individual plants without neighbor to evaluate the influence of selection treatment on traits without the impacts of plasticity induced by plant interactions. We measured leaf relative chlorophyll content, leaf area (LA), leaf mass per area (LMA) and leaf osmometric pressure before the drought; leaf stomatal conductance both before and

during the drought; and dry biomass ratio between root and shoot after the drought (in the third harvest). Leaf relative chlorophyll content was measured for three mature, fully expanded leaves per plant by using a SPAD-502 Plus chlorophyll meter from Konica Minolta. LA was obtained by scanning 3–4 mature, fully expanded leaves per plant with a LI-3100C Area Meter from LI-COR. LMA was calculated as the ratio between leaf dry mass (oven dried at 70°C for 48 hours, using the same leaves that for LA) and LA. Leaf osmotic potential at full hydration was considered as an important trait associated with plant tolerance to drought⁶⁷. We measured leaf osmotic potential with freeze-thaw leaf pieces cut from 1–2 mature, fully expanded leaves per plant by using a Wescor vapor pressure osmometer VAPRO (Model 5520) according to the method by Bartlett, et al.⁶⁷. Plants were fully hydrated one day before the leaf sampling for osmotic potential measurement. Leaf stomatal conductance is a measure of exchange rate of carbon dioxide and water vapor through the stomata⁶⁸. It was measured for 3–5 healthy mature leaves per plant by using a SC-1 Leaf Porometer from Decagon Devices. For grass species, 3 blades were placed adjacent to each other in order to have a large enough area for the measurement of stomatal conductance. For stomatal conductance during the drought event, we measured the individual plants from block 5 only due to limited time during the drought phase. We harvested aboveground and belowground plant biomass separately for alive individual plants at the end of the experiment (after the complete recovery from the drought). The oven-dried (70°C for 48 hours) aboveground and belowground biomass was used to calculate the biomass ratio between root and shoot. We took the average value of each trait of each plant for statistical analyses.

We used linear mixed-effects models to assess the influence (generalized across species) of selection treatments on trait values (red lines in Supplementary Figs. 4–6).

Block and selection treatment were set as fixed-effects terms; species and its interaction with selection treatment were set as random-effects terms. Alternatively, we set species, selection treatment and their interaction as fixed-effects terms to assess whether species responded differently to the selection treatments (Supplementary Table 9). LMA, LA, leaf osmotic potential, leaf stomatal conductance and root-shoot biomass ratio were log-transformed to improve normality of residuals.

We also measured leaf relative chlorophyll content, LA and LMA in mixtures before the drought event (Supplementary Table 10) to evaluate the influence of selection treatments on trait dissimilarity between interacting species within communities. We calculated the absolute trait distance between two species in each mixture both separately for each trait and jointly with the three traits. For multi-trait-based dissimilarity, we calculated the Euclidean trait distance in standardized three-dimensional trait space.

We used linear mixed-effects models to assess the effects of selection treatments on trait dissimilarity in mixtures (Supplementary Table 10). Block and selection treatment were set as fixed-effects terms; species composition and its interaction with selection treatment were set as random-effects terms. The model for LA dissimilarity did not converge so that we fit it with a general linear model, in which we tested the significance of selection treatment using its interaction with species composition as error term. For the models with LA, LMA and the joint three traits as dependent variables, we removed one pot (B1P674) because the LA value of *Alopecurus pratensis* in this pot was extremely small (about 1/3 of the second minimum value of the same species in mixtures). However, including or excluding this pot produced qualitatively similar results.

Author Contribution: M.S.-L and A.W. conceived the Jena Drought Experiment, Y.C., B.S., A.V. and C.W. conceived the glasshouse experiment to test selection effects. Y.C., M.I.G., C.W. and T.X. carried out the glasshouse experiment. Y.C., B.S. and A.V. developed the analytical procedure, and Y.C. did the statistical analyses. All authors discussed the results and helped write the paper.

Data Availability: The data supporting the findings of this study are available at the Figshare digital repository: <https://figshare.com/s/27107d80d374be6fe6c4>.

Code Availability: The code supporting the results are available at the Figshare digital repository: <https://figshare.com/s/8fdfb27d224e47f1a8e6>.

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FIGURES

Figure 1 | Experimental design. Seeds collected from different selection treatments (8-years treatments of recurrent summer droughts vs. ambient control) in the Jena Experiment, Germany, were sown in 2-species mixtures, in monocultures or individually in pots in a glasshouse at the University of Zurich, Switzerland. During a first phase of three months, pots were watered regularly (ambient conditions, “before drought”). This was followed by a second phase of two weeks without watering (drought conditions, “during drought”) and a third phase of seven weeks with regular watering (ambient conditions for recovery, “after drought”). Plants were harvested after 14–18 weeks (before the drought), 20 weeks (after the drought) and 27 weeks (after recovery from the drought) as represented by scissors.

Figure 2 | Effects of biodiversity on productivity among different 2-species mixtures for each selection treatment (ambient- vs. drought-selected plants) and harvest (before [a–f], during [g–l] and after [m–r] the drought event in the glasshouse). Biodiversity effects were calculated as net effect (first row), complementarity effect (second row) and sampling effect (third row). Lines connecting nodes (species) indicate species pairs within mixtures in the glasshouse. Blue and red lines indicate positive and negative average biodiversity effects, respectively, with the solid lines indicating significant effects based on Student's t test ($\alpha = 0.05$; mixtures of each selection treatment with less than three replicates at a harvest were not tested for significance and hence not shown in this figure). Node sizes are proportional to the corresponding monoculture biomass in each panel. Node colors indicate different functional groups (green=legume, grey=grass, orange=short herb, pink=tall herb). Full species names are shown in Supplementary Table 1.

Figure 3 | Difference in biodiversity effects on productivity between selection treatments (ambient- vs. drought-selected plants) across time (before [first column], during [second column] and after [third column] the drought event in the glasshouse). Biodiversity effects were calculated as net effect (a–c), complementarity effect (d–f) and sampling effect (g–i). The solid red lines indicate significant differences between the two selection treatments (see Supplementary Table 3). Red points and error bars show means $\pm$ standard error of 2-species mixtures composed of the corresponding selection treatment. The filled red points show significant differences from zero (horizontal dashed lines, see Supplementary Table 2), i.e., positive or negative average biodiversity effects. Grey points represent means for species pairs (standard errors for species pairs were not shown). Grey lines connect the same species pair between the two selection treatments.

Figure 4 | Difference in biodiversity effects on biomass stability in response to the drought event in the glasshouse between selection treatments (ambient and drought-selected plants). The solid red lines indicate significant differences between the two selection treatments (see Supplementary Table 5). Biomass stability was calculated as resistance (a), recovery (b) and resilience (c). Biodiversity effects were calculated as the differences in stability indices between mixtures and monocultures. Red points and error bars show the means $\pm$ standard error of 2-species mixtures composed of the corresponding selection treatment. Grey points represent means for species pairs (standard errors for species pairs were not shown). Grey lines connect the same species pair between the two selection treatments.

Figure 5 | Difference between heterospecific and conspecific interactions for species pairs of different selection treatments (ambient- vs. drought-selected plants) at each harvest (before [a–b], during [c–d] and after [e–f] the drought event in the glasshouse). Lines connecting nodes (species) indicate species pairs within mixtures in the glasshouse. Blue lines indicate weaker heterospecific than conspecific competition, or stronger heterospecific than conspecific facilitation, while red lines represent the opposite situations. The solid lines indicate significant difference from zero based on Student's t test ($\alpha = 0.05$; mixtures of each selection treatment with less than three replicates at a harvest were not tested for significance and hence not shown in this figure). Node sizes are proportional to the corresponding monoculture biomass in each panel. Node colors indicate different functional groups (green=legume, grey=grass, orange=short herb, pink=tall herb). Full species names are shown in Supplementary Table 1.

Figure 6 | Effects of selection treatment (ambient- vs. drought-selected plants) on the difference between heterospecific and conspecific interactions before (a), during (b) and after (c) the drought event in the glasshouse. The solid red line indicates a significant difference between the two selection treatments (see Supplementary Table 8). Red points and error bars show means $\pm$ standard error. The filled red point shows a significant difference from zero (horizontal dashed lines; see Supplementary Table 7), i.e., weaker heterospecific than conspecific competition. Grey points represent means for species pairs (standard errors for species pairs were not shown). Grey lines connect the same species pair between the two selection treatments.

Supplementary Files

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