

Review

Crop Diversity Experiment: towards a mechanistic understanding of the benefits of species diversity in annual crop systems

Christian Schöb^{1,*}, Nadine Engbersen², Jesús López-Angulo³, Anja Schmutz³ and Laura Stefan⁴

¹Área de Biodiversidad y Conservación, Universidad Rey Juan Carlos, 28933 Móstoles, Madrid, Spain, ²Agriculture and Forestry Division, Canton Lucerne, 6210 Sursee, Switzerland, ³Institute of Agricultural Sciences, ETH Zurich, 8092 Zurich, Switzerland, ⁴Cultivation Techniques and Varieties for Arable Crops, Agroscope, 1260 Nyon, Switzerland

*Corresponding author. E-mail: Christian.Schob@urjc.es

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Abstract

Inspired by grassland biodiversity experiments studying the impact of plant diversity on primary productivity, the Crop Diversity Experiment setup in 2018 aimed at testing whether these biodiversity benefits also hold for annual crop systems and whether crop mixtures also achieved transgressive overyielding, i.e. yield in mixture that was higher than the most productive monoculture. The first 3 years of the experiment demonstrated that crop mixtures do not only increase yield compared with an average monoculture but often also compared with the highest yielding monoculture. The crop diversity effects were stronger under more stressful environmental conditions and were often achieved in mixtures with legume crops. However, we observed transgressive overyielding also under favorable conditions and in mixtures without legumes. With our investigation of the underlying mechanisms of the yield benefits we found both direct complementarities between crop species and indirect effects via other organisms. The former included chemical, spatial and temporal complementarity in N uptake, complementary root distribution leading to complementary water uptake, as well as spatial and temporal complementarity in light use. Among the indirect mechanisms we identified complementary suppression of weeds and more abundant plant growth-promoting microbes in crop mixtures, apart from complementarity in pest and disease suppression not yet studied in the Crop Diversity Experiment but demonstrated elsewhere. In consequence, the Crop Diversity Experiment supports not only the assumption that the ecological processes identified in biodiversity experiments also hold in crop systems, but that diversification of arable crop systems provides a valuable tool to sustainably produce food.

Keywords intercropping, biodiversity, yield, competition, facilitation, complementarity effects, mixture

作物多样性实验：理解一年生作物系统物种多样性效应的机理

摘要：受到草地生物多样性实验研究植物多样性对初级生产力影响的启发，2018年建立的“作物多样性实验”旨在测试自然生态系统生物多样性的效应是否也适用于一年生作物系统，以及作物混合种植(简称作物混作)是否也能实现超产，即作物混作的产量超过作物单作的最高产量。实验的前3年结果表明，作物混作不仅增加了产量，而且通常也比最高产的作物单作产量高。作物多样性效应在环境胁迫下更显著，且

通常是在与豆科作物混作时实现超产。然而，我们也观察到在有利条件下和没有豆科植物的混作中，也有超产现象。对产量效应的潜在机制研究发现，作物物种之间存在直接的互补关系和通过其他生物的间接效应。前者包括氮吸收中的化学、空间和时间互补性，水分吸收的根分布互补性，以及光利用的空间和时间互补性。在间接机制中，除了“作物多样性实验”中未研究但在其他研究得到证明的对害虫和疾病的互补抑制之外，我们还证明作物混作中对杂草的互补抑制和植物生长促进微生物的丰度更高。因此，“作物多样性实验”不仅支持了生物多样性实验所证明的生态过程，也支持了作物系统中的生物多样性的生态系统功能假设，而且作物物种多样化的作物系统为可持续生产食物提供了有价值工具。

关键词：间作，生物多样性，产量，竞争，促进，互补效应，混合种植

INTRODUCTION

Biodiversity experiments in grasslands such as the Jena Experiment in Germany (Weisser *et al.* 2017), the BioDIV experiment in Cedar Creek, Minnesota, USA (Tilman *et al.* 2001) or the BIODEPTH experiment across Europe (Hector *et al.* 1999) have investigated the effect of plant diversity on primary productivity through a combination of changes in species richness and species composition. The outcome of all these experiments was a positive relationship between plant diversity and productivity. This outcome has further been supported by observations in real-world semi-natural grasslands beyond experimental plots through the Biodiversity Exploratories in Germany (Jochum *et al.* 2020) and in other ecosystems such as intensively managed grasslands (Finn *et al.* 2013) or forests (Tang *et al.* 2022). The mechanisms underlying these diversity effects on productivity have initially been partitioned into sampling and complementarity effects (Loreau and Hector 2001). Sampling effects represent those effects where the benefit of one species comes at the expense of another species, such as the dominance of a species with particular traits in a particular environment. Complementarity effects represent those effects where the benefits of one species do not come at the expense of other species in the community (Fox 2005). Sampling effects often explain differences in the sizes of biodiversity effects between specific species compositions but lack a general trend with increasing species richness or over space and time (Loreau and Hector 2001). In contrast, various studies have shown that complementarity effects explain differences in the size of biodiversity effects with increasing species richness, over space (Loreau and Hector 2001) and time (Reich *et al.* 2012; Zuppinger-Dingley *et al.* 2014). Therefore, given their omnipresent nature and their ability to achieve transgressive overyielding, i.e. where a mixture community yields more than the most

productive monoculture, complementarity effects deserve particular attention and are of great interest for application in agriculture and forestry.

For decades, ecologists have investigated processes underlying complementarity effects, such as niche differentiation or facilitation. Niche differentiation allows species to use resources in different chemical forms, at different times or in different spaces, thereby complementing each other in the uptake of resources and competing less. Evidence of specific niche differentiation processes directly linked to biodiversity effects is not as abundant as one might assume, not least because of both the difficulties in providing evidence for niche partitioning (e.g. Trinder *et al.* 2012) and the likelihood that biodiversity effects are the result of multiple complementarities rather than the complementarity in the uptake of a single resource (e.g. Jesch *et al.* 2018; Mommer *et al.* 2010). Furthermore, facilitative processes leading to positive biodiversity effects have generally been overlooked (Wright *et al.* 2017), with little evidence for their occurrence (but see Schöb *et al.* 2018). Therefore, despite the significant influence of biodiversity on ecosystem functioning and its relevance for human society (e.g. Brooker *et al.* 2023), our understanding of the ecological processes underlying this positive relationship between biodiversity and ecosystem functioning is still relatively poor. This explains the heated debates about the value and use of biodiversity effects in agriculture and forestry.

Despite the limited mechanistic understanding, the insight of ecological research over the past 40 years that plant diversity increases primary productivity is of great importance for society when considering ecosystems where primary productivity is an economic good, such as in agriculture and forestry. There are, however, concerns about the applicability of this knowledge in intensively used systems (Duru

et al. 2015). At the same time, there is a genuine desire to apply this knowledge in agriculture and to investigate whether this phenomenon holds for artificial, human-made systems such as arable crops or forest plantations.

Arable crop systems are plant communities with some fundamental differences to a perennial grassland system used in the long-term biodiversity experiments. Arable crops are almost exclusively annual plants with a fast generation time of usually around 100–150 days. Therefore, their growth is limited to the benign season of the year when crops are planted, grown and harvested. Furthermore, arable crop systems follow a highly controlled planting arrangement, with seeds sown in defined, regular distances within and between rows. They also traditionally hold very limited plant diversity, with the current standard being monocultures of a single species with a single genotype. Therefore, diversification of such an arable crop system tends to be at a very modest scale, e.g. including several genotypes of the same species (Reiss and Drinkwater 2018; Schöb *et al.* 2015) or very few, in general two, species (Brooker *et al.* 2015; Li *et al.* 2020). Finally, arable crops have undergone their domestication, with significant consequences on the plant phenotype (Milla 2023) and their functioning in a community (Chacón-Labela *et al.* 2019).

The Crop Diversity Experiment setup in 2018 aims to investigate the effects of plant diversity on yield in arable crops and identifying their underlying mechanisms. The experiment is largely inspired by the previously mentioned long-term grassland biodiversity experiments with the aim to assess the validity of this ecological knowhow in an agricultural setting. Despite the significant differences between arable crop systems and a semi-natural grassland, the null hypothesis for the Crop Diversity Experiment was that the underlying ecological processes leading to biodiversity effects in grasslands, such as niche partitioning and facilitation, also occur in crop fields. This is based on the assumption that they simply occur due to the coexistence of individuals interacting with each other and their environment. However, we expected differences in the frequency and intensity of these effects, both because many of the ecological processes underlying biodiversity effects depend on the environmental context (Brooker 2006), i.e. a context that is highly manipulated in arable systems, and because crops present the unique conditions described above.

THE CROP DIVERSITY EXPERIMENT

Objectives

To date, the main objective of the work in the Crop Diversity Experiment has been to quantify the effects of crop diversity on seed yield, with additional objectives of assessing the context dependence of these effects and the mechanisms underlying these effects, with a particular focus on complementarity effects, i.e. niche differentiation and facilitation processes. For complementarity effects, we considered both direct effects, such as complementary resource uptake patterns, and indirect effects through other organisms, such as weeds or the microbiome.

Study sites

This review presents numerous findings of the Crop Diversity Experiment initially conducted over 3 years (2018–2020) in Spain and Switzerland and since then with additional drought treatments (2021 to 2023) in Spain (not reported here). The study site in Spain is located at the experimental research station Aprisco, Torrejón el Rubio (Cáceres, Extremadura). The study site is characterized by a Mediterranean climate with wet and cold winters and hot and dry summers. The average precipitation during the period 2018–2020 was 393 mm per year and 181 mm during the growing season between February and June. Mean annual temperature during the same period was 17.0 and 15.7 °C during the growing season. The study site in Switzerland is located at the Irchel Campus of the University of Zurich, Zurich, except for the water isotope experiment, which was located in a farmer's field in Regensdorf near Zurich. The study site is characterized by a temperate climate with dry and cold winters and humid and warm summers. The average precipitation during the period 2018–2020 was 931.3 mm per year and 318.8 mm during the growing season between April and July. Mean annual temperature during the same period was 11.1 and 16.1 °C during the growing season. All climatic data from the period 2018 to 2020 were downloaded using the function `get_daily_climate()` from the `easyclimate` R package (Cruz-Alonso *et al.* 2023; Moreno and Hasenauer 2016; Rammer *et al.* 2022). The experimental gardens were irrigated during the growing season with the aim of maintaining the above-mentioned differences in precipitation between the two sites while assuring survival of the crops during drought periods. The automated irrigation system (PlantCare Ltd, Switzerland)

therefore maintained soil moisture between 17% and 25% of field capacity in Spain, and between 50% and 90% of field capacity in Switzerland.

Experimental setup

The experiments were set up in common gardens composed of raised beds of 1 m width and 7 (in Switzerland) and 10 m (in Spain) length. Each bed was composed of 0.5 m × 0.5 m plots separated by metal frames of 0.4 m depth. The beds were open at the bottom and placed on top of the naturally occurring soil at the field site. The raised beds were filled with locally available topsoil that represents a standard agricultural soil in the respective region. The soil in Spain was a sandy soil composed of 78% sand, 20% silt and 2% clay. It contained 0.05% nitrogen, 0.5% carbon and 253 mg total P/kg. In Switzerland, the soil was a sandy loam consisting of 45% sand, 45% silt and 10% clay. It contained 0.19% nitrogen, 3.39% carbon and 332 mg total P/kg. Spanish and Swiss soils had a mean pH of 6.30 and 7.25, respectively.

Crop species

The Crop Diversity Experiment was started in 2018 with eight annual crop species out of four different phylo-functional groups: *Triticum aestivum* L. (wheat, C₃ grass) and *Avena sativa* L. (oat, C₃ grass), *Lens culinaris* MEDIK. (lentil, legume) and *Lupinus angustifolius* L. (lupin, legume), *Linum usitatissimum* L. (linseed, herb [superrosids]) and *Camelina sativa* (L.) CRANTZ (camelina, herb [superrosids]), *Chenopodium quinoa* WILLD. (quinoa, herb [superasterids]) and *Coriandrum sativum* L. (coriander, herb [superasterids]). From 2019 onwards, quinoa was no longer used due to substantially longer maturation times, while in 2020, lupin was no longer used in Switzerland due to very poor performance in the slightly alkaline soil leading to insufficient seed production. Crop species were selected based on climatic requirements, frost resistance, maturation time and plant size. Specifically, the selected crop species were required to grow in Switzerland and Spain and tolerate moderate frost, had to mature between 90 and 120 days after sowing and be sufficiently small as to fit at least 40 individuals in 0.25 m² plots. Sowing density differed among the phylo-functional groups and was based on current cultivation practices: 160 seeds/m² for legumes, 240 seeds/m² for superasterids, 400 seeds/m² for cereals and 592 seeds/m² for superrosids. Sowing was done by hand every year in early February in Spain and in early April in Switzerland. Harvest of the mature

seeds was generally in June in Spain and between mid-July and mid-August in Switzerland.

Treatments

a) Planted crop diversity treatment

Each species was planted as a single plant without neighbour, in monoculture, 2- and 4-species mixtures (Chen *et al.* 2021). We initially planted 24 different 2-species mixtures, i.e. every possible combination of two species from different phylo-functional groups, and 12 different 4-species mixtures, i.e. every possible combination with all four phylo-functional groups present in the mixture. Specific combinations were removed due to the removal of species (i.e. quinoa from 2019 onwards) or lack of seeds (lupin in Switzerland in 2020).

b) Soil fertility treatment

Between 2018 and 2020, half of the beds were fertilized with mineral fertilizer containing 120 kg/ha N, 205 kg/ha P and 120 kg/ha K, i.e. a standard fertilizer application for the conditions in Spain. Fertilizer was applied just before sowing (50 kg/ha N), at tillering of wheat (50 kg/ha N) and at flowering of wheat (20 kg/ha N) (Engbersen *et al.* 2022b). The fertilizer treatment was randomly allocated to individual beds of the common garden in 2018 and was maintained in the same beds until 2020.

c) Local adaptation treatment

In 2018, we had grown both Swiss and Spanish cultivars in both sites to test for the adaptation of local cultivars to the prevailing climatic and soil conditions (Stefan *et al.* 2021a). From 2019 onwards, due to the relatively poor performance of some foreign cultivars only the locally adapted cultivars of each site were used, i.e. Spanish cultivars in Spain and Swiss cultivars in Switzerland.

d) Planting arrangement treatment

In 2019, the three species oat, lupin and camelina were used in a separate experiment where we manipulated the number and distance of neighbours with the idea to simulate densities and distances for each monoculture and mixture that optimize community-level yield (Stefan *et al.* 2022a). For this purpose, the number of neighbours at a distance of 8 cm from a single focal plant was varied between 0, 1, 2, 4 and 8 individuals, while the distance of 8 neighbouring plants around a single focal plant was varied between 5, 8, 12 and 20 cm.

e) Repetitive harvest treatment

In 2019, the three species oat, lupin and camelina were used in a separate experiment where monoculture and 2-species mixture plots were harvested every week beginning from the point at which all species had germinated and ending once all species had mature seeds (= 18 weeks; Engbersen *et al.* 2021). Each week, species-level biomass, N and P content and isotopic composition of N were determined.

f) Natural abundance of water isotopes

In a separate experiment conducted in a farmer's field in 2019, we measured the natural abundance of water isotopes to quantify niche differentiation in water uptake between crops in mixtures (Schmutz and Schöb 2023). This experiment was conducted with six crop species, including spring barley (*Hordeum vulgare* var. Atrika), spring wheat (*T. aestivum* var. Fiorina), faba bean (*Vicia faba* var. Fanfare), pea (*Pisum sativum* var. Astronaute), linseed (*L. usitatissimum* var. Marquise) and rapeseed (*Brassica napus* subsp. *napus* var. Campino). The naturally occurring gradient in the isotopic composition of H and O in water was used to quantify the relative proportion of water taken up by crop plants from different soil depths.

g) Coexistence history treatment

In 2018, we sowed seeds that were either commercially available or were obtained from germplasm collections, but from 2019 onwards we used the seeds produced in the experiment the previous year, with the objective to test for local adaptation of plants to their specific growing conditions (Stefan *et al.* 2022b). Therefore, seeds with a single coexistence history were produced as single plants and were grown once as a single plant (home), once as a monoculture (away) and once in all combinations of mixtures (away). Seeds with a monoculture coexistence history were produced in monoculture and were grown once as a single plant (away), once as a monoculture (home) and once in all combinations of mixtures (away). Seeds with a mixture coexistence history were produced in mixtures, where seeds of each mixture combination were once grown in the same mixture as their seed origin (home), while a seed pool of all combinations of the 4-species mixtures was used to grow a single plant (away) and a monoculture (away).

OUTCOMES AFTER 3 YEARS

Community-level yield

The Crop Diversity Experiment has demonstrated consistent positive effects of crop diversity on yield and vegetative biomass (López-Angulo *et al.* 2023). Based on the average production per species composition between 2018 and 2020 and averaged over country and fertilizer treatment, we found significant yield increases with increasing crop diversity from 2.02 ± 0.26 t/ha in monocultures to 2.56 ± 0.19 t/ha in 2-species mixtures and 3.00 ± 0.26 t/ha in 4-species mixtures (Supplementary Table S1), corresponding to a 27% and 49% yield increase in 2- and 4-species mixtures compared with monocultures, respectively. We found transgressive overyielding for 11 out of the 18 2-species mixtures and for six out of the eight 4-species mixtures (Table 1). Transgressive overyielding was found for all 2-species mixtures with legumes, except the combinations lupin/linseed and lentil/coriander, and for three 2-species mixtures without legumes, namely wheat/coriander, camelina/coriander and linseed/coriander. The two 4-species mixtures that did not show transgressive overyielding were those of oat/lentil/coriander either with camelina or linseed.

Yields were context dependent and significantly higher in Switzerland than Spain but with similar fertilizer effects between countries (CH + F: 3.72 ± 0.33 t/ha; CH – F: 3.08 ± 0.25 t/ha; ES + F: 1.84 ± 0.11 t/ha; ES – F: 1.57 ± 0.13 t/ha), resulting in yield increases with fertilizer of 17% in Spain and 21% in Switzerland (Fig. 1). Notably, the yield increases achieved by a 2-species mixture compared with a monoculture were slightly higher than those with mineral fertilizer application, while yield increases in 4-species mixtures compared with monocultures were substantially higher than the yield increases achieved with fertilizer addition. Importantly though, fertilizer effects remained in monocultures and mixtures, suggesting additive yield benefits of fertilizer addition and intercropping.

The land equivalent ratio (LER) significantly increased with increasing diversity, from 1.18 ± 0.03 in 2-species mixtures to 1.29 ± 0.04 in 4-species mixtures, and was higher under unfertilized (1.22 ± 0.04) than fertilized conditions (1.12 ± 0.03) (Supplementary Table S2). On average, over all species combinations and years, the LER for 2-species mixtures in Spain was 1.31 ± 0.08 and 1.15 ± 0.05 , and in Switzerland 1.15 ± 0.07 and 1.12 ± 0.07 under

Table 1: Plot-level yields (t/ha) averaged over all treatment levels

| (a) Monocultures | | | | | |
|--|--------------------|------------------|--------------------|--------------------|--------------------|
| | Mean ± SE | | | | |
| Av | 3.44 ± 1.47 | | | | |
| Ca | 1.93 ± 0.35 | | | | |
| Co | 2.13 ± 0.51 | | | | |
| Le | 1.44 ± 0.24 | | | | |
| Li | 1.24 ± 0.27 | | | | |
| Lu | 1.79 ± 0.65 | | | | |
| Tr | 2.17 ± 0.47 | | | | |
| (b) 2-Species mixtures (bold values represent transgressive overyielding) | | | | | |
| | Ca | Li | Le | Lu | Co |
| | Mean ± SE | Mean ± SE | Mean ± SE | Mean ± SE | Mean ± SE |
| Av | 3.20 ± 0.96 | 2.95 ± 1.28 | 3.65 ± 1.43 | 5.05 ± 1.50 | 3.35 ± 1.50 |
| Tr | 2.04 ± 0.41 | 1.84 ± 0.35 | 2.17 ± 0.38 | 2.97 ± 0.23 | 2.31 ± 0.34 |
| Ca | | | 2.18 ± 0.29 | 2.03 ± 0.28 | 2.19 ± 0.33 |
| Li | | | 1.50 ± 0.26 | 1.75 ± 0.46 | 2.21 ± 0.38 |
| Le | | | | | 1.95 ± 0.56 |
| Lu | | | | | 2.78 ± 0.30 |
| (c) 4-Species mixtures (bold values represent transgressive overyielding) | | | | | |
| | Mean ± SE | | | | |
| AvCaCoLe | 2.86 ± 0.83 | | | | |
| AvCaCoLu | 3.96 ± 0.98 | | | | |
| AvCoLeLi | 3.05 ± 1.00 | | | | |
| AvCoLiLu | 3.90 ± 1.20 | | | | |
| CaCoLeTr | 2.34 ± 0.34 | | | | |
| CaCoLuTr | 3.02 ± 0.20 | | | | |
| CoLeLiTr | 2.22 ± 0.52 | | | | |
| CoLiLuTr | 2.68 ± 0.37 | | | | |

Species abbreviations: Av = Oat [*Avena sativa*], Tr = Wheat [*Triticum aestivum*], Le = Lentil [*Lens culinaris*], Lu = Lupin [*Lupinus angustifolius*], Ca = Camelina [*Camelina sativa*], Li = Linseed [*Linum usitatissimum*], Co = Coriander [*Coriandrum sativum*].

unfertilized and fertilized conditions, respectively (Fig. 2). The LER for 4-species mixtures in Spain was 1.39 ± 0.09 and 1.18 ± 0.05 , and in Switzerland 1.35 ± 0.08 and 1.22 ± 0.07 , under unfertilized and fertilized conditions, respectively. In 2-species mixtures, highest average LERs without fertilizer

were achieved in Spain with mixtures including lentil (1.69) and in Switzerland with mixtures including lentil (1.35) or linseed (1.43), while lowest LERs without fertilizer were observed in Spain with mixtures including linseed (1.07) and in Switzerland with mixtures including camelina (0.95). Fertilization

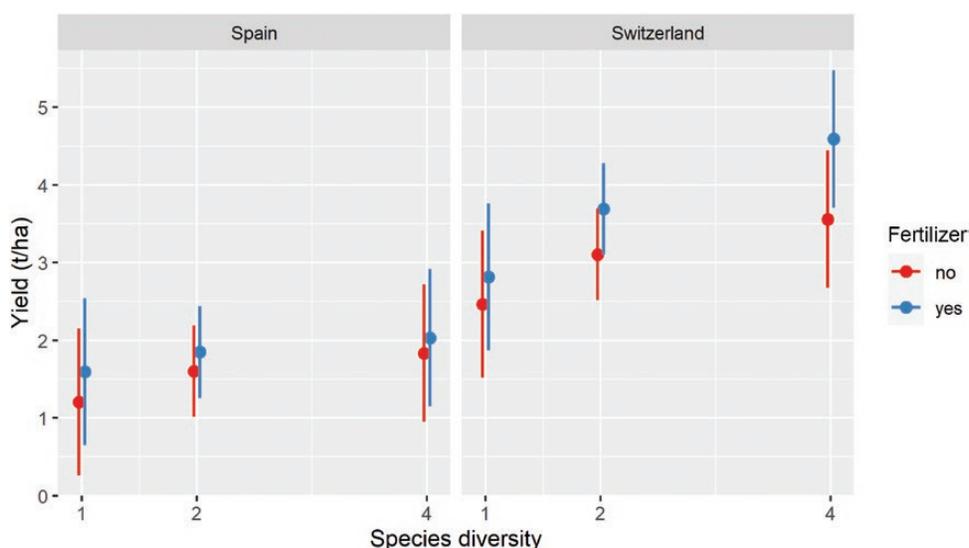


Figure 1: Average seed yield ($\pm 95\%$ CI) of the Crop Diversity Experiment between 2018 and 2020 per country, fertilizer treatment and species diversity level.

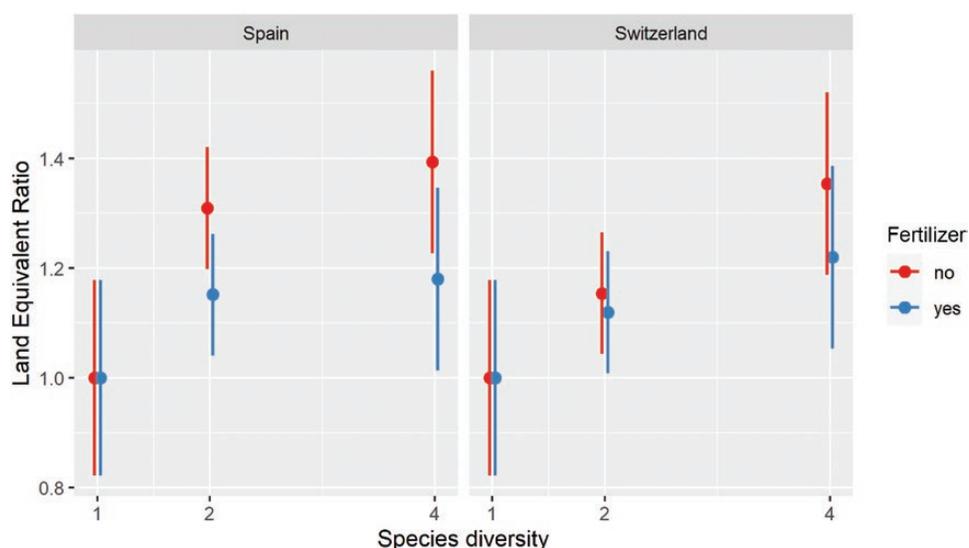


Figure 2: Average LER ($\pm 95\%$ CI) of the Crop Diversity Experiment between 2018 and 2020 per country, fertilizer treatment and species diversity level.

reduced the LER more for mixtures with oat or lentil than for mixtures with wheat and lupin, both in Spain and Switzerland (Table 2). Average positive effects of fertilization on the LER were only observed for mixtures with linseed in Spain, and for mixtures with camelina and coriander in Switzerland. The highest LERs were observed in Spain for oat/lentil (1.81), camelina/lentil (1.79) and wheat/lupin (1.53) without fertilizer, and for lentil/coriander (1.36), wheat/coriander (1.33) and wheat/lupin (1.29) with fertilizer. In Switzerland, highest LERs were observed for lupin/linseed (1.85), lentil/linseed (1.56) and wheat/lentil (1.52) without fertilizer, and for linseed/

coriander (2.04), linseed/wheat (1.37) and linseed/lentil (1.35) with fertilizer.

Species-level yield

Based on the average production per species in each species composition, we assessed the yields of individual species in monocultures, while their variation due to country and fertilizer treatment in mixtures was assessed by calculating the partial land equivalent ratio (pLER) as the average yield of the species in each mixture divided by the yield in the monoculture (Fig. 3). pLER is 1 in monocultures and expected to be 0.5 in 2-species mixtures and

Table 2: LERs averaged for each species combination, country and fertilizer treatment

| (a) 2-Species mixtures | | | | | | |
|-------------------------------|----------|---------------|--------------|-----------------|----------------|------------------|
| | | -F | | | | |
| | | Lentil | Lupin | Camelina | Linseed | Coriander |
| Spain | Oat | 1.81 | 1.42 | 1.23 | 1.01 | 0.88 |
| | Wheat | 1.48 | 1.53 | 0.97 | 0.88 | 1.24 |
| | Lentil | | | 1.79 | 1.37 | 2.00 |
| | Lupin | | | 0.92 | 0.97 | 1.50 |
| | Camelina | | | | | 1.48 |
| | Linseed | | | | | 1.10 |
| | | | +F | | | |
| | | Lentil | Lupin | Camelina | Linseed | Coriander |
| | Oat | 1.12 | 1.28 | 1.25 | 0.70 | 0.97 |
| | Wheat | 1.12 | 1.29 | 0.94 | 1.05 | 1.33 |
| | Lentil | | | 1.10 | 1.66 | 1.36 |
| | Lupin | | | 1.15 | 1.20 | 1.21 |
| | Camelina | | | | | 1.20 |
| | Linseed | | | | | 0.80 |

| | | -F | | | | |
|-------------|----------|---------------|--------------|-----------------|----------------|------------------|
| | | Lentil | Lupin | Camelina | Linseed | Coriander |
| Switzerland | Oat | 1.49 | 0.99 | 1.07 | 1.23 | 0.96 |
| | Wheat | 1.52 | 0.92 | 1.02 | 1.16 | 0.94 |
| | Lentil | | | 1.07 | 1.56 | 1.11 |
| | Lupin | | | 0.72 | 1.85 | 0.97 |
| | Camelina | | | | | 0.89 |
| | Linseed | | | | | 1.33 |
| | | | +F | | | |
| | | Lentil | Lupin | Camelina | Linseed | Coriander |
| | Oat | 1.11 | 0.88 | 1.09 | 1.03 | 1.00 |
| | Wheat | 1.06 | 0.74 | 1.22 | 1.37 | 0.85 |
| | Lentil | | | 1.24 | 1.35 | 1.02 |
| | Lupin | | | 1.01 | 1.08 | 0.96 |
| | Camelina | | | | | 1.11 |
| | Linseed | | | | | 2.05 |

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Table 2. Continued**(b) 4-Species mixtures**

| | Spain | |
|----------|-------|------|
| | –F | +F |
| AvCaCoLe | 1.63 | 1.24 |
| AvCaCoLu | 1.39 | 1.23 |
| AvCoLeLi | 1.64 | 1.30 |
| AvCoLiLu | 0.92 | 1.15 |
| CaCoLeTr | 1.57 | 1.09 |
| CaCoLuTr | 1.30 | 1.40 |
| CoLeLiTr | 1.45 | 1.07 |
| CoLiLuTr | 1.24 | 0.96 |

| | Switzerland | |
|----------|-------------|------|
| | –F | +F |
| AvCaCoLe | 1.36 | 1.20 |
| AvCaCoLu | 1.05 | 0.88 |
| AvCoLeLi | 1.32 | 1.39 |
| AvCoLiLu | 1.02 | 1.34 |
| CaCoLeTr | 1.53 | 1.03 |
| CaCoLuTr | 1.41 | 1.10 |
| CoLeLiTr | 1.50 | 1.48 |
| CoLiLuTr | 1.63 | 1.34 |

Species abbreviations as in [Table 1](#). Without fertilizer (-F) and with fertilizer (+F).

0.25 in 4-species mixtures if all components of the mixture do equally well in mixture as they do in monoculture. For the statistical analyses reported here we used the difference of the observed pLER from the expected pLER, which can be positive if the species yields more in a mixture than expected from its monoculture, or negative if it yields less than expected ([Supplementary Table S3](#)).

Wheat

Wheat yields in monoculture in Spain were 1.21 t/ha without fertilizer and 1.60 t/ha with fertilizer, while the corresponding yields in Switzerland were 2.58 and 3.28 t/ha, respectively. The pLER in mixtures was 0.16 ± 0.02 higher than expected, and particularly higher in Spain when grown without fertilizer (0.27 ± 0.05) than with fertilizer (0.10 ± 0.04), while pLERs in Switzerland were similar without (0.11 ± 0.04) and with fertilizer (0.14 ± 0.05).

Oat

Oat yields in monoculture in Spain were 0.76 t/ha without fertilizer and 1.09 t/ha with fertilizer, while the corresponding yields in Switzerland were 5.47 and 6.45 t/ha, respectively. The pLER in mixtures was 0.23 ± 0.04 higher than expected, and particularly higher in Switzerland (0.38 ± 0.05) than in Spain (0.08 ± 0.03). There was no significant effect of the fertilizer treatment on pLER.

Lentil

Lentil yields in monoculture in Spain were 0.91 t/ha without fertilizer and 1.18 t/ha with fertilizer, while the corresponding yields in Switzerland were 1.95 and 1.74 t/ha, respectively. The pLER in mixtures was higher than expected (0.13 ± 0.03), and significantly higher in Spain (0.20 ± 0.05) than in Switzerland (0.06 ± 0.02), and significantly higher without fertilizer (0.22 ± 0.04) than with fertilizer (0.04 ± 0.03).

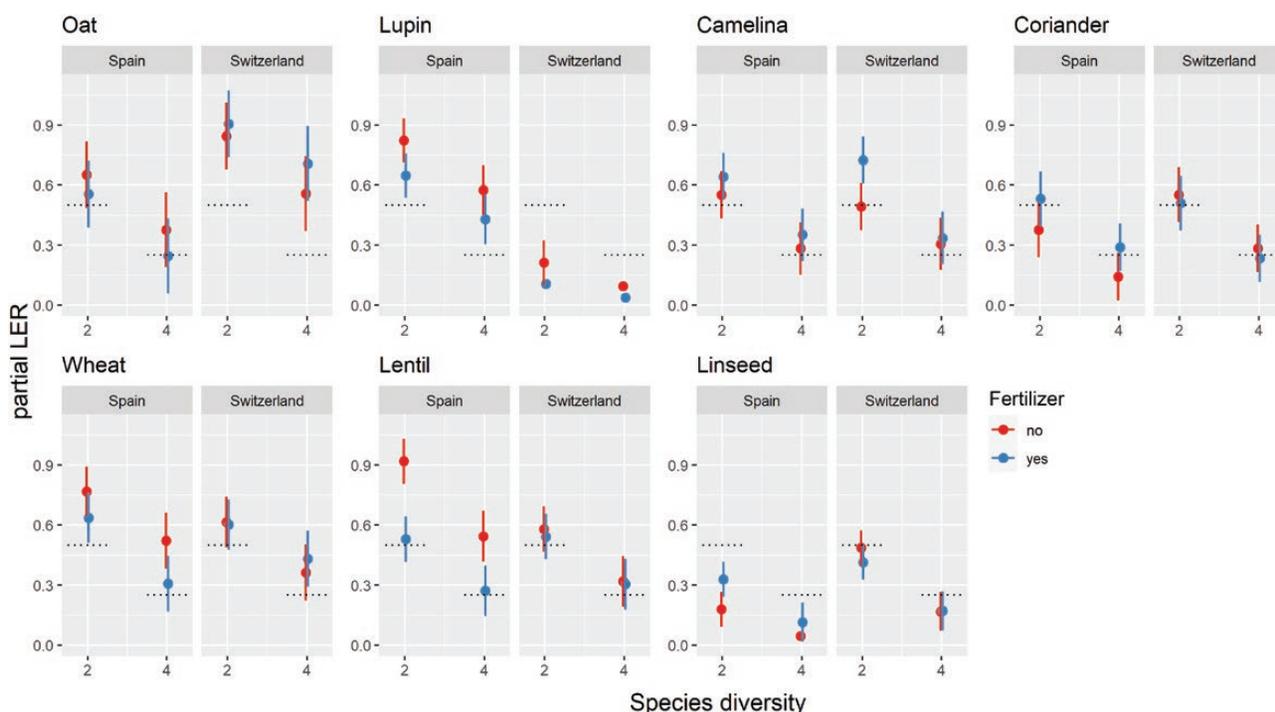


Figure 3: Average pLER ($\pm 95\%$ CI) of the Crop Diversity Experiment between 2018 and 2020 per species, country, fertilizer treatment and species diversity level. Expected pLER levels indicated with dotted lines are 0.5 for 2-species mixtures and 0.25 for 4-species mixtures based on a null hypothesis that crops will do equally well in monocultures and mixtures.

Lupin

Lupin yields in monoculture in Spain were 2.84 t/ha without fertilizer and 2.97 t/ha with fertilizer, while the corresponding yields in Switzerland were 0.47 and 0.87 t/ha, respectively. The pLER in mixtures was as expected (-0.01 ± 0.05), and significantly higher in Spain (0.24 ± 0.04) than in Switzerland (-0.27 ± 0.03), higher without fertilizer (0.05 ± 0.07) than with fertilizer (-0.08 ± 0.07), and higher in 4-species mixtures (0.03 ± 0.06) than 2-species mixtures (-0.05 ± 0.07).

Linseed

Linseed yields in monoculture in Spain were 0.64 t/ha without fertilizer and 0.91 t/ha with fertilizer, while the corresponding yields in Switzerland were 1.73 and 1.68 t/ha, respectively. The pLER in mixtures was significantly lower than expected (-0.14 ± 0.02), and significantly lower in Spain without fertilizer (-0.27 ± 0.04) than with fertilizer (-0.16 ± 0.03), and lower than in Switzerland both without (-0.04 ± 0.03) and with fertilizer (-0.08 ± 0.03).

Camelina

Camelina yields in monoculture in Spain were 1.08 t/ha without fertilizer and 1.70 t/ha with fertilizer,

while the corresponding yields in Switzerland were 2.66 and 2.29 t/ha, respectively. The pLER in mixtures was significantly higher than expected (0.09 ± 0.02), and significantly higher with fertilizer (0.14 ± 0.03) than without fertilizer (0.03 ± 0.03).

Coriander

Coriander yields in monoculture in Spain were 1.00 t/ha without fertilizer and 1.73 t/ha with fertilizer, while the corresponding yields in Switzerland were 2.40 and 3.38 t/ha, respectively. The pLER in mixtures was as expected (-0.01 ± 0.02), and significantly lower in Spain without fertilizer (-0.11 ± 0.04) than with fertilizer (0.04 ± 0.03).

DRIVERS UNDERLYING THE POSITIVE BIODIVERSITY EFFECTS

Direct effects

Over the last 5 years, the Crop Diversity Experiment has revealed a number of mutually non-exclusive processes that each partially explained the positive biodiversity effects presented above. Among the direct positive effects of crop diversity on yield through complementary resource use, the most striking effect

was the complementary nitrogen (N) use in mixtures with legumes that partially explained yield benefits in legume mixtures (Engbersen *et al.* 2021)—an effect that was stronger under low-nitrogen availability than under fertilized conditions, as also demonstrated elsewhere (Bedoussac *et al.* 2015). The role of legumes in explaining biodiversity effects is well known both in biodiversity experiments (Spehn *et al.* 2002) and intercropping (Fujita *et al.* 1992). In the Crop Diversity Experiment we found that lupin took up 70%–80% of its nitrogen through symbiotic N fixation from the atmosphere, thereby competing less with companion crops for the soil-derived N (Engbersen *et al.* 2021). This resulted in a higher cumulative N uptake of both lupin and oat in their 2-species mixture compared with their respective N uptake in monocultures. Furthermore, the uptake of N in different chemical forms went along with a temporal shift in the soil-N uptake of oat, where oat took up N earlier in a mixture with lupin than in monoculture and also earlier than lupin in the

same mixture (Fig. 4). This head-start in N uptake of oat due to a competitive release in the mixture with a legume translated into a higher cumulative biomass of oat in the oat/lupin mixture during the first 8 weeks. This went along with a higher light interception and higher photosynthetic capacity in the oat/lupin mixture compared with their monocultures in addition to the complementarity in N use (Engbersen *et al.* 2022a). The oat/camelina mixture on the other hand also showed a higher cumulative N-uptake than the monocultures, but this time not due to chemically different N sources. Rather there were temporal and most likely also spatial differences in the uptake of soil-derived N between these two species, with camelina taking up N later and deeper in the soil than oat (Engbersen *et al.* 2021). In addition, chlorophyll fluorescence measurements demonstrated higher photosynthetic efficiency of oat and camelina, combined with an overall higher light interception in mixture compared with their monocultures (Engbersen *et al.* 2022a).

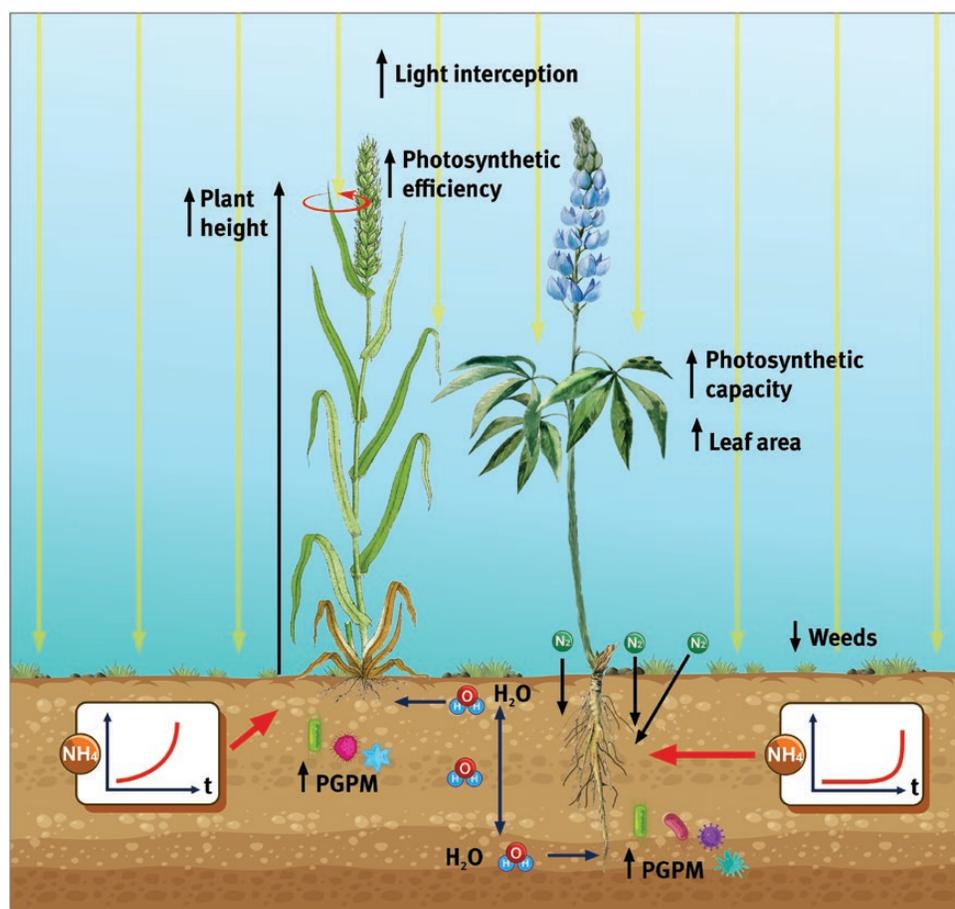


Figure 4: Direct and indirect mechanisms supporting the yield benefits of mixtures over monocultures identified in the Crop Diversity Experiment. Abbreviation: PGPM = plant growth-promoting microbes.

This light-use related complementarity observed in the oat/camelina and oat/lupin mixtures was indeed a general pattern in all mixtures, with higher plant height and increased SLA and leaf area in mixtures explaining positive diversity effects in the Crop Diversity Experiment throughout (Engbersen *et al.* 2022b).

The spatial complementarity in nutrient uptake is driven by a complementary spatial root distribution (Fig. 4), which we investigated through the natural proportion of stable isotopes of water. This method allowed us to demonstrate not only the inherent differences in the vertical distribution of roots but also plastic responses in the proportional uptake of water at different soil depths depending on the species composing the crop community (Schmutz and Schöb 2023).

Taken together, a number of niche differentiation processes have been identified in the Crop Diversity Experiment as becomes evident through the present review, including chemical, temporal and spatial differentiation in N and water uptake, increased light interception and higher photosynthetic capacity and efficiency in mixtures than in monocultures. In addition, we also found evidence for plant facilitation, namely in the case of lupin and camelina, where at low neighbourhood density an increasing density of lupin increased camelina growth (Stefan *et al.* 2022a). However, direct plant–plant facilitation was otherwise rare and presumably less important than niche differentiation in explaining the complementarity effects in the Crop Diversity Experiment. Beyond the Crop Diversity Experiment, additional facilitative mechanisms have been demonstrated in intercrops (Brooker *et al.* 2023), namely rhizosphere phosphorus facilitation (Li *et al.* 2007) and stimulation of nodulation and N₂ fixation via root exudates (Li *et al.* 2016), or when coculturing crops with animals (Ji *et al.* 2023). The Crop Diversity Experiment failed to demonstrate evidence for these or other effects of different organic acids identified in root exudates on P or N uptake and crop yield (Engbersen *et al.* 2021).

Indirect effects

Beyond the differences in direct interactions between plants in monocultures and mixtures, their indirect interactions via other organisms can significantly contribute to the observed yield benefits in mixtures (e.g. Buzhdygan and Petermann 2023; Cappelli *et al.* 2022). Among the indirect effects, in the Crop Diversity Experiment we specifically looked at weeds

and soil microbes (Fig. 4). In the case of weeds, we found a significant decrease in the abundance of weeds with increasing crop diversity and an increasing crop yield with reduced weed biomass depending on the environmental context (Stefan *et al.* 2021a). These results therefore suggest that crop diversity can suppress weeds and indirectly promote crop yield. It is reasonable to assume that the more complementary resource use in chemical, spatial and temporal forms in mixtures both above- and below-ground increases competition for resources with weeds and therefore reduces weed richness, abundance and biomass compared with monocultures.

The Crop Diversity Experiment also revealed crop diversity effects on the composition of soil microbes, in particular in Switzerland (Stefan *et al.* 2021b). Increased crop diversity went along with a higher diversity of soil fungi and, more importantly, a higher relative abundance of plant growth-promoting microbes such as members of the Actinobacteria, the latter being directly related to higher crop yield. Therefore, even though these compositional changes in soil microbes with increasing crop diversity did not explain all the yield benefits, they explained up to 35% of it and are therefore another key driver of crop diversity effects on yield.

Taken together, the present review demonstrates that alongside direct effects of crop diversity on yield, indirect ecological interactions via weeds and soil microbes also contribute to the observed yield benefits of mixtures (Fig. 4). Nevertheless, additional direct and indirect effects not investigated in the Crop Diversity Experiment so far are likely to occur, such as those mediated by pests and diseases (Letourneau *et al.* 2011).

ADDITIONAL POTENTIAL TO MAXIMIZE YIELD BENEFITS IN MIXTURES

The intercropping systems implemented so far and investigated in the Crop Diversity Experiment and elsewhere are generally set up with modern elite cultivars bred for growth in conventional monoculture cropping systems. Elite cultivars are characterized by uniformity and stability, meaning neglectable intraspecific diversity to fulfil the requirements for cultivar registration during variety testing (Donald 1968). However, the high level of uniformity comes with uniformity not only in maturity and nutritional properties (Fernandez *et al.* 2021), but also in resource uptake (Milla *et al.* 2014), interactions with other organisms

(Macfadyen and Bohan 2010) and potentially also reduced phenotypic plasticity in general (Matesanz and Milla 2018; but see Friedli *et al.* 2019). Therefore, modern cultivars are likely to have very limited complementarity between individual plants. Furthermore, elite cultivars are mostly bred for optimal growth conditions with non-limiting availability of nutrients and water (Milla *et al.* 2015). These conditions are achieved through external inputs, i.e. fertilization and irrigation, applied to the topsoil. Therefore, modern cultivars often do not require extensive root systems for sufficient below-ground resource uptake. Consequently, domestication and breeding for monocultures have led to a uniformity of crops not only within cultivars and species, but also among species, and to a superficial root system, resulting in the partial loss of complementarity between species based on their original properties. Therefore, currently available elite cultivars do not reach the same magnitude of proportional yield benefits in mixtures as their wild relatives (Chacón-Labelle *et al.* 2019). In addition, in the Crop Diversity Experiment we could show that the cultivation of crops in monocultures showed higher relative resource allocation to seeds than cultivation in mixtures (Chen *et al.* 2021). This reduction in resource allocation to reproductive organs with increasing plant diversity has not been observed in wild plants (Roscher and Schumacher 2016) and is therefore likely the result of extensive breeding activities for this trait in crops (Milla *et al.* 2015). In other words, resource allocation to reproductive organs has been a major domestication trait in grain crops (Milla 2023). This selection process for increased grain size has likely happened in monocultures, resulting in the selection of traits that favour grain size in monoculture, which are not necessarily the same as those favouring grain size in mixtures. Consequently, breeding for crop mixture ecotypes might have the potential to reverse this drop in the harvest index of current cultivars in mixtures, thereby achieving additional yield benefits.

Beyond targeting the harvest index, i.e. the relative allocation of resources to seeds, additional properties of crop plants might be specifically improved for cultivation in mixtures, including those relevant to promote direct and indirect positive effects on complementarity discussed above. Breeding for mixtures has been on the research agenda in recent years and different methods have been proposed to develop cultivars for mixture cropping (Bourke *et al.* 2021; Kopp *et al.* 2023). Based on the results

obtained in the Crop Diversity Experiment, besides the ideotype-driven or quantitative genetics-driven breeding, evolutionary plant breeding can bring back some traits relevant for high mixing ability. Namely, crop plant evolution in mixtures over 3 years demonstrated that plants tend to converge in their traits and become taller and with lower leaf dry matter content and larger leaves (Stefan *et al.* 2022b). Breeding for monocultures generally selected against these traits that are favoured in mixtures, likely due to the fact that monoculture ideotypes that perform best in a monoculture show reduced competitive ability (Weiner *et al.* 2010). In contrast, evolution in mixtures favours traits such as tall plants and large leaves, which would traditionally be interpreted as promoting competitive ability. However, the supposedly more competitive traits evolving in mixtures actually resulted in reduced competition and increased facilitation in mixtures compared with trait evolution in monoculture (Schöb *et al.* 2018; Stefan *et al.* 2022b), potentially further promoting yield benefits in mixtures. Evolutionary forces in plant communities are supposed to favour self-centred over cooperative ecotypes, thereby likely resulting in limited yield increases over time or even yield drops (Weiner *et al.* 2017). Therefore, a combination of the early evolutionary changes favouring mixing ability of crops combined with an artificial selection of cooperative traits (Wuest *et al.* 2022) might provide a promising way to optimize cultivars for growth in crop species mixtures and result in additional yield benefits compared with the currently optimized monocultures but also with mixtures set up with today's elite cultivars.

CONCLUSIONS

The diversity effects observed in perennial grassland experiments are also evident in annual crop systems, suggesting that the underlying primary ecological processes leading to the biodiversity effects are inherent to the effect of changes in richness and composition of plant species in a community. Furthermore, the yield benefits obtained in the Crop Diversity Experiment under highly controlled conditions and in small plots reasonably well correspond to those demonstrated a larger scale in farmers' fields (Li *et al.* 2020). Consequently, crop mixtures are a nature-based solution to overcome some of the challenges of modern agriculture and can likely be further improved with dedicated breeding for mixture-type cultivars.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Table S1: Yield (t/ha).

Table S2: LER.

Table S3: difpLER.

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