

# 1   **Diversity increases yield but reduces reproductive effort in crop** 2   **mixtures**

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## 17    **Abstract**

18    **Resource allocation to reproduction is a critical trait for plant fitness<sup>1,2</sup>. This**  
19    **trait, called harvest index in the agricultural context<sup>3-5</sup>, determines how plant**  
20    **biomass is converted to seed yield and consequently financial revenue of**  
21    **numerous major staple crops. While plant diversity has been demonstrated to**  
22    **increase plant biomass<sup>6-8</sup>, plant diversity effects on seed yield of crops are**  
23    **ambiguous<sup>9</sup>. This discrepancy could be explained through changes in the**  
24    **proportion of resources invested into reproduction in response to changes in**  
25    **plant diversity, namely through changes of species interactions and**  
26    **microenvironmental conditions<sup>10-13</sup>. Here we show that increasing crop plant**  
27    **diversity from monoculture over 2- to 4-species mixtures increased annual**  
28    **primary productivity, resulting in overall higher plant biomass and, to a lesser**  
29    **extent, higher seed yield in mixtures compared with monocultures. The**  
30    **difference between the two responses to diversity was due to a reduced**  
31    **reproductive effort of the eight tested crop species in mixtures, possibly because**  
32    **their common cultivars have been bred for maximum performance in**  
33    **monoculture. While crop diversification provides a sustainable measure of**  
34    **agricultural intensification<sup>14</sup>, the use of currently available cultivars may**  
35    **compromise larger gains in seed yield. We therefore advocate regional breeding**  
36    **programs for crop varieties to be used in mixtures that should exploit facilitative**  
37    **interactions<sup>15</sup> among crop species.**

38

## 39 Main text

40 Based on the vast ecological literature demonstrating positive relationships between  
41 plant diversity and annual primary productivity<sup>16,17</sup>, increasing crop plant diversity  
42 through intercropping, i.e. the simultaneous cultivation of more than one crop species  
43 on the same land, has been proposed as a promising sustainable intensification  
44 measure in agriculture<sup>14,15,18</sup>. However, evidence on positive crop plant diversity–seed  
45 yield relationships is ambiguous<sup>9,19,20</sup>. This could be due to non-linear reproductive  
46 allocation patterns, where increased annual primary productivity in mixtures would  
47 not translate into corresponding increases in seed yield.

48 The amount of resources allocated to seeds is a critical component of plant  
49 fitness<sup>1,2,21-23</sup> and directly determines grain yield and the economic value of annual  
50 grain crops, including the major staple crops wheat, maize, rice, soybeans, beans and  
51 barley<sup>23-25</sup>. For crops, resource allocation has therefore been a target trait under  
52 selection during plant domestication<sup>26</sup> and modern plant breeding<sup>3</sup>. In general,  
53 reproductive allocation is allometric<sup>27</sup>, i.e. seed yield increases alongside vegetative  
54 plant biomass<sup>28,29</sup>. However, varying abiotic and biotic conditions such as climate,  
55 resource availability, competition or genotype identity can modify the allometric  
56 resource allocation pattern<sup>13,30-33</sup>.

57 Plant community diversity is known to trigger changes in resource allocation  
58 patterns<sup>34</sup> through plastic responses of the constituent plants<sup>35,36</sup>. Plastic responses of  
59 plants can contribute to niche differentiation processes, which in turn promote  
60 positive biodiversity–productivity relationships<sup>37,38</sup>. In other words, plastic changes in

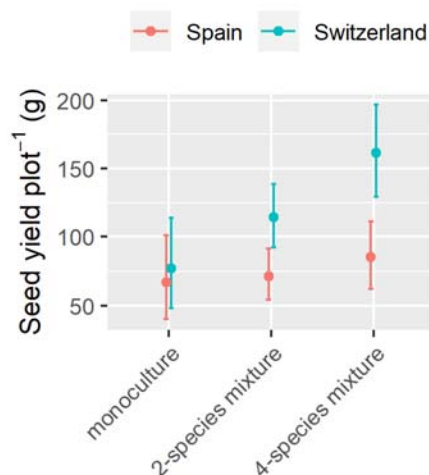
61 resource allocation strategies in response to increasing plant diversity, such as a  
62 reduced reproductive effort due to relatively higher resource investment in vegetative  
63 plant parts with higher plant diversity, could diminish the biodiversity–seed yield  
64 relationship. However, this ecologically and economically very relevant question has,  
65 to our knowledge, not been scientifically addressed.

66       Understanding the abiotic and biotic factors concomitantly controlling the  
67 proportion of resources allocated to seeds is crucial for efforts to maintain or increase  
68 crop yields and to contribute to food security under a range of environmental and  
69 farming conditions. However, we lack an ecological understanding on how plant  
70 diversity, in interaction with the physical environment, influences reproductive effort  
71 of the constituent species. For this study, we therefore selected eight annual grain crop  
72 species commonly cultivated in Europe to determine their reproductive effort under  
73 varying species diversity levels, different climatic and soil fertility conditions and  
74 with locally adapted (i.e. home) versus foreign cultivars (i.e. away). To do this we  
75 conducted a common garden experiment replicated over two countries (Switzerland  
76 and Spain), two soil fertility levels (unfertilized and fertilised), two cultivars (Swiss  
77 and Spanish) and four plant diversity levels (i.e. isolated single plants, monocultures  
78 and 24 different 2- and 16 different 4-species mixtures) in a replicated fully factorial  
79 design.

80       Increasing crop diversity from monoculture to 2-species mixture increased seed  
81 yield by 3.4% in Spain and by 21.4% in Switzerland, while seed yield increases

82 reached 12.7% and 44.3% from monoculture to 4-species mixture in Spain and  
83 Switzerland, respectively (Fig. 1).

84 **Fig. 1: Seed yield response to crop diversity**



Average seed yield of eight monocultures, 24 different 2- and 16 different 4-species mixtures planted with eight different annual crop species in 0.25 m<sup>2</sup> plots in Switzerland and Spain. Data are mean and 95% CI. n = 762. See Extended Data Table 1 for the complete statistical analysis.

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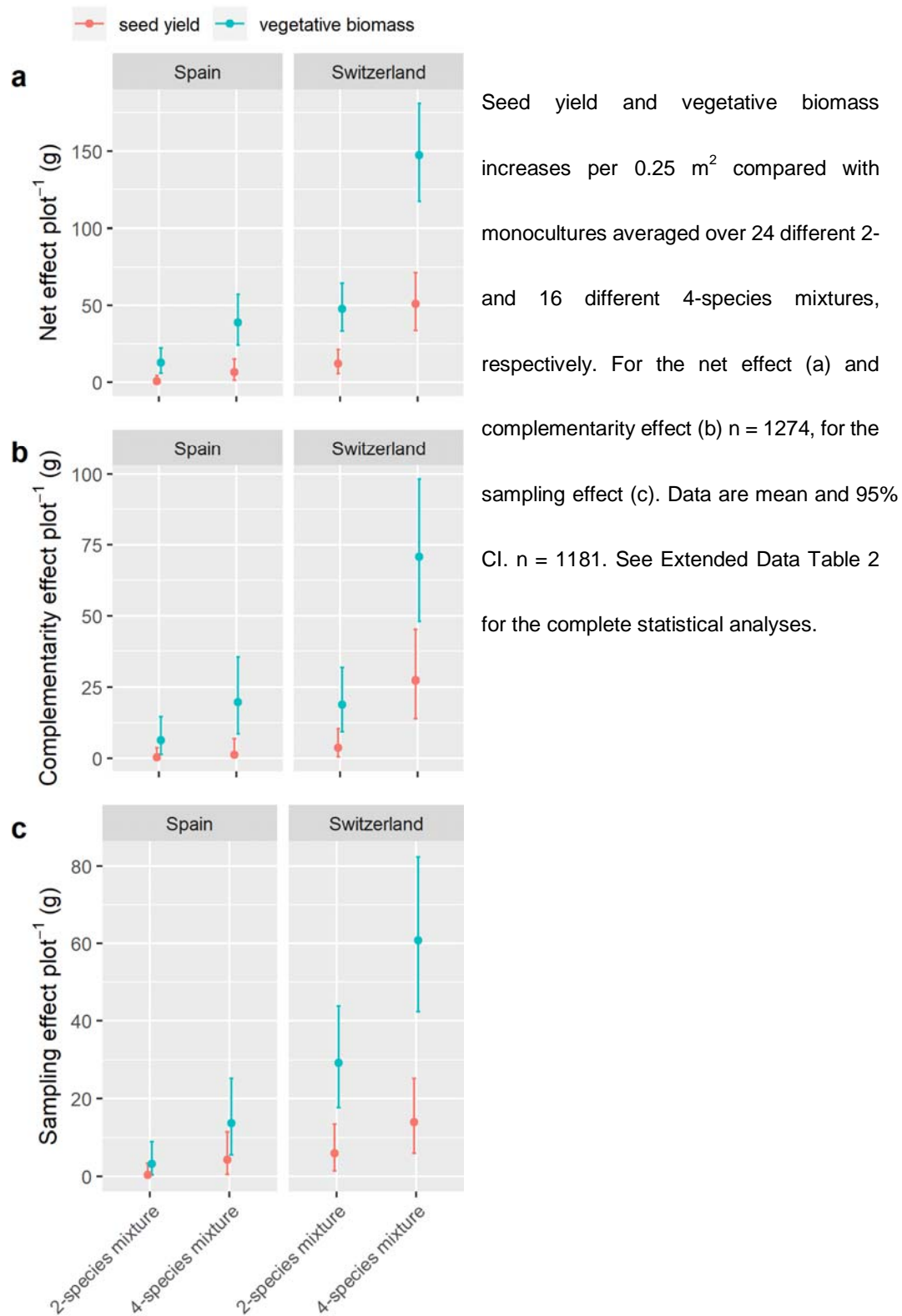
93 Even though crop diversity increased seed yield (Fig. 1), aboveground  
94 vegetative biomass increases with increasing crop diversity were 8.8- and 3.1-fold  
95 higher in Spain and Switzerland, respectively, than the increases in seed yield. The  
96 reduced benefit of crop diversity on seed yield compared with vegetative biomass was  
97 due to a reduction in both types of mechanisms underlying diversity effects on yield,  
98 i.e. complementarity and sampling effects<sup>17</sup> (Fig. 2). In Switzerland, complementarity  
99 effects contributed 25% more than sampling effects to the net biodiversity effect on  
100 seed yield, while in Spain only sampling effects could be detected. Complementarity  
101 effects in Switzerland were 59% lower for seed yield than for vegetative biomass.

102      Sampling effects were 70% and 83% lower for seed yield than for vegetative biomass

103      in Spain and Switzerland, respectively.

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105 **Fig. 2: Crop plant diversity effects on seed yield and vegetative biomass**



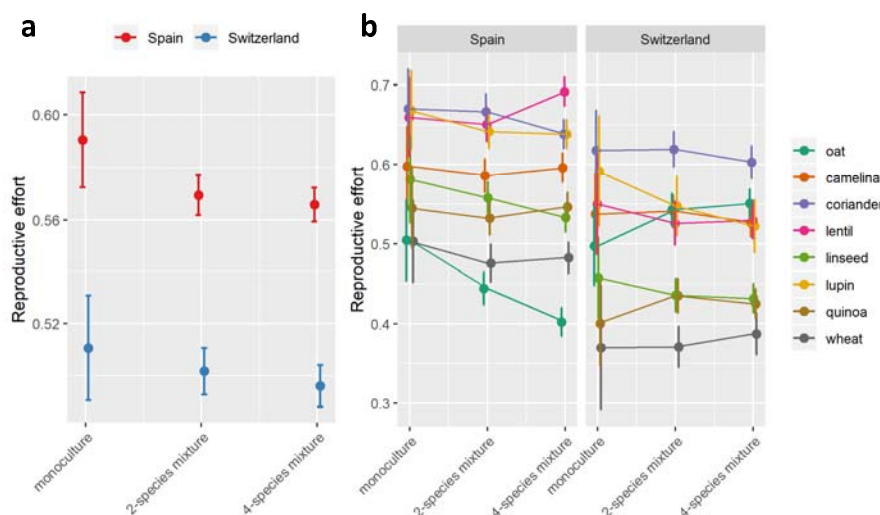
125 In line with these results at the plot level, we found at the individual plant level a  
126 clear trend towards reduced reproductive effort with increasing plant diversity (Fig.  
127 3a). Reproductive effort in monocultures was higher than in mixtures — an effect  
128 only weakly dependent on species and country (Fig. 3b). The strongest reductions in  
129 reproductive effort from monocultures to 4-species mixtures were observed in Spain  
130 for oat (−22%), linseed (−9%), wheat (−4%), lupin (−4%) and coriander (−4%), and in  
131 Switzerland for lupin (−13%), lentil (−7%), linseed (−7%), wheat (−5%) and coriander  
132 (−3%). Finally, reproductive effort was lower in 4-species mixtures than in 2-species  
133 mixtures (Fig. 3), except for locally adapted cultivars on fertilized soils (Extended  
134 Data Fig. 1).

135 Reproductive effort varied among species, being highest for legumes (i.e. *L.*  
136 *culinaris* (mean and 95% confidence interval): 0.60 [0.56, 0.63] and *L. angustifolius*:  
137 0.57 [0.53, 0.62]), followed by herbs (i.e. *C. sativum*: 0.64 [0.61, 0.68], *C. sativa*: 0.55  
138 [0.51, 0.59], *L. usitatissimum*: 0.51 [0.47, 0.55], *C. quinoa*: 0.49 [0.45, 0.53]), and  
139 lowest for cereals (i.e. *A. sativa*: 0.49 [0.48, 0.49], *T. aestivum*: 0.40 [0.37, 0.44]). The  
140 species-specific reproductive effort was also context-dependent and varied with  
141 ecotype and country and therefore with the home vs away environment. Reproductive  
142 effort was generally higher in Spain (0.56 [0.56, 0.57]) than in Switzerland (0.52  
143 [0.51, 0.53]), which is consistent with previous studies which found that plants  
144 allocated relatively more resources to reproductive structures under more severe  
145 environmental conditions<sup>39</sup>. In contrast, the higher reproductive efforts for legumes  
146 (lupin: +8%, lentil: +2%) and cereals (oat: +18%, wheat: +3.5%) in the home



147 compared with the away environment provides evidence for the importance of local  
148 adaptation<sup>40</sup> of crops for yield benefits (Extended Data Fig. 3).

149 **Fig. 3: Reproductive effort of crop species in response to plant diversity and**  
150 **country**



151  
152 Reproductive effort in response to plant diversity and country averaged over all species (a)  
153 and for each crop species separately (b). Data are mean and 95% CI. n = 4751. Reproductive  
154 effort of each species for each species combination is shown in Extended Data Fig. 2. See  
155 Extended Data Table 3 for the complete statistical analysis. Oat = *Avena sativa*, camelina =  
156 *Camelina sativa*, coriander = *Coriandrum sativum*, lentil = *Lens culinaris*, linseed = *Linum*  
157 *usitatissimum*, lupin = *Lupinus angustifolius*, quinoa = *Chenopodium quinoa*, wheat = *Triticum*  
158 *aestivum*.

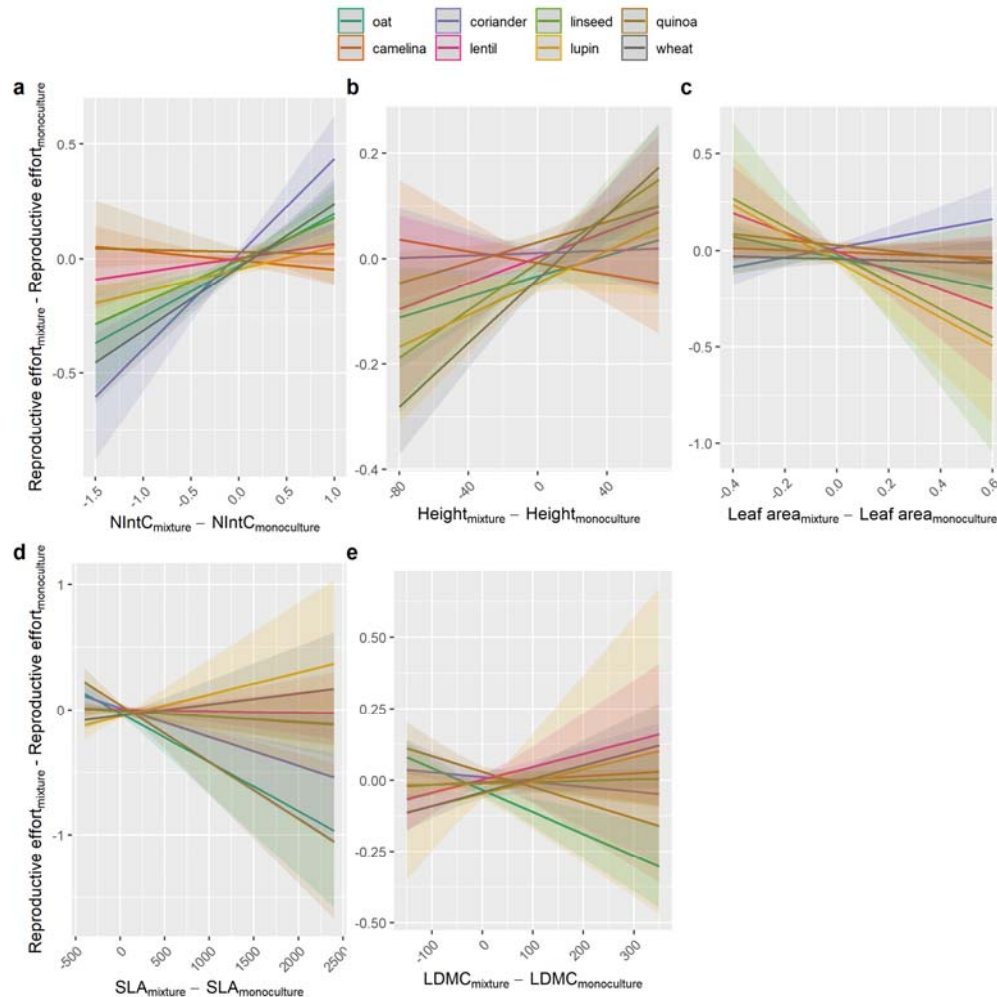
159  
160 Reduced reproductive effort in mixtures compared with monocultures was  
161 strongly linked to an increase in competition intensity (in particular for coriander,

162 wheat, linseed, oat, lupin and lentil). This is in line with previous research  
 163 demonstrating a drop of the harvest index with increasing planting density of crops<sup>41</sup>.  
 164 Beyond that, reduced plant height (in particular wheat, linseed, lupin, oat, lentil and  
 165 quinoa) together with increased leaf area (in particular lupin, linseed, lentil and oat)  
 166 and SLA (in particular quinoa, oat and coriander) in mixtures compared with  
 167 monocultures went along with reduced reproductive effort. Finally, reproductive  
 168 effort was reduced when LDMC was higher in mixtures than in monocultures for  
 169 linseed and quinoa, and when LDMC was lower in mixtures than in monocultures for  
 170 lentil, coriander and lupin.

171 Reproductive effort was highly responsive to the experimental treatments,  
 172 including the different plant diversity levels, suggesting a plastic response of currently  
 173 available crop plants to heterospecific neighbours in this trait. Specifically, the results  
 174 demonstrate a deviation of resources away from reproduction towards the shoot with  
 175 increasing neighbourhood plant diversity. This plastic response in resource allocation  
 176 of crop plants in more diverse cropping systems compromises the yield benefits of  
 177 crop mixtures. In the extreme case of oat in Spain, yield benefits in mixtures  
 178 compared with monocultures were reduced by 14 and 20% in 2- and 4-species  
 179 mixtures, respectively, only through the lower reproductive effort of this species in  
 180 mixtures compared with monocultures.

181

**Fig. 4: Relationship of reproductive effort of eight crop species with plant functional traits**



The difference in reproductive effort of eight crop species in mixtures compared with monocultures as a function of differences in competition intensity (NIntC; a), vegetative plant height (b), leaf area (c), specific leaf area (SLA; d) and leaf dry matter content (LDMC; e) between mixtures and monocultures. Data are mean and 95% CI. See Extended Data Table 4 for the complete statistical analysis. Oat = *Avena sativa*, camelina = *Camelina sativa*, coriander = *Coriandrum sativum*, lentil = *Lens culinaris*, linseed = *Linum usitatissimum*, lupin = *Lupinus angustifolius*, quinoa = *Chenopodium quinoa*, wheat = *Triticum aestivum*.

Our study demonstrates that beyond evidence for the benefits of intercropping for seed yield, growing currently available crop cultivars in mixtures does not result in the same amount of resources allocated to seed yield as in monocultures, i.e. the plant community type for which they have been bred and for which reproductive effort has been maximised<sup>3</sup>. Indeed, the little available evidence about diversity effects on reproductive effort in natural plant populations does not evidence such a reduction in reproductive effort with increasing diversity<sup>42</sup>. This suggests that the current suite of crop cultivars is not appropriate to fully exploit the benefits of crop diversification for global food security, and that specific breeding programs may be required that maximize reproductive effort of crops under mixture conditions. In the same way as breeding for high monoculture yields was based on short-statured genotypes that do not engage so much in intraspecific light competition in monocultures<sup>3</sup>, it may be possible to breed for high mixture yields if traits can be identified that reduce interspecific competition or increase complementarity and facilitation among species above and below ground in mixtures. According to our results, these breeding programs may benefit from going back to locally adapted cultivars with higher reproductive effort in mixtures.

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## 311 **Methods**

### 312 *Study sites*

313 The crop diversity experiment was carried out in outdoor experimental gardens in  
314 Zurich (Switzerland) and Torrejón el Rubio (Cáceres, Spain), i.e. two sites with  
315 striking differences in climate and soil. Spain is Mediterranean semiarid while  
316 Switzerland is temperate humid. In Zurich, the garden was located at the Irchel  
317 campus of the University of Zurich (47.3961 N, 8.5510 E, 508 m a.s.l.). In Torrejón el  
318 Rubio, the garden was situated at the Aprisco de Las Corchuelas research station  
319 (39.8133 N, 6.0003 W, 350 m a.s.l.). During the growing season, the main climatic  
320 differences between sites are precipitation (572 mm in Zurich between April and  
321 August vs 218 mm in Cáceres between February and June) and daily average hours of  
322 sunshine (5.8 h in Zurich vs 8.4 h in Cáceres), but there is little difference in terms of

323 temperature (average daily mean, min and max temperatures are 14.0 °C, 9.3 °C and  
324 18.6 °C in Zurich vs 14.6 °C, 9.6 °C and 19.6 °C in Cáceres). All climatic data are  
325 from the Deutsche Wetterdienst ([www.dwd.de](http://www.dwd.de)) and are average values over the years  
326 1961 to 1990.

327 Each experimental garden consisted of beds with square plots of 0.25 m<sup>2</sup> that  
328 were raised by 30 cm above the soil surface. In Switzerland, we had 554 plots spread  
329 over 20 beds of 1×7 m, with 26 to 28 plots per bed. In Spain, we had 624 plots spread  
330 over 16 beds of 1×10 m, with 38 to 40 plots per bed. The soil surface consisted of  
331 penetrable standard local agricultural soil, covered by a penetrable fleece. On top of  
332 the fleece, each box was filled with 30 cm standard, but not enriched, local  
333 agricultural soil. The local soil in Switzerland was a neutral loamy soil consisting of  
334 45% sand, 45% silt and 10% clay. Soil pH was 7.25, total C and N were 2.73% and  
335 0.15%, respectively, and total and available P were 339.7 mg/kg and 56.44 mg/kg,  
336 respectively. The local soil in Spain was a slightly acidic sandy soil consisting of 78%  
337 sand, 20% silt and 2% clay. Soil pH was 6.39, total C and N were 1.02% and 0.06%,  
338 respectively, and total and available P were 305.16 mg/kg and 66.34 mg/kg,  
339 respectively. Therefore, compared with the soil in Switzerland, the soil in Spain was  
340 sandier and poorer in soil organic matter.

#### 341 *Study species*

342 The eight selected crop species were: *Triticum aestivum* (wheat), *Avena sativa* (oat),  
343 *Lens culinaris* (lentil), *Coriandrum sativum* (coriander), *Camelina sativa* (camelina),

344 *Lupinus angustifolius* (blue lupin), *Linum usitatissimum* (linseed), and *Chenopodium*  
 345 *quinoa* (quinoa). These species are important annual seed crops that can be cultivated  
 346 in Europe. The eight species belong to four phylogenetic groups, with two species per  
 347 group. We had monocots [*A. sativa* (Poaceae) and *T. aestivum* (Poaceae)] vs dicots.  
 348 Then, among the dicots, we differentiated between superasterids [*C. sativum*  
 349 (Apiaceae) and *C. quinoa* (Amaranthaceae)] and superrosids. Among the superrosids,  
 350 we finally differentiated between legumes [*L. culinaris* (Fabaceae) and *L.*  
 351 *angustifolius* (Fabaceae)] and non-legumes [*C. sativa* (Brassicaceae) and *L.*  
 352 *usitatissimum* (Linaceae)]. Each species was represented by two cultivars (hereafter  
 353 called ecotypes), one local cultivar from Switzerland and another local cultivar from  
 354 Spain (Extended Data Table 5). For cultivar selection we considered, whenever  
 355 possible, traditional varieties with some inherent genetic variability within species.

### 356 *Experimental design*

357 The experimental design included a nested plant diversity treatment: (1) single control  
 358 plants for each species (between 4 and 10 replicates depending on species and country)  
 359 vs plant communities (i.e. factor ‘Community’); (2) within plant communities there  
 360 were monocultures for each species (2 replicates) vs species mixtures (i.e. factor  
 361 ‘Diversity’); (3) within species mixtures there were all possible 2-species mixtures  
 362 consisting of two phylogenetic groups each (2 replicates of 24 different species  
 363 combinations), and all possible 4-species mixtures consisting of four phylogenetic  
 364 groups each (2 replicates of 16 species combinations) (i.e. factor ‘Species number’).  
 365 To test for the context dependency of reproductive allocation patterns at different

366 plant diversity levels, this setup was replicated at two levels of soil fertility  
367 (unfertilized control plots vs fertilized plots; factor ‘Fertilisation’). In the fertilised  
368 plots we applied 120 kg/ha N, 205 kg/ha P and 120 kg/ha K divided over three  
369 fertilisation events of 50 kg N/ha applied one day before sowing, another 50 kg N/ha  
370 after tillering of wheat and the remaining 20 kg N/ha during the flowering stage of  
371 wheat. The described experimental setup was further replicated for the Swiss and the  
372 Spanish ecotypes (i.e. factor ‘Ecotype’) both in Switzerland and in Spain (i.e. factor  
373 ‘Country’). The interaction between ‘Ecotype’ and ‘Country’ was assessed as  
374 additional factor ‘Home’, with two factor levels: ‘home’ representing Spanish  
375 cultivars in Spain and Swiss cultivars in Switzerland and ‘away’ representing the  
376 opposite combinations.

#### 377 *Experimental setup and data collection*

378 In Spain, the seeds were sown between 2 and 4 February 2018 and in Switzerland  
379 between 4 and 6 April 2018. All the seeds were sown by hand at a standard sowing  
380 density for the corresponding crop species: 400 seeds/m<sup>2</sup> for cereals, 240 seeds/m<sup>2</sup> for  
381 superasterids, 592 seeds/m<sup>2</sup> for non-legume superrosids, and 160 seeds/m<sup>2</sup> for  
382 legumes. Sowing was conducted in four rows of 45 cm length per plot and an  
383 inter-row distance of 12 cm. Sowing depth was 0.5 cm for *C. sativa*, 5 cm for *L.*  
384 *culinaris* and 2 cm for all other species. For the isolated single-plant treatment we  
385 placed five seeds in the center of the plot, randomly selected one plant approx. three  
386 weeks after germination and manually removed the spare individuals. Weeds were  
387 manually removed from all monoculture and mixture plots approx. 80 days after

sowing, while weeds in the plots with isolated single plants were removed several times during the growing season to avoid competition of the single plants with the otherwise abundant weeds in these plots. No other interventions were made over the course of the experiment, e.g. no harrowing or pesticide application. Harvest was conducted for each species once it reached maturity and lasted in Spain between 15 June and 11 July for all species except *C. quinoa*, which was harvested between 26 July and 21 August. Harvest in Switzerland was between 11 and 13 July for *C. sativa* and between 26 July and 5 September for all other species. In each plot (except for isolated single plants) and for each species we randomly marked three individuals during the flowering stage (i.e. 6154 individuals). All the marked individuals were harvested separately and seeds (i.e. reproductive biomass) were separated from all other aboveground biomass, incl. stems, leaves and chaff (i.e. vegetative biomass). While seeds were air-dried, vegetative biomass was oven-dried at 80 °C for 48 h prior to weighing.

#### 402 *Data analyses*

Plot-level yield responses to the experimental treatments were assessed using a linear mixed effects model with (1) country, ecotype and home *vs* away; (2) fertilisation, and (3) diversity and species number, and their interactions as fixed effects and species composition and bed ID as random effects. Plot-level yield as the total mass of all seeds produced in a plot was square-root transformed to meet assumptions of parametric statistics. Significance of each factor was assessed using type-I analysis of variance with Satterthwaite's method.

410 In order to assess differences in biodiversity effects on vegetative biomass  
411 versus grain yield, we applied the additive partitioning method<sup>17</sup> of biodiversity  
412 effects and calculated net effects, complementarity effects and sampling effects  
413 separately for vegetative biomass and grain yield. Differences in their responses to  
414 experimental treatments were tested with a linear mixed-effects model with net effect,  
415 complementarity effect or sampling effect as response variables and organ (shoot *vs*  
416 seeds), country, ecotype, home *vs* away, fertilisation, species number (2 *vs* 4) and  
417 their possible interactions as fixed effects. Bed ID and plot ID were included as  
418 random terms. The three response variables were square-root transformed to meet  
419 assumptions of parametric statistics. Significance of each factor was assessed using  
420 type-I analysis of variance with Satterthwaite's method.

421 Reproductive effort was calculated for each sampled individual that produced  
422 seeds (i.e. 5107 individuals included, while 1047 individuals were excluded due to  
423 mortality, lack of mature seeds or missing data) as  $RE = \text{reproductive biomass} / (\text{vegetative biomass} + \text{reproductive biomass})$ . To detect the effects of (1)  
424 species, (2) country, ecotype and home, (3) fertilization, (4) species number (two- *vs*  
425 four-species) nested within diversity (monoculture *vs* mixture) nested within  
426 community (single individual *vs* community) and the possible interactions between  
427 these factors on reproductive effort of the crops, we used a linear mixed-effects model  
428 and type-I analysis of variance. Reproductive effort was square-root-transformed to  
429 meet normality and homoscedasticity of variance assumptions. We included bed ID  
430 and plot ID as well as the species composition as random factors into the model.

In order to test for functional plant traits related to reproductive effort of crops when neighbour diversity increased, we quantified differences in plant interaction intensity and plant functional traits between mixtures and monocultures and related them to the changes in reproductive effort of plants from monoculture to mixture. Plant interaction intensity in the plots was calculated for each individual by means of the neighbour-effect intensity index with commutative symmetry (NIntC)<sup>42</sup>. NIntC is based on the difference in aboveground net primary productivity in any monoculture or mixture compared to the average aboveground primary productivity of the same species and ecotype in the same country and soil fertility but growing as an isolated single plant without neighbours, and calculated as:

$$\text{NIntC} = 2 \times [\Delta P / (\Sigma P + |\Delta P|)].$$

As plant traits we used vegetative plant height, leaf area, SLA and LDMC. SLA and LDMC together reflect a fundamental trade-off in plant functioning between a rapid production of biomass (i.e. high SLA and low LDMC) and an efficient conservation of nutrients (i.e. low SLA and high LDMC)<sup>43</sup>, and the plant's capacity of endurance and resistance in harsh environment<sup>44-46</sup>. Vegetative plant height reflects plant's ability to capture light energy in competition through relatively high growth rates<sup>47,48</sup>.

In a linear mixed-effects model we assessed the response of  $\Delta \text{RE}_{\text{mixture-monoculture}}$  to  $\Delta \text{NIntC}_{\text{mixture-monoculture}}$ ,  $\Delta \text{height}_{\text{mixture-monoculture}}$ ,  $\Delta \text{leaf area}_{\text{mixture-monoculture}}$ ,  $\Delta \text{SLA}_{\text{mixture-monoculture}}$  and  $\Delta \text{LDMC}_{\text{mixture-monoculture}}$  and their interactions with species. Bed and plot ID were included as random terms. Statistical significance of each factor was tested with type-III analysis of variance.

454 All analyses were conducted with R version 3.6.2<sup>49</sup>. Reported figures, including  
455 means and confidence intervals are for estimated marginal means calculated using  
456 `ggemmeans()` in *ggeffects*<sup>50</sup> and plotted with `plot_model()` in *sjPlot*<sup>51</sup>.

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483

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#### 490 **Author contributions**

491 CS and JC conceptualised the study; CS designed the experiment with input from BS;

492 NE, LS and CS carried out the experiment, CS, BS and JC analysed the data; JC and

493 CS wrote the paper with input from BS, NE, LS and HS.

#### 494 **Competing interests**

495 The authors declare no competing financial interests.

496 **Materials & Correspondence**

497 Correspondence and requests for materials should be addressed to Christian Schöb.

498 **Data availability statement**

499 The data that support the findings of this study are available from the corresponding

500 author upon reasonable request.

501 **Supplementary Information** is available for this paper.

502 - R code

503 - data

## 504 Extended Data

### 505 Extended Data Table 1 | Type-I Analysis of Variance table testing the 506 experimental treatment effects on plot-level seed yield 507

Factor	SS	MS	numDF	denDF	F-value	P-value
Country	835.01	835.01	1	20.8	71.23	<0.001
Ecotype	966.21	966.21	1	688.7	82.43	<0.001
Home	127.35	127.35	1	689.1	10.86	0.001
Fertilisation	30.41	30.41	1	20.8	2.59	0.122
Diversity	32.81	32.81	1	45.1	2.80	0.101
Species number	34.04	34.04	1	44.9	2.90	0.095
Country × Fertilisation	32.76	32.76	1	20.8	2.80	0.110
Ecotype × Fertilisation	9.46	9.46	1	688.0	0.81	0.369
Home × Fertilisation	0.73	0.73	1	688.1	0.06	0.803
Country × Diversity	120.78	120.78	1	676.9	10.30	0.001
Country × Species number	60.13	60.13	1	678.5	5.13	0.024
Ecotype × Diversity	24.07	24.07	1	689.4	2.05	0.152
Ecotype × Species number	13.59	13.59	1	693.0	1.16	0.282
Home × Diversity	27.04	27.04	1	689.6	2.31	0.129
Home × Species number	5.02	5.02	1	693.0	0.43	0.513
Fertilisation × Diversity	3.05	3.05	1	676.8	0.26	0.610
Fertilisation × Species number	10.48	10.48	1	678.2	0.89	0.345
Country × Fertilisation × Diversity	0.89	0.89	1	676.7	0.08	0.782
Country × Fertilisation × Species number	0.32	0.32	1	678.2	0.03	0.869
Ecotype × Fertilisation × Diversity	4.83	4.83	1	689.2	0.41	0.521
Ecotype × Fertilisation × Species number	0.08	0.08	1	693.0	0.01	0.934
Home × Fertilisation × Diversity	9.15	9.15	1	689.2	0.78	0.377
Home × Fertilisation × Species number	0.04	0.04	1	693.0	0.00	0.956
Random factor	n	Variance	SD			
Species composition	48	5.65	2.38			
Bed ID	29	0.12	0.35			
Residual		11.72	3.42			

508  
509 Significance was tested with the Satterthwaite approximation method. n = 762.  
510 Marginal  $R^2 = 0.19$ , conditional  $R^2 = 0.46$ .

511

512 **Extended Data Table 2 | Type-I Analysis of Variance table testing the experimental treatment effects on net effect, complementarity effect**  
513 **and sampling effect**  
514

Factor	Net effect						Complementarity effect						Sampling effect					
	SS	MS	num DF	den DF	F-val ue	P-val ue	SS	MS	num DF	den DF	F-val ue	P-val ue	SS	MS	num DF	den DF	F-val ue	P-val ue
Organ (shoot vs seeds)	381			621.	231.	<0.0	161	1615.		621.	82.0	<0.0	195	1956.		575.	159.	<0.0
	9.2	3819.2	1	0	42	<b>01</b>	5.3	3	1	0	8	<b>01</b>	6.4	4	1	3	82	<b>01</b>
Country	585.				35.5	<0.0	212.				10.7	<b>0.00</b>	191.				15.6	<0.0
	9	585.9	1	23.1	0	<b>01</b>	3	212.3	1	23.4	9	<b>3</b>	6	191.6	1	22.7	5	<b>01</b>
Ecotype				610.		0.27					608.	0.12				565.		<b>0.03</b>
	19.4	19.4	1	9	1.17	9	47.4	47.4	1	7	2.41	1	55.1	55.1	1	1	4.50	<b>4</b>
Home vs Away				610.		0.46					608.	0.93				565.		0.50
	8.7	8.7	1	9	0.52	9	0.2	0.2	1	7	0.01	0	5.6	5.6	1	1	0.45	1
Fertilisation						0.10						0.70						0.09
	47.8	47.8	1	23.1	2.90	2	2.8	2.8	1	23.4	0.14	8	37.1	37.1	1	22.7	3.03	5
Species number				605.	41.4	<0.0	404.			603.	20.5	<0.0	200.			560.	16.3	<0.0
	683.4	683.4	1	9	1	<b>01</b>	3	404.3	1	9	4	<b>01</b>	4	200.4	1	2	7	<b>01</b>
Country × Fertilisation					<0.0	0.98						0.30						0.08
	<0.1	<0.1	1	23.1	1	5	21.8	21.8	1	23.4	1.11	3	39.0	39.0	1	22.7	3.19	8
Ecotype × Fertilisation				610.		<b>0.00</b>	148.			608.		<b>0.00</b>				565.		0.85
	119.7	119.7	1	9	7.25	<b>7</b>	4	148.4	1	6	7.54	<b>6</b>	0.4	0.4	1	1	0.04	0
Home vs Away × Fertilisation				610.	11.8	<0.0	264.			608.	13.4	<0.0				565.		0.43
	195.5	195.5	1	9	5	<b>01</b>	2	264.2	1	6	2	<b>01</b>	7.5	7.5	1	2	0.61	4
Country × Species number				605.		<b>0.02</b>	106.			603.		<b>0.02</b>				560.		0.84
	88.7	88.7	1	8	5.37	<b>1</b>	6	106.6	1	8	5.41	<b>0</b>	0.5	0.5	1	1	0.04	6
Ecotype × Species number				620.		0.67				617.		0.57				572.		0.41
	3.0	3.0	1	1	0.18	2	6.4	6.4	1	7	0.32	0	8.1	8.1	1	6	0.66	7
Home vs Away × Species number				620.		0.88				617.	<0.0	0.98				572.		0.61
	0.3	0.3	1	0	0.02	6	<0.1	<0.1	1	7	1	6	3.1	3.1	1	3	0.25	4
Fertilisation × Species number				605.		0.30				603.		0.53				560.		0.98
Organ × Country	17.2	17.2	1	8	1.04	8	7.7	7.7	1	8	0.39	1	<0.1	<0.1	1	2	0.00	5
	47.8	47.8	1	621.	2.89	0.08	14.3	14.3	1	621.	0.72	0.39	562.	562.6	1	574.	45.9	<0.0

				0		9				0		5		6		8		6	<b>01</b>
				621.	15.2	<b>&lt;0.0</b>	394.			621.	20.0	<b>&lt;0.0</b>				574.			0.77
Organ × Ecotype	250.9	250.9	1	0	0	<b>01</b>	9	394.9	1	0	7	<b>01</b>	1.0	1.0	1	9	0.08	6	
				621.	34.2	<b>&lt;0.0</b>	310.			621.	15.7	<b>&lt;0.0</b>	422.			574.	34.5	<b>&lt;0.0</b>	
Organ × Home vs Away	564.9	564.9	1	0	3	<b>01</b>	8	310.8	1	0	9	<b>01</b>	7	422.7	1	8	3	<b>01</b>	
				621.		<b>0.00</b>	145.			621.		<b>0.00</b>				574.		0.16	
Organ × Fertilisation	164.5	164.5	1	0	9.97	<b>2</b>	2	145.2	1	0	7.38	<b>7</b>	23.8	23.8	1	9	1.94	4	
				621.		<b>0.00</b>	101.			621.		<b>0.02</b>				575.		0.07	
Organ × Species number	150.6	150.6	1	0	9.13	<b>3</b>	8	101.8	1	0	5.17	<b>3</b>	40.3	40.3	1	1	3.30	0	
Country × Fertilisation × Species				605.		0.84				603.		0.61				560.		0.57	
number	0.6	0.6	1	8	0.04	4	4.9	4.9	1	8	0.25	9	3.9	3.9	1	1	0.32	1	
Ecotype × Fertilisation × Species				620.		0.72				617.		0.73				572.		0.81	
number	2.1	2.1	1	0	0.13	0	2.2	2.2	1	7	0.11	6	0.7	0.7	1	6	0.06	1	
Home vs Away × Fertilisation ×				620.		0.82				617.		0.89				572.		0.17	
Species number	0.8	0.8	1	0	0.05	4	0.4	0.4	1	7	0.02	1	22.1	22.1	1	3	1.81	9	
				621.		<b>0.01</b>	259.			621.	13.1	<b>&lt;0.0</b>				574.		0.44	
Organ × Country × Fertilisation	100.8	100.8	1	0	6.11	<b>4</b>	1	259.1	1	0	6	<b>01</b>	7.2	7.2	1	8	0.59	5	
				621.		0.83				621.		0.22				574.		<b>0.02</b>	
Organ × Ecotype × Fertilisation	0.7	0.7	1	0	0.04	8	28.8	28.8	1	0	1.46	7	60.3	60.3	1	9	4.92	<b>7</b>	
Organ × Home vs Away ×				621.	12.7	<b>&lt;0.0</b>				621.		0.08	102.			574.		<b>0.00</b>	
Fertilisation	210.9	210.9	1	0	8	<b>01</b>	57.9	57.9	1	0	2.94	7	3	102.3	1	7	8.35	<b>4</b>	
				621.		0.47				621.		0.36				574.		0.23	
Organ × Country × Species number	8.5	8.5	1	0	0.52	2	16.1	16.1	1	0	0.82	6	17.0	17.0	1	9	1.39	9	
				621.	<0.0	0.97				621.		0.32				575.		0.61	
Organ × Ecotype × Species number	<0.1	<0.1	1	0	1	3	19.1	19.1	1	0	0.97	5	3.1	3.1	1	0	0.25	7	
Organ × Home vs Away × Species				621.		0.17				621.		0.76				574.		<b>0.01</b>	
number	29.9	29.9	1	0	1.81	9	1.8	1.8	1	0	0.09	4	75.3	75.3	1	9	6.15	<b>3</b>	
Organ × Fertilisation × Species				621.		0.71				621.		0.44				575.		0.42	
number	2.3	2.3	1	0	0.14	1	11.4	11.4	1	0	0.58	7	7.9	7.9	1	1	0.64	3	
Organ × Country × Fertilisation ×				621.		0.79				621.		0.88				575.		0.61	
Species number	1.1	1.1	1	0	0.07	8	0.4	0.4	1	0	0.02	8	3.0	3.0	1	0	0.25	9	
Organ × Ecotype × Fertilisation ×				621.		0.84				621.	<0.0	0.94				575.		0.07	
Species number	0.7	0.7	1	0	0.04	1	0.1	0.1	1	0	1	8	38.5	38.5	1	1	3.14	7	

Organ × Home vs Away × Fertilisation × Species number				621.	0.87	621.	0.42	575.	0.39									
	0.4	0.4	1	0	0.03	1	12.5	12.5	1	0	0.63	7	9.0	9.0	1	0	0.73	2
				Varia			Varia			Varia								
Random effects	n		SD				n		SD				n		SD			
Plot ID	637	31.70	5.63				637	34.13	5.84				593	22.38	4.73			
Bed ID	29	1.14	1.07				29	2.24	1.50				29	2.13	1.46			
Residual		16.50	4.06					19.68	4.44					12.24	3.50			

Significance was tested with the Satterthwaite approximation method. For the net effect  $n = 1274$ , marginal  $R^2 = 0.20$ , conditional  $R^2 = 0.73$ ; for the complementarity effect  $n = 1274$ , marginal  $R^2 = 0.12$ , conditional  $R^2 = 0.69$ ; for the sampling effect  $n = 1181$ , marginal  $R^2 = 0.16$ , conditional  $R^2 = 0.72$ .

520 **Extended Data Table 3 | Type-I Analysis of Variance table of the experimental treatment effects on reproductive effort**

521

Factor	SS	MS	numDF	denDF	F-value	P-value
Species	18.87	2.70	7	635.5	191.14	<0.001
Country	0.96	0.96	1	21.5	68.10	<0.001
Ecotype	3.04	3.04	1	450.8	215.55	<0.001
Home vs Away	0.43	0.43	1	464.2	30.48	<0.001
Fertilisation	0.00	0.00	1	21.3	0.25	0.621
Diversity	0.07	0.07	1	77.7	4.81	0.031
Species number	0.01	0.01	1	28.4	1.01	0.323
Species × Country	7.04	1.01	7	3931.6	71.28	<0.001
Species × Ecotype	4.15	0.59	7	3938.0	42.03	<0.001
Species × Home vs Away	1.18	0.17	7	3963.5	11.91	<0.001
Species × Fertilisation	0.36	0.05	7	3728.1	3.66	<0.001
Species × Diversity	0.09	0.01	7	103.7	0.89	0.519
Species × Species number	0.19	0.03	7	693.2	1.88	0.070
Country × Fertilisation	0.01	0.01	1	21.6	0.51	0.482
Ecotype × Fertilisation	0.00	0.00	1	451.7	0.04	0.842
Home vs Away × Fertilisation	0.04	0.04	1	465.1	2.66	0.104
Country × Diversity	0.01	0.01	1	1461.3	0.50	0.479
Country × Species number	0.00	0.00	1	482.6	0.02	0.897
Ecotype × Diversity	0.01	0.01	1	1460.2	0.36	0.549
Ecotype × Species number	0.00	0.00	1	479.6	0.00	0.996
Home vs Away × Diversity	0.01	0.01	1	1462.0	0.95	0.331
Home vs Away × Species number	0.01	0.01	1	491.8	0.65	0.420
Fertilisation × Diversity	0.00	0.00	1	1443.9	0.06	0.803
Fertilisation × Species number	0.08	0.08	1	463.5	5.61	0.018
Species × Country × Fertilisation	0.43	0.06	7	3926.5	4.33	<0.001
Species × Ecotype × Fertilisation	0.14	0.02	7	3940.0	1.40	0.200
Species × Home vs Away × Fertilisation	0.19	0.03	7	3960.0	1.95	0.057

Species × Country × Diversity	0.23	0.03	7	1860.0	2.30	0.025
Species × Country × Species number	0.18	0.03	7	3938.9	1.81	0.080
Species × Ecotype × Diversity	0.08	0.01	7	1870.9	0.80	0.583
Species × Ecotype × Species number	0.09	0.01	7	3958.7	0.93	0.485
Species × Home vs Away × Diversity	0.09	0.01	7	1936.8	0.91	0.496
Species × Home vs Away × Species number	0.09	0.01	7	4006.5	0.93	0.480
Country × Fertilisation × Diversity	0.04	0.04	1	1474.3	3.04	0.082
Country × Fertilisation × Species number	0.01	0.01	1	472.5	0.69	0.408
Ecotype × Fertilisation × Diversity	0.03	0.03	1	1468.8	2.12	0.145
Ecotype × Fertilisation × Species number	0.01	0.01	1	479.8	0.43	0.514
Home vs Away × Fertilisation × Diversity	0.00	0.00	1	1481.0	0.09	0.765
Home vs Away × Fertilisation × Species number	0.06	0.06	1	489.2	4.06	0.044
Species × Country × Fertilisation × Diversity	0.20	0.01	14	1883.5	0.99	0.456
Species × Country × Fertilisation × Species number	0.27	0.02	14	3913.5	1.37	0.160
Species × Ecotype × Fertilisation × Diversity	0.07	0.01	7	1931.6	0.69	0.680
Species × Ecotype × Fertilisation × Species number	0.06	0.01	7	3965.8	0.65	0.715
Species × Home vs Away × Fertilisation × Diversity	0.18	0.03	7	2052.5	1.78	0.087
Species × Home vs Away × Fertilisation × Species number	0.11	0.02	7	4009.3	1.13	0.338
Random effects	n	Variance	SD			
Plot ID	762	0.00104	0.03227			
Species composition	48	0.00005	0.00726			
Bed ID	29	0.00021	0.01444			
Residual		0.01410	0.11875			

Significance was tested with the Satterthwaite approximation method.  $n = 4751$ . Marginal  $R^2 = 0.40$ , conditional  $R^2 = 0.45$ .



525 **Extended Data Table 4 | Type-III Analysis of Variance table of the relationship between the difference in reproductive effort between**  
 526 **mixtures and monocultures and corresponding changes in plant interaction intensity and plant traits**

Factor	SS	MS	numDF	denDF	F-value	P-value
Species	0.817	0.117	7	1579.6	11.18	<0.001
ΔNIntC	0.534	0.534	1	1588.5	51.09	<0.001
ΔHeight	0.212	0.212	1	1539.5	20.27	<0.001
ΔLeaf area	0.097	0.097	1	1588.8	9.31	0.002
ΔSLA	0.096	0.096	1	1576.9	9.23	0.002
ΔLDMC	<0.001	<0.001	1	1578.8	<0.01	0.984
Species × ΔNIntC	0.509	0.073	7	1580.9	6.96	<0.001
Species × ΔHeight	0.233	0.033	7	1583.6	3.19	0.002
Species × ΔLeaf area	0.212	0.030	7	1580.6	2.89	0.005
Species × ΔSLA	0.245	0.035	7	1579.7	3.35	0.002
Species × ΔLDMC	0.259	0.037	7	1582.1	3.54	<0.001
Random effects	n	Variance	SD			
Plot ID	637	<0.0001	<0.0001			
Bed ID	29	0.0004	0.0198			
Residuals		0.0104	0.1022			

527

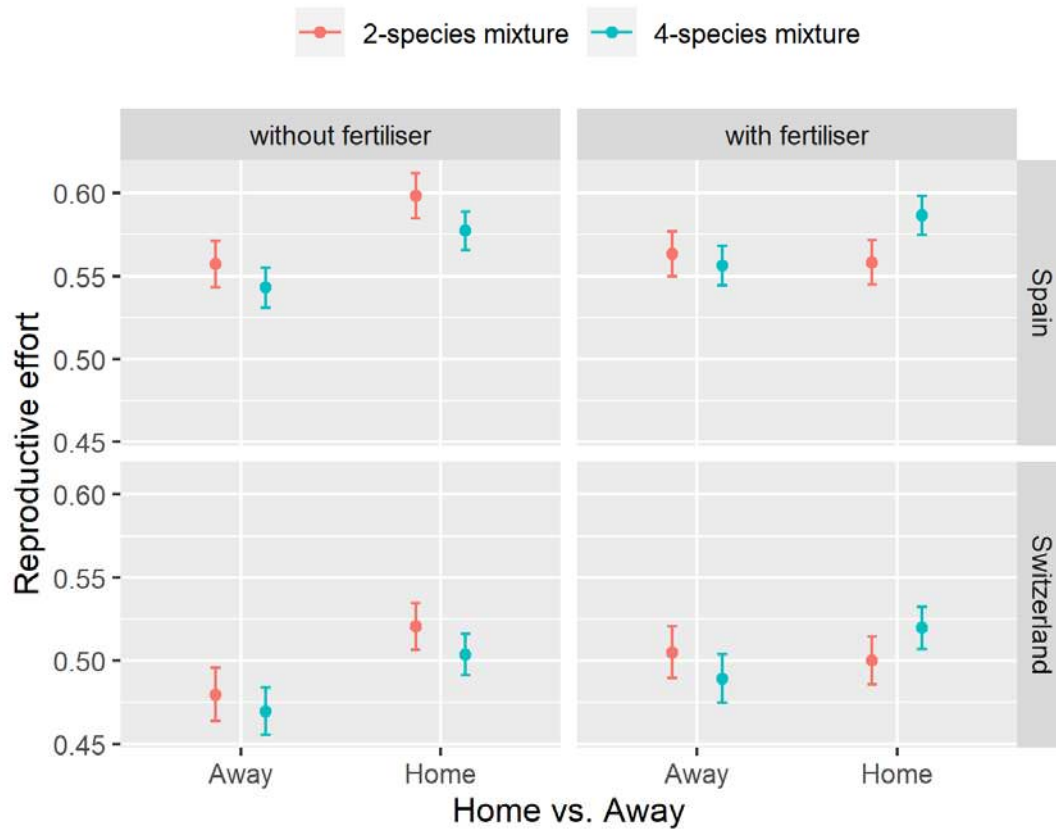
528 Significance was tested with the Satterthwaite approximation method. n = 1637. Marginal  $R^2 = 0.16$ , conditional  $R^2 = 0.19$ .

529

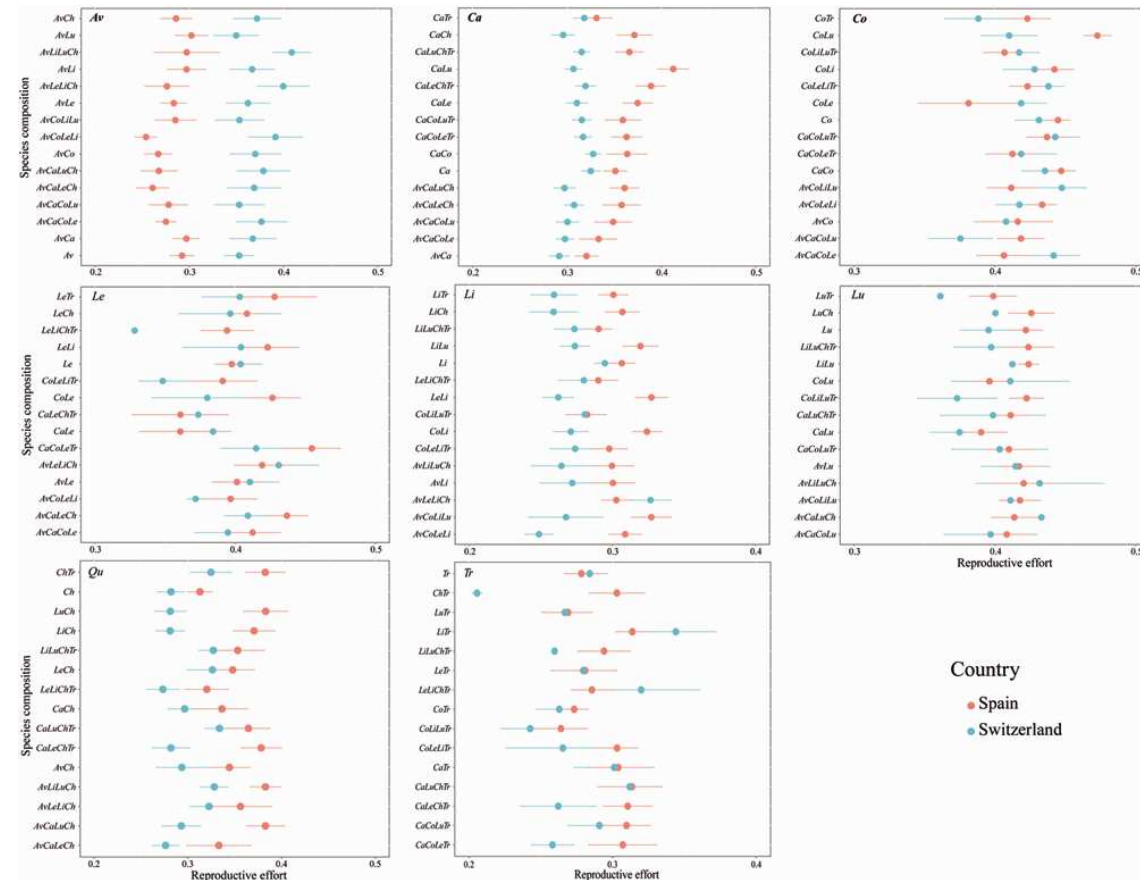
**Extended Data Table 5 | Cultivar and seed supplier for the crop species used in the experiment**

Species	Switzerland		Spain	
	Cultivar	Supplier	Cultivar	Supplier
<i>Avena sativa</i>	Canyon	Sativa Rheinau	Previsión	INIA, Madrid
<i>Triticum aestivum</i>	Fiorina	DSP, Delley	Cabezorro (BGE015403)	INIA, Madrid
<i>Coriandrum sativum</i>	Indian	Zollinger Samen, Les Evouettes	wild type	Semillas Cantueso, Córdoba
<i>Chenopodium quinoa</i>	n.a.	Artha Samen, Münsingen	Atlas	Algosur, Sevilla
<i>Lupinus angustifolius</i>	Boregine	Aspenhof, Wilchingen	wild type	Semillas Cantueso, Córdoba
<i>Lens culinaris</i>	Anicia	Agroscope, Reckenholz	de la Armuña	Legumer SL, Salamanca
<i>Camelina sativa</i>	n.a.	Zollinger Samen, Les Evouettes	n.a.	Camelina Company, Madrid
<i>Linum usitatissimum</i>	Lirina	Sativa Rheinau	wild type	Semillas Cantueso, Córdoba

**Extended Data Fig. 1 | Reproductive effort of crops in response to the Home vs Away, Fertilization, Country and Species number (2- vs 4-species mixtures) treatments**

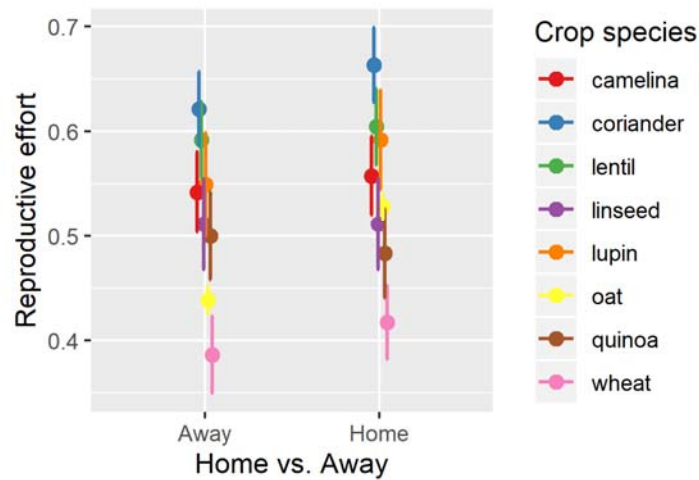


## Extended Data Fig. 2 | Reproductive effort of the eight crop species planted in communities of different species composition



Species were abbreviated as: *Avena sativa* = Av, *Triticum aestivum* = Tr, *Camelina sativa* = Ca, *Coriandrum sativum* = Co, *Lens culinaris* = Le, *Lupinus angustifolius* = Lu, *Linum usitatissimum* = Li and *Chenopodium quinoa* = Ch.

### Extended Data Fig. 3 | Reproductive effort for eight crop species in their Home vs Away environment



Reproductive effort quantifies the proportion of reproductive biomass, i.e. seed yield, from total aboveground biomass produced by the Spanish cultivars in Spain and the Swiss cultivars in Switzerland (Home) and vice versa (Away).