

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^{1,2}. This**
19 **trait, called harvest index in the agricultural context³⁻⁵, 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 biomass⁶⁻⁸, plant diversity effects on seed yield of crops are**
23 **ambiguous⁹. 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 conditions¹⁰⁻¹³. 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 intensification¹⁴, 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 **interactions¹⁵ 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^{16,17}, 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^{14,15,18}. However, evidence on positive crop plant diversity–seed
45 yield relationships is ambiguous^{9,19,20}. 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^{1,2,21-23} 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 barley²³⁻²⁵. For crops, resource allocation has therefore been a target trait under
52 selection during plant domestication²⁶ and modern plant breeding³. In general,
53 reproductive allocation is allometric²⁷, i.e. seed yield increases alongside vegetative
54 plant biomass^{28,29}. However, varying abiotic and biotic conditions such as climate,
55 resource availability, competition or genotype identity can modify the allometric
56 resource allocation pattern^{13,30-33}.

57 Plant community diversity is known to trigger changes in resource allocation
58 patterns³⁴ through plastic responses of the constituent plants^{35,36}. Plastic responses of
59 plants can contribute to niche differentiation processes, which in turn promote
60 positive biodiversity–productivity relationships^{37,38}. In other words, plastic changes in

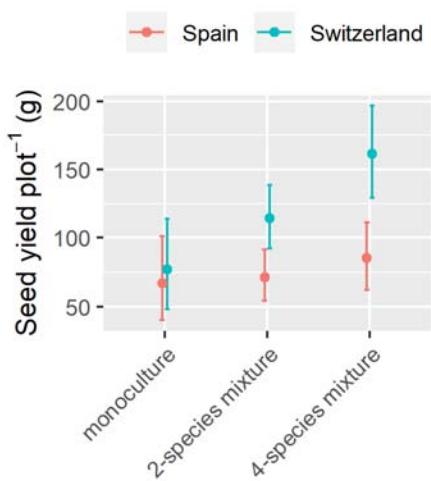
61 resource allocation strategies in response to increasing plant diversity, such as a
62 reduced reproductive effort due to relatively higher resource investment in vegetative
63 plant parts with higher plant diversity, could diminish the biodiversity–seed yield
64 relationship. However, this ecologically 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 m² 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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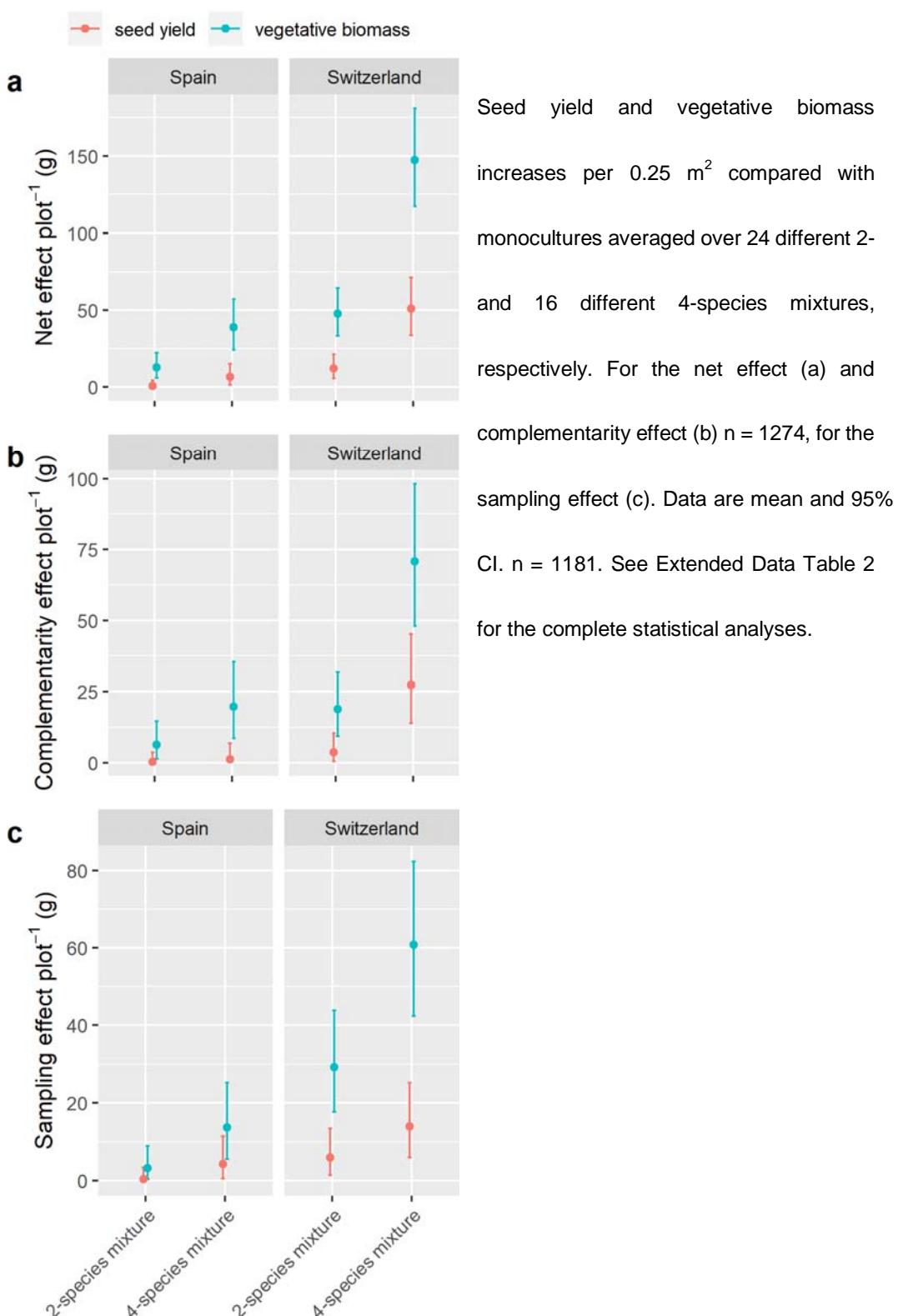
93 Even though crop diversity increased seed yield (Fig. 1), aboveground
94 vegetative biomass increases with increasing crop diversity were 8.8- and 3.1-fold
95 higher in Spain and Switzerland, respectively, than the increases in seed yield. The
96 reduced benefit of crop diversity on seed yield compared 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 effects¹⁷ (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.

104

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

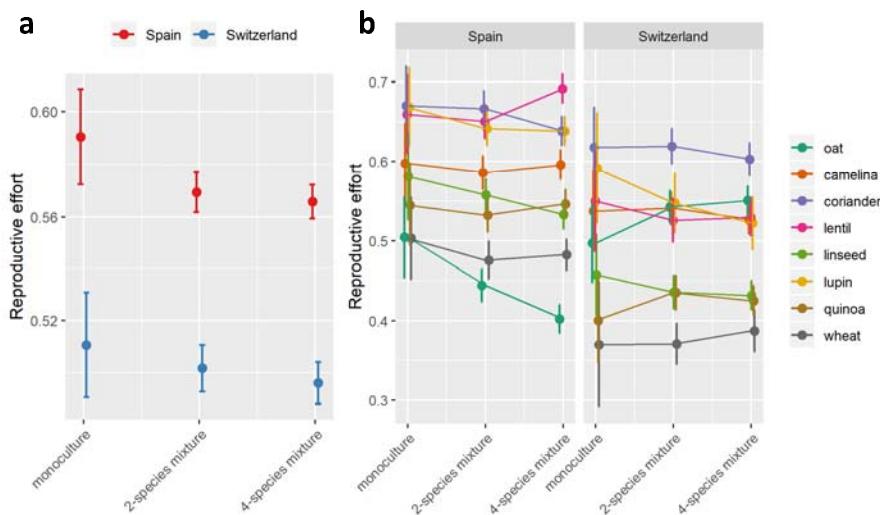


125 In line with these results at the plot level, we found at the individual plant level a
126 clear trend towards reduced reproductive effort with increasing plant diversity (Fig.
127 3a). Reproductive effort in monocultures was higher than in mixtures — an effect
128 only weakly dependent on species 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 conditions³⁹. 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 adaptation⁴⁰ 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*.

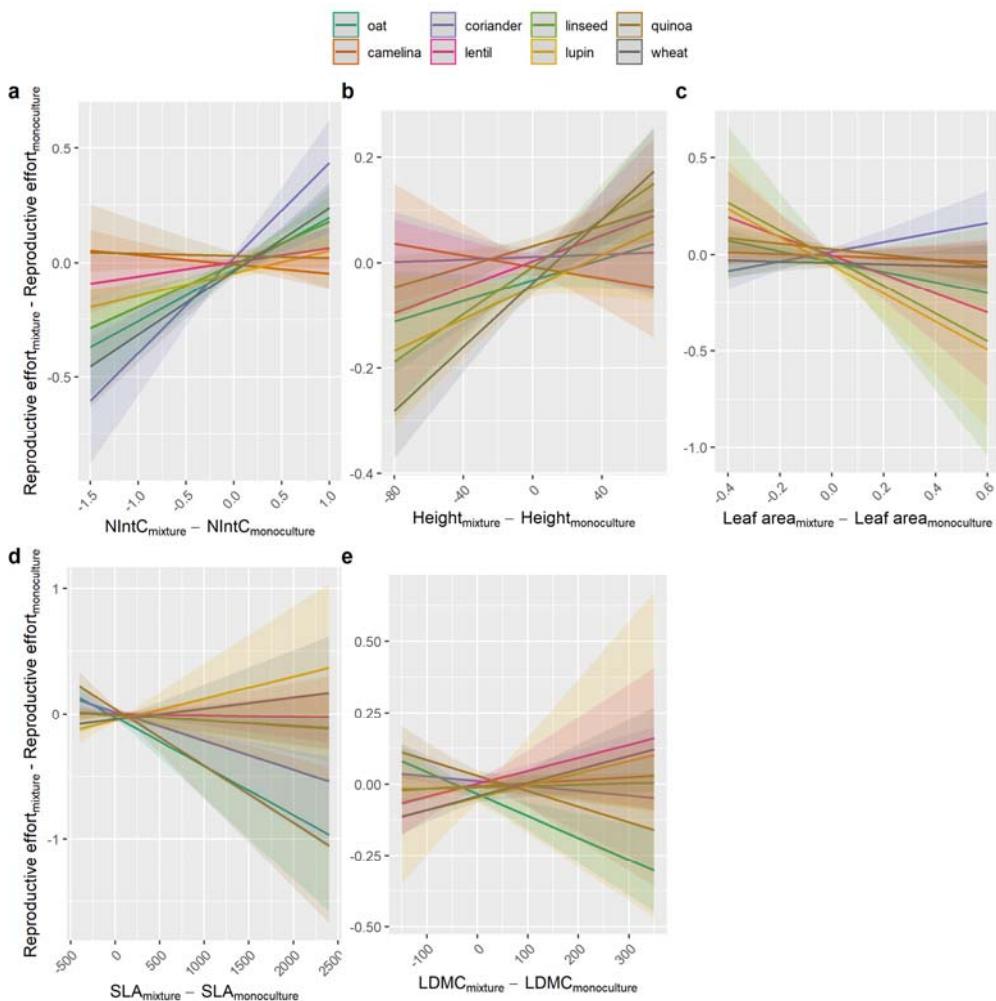
159
160 Reduced reproductive effort in mixtures compared with monocultures was
161 strongly linked to an increase in competition intensity (in particular for coriander,

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 crops⁴¹.
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

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



184
185 The difference in reproductive effort of eight crop species in mixtures compared with
186 monocultures as a function of differences in competition intensity (NIntC; a), vegetative plant
187 height (b), leaf area (c), specific leaf area (SLA; d) and leaf dry matter content (LDMC; e)
188 between mixtures and monocultures. Data are mean and 95% CI. See Extended Data Table 4
189 for the complete statistical analysis. Oat = *Avena sativa*, camelina = *Camelina sativa*,
190 coriander = *Coriandrum sativum*, lentil = *Lens culinaris*, linseed = *Linum usitatissimum*, lupin =
191 *Lupinus angustifolius*, quinoa = *Chenopodium quinoa*, wheat = *Triticum aestivum*.

192 Our study demonstrates that beyond evidence for the benefits of intercropping
193 for seed yield, growing currently available crop cultivars in mixtures does not result in
194 the same amount of resources allocated to seed yield as in monocultures, i.e. the plant
195 community type for which they have been bred and for which reproductive effort has
196 been maximised³. Indeed, the little available evidence about diversity effects on
197 reproductive effort in natural plant populations does not evidence such a reduction in
198 reproductive effort with increasing diversity⁴². This suggests that the current suite of
199 crop cultivars is not appropriate to fully exploit the benefits of crop diversification for
200 global food security, and that specific breeding programs may be required that
201 maximize reproductive effort of crops under mixture conditions. In the same way as
202 breeding for high monoculture yields was based on short-statured genotypes that do
203 not engage so much in intraspecific light competition in monocultures³, it may be
204 possible to breed for high mixture yields if traits can be identified that reduce
205 interspecific competition or increase complementarity and facilitation among species
206 above and below ground in mixtures. According to our results, these breeding
207 programs may benefit from going back to locally adapted cultivars with higher
208 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) and are average values over the years
326 1961 to 1990.

327 Each experimental garden consisted of beds with square plots of 0.25 m² 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/m² for cereals, 240 seeds/m² for
381 superasterids, 592 seeds/m² for non-legume superrosids, and 160 seeds/m² 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

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

402 *Data analyses*

403 Plot-level yield responses to the experimental treatments were assessed using a linear
404 mixed effects model with (1) country, ecotype and home *vs* away; (2) fertilisation,
405 and (3) diversity and species number, and their interactions as fixed effects and
406 species composition and bed ID as random effects. Plot-level yield as the total mass
407 of all seeds produced in a plot was square-root transformed to meet assumptions of
408 parametric statistics. Significance of each factor was assessed using type-I analysis of
409 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 method¹⁷ 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 = reproductive
424 biomass/(vegetative biomass + reproductive biomass). To detect the effects of (1)
425 species, (2) country, ecotype and home, (3) fertilization, (4) species number (two- *vs*
426 four-species) nested within diversity (monoculture *vs* mixture) nested within
427 community (single individual *vs* community) and the possible interactions between
428 these factors on reproductive effort of the crops, we used a linear mixed-effects model
429 and type-I analysis of variance. Reproductive effort was square-root-transformed to
430 meet normality and homoscedasticity of variance assumptions. We included bed ID
431 and plot ID as well as the species composition as random factors into the model.

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

442
$$NIntC = 2 \times [\Delta P / (\Sigma P + |\Delta P|)]$$
.

443 As plant traits we used vegetative plant height, leaf area, SLA and LDMC. SLA and
444 LDMC together reflect a fundamental trade-off in plant functioning between a rapid
445 production of biomass (i.e. high SLA and low LDMC) and an efficient conservation
446 of nutrients (i.e. low SLA and high LDMC)⁴³, and the plant's capacity of endurance
447 and resistance in harsh environment⁴⁴⁻⁴⁶. Vegetative plant height reflects plant's
448 ability to capture light energy in competition through relatively high growth rates^{47,48}.

449 In a linear mixed-effects model we assessed the response of $\Delta RE_{\text{mixture-monoculture}}$ to
450 $\Delta NIntC_{\text{mixture-monoculture}}$, $\Delta height_{\text{mixture-monoculture}}$, $\Delta leaf area_{\text{mixture-monoculture}}$,
451 $\Delta SLA_{\text{mixture-monoculture}}$ and $\Delta LDMC_{\text{mixture-monoculture}}$ and their interactions with species.
452 Bed and plot ID were included as random terms. Statistical significance of each factor
453 was tested with type-III analysis of variance.

454 All analyses were conducted with R version 3.6.2⁴⁹. Reported figures, including
455 means and confidence intervals are for estimated marginal means calculated using
456 `ggemmeans()` in *ggeffects*⁵⁰ and plotted with `plot_model()` in *sjPlot*⁵¹.

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483

484 **Acknowledgements**

485 This work was financially supported by the Swiss National Science Foundation (PP
486 PPOOP3_170645 to CS). JC was supported by the China Scholarship Council.
487 Thanks to C. Barriga Cabanillas, E. P. Carbonell, H. Ramos Marcos, E. Hidalgo
488 Froilán, A. García-Astillero Honrado, R. Hüppi and S. Baumgartner for field
489 assistance.

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

Factor	Net effect						Complementarity effect						Sampling effect																	
	SS	MS	num		den		F-val		P-val		SS	MS	num		den		F-val		P-val		SS	MS	num		den		F-val		P-val	
			DF	DF	DF	DF	ue	ue	DF	DF			DF	DF	DF	DF	ue	ue	DF	DF	ue	ue	DF	DF	DF	DF	ue	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	01			5.3	3	1	0	8	01			6.4	4	1	3	82	01								
	585.				35.5	<0.0			212.				10.7	0.00			191.				15.6	<0.0								
Country	9	585.9	1	23.1	0	01			3	212.3	1	23.4	9	3			6	191.6	1	22.7	5	01								
				610.		0.27					608.			0.12				565.			565.	0.03								
Ecotype	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	4								
				610.		0.46					608.			0.93				565.			565.	0.50								
Home vs Away	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								
						0.10								0.70								0.09								
Fertilisation	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								
				605.	41.4	<0.0			404.			603.	20.5	<0.0			200.			560.	16.3	<0.0								
Species number	683.4	683.4	1	9	1	01			3	404.3	1	9	4	01			4	200.4	1	2	7	01								
					<0.0	0.98							0.30								0.08									
Country × Fertilisation	<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								
				610.		0.00			148.			608.		0.00				565.			565.	0.85								
Ecotype × Fertilisation	119.7	119.7	1	9	7.25	7			4	148.4	1	6	7.54	6			0.4	0.4	1	1	0.04	0								
				610.	11.8	<0.0			264.			608.	13.4	<0.0				565.			565.	0.43								
Home vs Away × Fertilisation	195.5	195.5	1	9	5	01			2	264.2	1	6	2	01			7.5	7.5	1	2	0.61	4								
				605.		0.02			106.			603.		0.02				560.			560.	0.84								
Country × Species number	88.7	88.7	1	8	5.37	1			6	106.6	1	8	5.41	0			0.5	0.5	1	1	0.04	6								
				620.		0.67						617.		0.57				572.			572.	0.41								
Ecotype × Species number	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								
				620.		0.88						617.	<0.0	0.98				572.			572.	0.61								
Home vs Away × Species number	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								
				605.		0.30						603.		0.53				560.			560.	0.98								
Fertilisation × Species number	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								
Organ × Country	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	01
			621.	15.2	<0.0	394.		621.	20.0	<0.0		
Organ x Ecotype	250.9	250.9	1	0	0	01	9	394.9	1	0	7	01
			621.	34.2	<0.0	310.		621.	15.7	<0.0	422.	
Organ x Home vs Away	564.9	564.9	1	0	3	01	8	310.8	1	0	9	01
			621.		0.00	145.		621.		0.00		
Organ x Fertilisation	164.5	164.5	1	0	9.97	2	2	145.2	1	0	7.38	7
			621.		0.00	101.		621.		0.02		
Organ x Species number	150.6	150.6	1	0	9.13	3	8	101.8	1	0	5.17	3
Country x Fertilisation x Species number			605.		0.84			603.		0.61		
	0.6	0.6	1	8	0.04	4	4.9	4.9	1	8	0.25	9
Ecotype x Fertilisation x Species number			620.		0.72			617.		0.73		
	2.1	2.1	1	0	0.13	0	2.2	2.2	1	7	0.11	6
Home vs Away x Fertilisation x Species number			620.		0.82			617.		0.89		
	0.8	0.8	1	0	0.05	4	0.4	0.4	1	7	0.02	1
			621.		0.01	259.		621.	13.1	<0.0		
Organ x Country x Fertilisation	100.8	100.8	1	0	6.11	4	1	259.1	1	0	6	01
			621.		0.83			621.		0.22		
Organ x Ecotype x Fertilisation	0.7	0.7	1	0	0.04	8	28.8	28.8	1	0	1.46	7
Organ x Home vs Away x Fertilisation			621.	12.7	<0.0			621.		0.08	102.	
	210.9	210.9	1	0	8	01	57.9	57.9	1	0	2.94	7
			621.		0.47			621.		0.36		
Organ x Country x Species number	8.5	8.5	1	0	0.52	2	16.1	16.1	1	0	0.82	6
			621.	<0.0	0.97			621.		0.32		
Organ x Ecotype x Species number	<0.1	<0.1	1	0	1	3	19.1	19.1	1	0	0.97	5
Organ x Home vs Away x Species number			621.		0.17			621.		0.76		
	29.9	29.9	1	0	1.81	9	1.8	1.8	1	0	0.09	4
Organ x Fertilisation x Species number			621.		0.71			621.		0.44		
	2.3	2.3	1	0	0.14	1	11.4	11.4	1	0	0.58	7
Organ x Country x Fertilisation x Species number			621.		0.79			621.		0.88		
	1.1	1.1	1	0	0.07	8	0.4	0.4	1	0	0.02	8
Organ x Ecotype x Fertilisation x Species number			621.		0.84			621.	<0.0	0.94		
	0.7	0.7	1	0	0.04	1	0.1	0.1	1	0	1	8
								621.		38.5	38.5	1
										1	1	3.14
												7

Organ × Home vs Away ×															
Fertilisation × Species number	0.4	0.4	1	621.	0	0.03	0.87	12.5	12.5	1	621.	0	0.63	0.42	575.
															0.39
<hr/>															
Random effects	Varia			Varia			Varia			Varia			Varia		
	n	nce	SD	n	nce	SD	n	nce	SD	n	nce	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				

515

516 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
 517 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 $R^2 =$
 518 0.72.

519

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

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

522

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

524

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
ΔN_{IntC}	0.534	0.534	1	1588.5	51.09	<0.001
Δ Height	0.212	0.212	1	1539.5	20.27	<0.001
Δ Leaf area	0.097	0.097	1	1588.8	9.31	0.002
Δ SLA	0.096	0.096	1	1576.9	9.23	0.002
Δ LDMC	<0.001	<0.001	1	1578.8	<0.01	0.984
Species \times ΔN_{IntC}	0.509	0.073	7	1580.9	6.96	<0.001
Species \times Δ Height	0.233	0.033	7	1583.6	3.19	0.002
Species \times Δ Leaf area	0.212	0.030	7	1580.6	2.89	0.005
Species \times Δ SLA	0.245	0.035	7	1579.7	3.35	0.002
Species \times Δ LDMC	0.259	0.037	7	1582.1	3.54	<0.001
<hr/>						
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

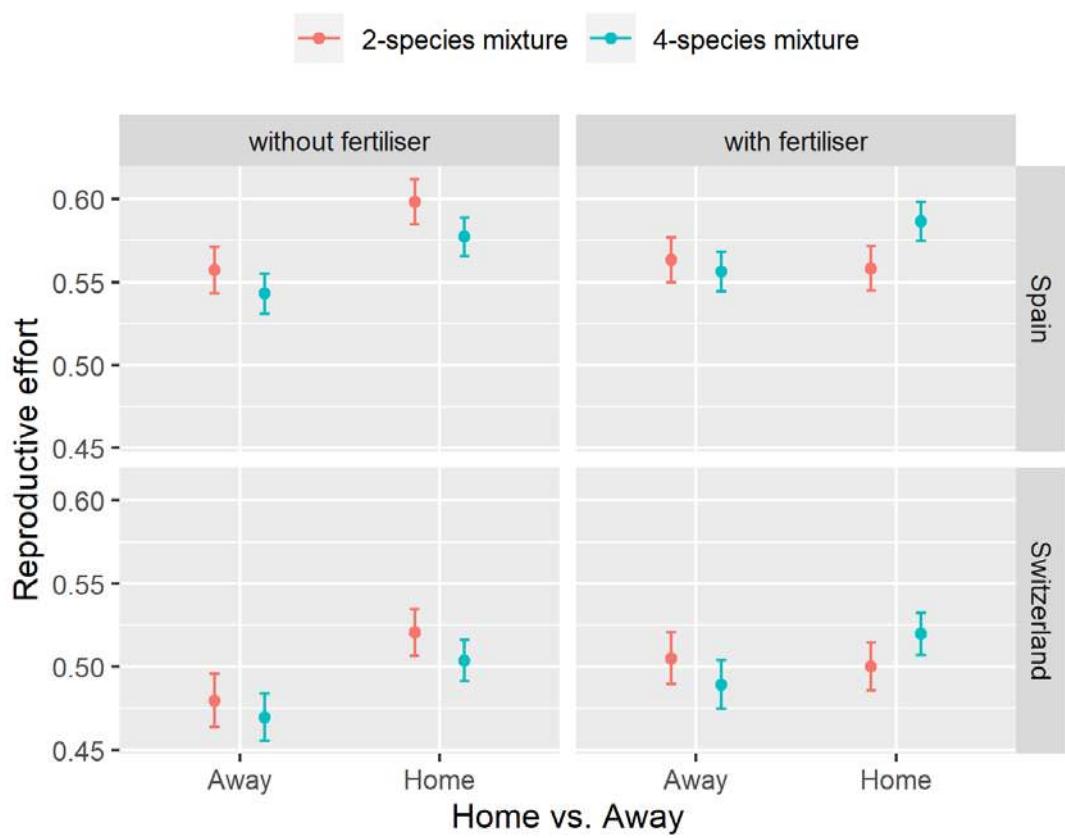
530 **Extended Data Table 5 | Cultivar and seed supplier for the crop species used in the**
531 **experiment**

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

532

533

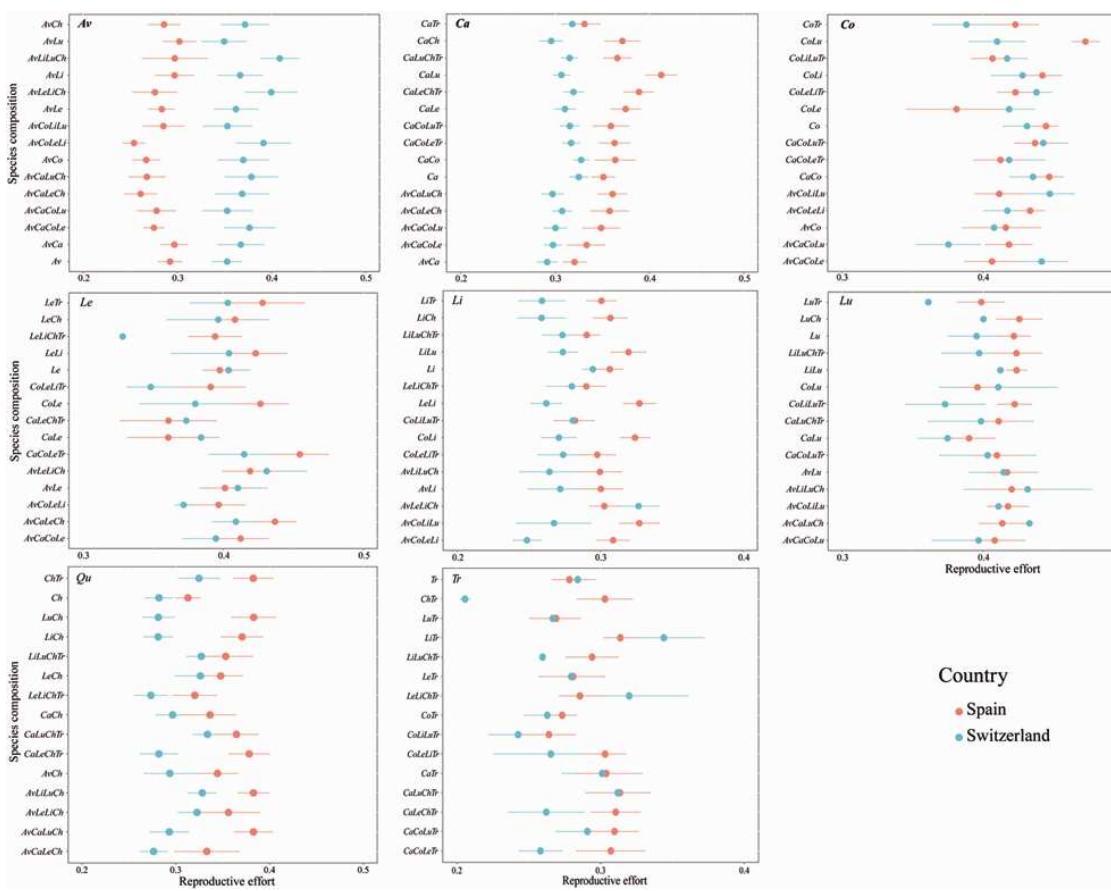
534 **Extended Data Fig. 1 | Reproductive effort of crops in response to the Home vs Away,**
535 **Fertilization, Country and Species number (2- vs 4-species mixtures) treatments**



536

537

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

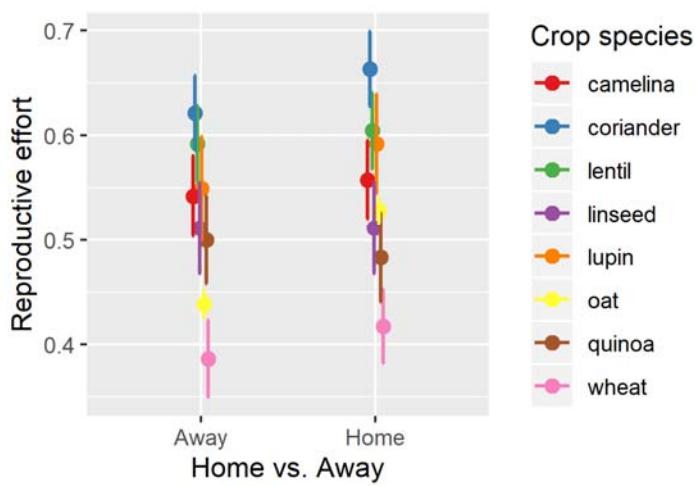


540

541 Species were abbreviated as: *Avena sativa* = Av, *Triticum aestivum* = Tr, *Camelina sativa* =
 542 *Chenopodium quinoa* = Qu, *Lens culinaris* = Le, *Lupinus angustifolius* = Lu, *Linum*
 543 *usitatissimum* = Li and *Chenopodium quinoa* = Ch.

544

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



547

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