




## LETTER

# Plant domestication disrupts biodiversity effects across major crop types

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### Abstract

Plant diversity fosters productivity in natural ecosystems. Biodiversity effects might increase agricultural yields at no cost in additional inputs. However, the effects of diversity on crop assemblages are inconsistent, probably because crops and wild plants differ in a range of traits relevant to plant–plant interactions. We tested whether domestication has changed the potential of crop mixtures to over-yield by comparing the performance and traits of major crop species and those of their wild progenitors under varying levels of diversity. We found stronger biodiversity effects in mixtures of wild progenitors, due to larger selection effects. Variation in selection effects was partly explained by within-mixture differences in leaf size. Our results indicate that domestication might disrupt the ability of crops to benefit from diverse neighbourhoods *via* reduced trait variance. These results highlight potential limitations of current crop mixtures to over-yield and the potential of breeding to re-establish variance and increase mixture performance.

### Keywords

Biodiversity-ecosystem functioning, complementarity effects, crop ecology, diversity-productivity relationship, evolution, functional traits, genetic variation, over-yielding, polycultures, selection effects.

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## INTRODUCTION

Global agricultural production needs to rise by 60–110% to accommodate the projected demands for food by 2050 (Tilman *et al.* 2011). This constitutes a major challenge, in particular if it is to be met without substantial expansion of croplands and reduced usage of synthetic fertilisers and pesticides (Foley *et al.* 2011; Gurr *et al.* 2016; Wan *et al.* 2018). Therefore, farming practices that increase crop production in a sustainable way are needed. The promotion and management of biodiversity effects, that is, higher productivity of species mixtures than expected from their respective monocultures, might contribute to address this challenge (Brooker *et al.* 2015; Isbell *et al.* 2017; Martin-Guay *et al.* 2018). However, while biodiversity effects have been solidly demonstrated in natural ecosystems (Loreau & Hector 2001; Tilman *et al.* 2001; Hooper *et al.* 2005; Cardinale *et al.* 2011), the literature reports contrasting responses in mixtures of arable crops, ranging from positive (Kjær *et al.* 2009; Lin 2011; Reiss & Drinkwater 2018) to negative (Pimentel *et al.* 2005; Letourneau *et al.* 2009; Snapp *et al.* 2010), with considerable variation between years, locations and crop species (Fridley 2002; Hauggaard-Nielsen *et al.* 2008; Smith *et al.* 2008; Snapp *et al.* 2010). Here, we argue that evolution of plant phenotypes after domestication might partly account for such discrepancies between the behaviour of wild and crop plants in mixtures.

Experiments in agricultural and natural settings use different experimental setups, which might explain part of the disparities (Brooker *et al.* 2015). For instance, biodiversity-

ecosystem functioning (BEF) experiments use regular spacing among plants and keep fixed plantation densities (Trenbath 1974; Schmid & Hector 2004; Bruelheide *et al.* 2014; Schmid *et al.* 2017). Experiments with crops use more variable spatial arrangements (e.g. intercropping patterns, Malézieux *et al.* 2009), and generally very different metrics (land equivalent ratios vs. additive partitioning of biodiversity effects; Adetiloye & Ezedinma 1983; Loreau & Hector 2001). Therefore, different methods might result in discordant biodiversity effects. Another cause of discrepancy might be the values of the traits of the plant species and genotypes involved in the mixtures.

Crop phenotypes are different from those of their wild progenitors (Meyer *et al.*, 2012) or other wild plants (Milla *et al.* 2018). Herbaceous crops are generally larger seeded than their wild relatives, have lost seed dormancy and dispersal mechanisms, and show erect and compact growth habits (Harlan *et al.* 1973; Meyer *et al.*, 2012). Further traits that might have changed after crop domestication can be relevant for plant performance in mixtures. For example, increased plant canopy height and leaf area after domestication (Milla *et al.* 2014; Milla & Matesanz 2017) suggest that crops are stronger competitors for light than their wild progenitors. Additionally, genetic bottlenecks (due to selection processes by early farmers) and crop breeding for maximum monoculture yield have substantially reduced the genetic diversity of crops (Tanksley & McCouch 1997; Doebley *et al.* 2006; Zeder 2006). This reduction in genetic diversity might lead to increased

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phenotypic uniformity, that is, constant phenotypes in different environments (Bloomfield *et al.* 2014). Genetic variability and phenotypic plasticity trigger resource use complementarity in mixtures (Malézieux 2012; Zeller *et al.* 2012; Zupping-Dingley *et al.* 2014; Prieto *et al.* 2015). Indeed, a recent study employing genetically divergent *Arabidopsis* accessions suggests that biodiversity effects can be partly tractable in the genotype (i.e. allelic mixtures at locus Chr4@16.92 were more productive in terms of biomass than the most productive monoallelic community; Wuest & Niklaus 2018). Thus, if domestication and further breeding have reduced genetic diversity and increased constancy of phenotypes, achieving higher productivity in crop mixtures through increased niche complementarity might be compromised.

In addition, recent evolution under monoculture might also have diminished the ability of crops to perform in mixtures. Current genotypes of major arable crops were selected to maximise yields in monospecific stands (Weiner *et al.* 2017), which entailed adaptations to perform in an intraspecific neighbourhood (e.g. high phenological synchrony). In contrast, wild plants composing the natural and seminatural grasslands typical of BEF experiments, as well as crop wild progenitors, have evolved in mixed plant communities for their entire evolutionary history. Local adaptations to a diverse neighbourhood can evolve over short-time periods and differently depending on the biotic (Zupping-Dingley *et al.* 2014) and abiotic conditions (i.e. elevated CO<sub>2</sub>; Kleynhans *et al.* 2016). Indeed, competitive hierarchies and further adaptations through niche differentiation or facilitation (which are the mechanisms underlying biodiversity effects) are more likely to evolve in diverse communities than in monospecific stands (Schöb *et al.* 2018). A recent study found that biodiversity effects in mixtures of genotypes with a recent history of coexistence were higher than in mixtures of genotypes with a monoculture history (Zupping-Dingley *et al.* 2014). Importantly, in a short period of 8 years of co-selection history in mixtures, plants evolved adaptations to improve over-yielding (Zupping-Dingley *et al.* 2014). Given

that most crop species have been selected under monoculture conditions over centuries, the results of Zupping-Dingley *et al.* (2014) suggest that crop plants might be less suited to over-yielding in mixtures, and might benefit less from biodiversity effects than their wild progenitors.

The primary goal of this study was to investigate how domestication has affected the ability of annual crops to deliver biodiversity effects. Specifically, we compared the performance and functional trait diversity of assemblages of annual crops and of their wild progenitors, set to grow in mesocosms of varying levels of diversity. We hypothesised that: (1) crop species will show lower biodiversity effects than their wild progenitors, and (2) weak biodiversity effects in crop mixtures will be driven by increased similarity in functional traits within assemblages.

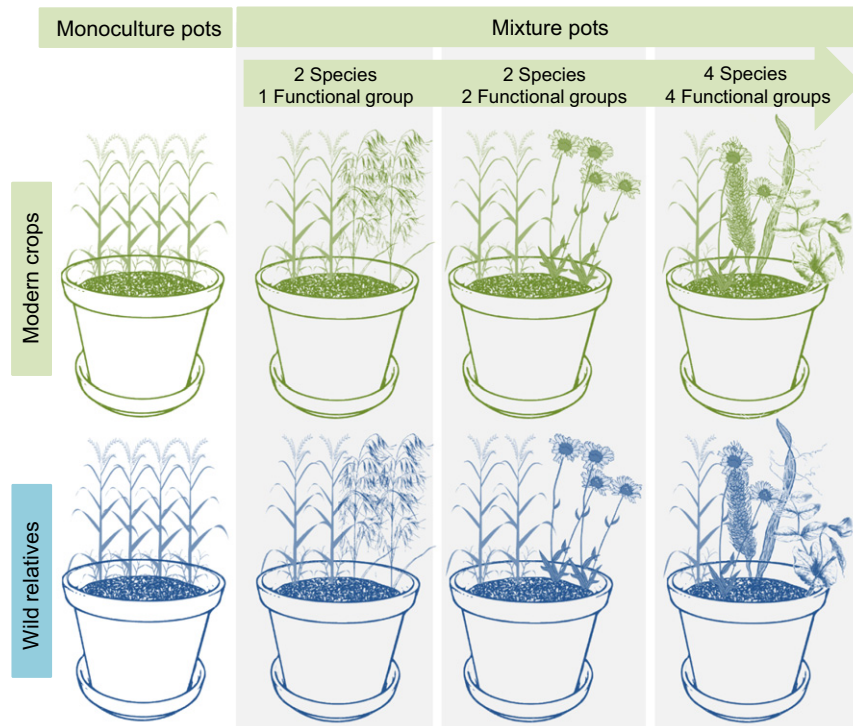
## MATERIAL AND METHODS

To test whether domestication has affected the ability of annual crops to perform in mixtures, we conducted a biodiversity-ecosystem functioning (BEF) experiment with annual crop species. We selected eight crops (two forbs, two C<sub>3</sub> grasses, two C<sub>4</sub> grasses, and two legumes), and gathered seeds of a domesticated and a wild progenitor accession of each (Table 1). We grew and harvested each species in monoculture and in three types of mixtures, separately for wild progenitor and domesticated accessions. To calculate biodiversity effects, we followed the additive partitioning method of Loreau & Hector 2001, and partitioned net biodiversity effects into complementarity and selection effects. Additionally, we measured a suite of plant traits (height, leaf area, leaf mass per area, and leaf mass fraction) that influence growth and plant–plant interactions in mixtures (Litrico & Violle 2015; Prieto *et al.* 2015). We calculated within-mixture trait differences (i.e. ratio between absolute differences and trait means) to address whether differences in the ability to over-yield are modulated by phenotypic diversity within assemblages.

**Table 1** Botanical and common names of the domesticated (crops) and wild progenitors and functional group of the set of species used in the experiment

Crop name	Botanical name	Domestication status	Botanic family	Functional group
Sunflower	<i>Helianthus annuus L.</i>	C	Asteraceae	Forbs
	<i>Helianthus annuus L.</i>	W		
Tomato	<i>Solanum lycopersicum L.</i>	C	Solanaceae	
	<i>Solanum pimpinellifolium L.</i>	W		
Durum wheat	<i>Triticum durum (Desf.)</i>	C	Poaceae	C <sub>3</sub> grasses
	<i>Triticum diccoides (Körn. Ex Asch. &amp; Graebn.) Schweir</i>	W		
Oats	<i>Avena sativa L.</i>	C		
	<i>Avena sterilis L.</i>	W		
Sorghum	<i>Sorghum bicolor (L.) Moench</i>	C		C <sub>4</sub> grasses
	<i>Sorghum arundinaceum (Desv.) Stapf.</i>	W		
Millet	<i>Pennisetum glaucum (L.) R.Br.</i>	C		
	<i>Pennisetum glaucum (L.) R.Br.</i>	W		
Peas	<i>Pisum sativum L.</i>	C	Fabaceae	Legumes
	<i>Pisum sativum subsp. elatius (M. Brieb) Asch. &amp; Graebn.</i>	W		
Cow peas	<i>Vigna unguiculata (L.) Walp.</i>	C		
	<i>Vigna unguiculata (L.) Walp.</i>	W		

Domestication status: C = crop; W = wild progenitor.



**Figure 1** Experimental setup. Monocultures hosted four individuals of a given genotype, and were replicated 5–6 times for each of the 16 genotypes in the experiment ( $n = 94$  pots). Three types of mixtures of increasing levels of functional diversity were set up, separately for domesticated genotypes (green) and wild progenitors (blue): (1) mixtures of two species of the same functional group ( $n = 63$  pots), (2) mixtures of two species of two functional groups ( $n = 141$  pots), and (3) mixtures of four species of four different functional groups ( $n = 63$  pots).

### Study system and experimental design

To include the most prominent functional groups in annual croplands, we used two species of each of the major functional groups of annual crops:  $C_3$  grasses,  $C_4$  grasses, legumes, and forbs (Table 1). Plants were grown in 6L pots with a fixed density of four individuals across all treatments. Individuals of the 16 accessions were grown in monocultures and in mixtures. Each type of mixture included all possible combinations of species and functional groups in the experiment, separately for wild progenitor and domesticated accessions. We built three types of mixtures: one type of within-functional group polycultures and two types of among-functional group polycultures (Fig. 1). Within-functional group polycultures were composed of two individuals of two different species of a given functional group. The among-functional group polycultures consisted either of a mix of two different species of two different functional groups, or a mix of four different species, belonging each to one of the four functional groups. We implemented four levels of increasing diversity: monocultures (16 combinations, 94 pots), within-functional group two species mixtures (two species of the same functional group; 8 combinations; 63 pots), among-functional group 2-species mixtures (two species from two different functional groups; 48 combinations; 141 pots), and among-functional group 4-species mixtures (four species of four different functional groups; 32 combinations; 63 pots). Experimental design, treatments, and species combinations within each treatment are summarised in Table S2. Detailed information about the

assignment of wild progenitors, or seed accession identifiers and seed donors can be found in Table S1.

### Growth conditions

In May 2016, seeds of each accession were germinated in small individual pots ( $6 \times 4 \times 4$  cm) filled with commercial topsoil (Klasmann; Traysubstrate 060). Once germinated, and as soon as transplanting was feasible without compromising plant establishment, randomly selected seedlings were transplanted to the experimental pots ( $25 \times 15.5 \times 15.5$  cm, 6L). The pots were filled with conventional, washed river sand and supplemented with slow-release fertiliser ( $8 \text{ gdm}^{-3}$ ; Basacote Plus 6M; Compo, Barcelona, Spain; see fertiliser components on Table S3). The amount of fertiliser was set to grow plants under high-nutrient availability conditions (Day *et al.* 2003). All pots were randomly located on three greenhouse benches at Universidad Rey Juan Carlos, Mostoles-Madrid, central Spain ( $40^\circ 18' 48''$  N,  $3^\circ 52' 57''$  W), and received full sun (mean midday photosynthetically active radiation [PAR] *c.*  $1200 \mu\text{mol m}^{-2}\text{s}^{-1}$ , measured in three consecutive clear days of the experiment; LI-COR, Lincoln, NE, USA). Watering was applied regularly via sprinklers to maintain the pots at 80–90% of their field water holding capacity. Pots were regularly weeded to keep the species composition as designed. Replacement of dead seedlings took place during the first 10 days of the experiment, by seedlings of the same age. After that period, all pots lacking one or more individuals were discarded. The experiment ran until reproductive development

was observed in the earliest flowering accessions, which set the harvest date of the experiment. Pesticides were not needed during the experiment. Details on the number of replicates per treatment and domestication status can be found in Table S2.

### Measurement of traits, harvest and calculation of within-pot trait differences

To explore how the variation in functional traits within pots (character displacement) underlies biodiversity effects, we measured plant height (h), leaf area (LA), leaf mass per area (LMA) and leaf mass fraction (LMF). Plants that hold more than optimal h or LA are competitively superior in intercepting light and generally displace shorter and smaller-leaved species (Westoby *et al.* 2002; Anten 2005). High variation in h and/or LA is often associated with increased productivity via selection effects (Cadotte 2017). LMF is directly and LMA is inversely related to plant relative growth rate (RGR; Reich *et al.* 1997; Poorter & Garnier 1999). Variation in LMA in stands is related to different light-use strategies and increased productivity via complementarity (Roscher *et al.* 2015; Cadotte 2017). LMF is the proportion of biomass allocated to leaves. At high densities, variation in LMF would indicate different strategies to capture light and other resources (Poorter *et al.* 2012).

Measurements of all traits were performed at the individual level. Plant height (h; cm) was measured just before harvest, when reproductive development started in the earliest flowering accession (5 weeks after transplanting into the experimental pots). Aboveground biomass was harvested at ground level separately for each individual in the experiment, separated into leaves and other organs, and oven dried at 65 °C for 3 days prior to weighting. Leaf area was measured as the lamina area (LA, in mm<sup>2</sup>) of a representative leaf by scanning a fresh leaf immediately after plant harvest, and its dry mass was used to calculate leaf mass per area (LMA, in g mm<sup>-2</sup>). Leaf mass fraction (LMF, unitless) was measured as the ratio of the total leaf mass to the total dry mass of each individual plant. To calculate the relative differences in height, leaf area, LMA and LMF within pots, we calculated all the absolute differences between each two individuals of a pot divided by the mean of the two, and then calculating the mean of all the values.

### Calculations of biodiversity effects

Biodiversity effects are based on the differences between the observed yields of each species in mixtures compared to monocultures, and may be partitioned into complementarity effects (CEs) and selection effects (SEs) following the approach of Loreau & Hector 2001. CEs measure if species' yields in a mixture are on average higher or lower than expected by the relative yields of the component species in monoculture. Positive CEs are indicative of niche partitioning and facilitative interactions resulting in an increase in total resource use, while negative complementarity effects indicate competitive interactions among plants resulting from either chemical or physical interferences (Loreau & Hector 2001). SEs are measured as the covariance between the deviation

from the expected relative yield of a species in a mixture and the yield of the same species in monoculture. SEs occur when the change in the relative yield of a species in a mixture is a function of its yield in monoculture (i.e. a species with high or low yield in a monoculture yields disproportionately more, or less, respectively, in mixture). Net effects (NEs) are the sum of CEs and SEs. All three effects can be either positive or negative. NE has an expected value of zero under the null hypothesis of no biodiversity effects (see the Supporting Information for calculation details).

### Statistical analyses

#### *Biodiversity effects in crops vs. wild progenitors and across diversity levels*

We compared the performance of wild and domesticated plant species mixtures using mixed effects models with residual maximum likelihood estimation. Significance tests were based on approximate *F*-tests. Biodiversity effects (NEs, CEs and SEs; g/pot) were the response variables in the models. Absolute values of NEs, CEs and SEs were square root- or log-transformed to meet assumptions of homoscedasticity, and after that, their original signs put back to the transformed values for analyses, which allowed maintaining the direction of the effects (Loreau & Hector 2001). The fixed terms of the model were, in this order, bench (three levels), domestication status (DOM: crop vs. wild), species richness (SPr: two vs. four species), functional group richness (FGr: one vs. two functional groups), functional group combination (FG comb: eleven levels), and their interactions. Not all possible combinations between functional group richness and species richness existed. Several of the combinations are impossible (e.g. four functional groups and one species) while others are possible but were not included in the design (e.g. one functional group and four species, or two functional groups and two species). To deal with such a non-fully factorial design, we used a nested structure of the fixed-effect terms. Thus, FGr (one vs. two functional groups) was nested within SPr (two vs. four species), in such a way that the factor FGr only applies to one level of SPr, that is, two species. A total of 267 biodiversity effects were calculated in mixture pots (more details in Table S2). Species combination was used as a random intercept term. No outliers were excluded from the analyses. The full model is shown in Table 2. To test whether the results were consistent across functional groups, we split the data into four smaller, overlapping, data sets, by the presence of each functional group (legumes, forbs, C<sub>4</sub> grasses or C<sub>3</sub> grasses) in the pots. Then, we performed the analyses for each of these new data sets and tested the effects of the different predictors on biodiversity effects separately per functional group.

#### *Relative differences in traits between domestication statuses and their relationships to biodiversity effects*

To test whether character displacement within pots is the underlying mechanism of biodiversity effects, we tested whether the relative differences in traits follow the same significant direction as CE or SE does for crops and wilds. For this purpose, we used the mean relative differences for a given trait in mixture pots as a response variable, using the same mixed model as the one employed for explaining the



**Table 2** Results of mixed effects ANOVA for the biodiversity effects in mixtures

Source of variation	numDf	NE			CE			SE		
		denDf	F	P	denDf	F	P	denDf	F	P
Bench	2	204.08	1.73	0.178	211.93	4.26	<b>0.015</b>	220.58	3.09	<b>0.047</b>
Domestication status: wild versus crop	1	211.89	4.82	<b>0.029</b>	211.82	0.61	0.433	211.96	8.33	<b>0.004</b>
Species richness: two versus four	1	32.01	0.20	0.656	31.90	0.62	0.435	31.80	4.08	<b>0.051</b>
Functional group richness: one versus two	1	20.72	0.16	0.692	18.41	0.07	0.788	13.28	6.78	<b>0.021</b>
Functional group combination	8	24.78	0.69	0.68	22.94	0.57	0.786	18.27	2.42	<b>0.055</b>
Domestication status: wild versus crop × Species richness: two versus four	1	211.39	0.03	0.842	211.65	0.01	0.913	212.27	0.15	0.694
Domestication status: wild versus crop × Functional group richness: one versus two	1	210.40	1.06	0.302	210.53	3.48	0.063	210.91	0.059	0.807
Domestication status: wild versus crop × Functional group combination	8	210.62	1.47	0.168	210.79	1.77	0.084	211.29	1.901	<b>0.061</b>
Random terms	<i>n</i>	vc			vc			vc		
Species combination	44	0.7378			5.884			0.209		
Residual	267	1.7757			19.532			1.471		

NE, net effects; CE, complementarity effects; SE selection effects; numDf, degrees of freedom term; denDf, degrees of freedom of the error term; *F*, variance ratio; *P*, error probability; statistical significance  $P \leq 0.5$ ;  $P < 0.01$ ,  $P < 0.001$  are indicated in bold; *n*, number of replicates for random effects; VC, variance component.

biodiversity effects (NE, CE and SE) in crops vs. wilds progenitors. The full model is presented in Table S5. To directly test the association between biodiversity effects and the differences in particular functional traits, we ran mixed models using the biodiversity effects (NE, CE and SE) as response variable, but adding the mean differences per trait as an explanatory variable. This model is presented in Table S6. When the variation in a given functional trait correlated with CEs or SEs, we explored these specific relationships further using standardised major axis (SMA) regressions (Warton *et al.* 2012). First, we fitted SMA regressions separately for crops and for wild progenitor pots and tested for a common slope using a Bartlett-corrected likelihood ratio test (Warton & Weber 2002). If the assumption of a common slope was justified, a Wald test was performed to identify significant differences in elevation and shifts along the common axis between crops and wild progenitors.

All statistical analyses were conducted using R version 3.4.2 (R Core Team 2017). Mixed models were fitted using the function *lmer* from package *lme4* (Bates *et al.* 2015). Significance of the fixed factors was assessed with type I ANOVA tests from the package *lmerTest* (Kuznestsova *et al.* 2017). We estimated conditional (variance explained by fixed and random factors) and marginal  $R^2$  (variance explained by fixed factors alone) using the function *r.squaredGLMM* from the *MuMIn* package (Barton 2014). SMA analyses were performed using the *smart* library in R (Warton *et al.* 2012). Plots were produced using *ggplot2* (Wickham 2016).

## RESULTS

### Biodiversity effects in mixtures of crops vs. mixtures of wild progenitors

Net biodiversity effects were significantly higher in mixtures of wild progenitors than in the mixtures of their domesticated counterparts (Fig. 2a; Table 2;  $P = 0.029$ ). Differences in NEs

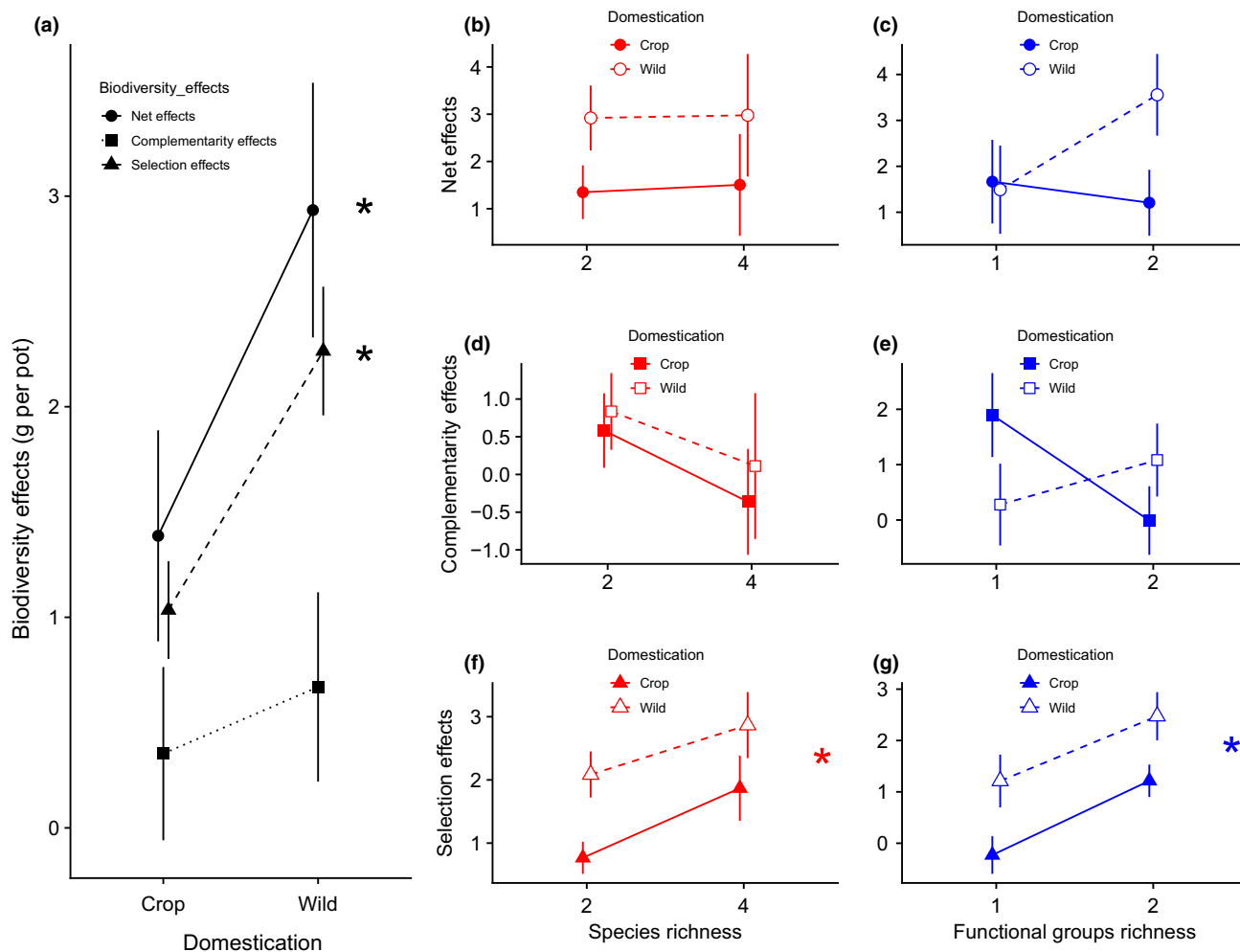
between domestication statuses were largely driven by stronger positive SEs in the mixtures of wild progenitors compared with the mixtures of crops (Fig. 2a; Table 2;  $P = 0.004$ ). Biomass was 12% higher, on average, in the mixtures of wild progenitors compared to the biomass expected from monocultures (Fig. S5). The effects of plant domestication status on SE were consistent across the four functional groups evaluated (Fig. S1; Table S2). Complementarity effects were also generally positive, but similar among domestication statuses (Fig. 2a).

Increasing diversity from two to four species or from one to two functional groups had no significant effects on NEs (Fig. 2b and c). The effects of species richness ( $P = 0.051$ ) and functional group richness ( $P = 0.021$ ) on SE were positive in both mixtures of crops and wild progenitors (Fig. 2f, g; Table 2). Although CE decreased with increasing levels of species richness (Fig. 2d), this negative effect of species richness on CE was not significant. Conversely, functional group richness increased CE in crop mixtures but decreased in mixtures of wild progenitors (interaction between domestication status and functional group richness;  $P = 0.06$ ; Table 2). This trend was stronger in the pots containing  $C_4$  grasses (Fig. S2b for  $C_4$  grasses; Table S2;  $P = 0.001$ ).

### Functional trait differences as drivers of variation in biodiversity effects

Character displacement within mixtures varied between domesticated crops and their wild progenitors in a trait-specific manner. Crop mixtures showed lower variation in leaf area than their wild progenitors (Fig. 3b;  $P < 0.001$ ), and higher variation in LMA and LMF ( $P = 0.011$  and  $P < 0.001$  respectively; Fig. S4; Table S5). Variation in plant height was similar in pots of wilds and domesticated crops ( $P = 0.118$ ; Figure S4; Table S5).

Selection effects correlated positively with the relative differences in leaf area ( $P = 0.019$ ;  $R_m^2 = 0.38$ ;  $R_c^2 = 0.71$ ; Fig. 3a;



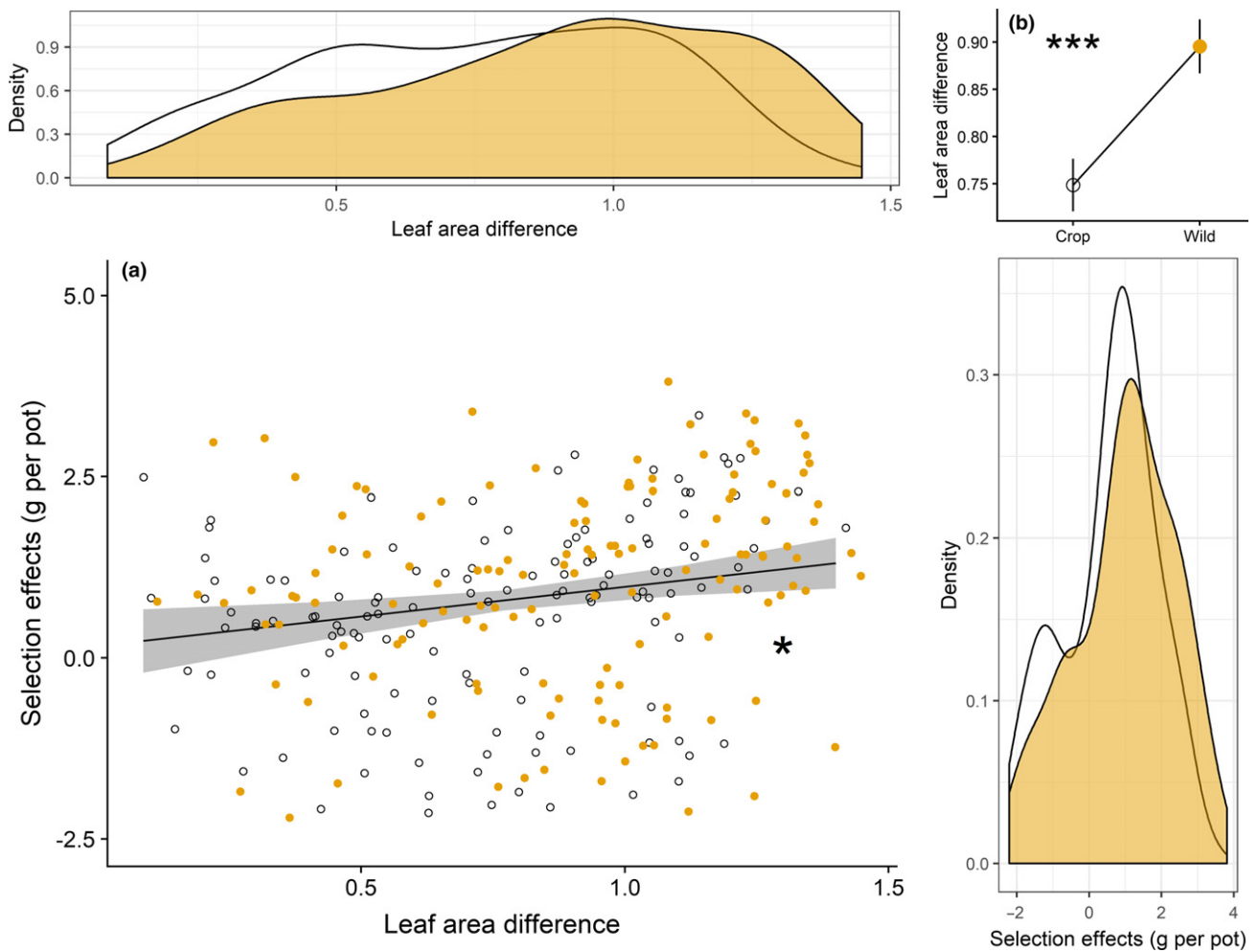
**Figure 2** Biodiversity effects across domestication statuses and diversity levels. (a) Biodiversity effects (net, complementarity and selection effects) in the mixtures of domesticated crops and wild progenitors. Biodiversity effects were assessed by additive partitioning of net effects, and decomposed into complementarity and selection effects ( $n = 272$ ). (b–g) Biodiversity effects split into net, complementarity and selection effects of crops and their wild progenitors, grouped per increasing species richness (red) and functional group richness (blue). Values are means  $\pm$  standard error of the mean (sem) calculated from raw data. These data are shown separately per functional group (legumes, forbs, C<sub>3</sub> or C<sub>4</sub> grasses) in the Supporting Information (Figures S1, S2 and S3)

Table S6) and plant height ( $P < 0.001$ ;  $R_m^2 = 0.39$ ;  $R_c^2 = 0.69$ ; Figure S4; Table S6). Therefore, given that wild mixtures showed higher variation in leaf area than crops, and that such variation correlated with SEs, we explored this relationship further using SMA regression (Warton *et al.* 2012). SEs were significantly correlated with leaf area differences across domestication statuses ( $P < 0.001$ , slope = 4) and individually for both samples. SMA slopes were significantly different from zero (domestic crops:  $P < 0.01$ , slope = 3.96, wild progenitors:  $P < 0.01$ , slope = 4.12), homogeneous among domesticated and wild progenitors ( $P > 0.05$ ), and with a significant shift along the common slope ( $P < 0.001$ ). Thus, SMA analyses support the results (1) that SEs are partly explained by differences in leaf area within pots, and (2) that pots of wild progenitors have more diverse leaf area scores compared to domesticated crops (see Fig. 3). Additionally, SMA analyses show that diversity in leaf area within pots affects SEs in a similar way and intensity (i.e. slope) in domesticated and wild

assemblages, though at different positions along the difference-in-leaf-area range.

## DISCUSSION

Our results show that diversity promotes productivity also in arable crops, but suggest that through the course of plant domestication crop varieties have lost part of their capability of delivering biodiversity effects. We found greater biodiversity effects in wild progenitors' assemblages, compared to their crop counterparts, and provide evidence that crops might have lost their ability to benefit from biodiversity effects via reduced functional trait variation within mixtures. Interestingly, the stronger biodiversity effects shown by wild progenitors are attributable to stronger selection effects, which in turn were primarily associated with larger differences in leaf size. Positive selection effects occur when species with higher than average biomass in monoculture yield higher than



**Figure 3** Relative differences in leaf area between domestication statuses and their relationships to selection effects. (a) Relationship between selection effects and the relative differences between species within mixtures pots. The solid line shows the slope of a mixed effects model. The grey area shows the 95% confidence intervals of the fit line. Data points are observed scores for crops (hollow dots) and wild progenitors (yellow). The marginal density plots for the selection effects and the relative differences in leaf area are shown split for crops (hollow area) and wild progenitors (yellow area). (b) Relative differences of leaf area within pots, for each domestication status in mixture assemblages. Values are means  $\pm$  standard error of the mean, calculated from raw data. Significance of the regression slope and significant differences between domestication statuses at the inset are indicated by asterisks ( $***P < 0.001$ ;  $**P < 0.01$ ;  $*P < 0.05$ ). The same relationships for the relative differences in height, leaf mass fraction (LMF) and leaf mass area (LMA), and the selection effect are provided in Supporting Information (Figure S4).

expected in mixture. Functional differences within assemblages are relevant to plant–plant interactions and underlie biodiversity effects, either because they promote a complementary use of resources or because they trigger selection effects (Fox 2005; Malézieux *et al.* 2009; Zuppinger-Dingley *et al.* 2014; Prieto *et al.* 2015). However, functional differences are different between crops and wild plants (Meyer *et al.*, 2012; Milla *et al.* 2014). Thus, it is possible that some trait values, or combinations of trait values, necessary for enhancing yield in mixtures are absent or downplayed in current crop varieties, as shown here for leaf area. The consequences for fostering crop yields in a sustainable way are wide, as crops might carry an evolutionary legacy that impacts the capacity of crop mixtures to over-yield.

Although wild progenitors showed higher net biodiversity effects than crops, we show that both domestication statuses over-yielded in mixtures. Our results for arable crops are in

line with diversity–productivity relationships reported for other types of plant communities (Loreau & Hector 2001; Tilman *et al.* 2001; Hooper *et al.* 2005; Cardinale *et al.* 2011), and concur with previous studies reporting positive biodiversity effects in crop mixtures (Li *et al.* 1999, 2006, 2007; Kiær *et al.* 2009; Lin 2011; Davis *et al.* 2012; Reiss & Drinkwater 2018; but see Pimentel *et al.* 2005; Letourneau *et al.* 2009; Snapp *et al.* 2010). Our study expands the current knowledge for arable crops by using a BEF experiment approach, which specifically tests the role of increasing diversity, thereby ruling out the confounding effects of disparate spatial scales (Malézieux *et al.* 2009; Brooker *et al.* 2015), compositional differences (no balanced combination of functional types or gradients of diversity; Malézieux *et al.* 2009) and temporal scales (Smith *et al.* 2008) of agricultural trials.

Biodiversity can promote over-yielding through complementarity and/or selection effects (Fox 2005; Barot *et al.* 2017),

whose relative relevance varies among study cases and duration of experiments (Fargione *et al.* 2007). In our experiment, SEs were much stronger than CEs. Selection effects are frequently disregarded as relevant contributors to over-yielding because they might signal strong competitive hierarchies, and thus suppressed species and preclusion to achieve transgressive over-yielding (Loreau 2000). However, the fact that productive species over-yield disproportionately does not necessarily come at the cost of other species under-yielding. In our experiment, the patterns of relative yields of individual species suggest that dominance was not a relevant mechanism triggering SEs (see Fig. S6), which highlights that SEs are useful drivers of biodiversity effects and should not be overlooked in crop mixtures.

Interestingly, SEs were stronger in assemblages of wild progenitors than in assemblages of crops, consistently across species and functional group richness levels. Moreover, dissimilarity in leaf areas, which were larger in mixtures of wilds, partly accounted for the lower capacity of crops to over-yield in mixtures. There is general consensus that functional differences between co-occurring species underlie the link between diversity and productivity (Cardinale *et al.* 2011). This link strengthens over time, due to adaptations through natural selection (Zupping-Dingley *et al.* 2014). Thus, given time, populations of diverse mixtures are expected to be better adapted to growing with interspecific partners (Dawson & Goldringer 2012). For example, Allard & Adams 1969 found that mixtures formed by varieties of barley selected as pure lines were less productive compared to mixtures of barley lines cultivated together for many generations. This is consistent with grassland BEF experiments showing that species with a co-selection history in mixtures develop functional trait divergence and increase biodiversity effects (both complementarity and selection effects; Zupping-Dingley *et al.* 2014). Indeed, frequent biotic interactions have been documented to impose selection on plasticity in functional traits and result in functional divergence between neighbouring plants in experimental (Lipowsky *et al.* 2011) and natural grasslands (Abakumova *et al.* 2016). Our results concur with these findings and provide evidence that crop breeding, as a selection process that generally occurs in monospecific stands, might have disrupted the ability of crops to develop strong biodiversity effects in diverse environments. These differences between crop plants and wild progenitors might arise either from directional selection in crops, or from reduced plasticity after domestication in certain traits (Matesanz & Milla 2017), which remains to be investigated.

In addition, arable cropping systems might pose limitations to co-evolutionary adaptations that promote complementarity (Zupping-Dingley *et al.* 2014). CEs generally increase over time (Fargione *et al.* 2007; Lipowsky *et al.* 2011; Reich 2012; Zupping-Dingley *et al.* 2014), which indicates co-adaptation of the genotypes at play (Zupping-Dingley *et al.* 2014), and might facilitate transgressive over-yielding in the long term (Cardinale *et al.* 2007). Since intercrops are rarely re-seeded on-farm in arable systems, which was mirrored in our experiment by using seeds with no previous history of coexistence, such opportunities for co-adaptation are precluded. We speculate that the ability of domesticated crops to adapt to local neighbourhoods would be hampered, either because they

exhibit lower genetic variation and evolutionary potential (Doebley *et al.* 2006; Miller & Gross 2011; Zhang *et al.* 2015) and/or lower potential for plasticity due to an evolutionary history of coexistence in monocultures (Abakumova *et al.* 2016). In other words, mixing pure varieties that exhibit local adaptation is probably significantly advantageous in terms of monoculture yield and other ecosystem services, but not necessarily optimal for the performance in mixtures. Thus, we suggest identifying traits, or trait combinations, that make mixtures of wild progenitors more productive, and bringing back the genes underlying those phenotypes to current varieties (Zhang *et al.* 2015; Wuest & Niklaus 2018). Alternatively, instead of focusing on single beneficial traits, breeding for mixing ability can be oriented to increase genetic diversity and/or plasticity within crop varieties. Such strategies can be reinforced with classical breeding on standing variation within crops, and with multi-generation programs that allow *de novo* adaptations to multi-specific settings.

Finally, it is important to acknowledge that some specificity of our set up and study system call for caution when generalising our findings, and might explain some discrepancies with preceding literature. For instance, it is remarkable that CEs in our experiment, even if positive, were generally weak. Previous studies on intercropping suggest that CEs can be quite large (Li *et al.* 2006, 2007, 2014; Davis *et al.* 2012). Free-rooting intercrop experiments allow root growth complementarity, and displacement in phenological traits, more easily than in greenhouse settings (Li *et al.* 2006, 2007). Other benefits of diversification, like increases in soil biodiversity or in soil carbon storage, are better captured in the long term and at larger spatial scales (Davis *et al.* 2012). Additionally, in spite of our efforts to include diverse crops from diverse functional types, our set up was limited to eight crop species, and ignored varietal and geographical diversity within the gene pool of each crop. Clearly, further studies addressing more crop species, and wider genetic, varietal and domestication status diversities within species, are needed. In this sense, to test if genotypes that are more closely related to their wild progenitors also show stronger biodiversity effects a set up that includes multiple stages along a sequence of domestication of a given species would be suitable (see e.g. Roucou *et al.*, 2018). Such an approach would reveal if a true 'dose-response' relationship exists between biodiversity effects and domestication.

## CONCLUSIONS

Our BEF experiment on eight arable crops revealed that domestication has reduced the ability of domesticated crops to benefit from biodiversity effects. We have shown that mixtures of wild progenitors attain higher biodiversity effects than mixtures of crops, driven by larger selection effects that are associated to larger differences in leaf area within assemblages. Our analysis showed that mixing annual crops might bring yield benefits if the composing species exhibit contrasting values of key functional traits. Since crop plants have a recent history of selection under monoculture, we argue that crop breeding might have hindered the ability of crop plants to perform in interspecific neighbourhoods through reduced genetic variance or plasticity in key traits. It will be interesting to explore to what extent the different



functional divergences found within crops vs. wild mixtures arise from a directional selection of certain phenotypes or from a reduced plasticity in certain traits in crops. Moreover, as the adaptations to diverse coexistence environments are expected to increase over time, we propose breeding strategies including multiple generation programs that permit local adaptations to arise. Thus, further breeding programs should re-establish genetic diversity and plasticity to increase the performance of mixtures. Provided that implementing genes from wild progenitors has proved useful for multiple breeding purposes (Zhang et al. 2015; Wuest & Niklaus 2018), and that we show here that wild progenitors might also have useful traits for coexistence in mixtures, we recommend a focus on wild relatives to breed crops for optimal polycultures.

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#### AUTHORSHIP

RM originally formulated the idea and designed the experiment. RM, PGP and SM conducted the experiment. JCL analysed the data and wrote the manuscript with inputs from all other authors. All authors provided technical assistance and contributed substantially to revisions.

#### DATA AVAILABILITY STATEMENT

Data supporting the results are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.3q7p6b5>.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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