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# Understanding the combined impacts of weeds and climate change on crops

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## Classification

Biological Sciences, Ecology.

## Keywords

Drought, elevated $CO_2$, meta-analysis, non-native plants, plant competition, warming

## Author Contributions

Author contributions: M.V. and I.I. designed research; M.V., E.B., D.B., B.A.B., R.E., B.B.L. and A.T. performed research; I.I. and MV analyzed data; M.V. and I.I. wrote the paper; E.B., D.B., B.A.B., R.E., B.B.L., A.T., J.D. and C.J.B.S. commented several versions of the manuscript.

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Main Text
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Tables 1

## Abstract

Crops worldwide are simultaneously affected by weeds, which reduce yield, and by climate change, which can negatively or positively affect both crop and weed species. While the individual effects of environmental change and of weeds on crop yield have been assessed, the combined effects have not been broadly characterized. To explore the simultaneous impacts of weeds with changes in climate-related environmental conditions on future food production, we conducted a meta-analysis of 171 observations measuring the individual and combined effects of weeds and elevated $CO_2$, drought or warming on 23 crop species. The combined effect of weeds and environmental change tended to be additive. On average, weeds reduced crop yield by 28 %, a value that was not significantly different from the simultaneous effect of weeds and environmental change (27%), due to increased variability when acting together. The negative effect of weeds on crop yield was mitigated by elevated $CO_2$ and warming, but added to the negative effect of drought. The impact of weeds with environmental change was also dependent on the photosynthetic pathway of the weed/crop pair and on crop identity. Native and non-native weeds had similarly negative effects on yield, with or without environmental change. Weed impact with environmental change was also independent of whether the crop was infested with a single or multiple weed species. Since weed impacts remain negative under environmental change, our results highlight the need to evaluate the efficacy of different weed management practices under climate change. Understanding that the effects of environmental change and weeds are, on average, additive brings us closer to developing useful forecasts of future crop performance.

## Main text

## Introduction

As the human population grows, global demand for food production is increasing. Concurrently, factors affecting food supply are changing. The spread of weed species and the prevalence of herbicide-resistant weeds is increasing. Weeds already cause greater global crop losses than either insect pests or pathogens (Oerke 2006, Fried *et al* 2017); yield losses to non-native weeds can amount to 42% of crop production (Vilà *et al* 2004). Weed control costs farmers over €150 million per year in the UK (Williamson 2002) and $3 billion per year in the U.S. (Pimentel *et al* 2005). Simultaneously, changes in Earth's climate and atmosphere are directly affecting growing conditions for plants; colder regions are experiencing longer growing seasons (Mueller *et al* 2015), drought conditions are increasing in many regions (Naumann *et al* 2018), and rising atmospheric $CO_2$ is affecting plant growth worldwide (Zhu *et al* 2016). Some of these changes are causing widespread yield losses in crops (Porter *et al* 2014). For example, in South Asian smallholder farms, drought and other water constraints cause yield losses that average 9.1% in wheat, rice, sorghum and chickpea crops (Li *et al* 2011). Furthermore, a recent meta-analysis of studies modeling climate warming impacts on crops found that models project yield losses of wheat, rice and maize to increase in tropical and temperate regions in the second half of the century (Challinor *et al* 2014). However, most predictions of future crop yields are based solely on crop performance under forecasted climates without accounting for changes in weed competition.

Combined effects of climate change and weeds on crop production have not been broadly synthesized, but have important implications for future crop management practices (Thomson *et al* 2010). A primary question is whether the combined effect of weeds and climate change is additive (individual effects sum together), synergistic (effects amplify each other) or antagonistic (effects offset each other) (Crain *et al* 2008, Darling and Côté 2008, Jackson 2015). Some studies that have tested multiple abiotic global change factors have found additive effects (Dieleman *et al* 2012). However, many of these effects are not additive (16) and interactions between abiotic and biotic global factors can be complex (Tylianakis *et al* 2008). If non-additive effects of climate and weeds are common, predictions of future crop yields will have to include them to be realistic (Tubiello *et al* 2007, Ramesh *et al* 2017).

In agricultural systems, both crops and weeds are influenced by multiple climate-related environmental conditions (Korres *et al* 2016). Changes in atmospheric $CO_2$, temperature and precipitation influence weed and crop species' metabolic rates, phenology and performance (Bunce and Ziska 2000). However, weeds and crops may respond to these changes differently because they have been subjected to distinct selective pressures (Korres *et al* 2016). Further, research on biological invasions suggests that the interaction between environmental change and weed effects could depend on the functional traits of the species involved, the origin of the weeds, and whether one or more weeds are present. For example, the impact of weeds on crops often depends on the plants' functional traits, such as their photosynthetic pathways (Ziska 2003, Fried *et al* 2017). Everything else being equal, increased atmospheric $CO_2$ increases primary production and water-use efficiency in C3 plants, while C4 plants are less likely to benefit from $CO_2$ enhancement. In contrast, C4 plants are more likely than C3 plants to thrive under warm and dry conditions (Ainsworth and Long 2005, Prior *et al* 2011). Thus, the competitive outcome between C3 and C4 plants could depend on the specific environmental component of climate change under consideration (Korres *et al* 2016). Since both crops and weeds include C3 and C4 plants, we expect that impacts on crop yield will depend on interactions between photosynthetic pathway and environmental change (Ainsworth and Rogers 2007).

Effects of weeds on crops might also depend on weed origin (native versus non-native). Non-native plants have left behind natural enemies that keep their populations in check in their native ranges (Maron and Vilà 2001). Release from natural enemies can allow non-native plants to allocate more resources to growth and reproduction in the new regions, and become more competitive (Blossey and Notzold 1995). Many successful non-native plant species also have broad environmental tolerances, high phenotypic plasticity or the ability to evolve more rapidly than native plants (Davidson *et al* 2011, Simberloff *et al* 2012) potentially allowing them to benefit more from global environmental change than native plants (Davidson *et al* 2011). Thus, with environmental change, we expect non-native weeds to have greater impacts on crop yield than native weeds.

The magnitude of weed impacts on crops under environmental change might also depend on whether a crop is infested by one or multiple weed species. Most crops contain diverse communities of weeds, which respond to environmental change through shifts in relative abundance (Booth and Swanton 2002). Ecological theory and empirical evidence suggest that a community of multiple species could be more resilient to environmental change than poor species communities (Tilman *et al* 2014, van der Plas 2019). Thus, in agricultural systems, we expect infestation by multiple weed species to have greater impacts on crop yield under environmental change.

Understanding the interactive effects of climate and weeds requires empirical studies that compare crop yields under different environmental conditions in the presence of weeds (Parmesan *et al* 2018). Some experiments have tested these effects, but these studies have yet to be synthesized quantitatively. As a result, we do not have clear expectations for how climate change and weeds will affect crops, simultaneously. To test the above hypotheses and identify the contexts in which crop yield is most vulnerable to the simultaneous effects of weeds and environmental change, we conducted a systematic review and meta-analysis. Specifically, we analyzed results from experiments addressing the combined and direct effects of weeds and elevated $CO_2$, drought or warming on the yield-related variables of 23 crop species, and asked the following questions: (i) Is the effect of weeds on crop yield altered by environmental change? (ii) Are the combined effects of weeds and environmental change on crops additive, synergistic or antagonistic? (iii) Do the combined effects of weeds and environmental change depend on the photosynthetic pathway (C3 vs. C4) of the crop/weed species pair, (iv) on the origin of the weed (native vs. non-native), or (v) on whether single or multiple weed species are competing with the crop? Finally, (vi) how might the main crop species around the world be affected by weeds under environmental change?

## Materials and Methods

### *Literature search and data selection criteria*

Our database development was based on a systematic literature search protocol, paper selection criteria and data extraction protocol (Pullin and Stewart 2006). For quality control, at each step, we trained data collectors using an example subset of the data and discussed eligibility of all included data.

To identify studies that experimentally tested the interactive effects of weeds and climate changes (elevated $CO_2$, warming or drought), we searched the Web of Science core collection for all records until 25/07/2018 using the following keywords: (i) “crop AND (weed control OR herbicide OR weed competition OR weed management) AND weed AND (Warm* OR heat* Or thermal OR temperature increase OR temperature manipulation* OR climate change)”; (ii): “crop AND (weed control OR herbicide OR weed competition OR weed management) AND weed AND ($CO_2$ OR carbon dioxide) AND (increase* OR enhance* OR enrich* OR elev*)”; and (iii) “crop AND (weed control OR herbicide OR weed competition OR weed management) AND weed AND (Drought OR water stress* OR rainout OR rain out OR rain-out OR precipitation exclusion* OR rain exclusion* OR precipitation removal*)”.

This search retrieved 1,436 publications. By reviewing titles and abstracts, we identified studies for which the following criteria for data inclusion were met: (i) the study independently tested the effects on crop performance of both the weed and environmental change ; (ii) the study tested the combined effects of the weed and environmental change either through experimental manipulation of both factors, or by experimentally manipulating one factor across a gradient of the other factor (e.g. a weed removal experiment across an irrigation gradient); (iii) the study included control treatments (no weed and no environmental change); and finally; (iv) the response variables were measured simultaneously in all treatments. These criteria for inclusion yielded a set of 57 publications (SI References, Figure S1).

A single publication could include results of multiple observations. If the publication reported results fitting our criteria for data inclusion for multiple weed and/or crop species, we considered each weed-crop combination to be a unique observation. If several varieties of the same crop were tested independently, we also considered these to be unique observations. If an article included observations conducted on the same crop but located in two or more regions or sites, we considered the studies as independent. Similarly, if the treatments were conducted several times, or the crop was planted at different times, each treatment was used as an independent observation. When the observation incorporated information on more than one control treatment (e.g. different herbicides used to suppress weeds), we included them as independent observations. Following the same reasoning, when the article incorporated information on more than one experimental method for the same environmental change variable (e.g. $CO_2$ enrichment conducted in both growth chambers and a field experiment), we considered each separately. When more than two treatment levels were examined (e.g. different weed densities, different $CO_2$ concentrations), only the most extreme treatment was included. Thus, if the degree of weed infestation varied, we compared the effects of the lowest (“control”) vs. highest (“treatment”) level of infestation.

Studies reported different crop response variables (e.g. plant biomass, seed production, plant height, leaf area, etc.). We considered the response variable most associated to the specific crop yield (crop yield hereafter). If the response variables were measured several times, we provided the average value of the time series. If the time series was not provided, we included the measure that we considered ecologically most representative (e.g. the last one in the time series; spring measurement of an annual series during season of maximum activity; measurement closest to maximum crop yield).

For every unique observation, we recorded the weed species and the location of the observation, using this information to determine whether the weed was native or non-native to the study region based on range information provided in several information sources (e.g. CABI Invasive Species Compendium). We also recorded whether the observation focused on a single weed or a mixture of weeds. Crop and weed species were also classified by their photosynthetic pathway (C3 vs. C4).

The analysis included field, greenhouse and chamber experiments. Weed treatments were rather heterogeneous. Weed treatments used included: planting weeds at different densities, removing weeds manually or mechanically, use of herbicides or combinations of these removal methods. In field conditions, drought has mostly tested by different irrigation treatments or by comparing wet and dry seasons or years. Similarly, the effect of warming was tested in experiments that elevated soil or air temperature but also in studies that compared years with different mean temperature but similar precipitation. The effect of increased $CO_2$ included similar numbers of studies in outdoor open-top chambers as in indoor chambers.

### ***Data analysis***

We examined the effect of weeds and environmental change using standard meta-analytical models (Koricheva *et al* 2013). For each observation, we extracted data on the number of replicates, mean and variability around the mean (e.g. standard deviation or standard error) for controls, individual treatments, and interactive weed and environmental change treatments. We used the Web Plot Digitizer online application (http://arohatgi.info/WebPlotDigitizer/app/) to extract values from figures in the papers. When empirical data were not presented, or were presented only in summarized format, we emailed corresponding authors to request raw data and included any raw data received in the analysis. A description of the flowchart for the publication selection process following Moher *et al* (2009) can be found in Figure S1.

#### *Effect size calculation*

We compared treatment effects across cases by estimating effect size (ES) as: *ln (Treatment mean/Control mean)*. We used simulations (1,000 iterations) to estimate ES mean and SD, ES for each observation was drawn from normal distributions with reported means and SDs (see

Supplemental Information for code). Effect size was estimated at each iteration and from that output (1,000 values) we estimated ES mean and SD (SI text S1). Sample size was also considered in these estimations by weighing reported variances by sample size (Gurevitch and Hedges 2001). We used simulations to estimate ES, instead of standard metrics (e.g. Hedges' g) because a large proportion of observations did not report a measure of variability associated with the mean (57%). We included these observations by estimating the variance around their ES as a latent variable.

Although there is a lack of consistency about how to handle missing variance data (Wiebe *et al* 2006), there are three common methods of dealing with this: an algebraic calculation which requires parametric summary statistics, trial-level imputation (averaging, or running regressions, across observations with known variances), and no imputation (excluding observations with no variance) (Batson and Burton 2016). We did not want to bias our results by excluding such a large proportion of the data, as a result, in our analyses, we opted for the most conservative, lowest bias, imputation method. We estimated the missing variances as a function of the largest ES variance calculated from observations with reported variances. We sampled from normal distributions (limited to be positive) with estimated largest variance as the mean and a SD of 1. There were also nine observations that did not report sample size. For these observations, we followed the most conservative approach and assigned them a sample size N=1.

We calculated the expected additive effect of weeds plus environmental change by summing the individual experimental results (Weed+ Environmental Change) and compared the expected additive effect to the measured combined effect reported in each observation (Weed& Environmental Change). We followed Jackson (2015) to estimate the mean and pooled SD of the additive effect (see ES4 in Table 1).

To address our specific research questions, we calculated several effect sizes (ES), all based on crop performance under different treatments, C: control, W: with weeds, EC: under environmental change, and W&EC: with weeds and under environmental change (Table 1, SI text S1).

**Table 1. Calculations of effect size (ES) estimates** to assess the combined effects of environmental change and weeds on crop performance. C: control, crop performance without weeds & without environmental change; W: crop performance under weed treatment & without environmental change; EC: crop performance under environmental change & without weeds; W&EC: observed crop performance with weeds and environmental change; W+EC: expected additive performance (i.e. sum of the individual experimental results) with weeds and environmental change.

| Effect size | Comparison | Calculation |
|---|---|---|
| ES1 | Weed effect on crops under current climatic conditions | ln(W/C) |
| ES2 | Environmental Change (elevated $CO_2$, drought or warming) effect on crops | ln(EC/C) |
| ES3 | Observed weed effect under Environmental Change | ln(W&EC/EC) |
| ES4 | Additive expectation relative to the observed combined effect | ln(W+EC/W&EC) |

*Analysis of effect sizes*

Individual values of effect size were then analyzed to assess effects of weeds and environmental change factors on crop production. Effect sizes were analyzed using mixed effects models with publication as a random effect. This accounted for the lack of independence among observations from the same study. By using study random effects in our analyses, individual observations were nested within each study, thus the study random effect is a 'combined' mean, as in Ponisio *et al* (2015). Given the low number of studies considering the combined effects of weeds and environmental change on crops, including other potential random effects (e.g., for crop and weed species) was not feasible. For each ES calculation the effect of different environmental change factors (elevated $CO_2$, drought or warming) were estimated. Since we were using latent estimates of effect size variability (for those observations with missing variance), we used a hierarchical Bayesian approach in this analysis; parameters were all estimated from non-informative prior distributions except for the missing variances (see description of methods above). All the prior distributions for the effect size were: ES*~Normal (0,100), and all the precision terms prior distributions were: 1/variance~Gamma (0.001, 0.001).

We ran similar analyses, using ES1-effect of weeds alone and ES3-weed effect under environmental change, for each combination of crop/weed photosynthetic pathway (C3 and C4), for each crop species, for each type of weed origin (native and non-native), and for single vs. multiple weed species systems. Due to the low number of data points for some of the subgroups, this second analysis was done without publication random effects. Effect size calculations and analyses were carried out in OpenBUGS (Thomas *et al* 2006; see SI text S1 for analysis code).

Effect size posterior estimates that did not include zero in their 95% credible intervals were considered statistically significant. Effect sizes with 95% credible intervals that did not overlap were considered significantly different from each other.

### *Publication bias*

Meta-analysis results may be distorted by publication bias, that is, the selective publication of articles finding significant effects over those that find non-significant effects (Rothstein 2008). In our case, this bias in publication could lead to an overestimate of the effects of weeds and environmental change variables on crop yield. We visually checked for potential bias using funnel plots (see Figure S2; although see Tang and Liu 2000, Lau *et al* 2006).

## Results and Discussion

Our final database contained 171 observations from 57 publications (Table S1) on the effect of more than 47 weed species on 23 crop species. Most observations were conducted in North America (72) and Asia (44), followed by Europe (Fig. 1), with a clear lack of observations conducted in Africa, South America, and Australasia. The majority of observations (84) were on the effect of drought, with 49 on the effect of elevated $CO_2$ and 31 on the effect of increased temperature. The most frequently studied crops were rice (42 observations), mostly in Eastern Asia, followed by soybean (31), tomato (30) and corn (12). Wheat, the most widely grown crop in the world and second most important food source in low-income countries, was represented in only seven observations, none of them testing the effects of elevated $CO_2$. Nine crop species were represented by a single observation (Fig. 1).

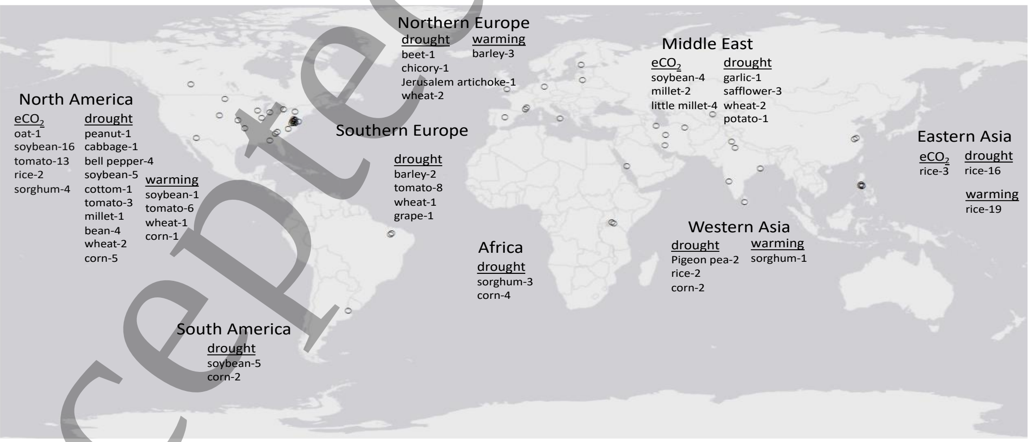

**Figure 1.** Geographic distribution of study sites used in the analysis. Tables show crop species studied and environmental factor considered. Numbers indicate number of observations included in the meta-analyses (See Table S1 for more information).

*Is the effect of weeds on crop yield altered by environmental change?*

Weeds alone significantly reduced crop performance by 27.99 % on average (Fig. 2, Table S3). Elevated $CO_2$ increased crop performance by 45.90% while drought decreased it by 29.85%; warming did not have a significant effect due to its large variation across studies (Fig. 2, Table S3). Elevated levels of atmospheric $CO_2$ often increase growth and water use efficiency of crop species that translate to increased crop production (Ainsworth and Rogers 2007). On the contrary, drought can have devastating effects to crop yields especially in non-irrigated systems (Li et al. 2011). The effect of warming is more context-dependent. Warming can accelerate and improve growing conditions in temperate regions by lengthening growing seasons and periods of time with optimal temperature but can also increases the risk of exposure to damaging heat (Tubiello *et al* 2007).

We assessed whether the negative effects of weeds were likely to change with environmental change by comparing ES1 (weed effect under current environmental conditions) and ES3 (weed effect under environmental change). Overall, the simultaneous effect of weeds and environmental change reduced crop performance by 26.64% a value that was not significantly different from the single effect of weeds without environmental change. Crop yield became more variable with warming, such that there was no significant effect under increased temperature (Fig. 2). ES3 was dependent on the biome (SI text S1, Table S2). The effect of the weeds under drought was most negative in Mediterranean, arid or semiarid climates, intermediate in temperate climates and the lowest in tropical and subtropical climates. This indicates that the impact of weeds on major crops might be exacerbated in dry regions such as the Mediterranean biome where models predict decreasing precipitation with climate change (Rojas *et al* 2019). In contrast, the effect of the weeds under warming was negative in tropical climates but not significant in temperate climates.

These results shed some light on how the simultaneous effects of environmental change on crop and weed species may alter their interaction. Weed species tend to have a strong, positive response to elevated atmospheric $CO_2$ (Ziska 2003), and weed presence counteracted any benefits of elevated $CO_2$ to crops. In the case of drought, the lack of change in overall weed impact suggests that reduced water availability has a similar negative effect on both crops and weeds, despite the fact that that the impact is larger in water stressed regions. In the case of warming, ES3 was highly variable. A correlation analysis between the magnitude of the change and ES3 indicated an increase in the effect size with increasing temperature differences (SI Fig. S3). Both crops and weeds are likely to benefit from warming, leading to both positive and negative outcomes on the impact of weeds. Overall, our results suggest more variable effects of weeds on crops under environmental change, and a need to adapt weed management practices where weed impacts increase (Peters *et al* 2014).

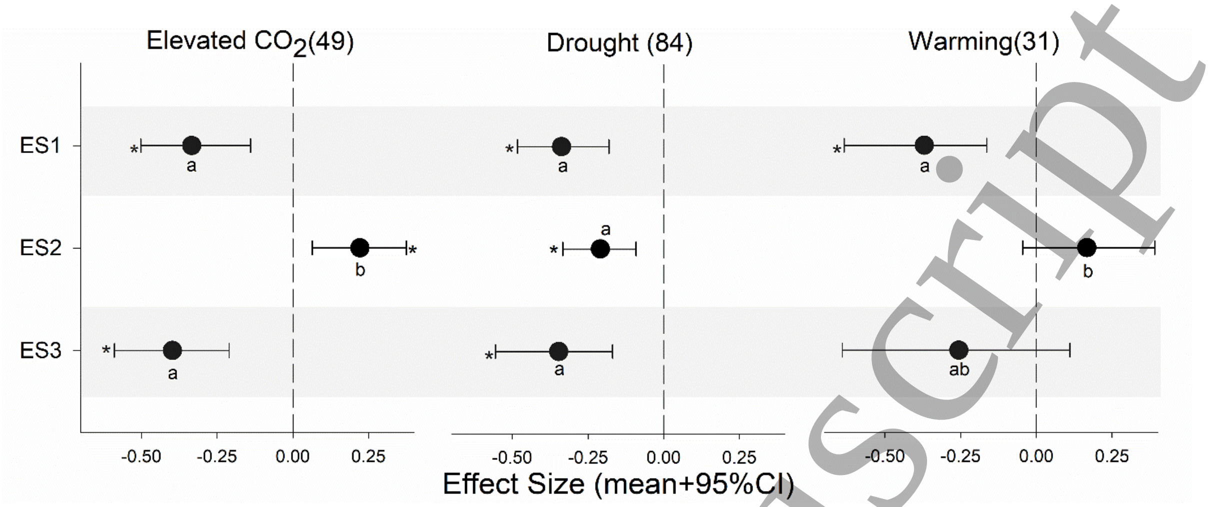

**Figure 2.** Effect size (ES) estimates comparing crop performance under current environment conditions and without weeds (control) with weeds (ES1), with environmental change (ES2), and the effect of weeds under environmental change (ES3). Credible intervals (95%CI) that do not include zero are considered statistically significant (indicated by an asterisk). Within each environmental change factor, different letters indicate that credible intervals are statistically different from each other. Numbers indicate sample sizes. See Table S2 for parameter values.

*Is the combined effect of weeds and environmental change on crops additive, synergistic or antagonistic?*

To answer this question, we compared the additive expectation against the observed combined effect of weeds and environmental change (ES4). There is wide variation among observations (Fig. 3). A correlation analysis between the magnitude of the change and ES4 indicated a trend towards synergistic effects with increasing temperature differences (SI Fig. S4). However, the combined effects of environmental change and weeds are on average additive. The effects of weeds are similar in present and predicted future environmental conditions, even though environmental change can dramatically alter competitive interactions among weeds and crops within particular cropping systems (Tylianakis *et al* 2008, Ziska and Dukes 2011). This result is in line with the additive effects found between other global change drivers (Wu *et al* 2011), but see Dieleman *et al* 2012). To realistically assess future crop production and inform management, we need to consider these combined effects of environmental change and weeds. As it stands, most experimental and synthetic work aimed at predicting crop yield only accounts for one of these two factors. Understanding that the effects of environmental change and weeds are, on average, additive brings us closer to developing useful forecasts of future crop performance.

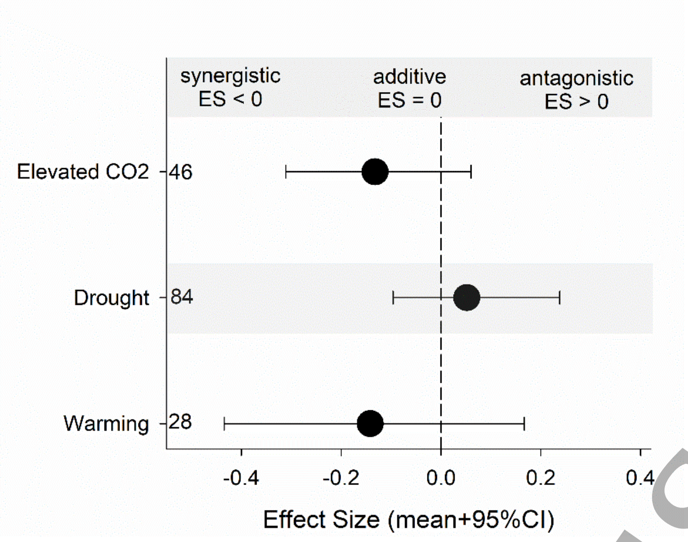

**Figure 3.** Effect size (ES4:W+EC/W&EC) estimates to test if the combined effect of environmental change factors (EC) and weeds (W) on crop yield are additive, synergistic or antagonistic. We consider effects with credible intervals (95%) overlapping zero to be additive. Numbers are sample sizes. See Table S2 for parameter values.

*Does the combined effect of weeds and environmental change depend on the photosynthetic pathway (C3 vs. C4) of the crop/weed species pair?*

We addressed this question by comparing estimates between ES1 and ES3 for the four potential combinations of crop/weed photosynthetic pathway, C3/C3, C3/C4, C4/C3, and C4/C4 (SI Table S2). We found that the impact of weeds on crops grown under environmental change conditions depended on the species' respective photosynthetic pathways and on the environmental change component under consideration (Fig. 4).

Elevated $CO_2$ increased the effect of the weeds on crops if they had the same photosynthetic pathway, decreased the effect of C4 weeds on C3 crops, and was not significant in C4 crop/C3 weed pairs. Thus, under elevated $CO_2$, weeds might increase their performance and be more competitive than crops if they are of the same photosynthetic pathway. In contrast, a greater responsiveness of C3 crops to $CO_2$ would benefit them when competing with C4 weeds (e.g. Patterson 1995) such as in rice crops (C3) invaded by C4 weeds (Rodenburg *et al* 2011).

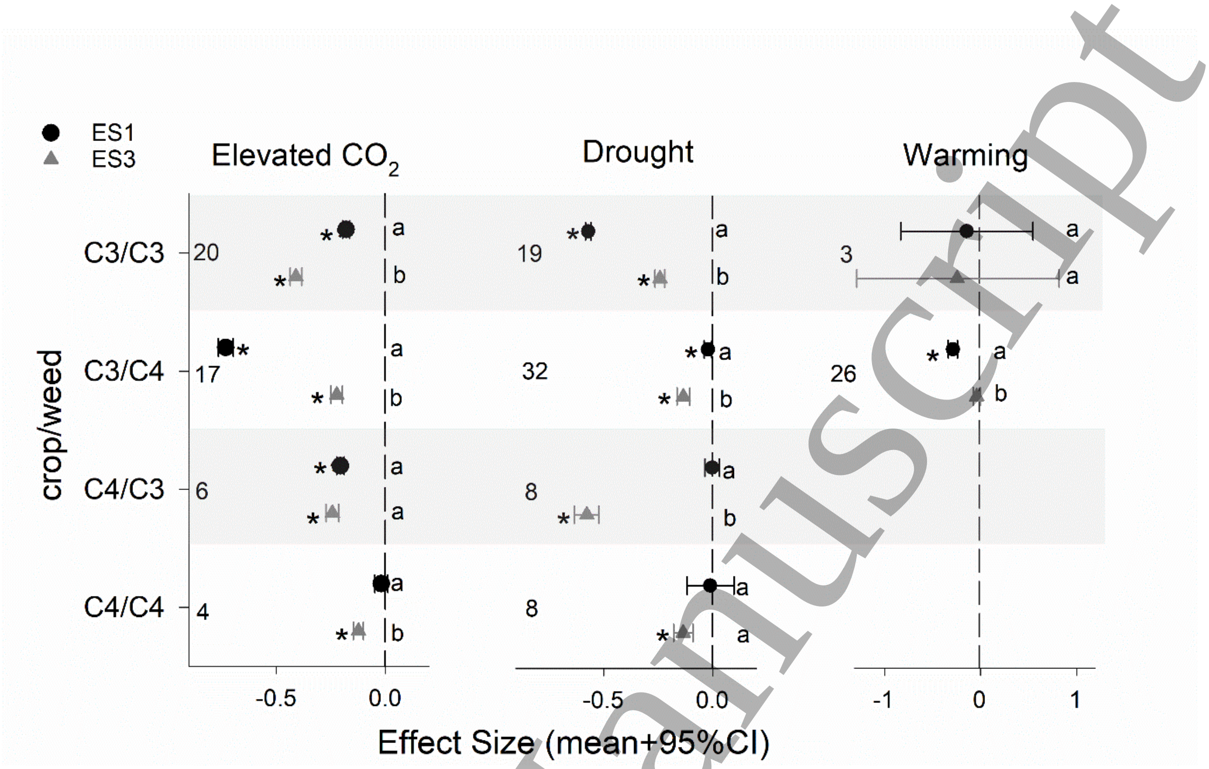

**Figure 4.** Effect size (ES) estimates of the effect of weeds, both under current environmental conditions (ES1) and with environmental change (ES3), categorized by weed and crop photosynthetic pathways (C3 or C4). Credible intervals (95%) that do not include zero are considered statistically significant (indicated by asterisks). For each photosynthetic pathway and environmental change factor combination, different letters indicate that the effect of the weeds is significantly different between current and changing environmental conditions (credible intervals do not overlap). There are no data to test for the effect of weeds under warming for C4/C3 and C4/C4 pairs. Numbers indicate sample sizes. See Table S2 for parameter values.

Drought increased the impact of the weeds in mixed pairs, decreased it in the C3/C3 pairs and was not significant in the C4/C4 pairs. Surprisingly, warming decreased the impact of C4 weeds on C3 crops but did not significantly affect C3 weeds' impacts on C3 crops; this combination had a small sample size (only 3 observations) and large variation. Warmer or drier conditions have been hypothesized to benefit C4 over C3 species (Patterson 1995). However, this pattern was not supported by our meta-analysis, indicating that other functional traits beside photosynthetic pathway might be more important to determine competitive superiority under climate change.

*Does the combined effect of weeds and environmental change depend on the weed origin?*

We addressed this question by comparing estimates between ES1 and ES3 for native and non-native weeds (SI Table S2). We did not find differences between the impact of native and non-native weeds on crops under current climatic conditions (Fig. 5). This supports other research findings that non-native plants are not more competitive than common native plants (Zhang and van Kleunen 2019). Contrary to our expectations, environmental change did not increase the impact of non-native weeds relative to native weeds. Indeed, due to large variation across observations, non-native weeds did not consistently reduce crop performance with drought or warming. Rather, the non-native weed effects remained non-significant with environmental change (Fig. 5). This result does not align with differences found between native and non-native plant performance (i.e. survival, growth and fecundity) with climate change in natural ecosystems (Sorte *et al* 2013, Liu *et al* 2017).

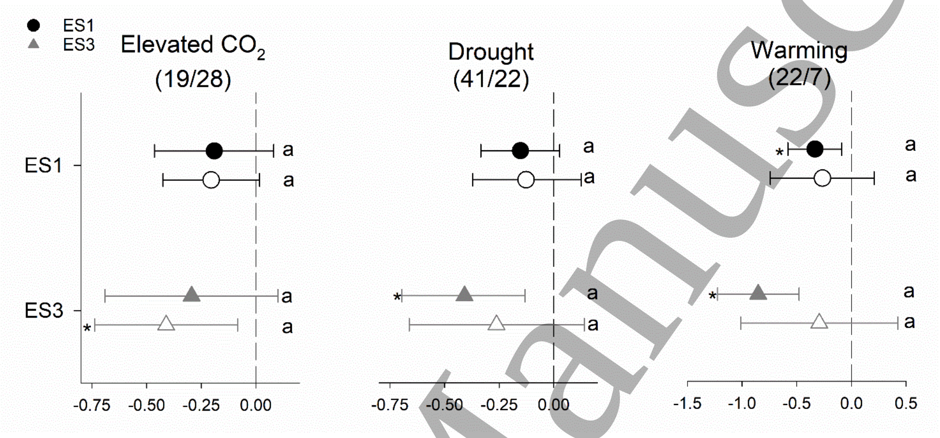

**Figure 5.** Effect size (ES) estimates of weeds under current environmental conditions (ES1) versus weeds with environmental change (ES3) relative to weed origin (native-solid symbols or non-native-white symbols). Credible intervals (95%) that do not include zero are considered statistically significant (indicated by asterisks). Within each panel, different letters indicate that the effects are statistically different from each other (credible intervals do not overlap). Numbers indicate sample sizes (native/non-native). See Table S2 for parameter values.

*Is the combined effect of weeds and environmental change on crops similar when there is a single weed species versus multiple weed species?*

We addressed this question by comparing estimates between ES1 and ES3 for single weed species versus mixtures of weeds (SI Table S2). We expected that multiple weed species would have stronger impacts on crops, and the impacts would be less affected by environmental change than single weed species. However, the impact of weeds did not differ depending on the number of weeds present, and the impact of multiple weeds was not modified by environmental change (Fig. 6). Our results suggest that the potential for diffuse competition among plant species in the community reduces the impacts on a particular species within the community (Goldberg 1987). It is possible that competition among weed species limits their impact on the crop (Lohrer and Whitlatch 2002). We also note that variability in the impacts of weed mixtures was much greater than for single weeds, particularly in the environmental change treatments.

While our results do not support the hypothesis that multiple weed species would have stronger impacts than a single weed, and that multiple weed species become more problematic for crops under environmental change, our sample sizes were too low to confidently reject these hypotheses, particularly under the environmental change treatments. Some studies have indeed found the reverse, that more diverse weed communities are less competitive with the crop than poor weed communities (Storkey and Neve 2018).

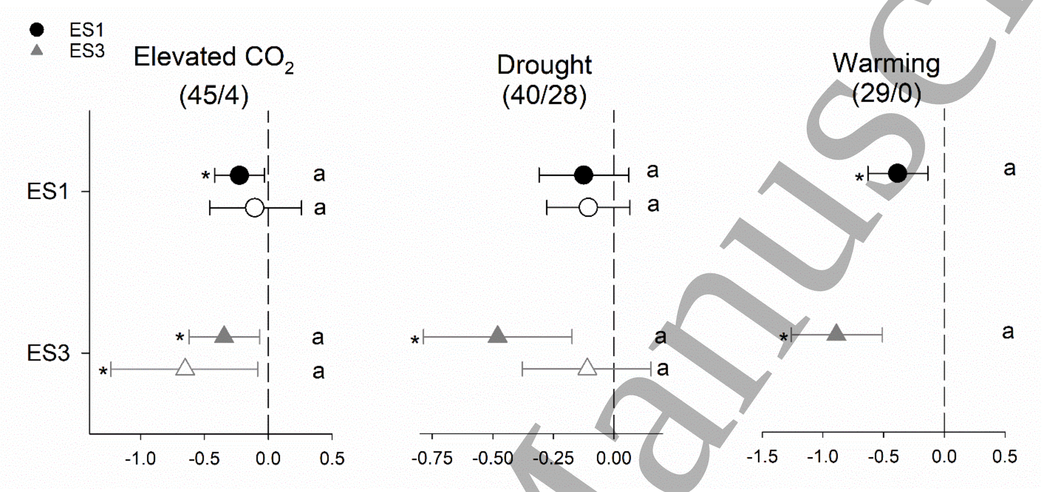

**Figure 6.** Effect size (ES) estimates of weeds under current environmental (ES1) versus weeds with environmental change (ES3) for studies with single weed species (solid symbols) vs. multiple weeds (white symbols). Credible intervals (95%) that do not include zero are considered statistically significant (indicated by an asterisk). Within each panel, different letters indicate that the effects are statistically different from each other (credible intervals do not overlap). Numbers indicate sample sizes (single/multiple). See Table S2 for parameter values.

*Is the effect of weeds under environmental change similar among major crop species?*

Ultimately, in order to effectively inform crop selection and management, we need predictions of individual crop species performance under the combined effects of weeds and environmental change. Despite the general effects of weeds and environmental change on crops (Fig. 2), individual crop species showed differing responses to environmental change (Fig. 7).

Surprisingly, without environmental change, crop yield was significantly reduced in only seven species, with the performance of only one crop, oat, showing an increase in yield with weeds (Fig. 7, ES1). Data were available to assess the effect of weeds under elevated $CO_2$ for seven crops. Elevated $CO_2$ reversed the negative effect of weeds in millet, a C4 plant, and increased the negative effects of weeds in little millet (C4) and oat (C3).

The impact of weeds under drought conditions become more detrimental for corn (C4), Jerusalem artichoke (C3) and safflower (C3), and were less detrimental (non-significant) in soybean (C3), wheat (C3) and millet (C4); for common beans (C3), the effect of weeds became positive with drought. Under warming, the impact of weeds remained negative for rice and decreased for barley, soybean, wheat and tomato becoming non-significant.

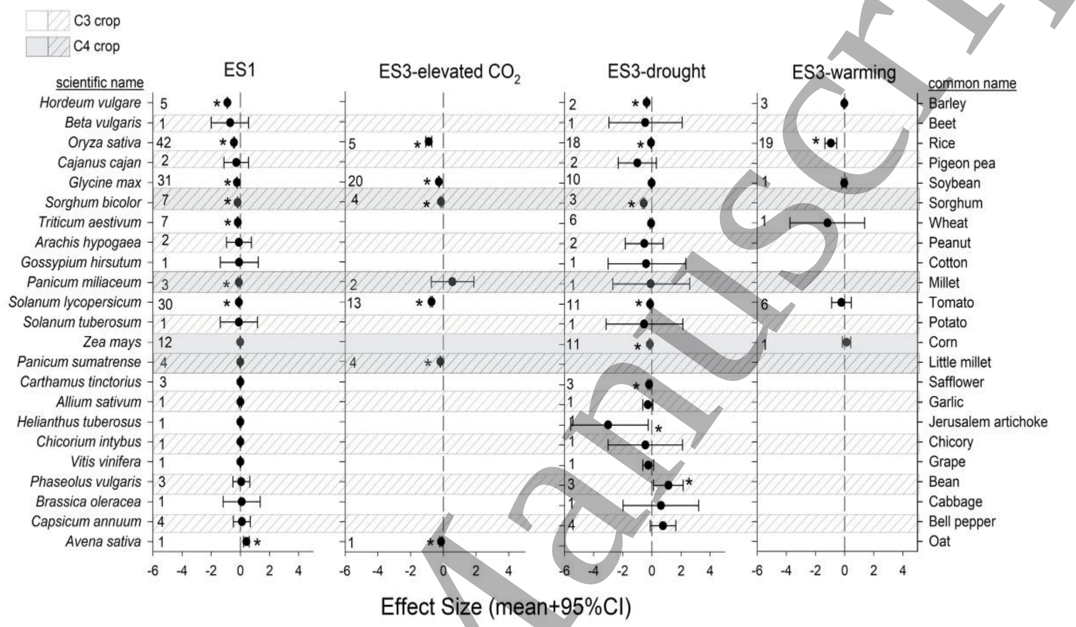

**Figure 7.** Effect size (ES) estimates of weeds, either under current environmental (ES1) or with environmental change (ES3), for studies of particular crop species. Credible intervals (95%) that do not include zero are considered statistically significant (indicated by an asterisk). Numbers indicate sample sizes. See Table S2 for parameter values.

Differences among crop species should be interpreted with caution due to the uneven taxonomic and geographical distribution of the studies (Fig. 1) and the small number of observations on the combined effects of weeds under environmental change for many crops. More than half of the observations used rice, soybean and tomato crops, while nine crop species were represented by a single observation (Fig. 7). We should also be aware that differences in weed composition and densities across observations might influence their impact (Vilà *et al* 2004, Zimdahl 2004).

## Conclusions and the way forward

Understanding how global change will affect crop yield is critical for projecting future food production. For this reason, many studies have quantified the effects of two major factors affecting crop yields: climate change and weeds. However, most studies have examined these factors in isolation (Juroszek and Von Tiedemann 2013), leaving uncertainty about the validity of extrapolations (Ward *et al* 2014). Studies that simultaneously address the effects of environmental conditions related to climate change and weeds on crops are not common, and surprisingly, many have experimental design limitations that precluded their inclusion in meta-analysis (Gurevitch *et al* 1992). Many studies did not explore the single and interactive effects of weeds and environmental change under the same experimental conditions or on the same crop varieties. Other studies lacked control treatments, had no replication, or did not present variance data. This information is often missing in agronomic studies of competition (Vilà *et al* 2004), which limited the dataset of studies available for synthesis. To present a comprehensive dataset, we included studies where the primary aim was not to test for the effect of climate change, but which provided proxies (i.e., contrasting environmental differences) to test for the effect of environmental change on crops with and without (or with low levels of) weeds. To better assess how climate change affects weed constraints on crops, future research should implement replicated well designed experiments with controls that provide full statistics and that explicitly test realistic environmental changes in field conditions. Future studies should also evaluate the effects of multiple environmental change components on crops with and without weeds (Peters *et al* 2014).

Of all pests, weeds have the greatest potential to reduce worldwide crop yields (Oerke 2006). Moreover, our meta-analysis indicates that the effects of weeds alone can be more detrimental on crop yield than environmental change alone. Our results also suggest that weeds will reduce crop yield under climate change by a similar magnitude to their effects under current climatic conditions. Therefore, weed management will remain a critically important activity climatic change. Weed management is facing major challenges such as the increasing rates of weed dispersal through global trade and climate change, the environmental damage caused by weed control, and weed resistance to herbicides (Liebman *et al* 2016). Because our results indicate that under forecasted climate change, the negative effects of weeds will persist to similar magnitude, we propose the following priority research areas: (i) comparing the effects of different weed management practices (e.g. chemical vs. mechanical) to minimize crop yield losses and costs under climate change (Peters *et al* 2014); (ii) focusing on rarely studied subsistence crops (e.g. vegetables) that depend on manual labor for weed management and on farming systems that cannot compensate for drought with irrigation (Altieri 2019); (iii) exploring differences among crop varieties (e.g. weed-suppressive crop genotypes) in the impact of weeds and climate change (Korres *et al* 2016), (iv) conducting research in regions where there are few studies, such as in the southern hemisphere, especially on weed effects with warming and (v) exploring if there are thresholds of environmental change that might cause non-additive effects with weeds.

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Main data that support the findings of this study are included in Table S1.

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