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RESEARCH ARTICLE

Crop rotational diversity can mitigate climate-induced grain yield losses

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Abstract

Diversified crop rotations have been suggested to reduce grain yield losses from the adverse climatic conditions increasingly common under climate change. Nevertheless, the potential for climate change adaptation of different crop rotational diversity (CRD) remains undetermined. We quantified how climatic conditions affect small grain and maize yields under different CRDs in 32 long-term (10–63 years) field experiments across Europe and North America. Species-diverse and functionally rich rotations more than compensated yield losses from anomalous warm conditions, long and warm dry spells, as well as from anomalous wet (for small grains) or dry (for maize) conditions. Adding a single functional group or crop species to monocultures counteracted yield losses from substantial changes in climatic conditions. The benefits of a further increase in CRD are comparable with those of improved climatic conditions. For instance, the maize yield benefits of adding three crop species to monocultures under detrimental climatic conditions exceeded the average yield of monocultures by up to 553 kg/ha under non-detrimental climatic conditions. Increased crop functional richness improved yields under high temperature, irrespective of precipitation.

For affiliations refer to page 15.

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Conversely, yield benefits peaked at between two and four crop species in the rotation, depending on climatic conditions and crop, and declined at higher species diversity. Thus, crop species diversity could be adjusted to maximize yield benefits. Diversifying rotations with functionally distinct crops is an adaptation of cropping systems to global warming and changes in precipitation.

KEYWORDS
climate change adaptation, climate resilience, crop diversification, Europe, long-term experiments, North America, sustainable agriculture

1 | INTRODUCTION

Climate change negatively affects crop production (Jägermeyr et al., 2021), which is the basis of food systems globally. More than a third of global crop yield variability is explained by climatic variability (Ray et al., 2015). Growing season temperature is increasing and, in some regions, precipitation is becoming more intense and interspersed with more frequent and longer dry spells (IPCC, 2021). Both high temperature and low precipitation can independently or simultaneously lower crop productivity, by limiting carbon fixation, growth and investment in reproduction (Hatfield & Prueger, 2015; Prasad et al., 2011). High precipitation can reduce crop yields through waterlogging and lodging (Beillouin et al., 2020). Crop yields can thus be negatively affected by both dry spells and excessive precipitation (Li et al., 2019; Troy et al., 2015). Even short periods of extreme conditions or co-occurring adverse but not extreme growing conditions, like heat and water stress, can severely reduce yields (Brás et al., 2021; Hamed et al., 2021; Luan et al., 2022; Matiu et al., 2017; Vogel et al., 2019). There is an urgent need to adapt our cropping systems to reduce yield losses due to climate change (Challinor et al., 2014; Khanal et al., 2021).

Cropping systems are becoming increasingly simplified in many regions, with fewer and fewer crops grown in rotation (Bennett et al., 2012; Crossley et al., 2021; Schaak et al., 2023). Nevertheless, increasing crop diversity by including more crops and/or cover crops in the rotation could increase yields in several crops, particularly at low fertilization (MacLaren et al., 2022; Smith et al., 2023). In diverse rotations, soil fertility and water and nutrient use efficiency could be enhanced (Jian et al., 2020; Tanaka et al., 2005; Wang et al., 2018), which might help buffer against detrimental climatic conditions (Isbell et al., 2017). Indeed, higher crop rotation diversity (CRD) reduced maize yield losses in unfavourable years in several North American long-term experiments (Bowles et al., 2020; Gaudin et al., 2015). However, yields were not linked to specific climatic conditions in these studies, so the joint effect of changes in CRD and climatic conditions was not quantified. When explicitly taking into account growing season conditions, the benefits of a diverse rotation to small grain cereal yields were especially high during dry years in seven long-term experiments across Europe (Marini et al., 2020), but CRD level was not explicitly considered, potentially confounding effects of climatic conditions and diversity level. Therefore, it remains unclear how climatic conditions affect yield outcomes as CRD is changed by small increments, that is, beyond considering monocultures and diverse rotations as a dichotomy. Exploring these relationships could indicate how diverse the rotation needs to be to buffer yield losses under specific detrimental growing conditions.

Crop performance under variable climatic conditions is often assessed using averages of temperature and cumulative precipitation over the entire growing season or parts of it (e.g., Huang et al., 2021; Marini et al., 2020). However, these averages do not account for the effects of short but potentially damaging events such as heat waves and dry spells, and their combinations, which are becoming increasingly more frequent. It remains uncertain whether increasing CRD reduces yield losses under detrimental short-term conditions and how this might vary with the duration and intensity of single or compounded weather events.

The benefits of a more diverse rotation depend not only on the number of species included in the rotation but also on their role in the ecosystem (Nilsson et al., 2022; Smith et al., 2023). Species belonging to the same functional group share some traits and functions, for example, two cereal species are more similar in resource acquisition than a cereal and a legume species are. Therefore, functional redundancies might limit the benefits of diversification. Conversely, distinct functional groups, such as cereals, annual legumes, broadleaf crops (e.g., *Brassicaceae* and *Solanaceae*) and leys, that is, a mix of perennial or biennial grasses and legumes, have complementary traits and deliver functions that can enhance performance. Examples of functions are atmospheric nitrogen fixation for legumes and permanent soil cover for leys. Trait and functional complementarity are particularly effective in promoting several key ecosystem services, such as enhanced pathogen regulation, soil fertility, and resource use efficiency, and diverse response to stress (Cadotte et al., 2011; Duchene et al., 2020; Griffiths et al., 2022; Peralta et al., 2018). This likely explains why functional richness steadily enhances cereal yields, whereas species diversity leads to a maximum yield at intermediate levels (Smith et al., 2023). Understanding whether it is sufficient to increase crop species diversity rather than functional richness to mitigate yield losses from detrimental climatic conditions is critical to effectively adapt to climate change.

To evaluate the effects of increasing CRD on crop yields in relation to climatic conditions and over time, we collected meteorological and grain yield data of spring and winter small grains, and maize from 32 European and North American long-term (10–63 years) field experiments (LTEs) (Smith et al., 2023). We characterized growing season conditions both via anomalies in average temperature and precipitation, and via the occurrence of dry spells. We define detrimental climatic conditions as seasonal or shorter-term conditions that reduce monoculture yields below local averages. Our two main hypotheses were: (1) yield losses due to detrimental climatic conditions are mitigated with increasing CRD, and (2) grain yield benefits from increasing CRD are more pronounced under detrimental than average or high-yielding climatic conditions. We also explored how changes in grain yield across gradients of climatic conditions differ depending on whether functional richness or species diversity is used to characterize CRD. Our findings could support designing climate-resilient cropping systems.

2 | METHODS

2.1 | Crop yield data

Our dataset comprised 21 LTEs in Europe and 11 in North America, for a total of 941 site-year combinations, 117 rotations and 27,402 observations and spanning a wide gradient of climates, from Mediterranean to Sub-arctic ones. All crops were rain-fed. Crop rotations ranged from continuous monocultures, that is, a single crop species grown every growing season, to increasingly diverse rotations, that is, up to six crop species grown in succession over a certain number of growing seasons. Some experiments also included a fallow period (7% of rotations), cover crops (28% of rotations) and more than one crop grown during the same growing season, that is, intercropping and undersowing (26% of rotations). Experiments included at least two different crop rotations, but not necessarily a monoculture. For robust inference, we restricted the analyses to experiments that had been in place for at least 10 years. This ensured that a minimum of two full rotation cycles of the longest rotation were completed for all LTEs, except for Woodside LTE, for which the last 4 years of the second rotation cycle were missing. Furthermore, to avoid confounding effects between rotations and other management practices, we selected experiments where all crop rotations received similar treatments or adaptive management was applied (e.g., applications of pesticides or herbicides as needed). Details on the LTE experimental design, climatic conditions and diversity levels are summarized in the Supplementary Information (Table S1). Additional information is reported in Smith et al. (2023), which used the same yield dataset, but did not explore the role of climatic conditions.

In most LTEs, each phase of the rotation was present every year, with the exception of El Encín and Foggia LTEs, where the indicator crop—winter wheat in both cases—was harvested once every 2 years. Yields were collected for 10–63 years, except for El Encín and Foggia LTEs for which 7 years of data spanning 14 years were available. Some experiments included treatments applied to all rotations, related to, for example, amount of fertilizer, tillage intensity and management of residues. Since the effects of these options were not the focus of this study, but greatly affect crop yields, we combined them with replicates into the variable "Group" to simultaneously take into account the variation relative to replicate and treatment effects (see Section 2.4). For example, a LTE with replicates (1, 2, etc.) and two fertilizer treatments (A and B) would have several distinct Groups: A1, B1, A2, B2, etc.

We chose cereal crops as indicator crops because they are key in human and animal nutrition, widely grown, economically important and well represented in our dataset. We analysed spring small grains, winter small grains and maize separately, because we expected substantial differences in yield outcomes based on physiological and phenological dissimilarities and previous results (Fan et al., 2016; Kadam et al., 2014; Marini et al., 2020). Small grain yield data were only available from the European LTEs and maize from the North American LTEs. All yield data of the individual crops refer to grain dry matter. To reduce yield variability due to crop species and geographic location, we considered yield anomalies as mean-centred yield data obtained by subtracting the indicator crop-specific long-term mean yield from individual yield observations at each LTE. We did not detrend the yield anomalies (and climatic indices; see below) to be able to capture the net effects of the interactions of diversity with technological improvements and climate change occurred over the duration of the LTEs.

2.2 | CRD metrics

To capture different aspects of crop diversity in the rotation and likely pathways of impact, we considered two indices to measure CRD: (i) species diversity, measured by a modified version of Simpson's reciprocal diversity index (D) (Simpson, 1949), accounting for both the total number of species and their relative abundance over the length of the rotation, and (ii) the count of functional groups present in the rotation, that is, "functional richness" (FR) (Smith et al., 2023).

We calculated the species diversity D as

$$D = \frac{1}{\sum_{i=1}^{c} p_i^2}, \tag{1}$$

where c is the total number of crop species in the rotation, p_i is the ratio of the number of years during which the i^{th} species occurs to the length of the rotation in years. In other words, we modified the commonly employed Simpson's index to consider the proportion of co-existing species in a certain time period rather than a defined space. When the rotations included intercrops (in 26% of the cases), we divided p_i by the number of crop species intercropped with the ith species, thus effectively increasing D. While different rotation lengths and number of species can result in the same D, this index provides an approximation of how many species are included in a given rotation. For example, $D=1$ corresponds to a monoculture and $D=2$ to a 2-year rotation with two crop species.

We used functional richness (FR) as an alternative measure of CRD to take into account niche differentiation among four functional groups: cereals (present in all rotations), legumes, broadleaves and biennial or perennial leys. FR = 1 indicates a rotation including one or more cereal species (i.e., a cereal monoculture or a cereal-only rotation), and FR = 2 indicates a rotation including cereals together with an additional functional group, for example, one or more legume or broadleaf or ley species, while FR = 3 indicates cereals and two additional functional groups.

2.3 | Climatic data and climatic index calculation

Daily gridded meteorological data relative to the pixel in which each LTE is located were extracted from the E-OBS database, v 23.1 (Cornes et al., 2018) in Europe and from the CONUS dataset (Livneh et al., 2015) in North America. The data included daily maximum temperature and daily precipitation, at a spatial resolution of 0.1° × 0.1° for Europe and 0.0625° × 0.0625° for North America. While some LTEs had field weather stations available, we chose to use gridded data for all LTEs for consistency.

To summarize the growing conditions, we considered two sets of climatic indices: (i) growing season climatic indices, represented by average maximum daily temperature and cumulated precipitation during each growing season, and (ii) intra-seasonal climatic indices, quantifying potentially short but detrimental conditions expected to become more common. As intra-seasonal climatic indices, we chose length of the longest dry spell, that is, maximum number of consecutive days with daily precipitation <2 mm, and their average maximum temperature. The two sets of indices had a similar explanatory power of yield variations across a wide climatic gradient (Luan et al., 2021). We included intra-seasonal climatic indices because averaging climatic conditions over entire growing seasons potentially exclude short-term damaging events (Troy et al., 2015). We represented the growing season temperature as the average maximum daily temperature instead of mean daily temperature as the former had a higher explanatory power in most of our models (Table S2). Nevertheless, using mean daily temperature provided similar results (not shown).

We defined the site-specific growing season for spring crops and maize based on locally available planting and harvesting information. For winter crops, we considered only the main growing season, starting at the end of winter dormancy, as defined based on the rate of accumulation of growing degree days (see Section S1 for details).

Local climate effects were limited because the timing of the growing season was such that growing season climatic indices often overlapped in range and distribution despite large differences in annual conditions across sites (Figures S1–S4). Despite this substantial overlap, to focus on the effects of inter-annual variability of the climatic indices on yield anomalies, we used the climatic condition anomalies, thus removing the effects on yields attributable to the local climate. The climatic indices included in analyses were the anomalies of cumulated precipitation (*P*) and average temperature (*T*) as seasonal indices, and anomalies in the highest number of consecutive dry days (*CDD*) and the average maximum temperature during these dry days (*TDD*) as within-season indices. For each index, the anomalies were calculated by subtracting the LTE long-term mean from each year value. As LTE long-term mean we used the mean over the duration of each experiment. Choosing longer-term means, for example, relative to a period common to all sites, did not alter the results (not shown).

2.4 | Statistical analyses

We explored how yield anomalies of winter and spring small grains and maize vary with CRD, and pairs of climatic indices via two sets of mixed-effect models. In the first set of models, CRD was represented by the continuous species diversity *D*, in the second set of models as categorical functional richness FR. Beyond CRD, additional fixed factors were as follows: years since the beginning of the experiment (*t*: continuous), climatic index 1 (X_1: *T* or *TDD*) and climatic index 2 (X_2: *P* or *CDD*). For all models, as random factors, we used calendar year of sampling (year: categorical) and the variable "Group" nested within LTE to account for variation relative to spatial, temporal and design dependence. We differentiated *t* and year to separate yield variations explained by technological improvements over time and legacy effects of rotations since their implementation, captured by *t*, from variations due to LTE-specific effects of sampling year on yield, captured by year. Temperature and precipitation can have compound effects on yield outcome (Luan et al., 2021; Prasad et al., 2011; Zscheischler et al., 2020). We therefore included the interaction between the climatic indices, X_1: X_2 (*T*:*P* or *TDD*:*CDD*), as a fixed effect. Further, we considered a quadratic dependence on the temperature index, ${X_1}^2$ (i.e., T^2 or TDD^2), because several plant processes have an intermediate thermal optimum (Wang et al., 2017). We included the two-way interaction term between CRD and either X_1 or X_2 to assess how the response to temperature and precipitation anomalies, or to number of consecutive dry days and their temperature, change with CRD. We assumed non-linear relationships between CRD and yield responses, alone and in interactions with the climatic conditions, to account for possible diminishing returns of diversity on yield (Smith et al., 2023). Models were fitted separately for the three groups of indicator crops—spring small grains, winter small grains and maize.

In summary, the fixed part of the model considering species diversity *D* was

$$\begin{aligned} Yield = {} & \beta_0 + \beta_t t + \beta_D D + \beta_{D^2} D^2 + \beta_{X_1} X_1 + \beta_{{X_1}^2} {X_1}^2 + \beta_{X_2} X_2 \\ & + \beta_{Dt} Dt + \beta_{D^2t} D^2 t + \beta_{X_1X_2} X_1 X_2 + \beta_{{X_1}^2 X_2} {X_1}^2 X_2 + \beta_{DX_1} DX_1 \\ & + \beta_{DX_2} DX_2 + \beta_{D{X_1}^2} D{X_1}^2 + \beta_{D^2X_1} D^2 X_1 + \beta_{D^2X_2} D^2 X_2 \\ & + \beta_{D^2{X_1}^2} D^2 {X_1}^2, \end{aligned} \tag{2}$$

where β_0 is the intercept, β_t is the yield change resulting from a unitary increase in *t*, β_D and β_{D^2} are, respectively, the linear and quadratic yield change corresponding to a unitary increase in *D*, β_{X_i} and $\beta_{{X_i}^2}$ are, respectively, the linear and quadratic yield changes corresponding to a unitary increase in the climatic index X_i, β_{Dt} and β_{D^2t} quantify the interactions between time and *D* and D^2, respectively, that is, the change in β_D and β_{D^2} in response to a unitary change in t, $\beta_{X_1X_2}$ and $\beta_{X_1{}^2X_2}$ quantify the interactions between X_1 and X_2, that is, the change of β_{X_1} and $\beta_{X_1{}^2}$ in response to a unitary increase in explanatory variable X_2, while β_{DX_i}, $\beta_{DX_i{}^2}$, $\beta_{D^2X_i}$ and $\beta_{D^2X_i{}^2}$ represent the interactions between D or D^2 and X_i or X_i^2. For FR, the fixed part of the model was

$$\begin{aligned} Yield = {} & \beta_0 + \sum_{j=2}^{4} \beta_{FR_j} FR_j + \beta_t t + \beta_{X_1} X_1 + \beta_{X_1{}^2} X_1{}^2 + \beta_{X_2} X_2 + \sum_{j=2}^{4} \beta_{FR_j t} FR_j t \\ & + \sum_{j=2}^{4} \beta_{FR_j X_1} FR_j X_1 + \sum_{j=2}^{4} \beta_{FR_j X_2} FR_j X_2 + \sum_{j=2}^{4} \beta_{FR_j X_1{}^2} FR_j X_1{}^2 \\ & + \beta_{X_1 X_2} X_1 X_2 + \beta_{X_1{}^2 X_2} X_1{}^2 X_2, \end{aligned} \tag{3}$$

where β_{FR_j} is the yield change of having j ($j=2$, 3, 4) functional groups in a rotation (FR2, FR3 or FR4) compared with a rotation with only cereals (FR1, β_0), β_{FR_jt}, $\beta_{FR_jX_i}$, $\beta_{FR_jX_1{}^2}$ quantify the interactions of FR with time t and the climatic index X_i or X_i^2, and the other symbols have the same meaning as in Equation (2) but different values.

The mixed-effects statistical models were fitted using the "lme4" package version 1.1-26 (Bates et al., 2015) in R version 4.1.0 (R Core Team, 2021). The R statements are reported in the Supplementary Information (Section S2, Equations S2 and S3). The model assumptions were checked by visual interpretation of the residual plots using the "DHARMa" package in R (Hartig, 2021). We detected 3.2% outlier observations when running the first model (Equation 2) on maize and 0.13% outliers when running it on spring small grains, and no outliers when running any of the models on winter small grains. Removing the outliers did not alter the statistical significance of the model variables, or our conclusions. Therefore, we kept the outliers in the analyses. We tested all models for multi-collinearity, based on generalized variance inflation factor (GVIF), using the "car" package in R (Fox & Weisberg, 2019). We found no multi-collinearity in any of the models (Tables S3–S6). To establish the robustness of our results to the choice of LTEs, we removed one site at a time and repeated the analyses for each model and indicator crop. None of our conclusions were noticeably affected by removing any site. Predicted yields were calculated including the random component using the "ggeffects" package in R (Lüdecke, 2018), setting time at $t=15$ years, an arbitrary intermediate value. The same patterns hold for other choices of t (not shown). Model trends and estimated marginal means were calculated using "emmeans" package in R (Lenth, 2021), setting time at $t=15$ years.

When exploring the potential of CRD as climate change adaptation, we considered reference changes commensurate with the observed local variability and expected shifts under climate change. In the following, we present the changes in yield anomalies for selected changes in CRD and *T*, *P*, *TDD* and *CDD*. These changes in anomalies were calculated by substituting the estimated model coefficients (Tables 1–4) into Equations (2) and (3). For *T* and *TDD*, we assessed yield responses to a 1.5°C increase, and hence anomaly, in line with the average long-term temperature goal set by the Paris Agreement (UNFCCC, 2016). For *P* and *CDD*, we determined the cumulative frequency distribution of each index, LTE and indicator crop, and divided the LTEs into subsets with low and high variability of *P* and *CDD* (Figures S5 and S6). For *P*, we considered ranges between the first and third quartiles that exceeded an interval of 10 cm per growing season as sites having high variability, and ranges within an interval of 10 cm as sites having low variability. For *CDD*, we considered ranges between the first and third quartiles that exceeded an interval of 10 days per growing season as having high variability, and ranges within an interval of 10 days as having low variability. To exemplify the effects of a drier climate, within each subset, we chose the rounded averages of the first quartiles above 0 (i.e., the local mean) for *CDD*, or below 0 for *P*, as reference deviations from the long-term averages worsening the growing conditions. Using more extreme values, for example, the 15th and 85th percentiles, did not change the patterns discussed below, although predicted values differ, as expected (not shown).

3 | RESULTS

With fixed climatic conditions, yield anomalies (and hence yields) of small grains generally increased from low to intermediate species diversity (*D*; Equation 1) and declined at higher levels of diversity, while for maize yields increased up to the maximum species diversity present in the dataset (Figures 1 and 2), as previously shown (Smith et al., 2023). Conversely, increasing functional richness consistently increased or maintained the yield benefit even at high richness. With fixed CRD, yields increased with decreasing growing season temperature anomalies (*T*, and hence temperature) in all indicator crops, whereas decreasing cumulated precipitation anomalies (*P*, and hence precipitation) reduced yield anomalies (and therefore yields) of maize, had little effects on winter small grain cereals and was beneficial for spring small grain cereals (Figure 1). With fixed CRD, increasing anomalies of a number of consecutive dry spells (*CDD*, and hence length of dry spells) and temperature during dry spells (*TDD*) reduced yields for maize and winter small grain cereals, and had little effects on spring small grain cereals (Figure 2). The strength and shape of the relationship between CRD and grain yield anomalies depended on climatic conditions and their interaction, and on the indicator crop (Tables 1 and 2).

3.1 | The maximum yield benefits of species diversity depended on climatic anomalies

The maximum yield benefit attainable via increasing species diversity was reduced, but not cancelled, by detrimental climatic conditions (Figure 1; Table 1). Here, we present the difference in yield benefit between continuous monoculture (i.e., species diversity 1) and the highest yielding diverse rotation at anomalously low (first

TABLE 1 Model estimates, their standard errors (SE) and significance (p) from the linear mixed-effect model considering species diversity (D; Equation 1) and growing season climatic indices (T and P) for (a) spring small grains, (b) winter small grains and (c) maize yield anomalies (ton/ha), based on fitted Equation (2).

Model			(a) Spring small grains			(b) Winter small grains			(c) Maize		
Coefficients (Eq 2)	Predictors	Unit	Estimates	SE	p	Estimates	SE	p	Estimates	SE	p
β_0	Intercept	t ha^{-1}	-3.77×10^{-1}	1.27×10^{-1}	.004**	-5.52×10^{-1}	1.86×10^{-1}	.003**	-4.90×10^{-1}	1.41×10^{-1}	.001**
β_D	D	t ha^{-1}	8.58	1.84	<.001***	3.29×10^{1}	2.21	<.001***	4.04	2.48	.103
$\beta_D{}^2$	D^2	t ha^{-1}	9.04×10^{-1}	1.79	.613	−9.16	2.44	<.001***	-2.04×10^{1}	1.82	<.001***
β_t	t	t ha^{-1} year^{-1}	1.84×10^{-2}	3.45×10^{-3}	<.001***	4.14×10^{-2}	7.02×10^{-3}	<.001***	2.74×10^{-2}	4.50×10^{-3}	<.001***
β_{X1}	T	t ha^{-1} °C^{-1}	-1.62×10^{1}	5.02	.001**	-3.39×10^{1}	1.12×10^{1}	.003**	-1.50×10^{1}	5.80	.010*
$\beta_{X1}{}^2$	T^2	t ha^{-1} °C^{-2}	-1.51×10^{-1}	4.24	.972	2.38	1.17×10^{1}	.840	−3.15	5.32	.554
β_{X2}	P	t ha^{-1} cm^{-1}	-1.21×10^{-2}	6.53×10^{-3}	.065	4.79×10^{-2}	8.21×10^{-3}	<.001***	-1.24×10^{-2}	7.39×10^{-3}	.094
β_{Dt}	$D\times t$	t ha^{-1} year^{-1}	3.07×10^{-1}	7.37×10^{-2}	<.001***	1.09	1.31×10^{-1}	<.001***	5.49×10^{-1}	9.30×10^{-2}	<.001***
$\beta_D{}^2{}_t$	$D^2\times t$	t ha^{-1} year^{-1}	-5.52×10^{-1}	7.07×10^{-2}	<.001***	2.36×10^{-1}	1.20×10^{-1}	.050*	-4.62×10^{-2}	8.12×10^{-2}	.570
β_{DX1}	$D\times T$	t ha^{-1} °C^{-1}	7.86×10^{1}	9.27×10^{1}	.396	-1.82×10^{2}	1.34×10^{2}	.174	-7.14×10^{2}	1.34×10^{2}	<.001***
$\beta_D{}^2{}_{X1}$	$D^2\times T$	t ha^{-1} °C^{-1}	3.06×10^{2}	9.47×10^{1}	.001**	-1.86×10^{2}	1.52×10^{2}	.220	-1.33×10^{2}	1.00×10^{2}	.186
$\beta_{DX1}{}^2$	$D\times T^2$	t ha^{-1} °C^{-2}	-3.12×10^{2}	7.41×10^{1}	<.001***	8.50×10^{1}	1.12×10^{2}	.449	-2.87×10^{2}	1.19×10^{2}	.016*
$\beta_D{}^2{}_{X1}{}^2$	$D^2\times T^2$	t ha^{-1} °C^{-2}	6.93×10^{1}	7.84×10^{1}	.377	-1.35×10^{2}	1.40×10^{2}	.334	-2.77×10^{1}	9.62×10^{1}	.774
β_{DX2}	$D\times P$	t ha^{-1} cm^{-1}	-1.17×10^{-1}	1.45×10^{-1}	.423	3.33×10^{-1}	1.15×10^{-1}	.004**	−1.01	1.99×10^{-1}	<.001***
$\beta_D{}^2{}_{X2}$	$D^2\times P$	t ha^{-1} cm^{-1}	1.88×10^{-1}	1.45×10^{-1}	.195	-8.68×10^{-2}	1.30×10^{-1}	.505	-3.79×10^{-1}	1.38×10^{-1}	.006**
β_{X1X2}	$T\times P$	t ha^{-1} °C^{-1} cm^{-1}	8.39×10^{-1}	6.36×10^{-1}	.188	2.02	8.79×10^{-1}	.022*	-6.54×10^{-1}	6.33×10^{-1}	.303
$\beta_{X1}{}^2{}_{X2}$	$T^2\times P$	t ha^{-1} °C^{-2} cm^{-1}	-2.00×10^{-1}	6.00×10^{-1}	.739	-6.46×10^{-1}	6.97×10^{-1}	.355	-8.99×10^{-1}	5.19×10^{-1}	.084
Observations			8429			7198			11,231		
Marginal R^2/Conditional R^2			.0680/.731			.103/.776			.176/.766		

Note: The marginal R^2 represents the variation explained by the fixed factors alone, while the conditional R^2 is the variation explained by the entire model including fixed and random factors (Barton, 2020).

Abbreviations: D, species diversity; P, growing season cumulated precipitation anomaly; T, growing season average daily maximum temperature anomaly; t, years since the beginning of the experiment.

Significance levels: $^{*}p < .05$; $^{**}p < .01$; $^{***}p < .001$.

TABLE 2 Model estimates, their standard errors (SE) and significance (p) from the linear mixed-effect model considering species diversity (D; Equation 1) and intra-seasonal climatic indices (CDD and TDD) for (a) spring small grains, (b) winter small grains and (c) maize yield anomalies (ton/ha), based on fitted Equation (2).

Model			(a) Spring small grains			(b) Winter small grains			(c) Maize		
Coefficients (Eq 2)	**Predictors**	**Unit**	**Estimates**	**SE**	p	**Estimates**	**SE**	p	**Estimates**	**SE**	p
β_0	Intercept	$t\,ha^{-1}$	-2.66×10^{-1}	1.19×10^{-1}	.028*	-6.54×10^{-1}	1.80×10^{-1}	<.001***	-3.77×10^{-1}	1.31×10^{-1}	.005**
β_D	D	$t\,ha^{-1}$	9.64	1.56	<.001***	3.30×10^{1}	2.21	<.001***	1.15×10^{1}	2.15	<.001***
β_D^{2}	D^2	$t\,ha^{-1}$	−1.63	1.52	.283	−8.84	2.39	<.001***	-1.79×10^{1}	1.60	<.001***
β_t	t	$t\,ha^{-1}\,year^{-1}$	1.20×10^{-2}	2.88×10^{-3}	<.001***	4.10×10^{-2}	6.93×10^{-3}	<.001***	2.16×10^{-2}	3.82×10^{-3}	<.001***
β_{X1}	TDD	$t\,ha^{-1}\,°C^{-1}$	6.93×10^{-1}	3.46	.842	-4.07×10^{1}	1.02×10^{1}	<.001***	−9.25	4.43	.037*
β_{X1}^{2}	TDD^2	$t\,ha^{-1}\,°C^{-2}$	−2.57	3.60	.476	-2.58×10^{1}	1.11×10^{1}	.021*	5.06×10^{-1}	4.60	.912
β_{X2}	CDD	$t\,ha^{-1}\,day^{-1}$	2.36×10^{-3}	4.47×10^{-3}	.598	-4.61×10^{-2}	1.33×10^{-2}	.001**	-5.71×10^{-3}	5.22×10^{-3}	.274
β_{Dt}	$D\times t$	$t\,ha^{-1}\,year^{-1}$	2.64×10^{-1}	5.98×10^{-2}	<.001***	1.10	1.32×10^{-1}	<.001***	2.22×10^{-1}	7.75×10^{-2}	.004**
$\beta_{D^2\,t}$	$D^2\times t$	$t\,ha^{-1}\,year^{-1}$	-4.36×10^{-1}	5.69×10^{-2}	<.001***	2.30×10^{-1}	1.18×10^{-1}	.052	-1.61×10^{-1}	6.98×10^{-2}	.021*
β_{DX1}	$D\times TDD$	$t\,ha^{-1}\,°C^{-1}$	2.80×10^{2}	7.56×10^{1}	<0.001***	-5.92×10^{1}	1.53×10^{2}	0.698	2.06×10^{2}	1.09×10^{2}	0.058
$\beta_{D^2\,X1}$	$D^2\times TDD$	$t\,ha^{-1}\,°C^{-1}$	-5.96×10^{1}	7.13×10^{1}	.403	-1.50×10^{2}	1.54×10^{2}	.332	-1.23×10^{2}	8.05×10^{1}	.126
β_{DX1^2}	$D\times TDD^2$	$t\,ha^{-1}\,°C^{-2}$	1.14×10^{2}	7.78×10^{1}	.143	2.95×10^{2}	2.05×10^{2}	.150	9.27×10^{1}	1.13×10^{2}	.412
$\beta_{D^2\,X1^2}$	$D^2\times TDD^2$	$t\,ha^{-1}\,°C^{-2}$	2.92×10^{1}	7.04×10^{1}	.678	7.94×10^{2}	1.76×10^{2}	<.001***	-1.06×10^{2}	8.86×10^{1}	.230
β_{DX2}	$D\times CDD$	$t\,ha^{-1}\,day^{-1}$	-9.61×10^{-2}	9.97×10^{-2}	.335	−1.26	2.10×10^{-1}	<.001***	5.92×10^{-2}	1.19×10^{-1}	.618
$\beta_{D^2\,X2}$	$D^2\times CDD$	$t\,ha^{-1}\,day^{-1}$	8.93×10^{-2}	8.91×10^{-2}	.316	-1.12×10^{-1}	2.27×10^{-1}	.621	1.45×10^{-1}	8.91×10^{-2}	.103
β_{X1X2}	$TDD\times CDD$	$t\,ha^{-1}\,°C^{-1}\,day^{-1}$	-4.53×10^{-1}	4.46×10^{-1}	.310	−1.13	1.75	.519	-2.10×10^{-1}	4.93×10^{-1}	.670
$\beta_{X1^2\,X2}$	$TDD^2\times CDD$	$t\,ha^{-1}\,°C^{-2}\,day^{-1}$	-7.48×10^{-1}	4.26×10^{-1}	0.080	3.44	2.20	0.118	−1.38	5.02×10^{-1}	0.006**
Observations			8429			7198			11,231		
Marginal R^2/Conditional R^2			.0578/.728			.101/.774			.144/.770		

Note: The marginal R^2 represents the variation explained by the fixed factors alone, while the conditional R^2 the variation explained by the entire model including fixed and random factors (Barton, 2020).

Abbreviations: CDD, anomaly of the highest number of consecutive dry days; D, species diversity; t, years since the beginning of the experiment; TDD, average maximum temperature anomaly during the consecutive dry days.

Significance levels: $^{*}p < .05$; $^{**}p < .01$; $^{***}p < .001$.

TABLE 3 Model estimates, their standard errors (SE) and significance (p) from the linear mixed-effect model considering functional richness (FR) and growing season climatic indices (P and T) for (a) spring small grains, (b) winter small grains and (c) maize yield anomalies (ton/ha), based on fitted Equation (3).

Model			(a) Spring small grains			(b) Winter small grains			(c) Maize		
Coefficients (Eq 3)	Predictors	Unit	Estimates	SE	p	Estimates	SE	p	Estimates	SE	p
β_0	Intercept	$\mathrm{t\,ha^{-1}}$	-5.20×10^{-1}	1.30×10^{-1}	<.001***	-8.19×10^{-1}	1.44×10^{-1}	<.001***	−1.05	1.90×10^{-1}	<.001***
β_{FR2}	FR2	$\mathrm{t\,ha^{-1}}$	2.02×10^{-1}	4.33×10^{-2}	<.001***	5.43×10^{-1}	5.73×10^{-2}	<.001***	6.66×10^{-1}	4.99×10^{-2}	<.001***
β_{FR3}	FR3	$\mathrm{t\,ha^{-1}}$	1.04×10^{-1}	5.19×10^{-2}	.0463*	6.82×10^{-1}	5.69×10^{-2}	<.001***	9.19×10^{-1}	8.86×10^{-2}	<.001***
β_{FR4}	FR4	$\mathrm{t\,ha^{-1}}$	2.52×10^{-1}	7.81×10^{-2}	.00125**	—	—	—	—	—	—
β_t	t	$\mathrm{t\,ha^{-1}\,year^{-1}}$	1.17×10^{-2}	3.59×10^{-3}	.0012**	2.48×10^{-2}	4.56×10^{-3}	<.001***	3.07×10^{-2}	7.17×10^{-3}	<.001***
β_{X1}	T	$\mathrm{t\,ha^{-1}\,°C^{-1}}$	-1.57×10	5.23	.00281**	-1.23×10	5.90	.037*	-3.47×10	1.14×10	.00249**
$\beta_{X1}{}^2$	T^2	$\mathrm{t\,ha^{-1}\,°C^{-2}}$	4.47	4.35	.304	−2.65	5.37	.621	−2.00	1.19×10	.867
β_{X2}	P	$\mathrm{t\,ha^{-1}\,cm^{-1}}$	-9.98×10^{-3}	6.95×10^{-3}	.152	-8.80×10^{-3}	7.60×10^{-3}	.248	4.20×10^{-2}	8.50×10^{-3}	<.001***
β_{FR2t}	FR2 × t	$\mathrm{t\,ha^{-1}\,year^{-1}}$	3.31×10^{-3}	1.76×10^{-3}	.0593	-2.64×10^{-4}	2.63×10^{-3}	.92	7.22×10^{-3}	2.21×10^{-3}	.00106**
β_{FR3t}	FR3 × t	$\mathrm{t\,ha^{-1}\,year^{-1}}$	2.02×10^{-2}	1.81×10^{-3}	<.001***	9.16×10^{-3}	2.00×10^{-3}	<.001***	3.95×10^{-2}	6.28×10^{-3}	<.001***
β_{FR4t}	FR4 × t	$\mathrm{t\,ha^{-1}\,year^{-1}}$	1.25×10^{-2}	3.38×10^{-3}	<.001***	—	—	—	—	—	—
β_{FR2X1}	FR2 × T	$\mathrm{t\,ha^{-1}\,°C^{-1}}$	2.89	2.21	.191	−7.23	3.01	.0161*	3.72×10^{-1}	3.18	.907
β_{FR3X1}	FR3 × T	$\mathrm{t\,ha^{-1}\,°C^{-1}}$	-1.01×10	2.76	<.001***	−9.36	2.94	.00146**	2.66	6.38	.677
β_{FR4X1}	FR4 × T	$\mathrm{t\,ha^{-1}\,°C^{-1}}$	7.36	4.41	.0953	—	—	—	—	—	—
$\beta_{FR2X1}{}^2$	FR2 × T^2	$\mathrm{t\,ha^{-1}\,°C^{-2}}$	−5.57	1.73	.00128	−3.59	2.23	.108	7.04	2.88	.0144*
$\beta_{FR3X1}{}^2$	FR3 × T^2	$\mathrm{t\,ha^{-1}\,°C^{-2}}$	−9.83	2.13	<.001***	−6.20	2.29	.00684**	6.48	5.83	.266
$\beta_{FR4X1}{}^2$	FR4 × T^2	$\mathrm{t\,ha^{-1}\,°C^{-2}}$	−3.59	3.37	.287	—	—	—	—	—	—
β_{FR2X2}	FR2 × P	$\mathrm{t\,ha^{-1}\,cm^{-1}}$	5.22×10^{-4}	3.42×10^{-3}	.878	-8.88×10^{-3}	4.34×10^{-3}	.0407*	6.29×10^{-3}	2.81×10^{-3}	.0252*
β_{FR3X2}	FR3 × P	$\mathrm{t\,ha^{-1}\,cm^{-1}}$	-9.80×10^{-3}	4.24×10^{-3}	.0209	-1.32×10^{-2}	4.53×10^{-3}	.00356**	1.97×10^{-2}	4.79×10^{-3}	<.001***
β_{FR4X2}	FR4 × P	$\mathrm{t\,ha^{-1}\,cm^{-1}}$	6.18×10^{-3}	6.18×10^{-3}	.317	—	—	—	—	—	—
β_{X1X2}	T × P	$\mathrm{t\,ha^{-1}\,°C^{-1}\,cm^{-1}}$	7.90×10^{-1}	6.31×10^{-1}	.211	-8.62×10^{-1}	6.27×10^{-1}	.17	1.98	8.81×10^{-1}	.0254*
$\beta_{X1}{}^2{}_{X2}$	T^2 × P	$\mathrm{t\,ha^{-1}\,°C^{-2}\,cm^{-1}}$	-1.02×10^{-1}	5.95×10^{-1}	.863	-9.02×10^{-1}	5.14×10^{-1}	.08*	-7.51×10^{-1}	6.98×10^{-1}	.283
Observations			8429			7198			11,231		
Marginal R^2/Conditional R^2			.17/.76			.13/.78			.071/.73		

Note: The marginal R^2 represents the variation explained by the fixed factors alone, while the conditional R^2 the variation explained by the entire model including fixed and random factors (Barton, 2020).

Abbreviations: FR, functional richness; P, growing season cumulated precipitation anomaly; T, growing season average daily maximum temperature anomaly; t, years since the beginning of the experiment.

Significance levels: $^{*}p < .05$; $^{**}p < .01$; $^{***}p < .001$.

TABLE 4 Model estimates, their standard errors (SE) and significance (*p*) from the linear mixed-effect model considering functional richness (FR) and intra-seasonal climatic indices (*CDD* and *TDD*) for (a) spring small grains, (b) winter small grains and (c) maize yield anomalies (ton/ha), based on fitted Equation (3).

Model			(a) Spring small grains			(b) Winter small grains			(c) Maize		
Coefficients (Eq 3)	Predictors	Unit	Estimates	SE	*p*	Estimates	SE	*p*	Estimates	SE	*p*
β_0	Intercept	tha^{-1}	-4.32×10^{-1}	1.22×10^{-1}	.001**	-7.35×10^{-1}	1.35×10^{-1}	<.001***	−1.16	1.83×10^{-1}	<.001***
β_{FR2}	FR2	tha^{-1}	2.23×10^{-1}	3.73×10^{-2}	<.001***	5.92×10^{-1}	5.32×10^{-2}	<.001***	6.76×10^{-1}	4.91×10^{-2}	<.001***
β_{FR3}	FR3	tha^{-1}	2.29×10^{-1}	4.41×10^{-2}	<.001***	7.89×10^{-1}	4.98×10^{-2}	<.001***	9.23×10^{-1}	9.16×10^{-2}	<.001***
β_{FR4}	FR4	tha^{-1}	2.14×10^{-1}	7.19×10^{-2}	.003**	—	—	—	—	—	—
β_t	*t*	$\text{tha}^{-1}\,\text{year}^{-1}$	6.26×10^{-3}	3.01×10^{-3}	.038*	2.06×10^{-2}	3.85×10^{-3}	<.001***	2.99×10^{-2}	7.03×10^{-3}	<.001***
β_{X1}	*TDD*	$\text{tha}^{-1}\,°\text{C}^{-1}$	−4.48	3.70	.227	-1.28×10	4.50	.005**	-3.90×10	1.04×10	<.001***
$\beta_{X1}{}^2$	TDD^2	$\text{tha}^{-1}\,°\text{C}^{-2}$	−4.84	3.80	.204	−1.78	4.65	.702	$-2.08\times10^{+01}$	1.12×10	.063
β_{X2}	*CDD*	$\text{tha}^{-1}\,\text{day}^{-1}$	4.89×10^{-3}	4.78×10^{-3}	.307	-4.03×10^{-3}	5.37×10^{-3}	.453	-3.65×10^{-2}	1.36×10^{-2}	.008**
$\beta_{\mathrm{FR2}t}$	FR2 × *t*	$\text{tha}^{-1}\,\text{year}^{-1}$	2.92×10^{-3}	1.45×10^{-3}	.045*	-3.48×10^{-3}	2.35×10^{-3}	.138	7.30×10^{-3}	2.14×10^{-3}	.001**
$\beta_{\mathrm{FR3}t}$	FR3 × *t*	$\text{tha}^{-1}\,\text{year}^{-1}$	1.49×10^{-2}	1.44×10^{-3}	<.001***	4.53×10^{-3}	1.66×10^{-3}	.006**	4.51×10^{-2}	6.36×10^{-3}	<.001***
$\beta_{\mathrm{FR4}t}$	FR4 × *t*	$\text{tha}^{-1}\,\text{year}^{-1}$	1.43×10^{-2}	2.99×10^{-3}	<.001***	—	—	—	—	—	—
β_{FR2X1}	FR2 × *TDD*	$\text{tha}^{-1}\,°\text{C}^{-1}$	7.45	1.87	<.001***	4.53	2.35	.054	−2.82	2.89	.329
β_{FR3X1}	FR3 × *TDD*	$\text{tha}^{-1}\,°\text{C}^{-1}$	5.55	2.01	.006**	1.05×10	2.55	<.001***	3.10	6.29	.622
β_{FR4X1}	FR4 × *TDD*	$\text{tha}^{-1}\,°\text{C}^{-1}$	1.04×10	3.92	.008**	—	—	—	—	—	—
$\beta_{\mathrm{FR2X1}}{}^2$	FR2 × TDD^2	$\text{tha}^{-1}\,°\text{C}^{-2}$	6.19	1.97	.002**	4.80	2.42	.047*	$-1.05\times10^{+01}$	2.66	<.001***
$\beta_{\mathrm{FR3X1}}{}^2$	FR3 × TDD^2	$\text{tha}^{-1}\,°\text{C}^{-2}$	1.54	1.84	.403	5.31	2.36	.024*	1.86×10	9.27	.045*
$\beta_{\mathrm{FR4X1}}{}^2$	FR4 × TDD^2	$\text{tha}^{-1}\,°\text{C}^{-2}$	−2.45	4.22	.561	—	—	—	—	—	—
β_{FR2X2}	FR2 × *CDD*	$\text{tha}^{-1}\,\text{day}^{-1}$	-4.24×10^{-3}	2.35×10^{-3}	.071	-1.90×10^{-3}	3.17×10^{-3}	.549	-1.05×10^{-2}	4.60×10^{-3}	.022*
β_{FR3X2}	FR3 × *CDD*	$\text{tha}^{-1}\,\text{day}^{-1}$	-4.55×10^{-3}	2.69×10^{-3}	.091	-1.79×10^{-3}	3.00×10^{-3}	.550	-4.40×10^{-2}	7.19×10^{-3}	<.001***
β_{FR4X2}	FR4 × *CDD*	$\text{tha}^{-1}\,\text{day}^{-1}$	-1.37×10^{-3}	4.69×10^{-3}	.771	—	—	—	—	—	—
β_{X1X2}	*TDD* × *CDD*	$\text{tha}^{-1}\,°\text{C}^{-1}\,\text{day}^{-1}$	-4.61×10^{-1}	4.45×10^{-1}	.301	-1.46×10^{-1}	4.88×10^{-1}	.765	-8.69×10^{-1}	1.74	.619
$\beta_{X1}{}^2{}_{X2}$	TDD^2 × *CDD*	$\text{tha}^{-1}\,°\text{C}^{-2}\,\text{day}^{-1}$	-7.53×10^{-1}	4.25×10^{-1}	.077	−1.34	4.97×10^{-1}	.007**	3.08	2.18	.160
Observations			8429			7198			11,231		
Marginal R^2/Conditional R^2			.06/.73			.13/.78			.14/.76		

Note: The marginal R^2 represents the variation explained by the fixed factors alone, while the conditional R^2 the variation explained by the entire model including fixed and random factors (Barton, 2020).

Abbreviations: *CDD*, anomaly of the highest number of consecutive dry days; FR, functional richness; *t*, years since the beginning of the experiment; *TDD*, average maximum temperature anomaly during the consecutive dry days.

Significance levels: $^{*}p < .05$; $^{**}p < .01$; $^{***}p < .001$.

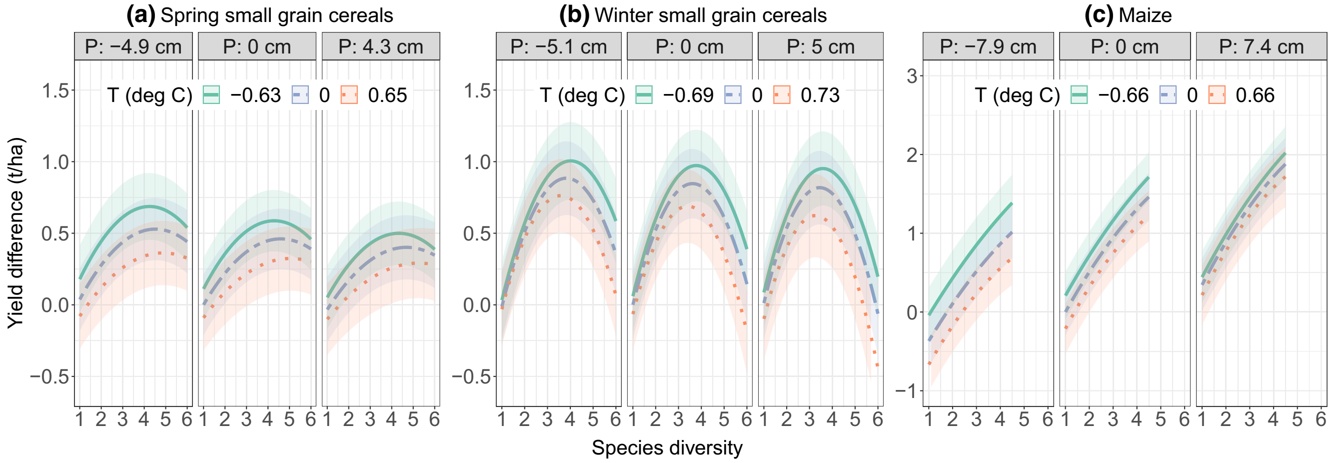

FIGURE 1 Model-predicted yield difference from baseline yield anomaly for (a) spring small grains, (b) winter small grains and (c) maize, as a function of species diversity, growing season average daily maximum temperature anomalies (*T*) and cumulated precipitation anomalies (*P*) based on fitted Equation (2). To facilitate the comparisons across climatic conditions and species diversity, the baseline of yield anomaly (i.e., 0 t ha^{-1} on the *y*-axis) is set to the yield anomaly, that is, deviations from the site- and crop-specific local mean, of the monoculture under long-term average of *T* and *P* and at $t = 15$ year—an arbitrary intermediate value of the time elapsed from the beginning of the experiment; similar patterns occur when selecting other *t*. Colours and lines represent yield anomaly predictions for the first quartile (green solid lines), long-term average (blue dashed lines) and third quartile (red dotted lines) of *T*. For each indicator crop, the left, central and right panels show model predictions for the first quartile, the long-term average, and the third quartile of *P*. The shaded areas extend over the 95% confidence intervals.

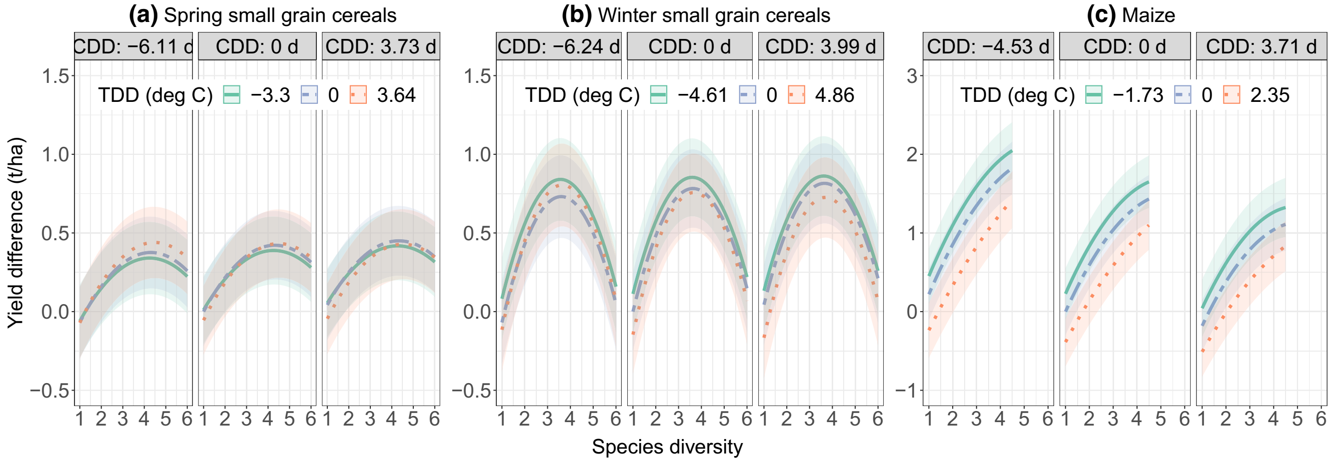

FIGURE 2 Model-predicted yield difference from baseline yield anomaly for (a) spring small grains, (b) winter small grains and (c) maize as a function of species diversity, the anomalies of the highest number of consecutive dry day (*CDD*) and average temperatures during that period (*TDD*), based on fitted Equation (2). To facilitate the comparisons across conditions and species diversity, the baseline of yield anomaly (i.e., 0 t ha^{-1} on the *y*-axis) is set to the yield anomaly, that is, deviations from the site- and crop-specific local mean, of the monoculture under long-term average *CDD* and *TDD* at $t = 15$ years. Left, central and right panels for each crop refer to model predictions within the first quartile, the long-term average and the third quartiles of *CDD*. The lines refer to the first quartile (solid green), the long-term average (dashed blue) and the third quartile (dotted red) of *TDD*. The shaded areas extend over the 95% confidence intervals.

quartile) or high (third quartile) *P* and *T* (or *CDD* and *TDD*), at Year 15, that is, the largest possible benefit of species diversity.

Under high-yielding seasonal conditions for small grains (first *T* quartile and first *P* quartile, Figure 1), the maximum yield benefits attainable via species diversity were 508 kg/ha (95% CI [274, 742]) and 973 kg/ha (95% CI [701, 1244]) for spring and winter small grains respectively. Under low-yielding conditions (third *T* and *P* quartiles, Figure 1), the maximum yield benefits attainable via species diversity were reduced to 393 kg/ha (95% CI [148, 637]) and 722 kg/ha (95% CI [431, 1013]) for spring and winter small grains respectively. For maize, the maximum yield benefits attainable via species diversity were 1601 kg/ha (95% CI [1268, 1935]), under high-yielding conditions (first *T* quartile and third *P* quartile, Figure 1). Low-yielding conditions (first *P* quartile and third *T* quartile) reduced the maximum yield benefits attainable via species diversity to 1368 kg/ha (95% CI [1026, 1710], Figure 1).

The maximum yield benefits attainable via species diversity were also affected by intra-seasonal climatic conditions, that is, anomalies in *CDD* and *TDD*, in directions dependent on the indicator crop (Figure 2; Table 2). Maximum yield benefits attainable via species diversity for spring small grains increased with *TDD* (Table 2, $D \times TDD$ interaction), but the effect was only noticeable under low *CDD* (Figure 2). For winter small grains, the maximum yield benefits attainable via species diversity decreased as *TDD* increased under average and high *CDD* (Figure 2). For maize, the difference between monoculture yields and the maximum yield benefit attainable via species diversity decreased as *CDD* and *TDD* increased (Figure 2). Taking maize as example, the difference in yield benefit between a monoculture and the highest yielding rotation at Year 15 was 1608 kg/ha (95% CI [1245, 1971]) under the first *CDD* and *TDD* quartiles, and was reduced to 1360 kg/ha (95% CI [1039, 1682]) under the third *CDD* and *TDD* quartiles.

3.2 | The yield-maximizing species diversity changed with climatic conditions

As *P* and *T* increased, the yield-maximizing species diversity increased in spring small grains, but decreased in winter small grains (Figure 1). Species diversity in maize also interacted with growing season temperature and precipitation (Table 1), but the yield-maximizing species diversity was likely outside the range of species diversity included in our dataset (Figure 1).

The yield-maximizing species diversity also shifted depending on the length and temperature anomaly of the longest dry spell. For small grains, the yield-maximizing species diversity increased under longer and warmer dry spells (Figure 2). For maize, the length and temperature of dry spells did not affect the relation between yields and species diversity (Table 2), but the yield-maximizing species diversity was higher than the species diversity range among the LTEs (Figure 2).

3.3 | Yield benefits of species diversity compensated for warming-induced monoculture yield losses

Warming caused a yield reduction in monocultures that could be balanced by relatively small increases in species diversity (Figure 1). Taking maize as example, an increase in growing season temperature of 1.5°C, that is, a shift from the long-term average to the 93rd percentile of *T*, reduced maize yield by 486 kg/ha (95% CI [−990, 18]) under a monoculture at Year 15 under local average precipitation (Equation 2). A species diversity of 2, in this case, would be sufficient to maintain the yield of the monoculture under long-term average *T* and *P* ($T=0$ and $P=0$).

Co-occurring warming and negative precipitation anomalies led to even higher yield losses than warming alone for maize, and required higher species diversity to compensate monoculture yield losses (Table 1, $T \times P$ interaction). In the following examples, we present modelled yields in relation to the yields of a monoculture occurring under long-term average of *T* and *P*, at Year 15. For example, if a 1.5°C increase in *T* co-occurred with a 5 cm decline in *P*, representing a frequent anomaly in LTEs with relatively low variability in *P* (see Section 2.3), transforming a monoculture into a rotation with species diversity of 2.59 would compensate the potential loss of 1150 kg/ha (95% CI [−1553, −746]) (Equation 2; Table 1). An additional maize yield of 553 kg/ha (95% CI [125, 980]) could be gained by further increasing species diversity to the yield-maximizing level under such conditions, that is, to 4.57. The compensatory effect of species diversity held also in LTEs with higher precipitation variability. If the warming of 1.5°C occurred with a 8 cm decline in *P*, a frequent *P* anomaly in LTEs with relatively high variability in *P*, increasing species diversity to 3.19, could buffer the expected monoculture yield loss of 1017 kg/ha (95% CI [−1419, −615]) (Equation 2; Table 1).

Yield reductions associated with high *CDD* and *TDD* in monocultures could be balanced by the yield benefit increases in species diversity (Figure 2). Monoculture yields were reduced by increasing *CDD* and *TDD*, from local average to the third *CDD* and *TDD* quartiles by an average of 45 kg/ha (95% CI [−270, 180]) for spring small grains, 166 kg/ha (95% CI [−423, 91]) for winter small grains and 511 kg/ha (95% CI [−827, −195]) for maize (Figure 2). In those conditions, increasing species diversity from 1 (monoculture) to 1.18 for spring small grains, 1.27 for winter small grains and 2.04 for maize was sufficient to compensate for these monoculture yield losses (Figure 2). Yield reductions caused by expected shifts in *TDD* and *CDD* towards a warmer and more variable climate, required higher species diversity to be mitigated. For example, an increase of 1.5°C in *TDD* co-occurring with a 3-day lengthening of *CDD*—a level frequent in LTEs with relatively low variability in *CDD*—was predicted to reduce maize yield by 359 kg/ha (95% CI [−662, −56]) in a maize monoculture (Equation 2; Table 2). A species diversity of 1.65 would compensate for the yield loss, and a surplus of 1000 kg/ha (95% CI [691, 1308]) could be gained at the maximum species diversity included in our dataset (4.57). An increase of 7 days in *CDD*—typical of LTEs with relatively high variability in *CDD*—co-occurring with an increase of 1.5°C in *TDD* would require a species diversity of 2.06 to buffer a monoculture loss of 522 kg/ha (95% CI [−874, −170]) (Equation 2; Table 2).

Increasing species diversity did not reduce the sensitivity of yield anomalies to changes in temperature anomalies, except for small grains under low precipitation and high temperatures, and winter small grains under long-term average conditions (Figure S7). Warming had a stronger negative effect on small grain yields for species diversity from 2 to 5 for spring grains and from 2 to 6 for winter grains (Figure S7). The sensitivity of yield anomalies to yield-reducing precipitation anomalies did not change as species diversity increased for all indicator crops (not shown).

3.4 | Functional richness compensated for yield losses associated with detrimental conditions

Similar to species diversity, modest increases in functional richness compensated for yield losses associated with warming occurring at functional richness 1, that is, cereal-only rotations. For example, a functional richness of 2, that is, adding one non-cereal crop to the rotation, was sufficient to balance the expected yield loss of cereal-only rotations under an increase in *T* from the average value to the third quartile at average *P* (Figure 3; Table 3). Under these conditions, the yield benefit of an increase in functional richness from 1 to 2 gave a surplus of 199 kg/ha (95% CI [−25, 424]) for spring small grains, 389 kg/ha (95% CI [127, 650]) for winter small grains and 526 kg/ha (95% CI [210, 843]) for maize, compared with a cereal-only rotation grown under long-term average conditions. The yield surplus was even larger when functional richness was higher than 2 under the same warming conditions (Figure 3). We observed analogous outcomes for warm dry spells, that is, *TDD* in the third quartile (Figure 4; Table 4).

Increasing functional richness compensated yield losses in cereal-only rotations even under warming expected due to climate change. Taking maize as example, a 1.5°C warming under long-term average precipitation caused a maize yield loss of 518 kg/ha (95% CI [−1022, −15]) in cereal-only rotations, which was more than compensated by a functional richness of 2. The yield benefit of this functional richness increase exceeded the yields under the current long-term average temperature by 310 kg/ha (95% CI [−188, 808]) (Equation 3; Table 3). If the 1.5°C warming co-occurred with a 5 or 8 cm decline in *P*, anomalies frequently observed in LTEs with low and high variability in *P* respectively, the cereal-only rotation would require two additional functional groups (i.e., a functional richness of 3) to compensate for the yield loss of 842 kg/ha (95% CI [−1263, −421]) or 1037 kg/ha (95% CI [−1437, −636]), respectively (Equation 3; Table 3). Similar patterns emerged also for spring and winter small grains.

4 | DISCUSSION

4.1 | Increased CRD more than compensated yield losses in low diversity rotations under detrimental climatic conditions in all crops

Increasing CRD mitigated staple cereal yield losses occurring in monocultures and cereal-only rotations due to detrimental climatic conditions, confirming our first hypothesis (Tables 1–4). Yield benefits of relatively small increases in CRD, that is, one additional crop added to monocultures or one functional group added to cereal-only rotations, compensated for yield losses in these low diversity rotations occurring under detrimental climatic conditions. Hence, increasing CRD could support climate change adaptation of cereal production under European and North American growing conditions. Analyses of additional long-term experiments are needed to explore whether diversified crop rotations buffer yield losses due to climate change also in other regions and crops.

For small grains, the maximum yield benefits attainable via diversification increased with decreasing temperature and precipitation, that is, under favourable conditions. This stood in contrast to our second hypothesis and observations in grasslands (Wright et al., 2021). In maize, the maximum attainable yield benefit was

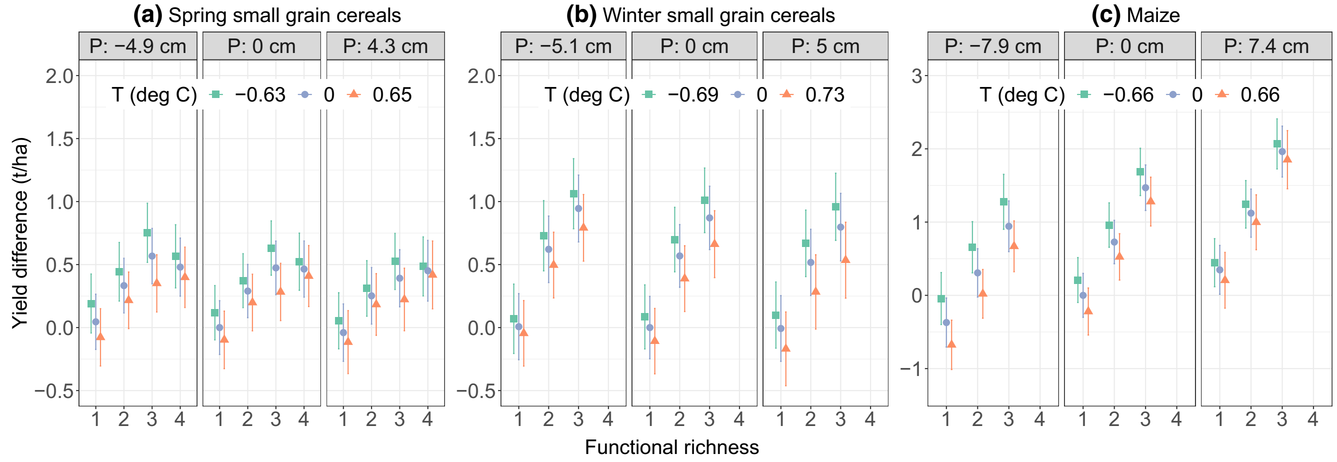

FIGURE 3 Model-predicted yield difference from baseline yield anomaly for (a) spring small grains, (b) winter small grains and (c) maize, in response to functional richness, growing season average daily maximum temperature anomalies (*T*) and cumulated precipitation anomalies (*P*), based on fitted Equation (3). To facilitate the comparisons across conditions and functional richness, the baseline of yield anomaly (i.e., 0 t ha^{-1} on the *y*-axis) is set to the yield anomaly, that is, deviations from the site- and crop-specific local mean, of a rotation with functional richness 1, that is, cereal-only, under long-term average of *T* and *P*, and at *t* = 15 years, an arbitrary intermediate value; similar patterns occur when selecting other *t*. Symbols represent yield anomaly predictions under the first quartile (green squares), long-term average (blue diamonds) and third quartile (red triangles) of *T*. For each indicator crop, the left, central and right panels show model predictions within the first quartile, the long-term average and the third quartile of *P*. The whiskers indicate the 95% confidence intervals.

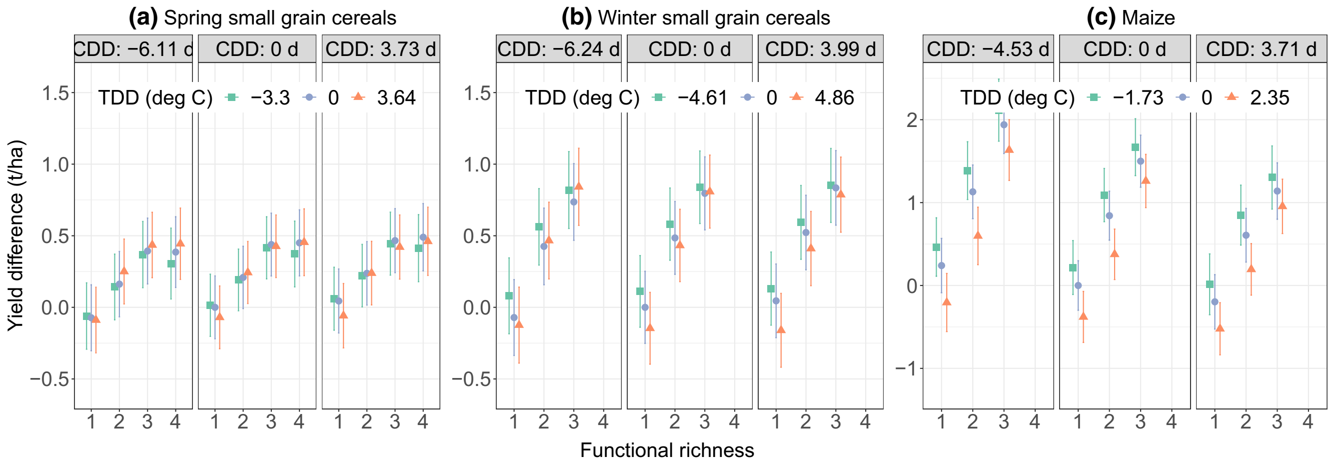

FIGURE 4 Model-predicted yield difference from baseline yield anomaly, that is, deviations from the site- and crop-specific local mean, for (a) spring small grains, (b) winter small and (c) maize, in response to functional richness, and the anomalies of the highest number of consecutive dry days (*CDD*) and average temperatures during that period (*TDD*), based on fitted Equation (3). To facilitate the comparisons across conditions and functional richness, the baseline of yield anomaly (i.e., 0 t ha^{-1} on the *y*-axis) is set to the anomaly, that is, deviations from the site- and crop-specific local mean, of a rotation with functional richness 1, that is, cereal-only, under long-term average of *CDD* and *TDD*, and at $t = 15$ years. For each indicator crop, the left, central and right panels show model predictions within the first quartile, the long-term average and the third quartile of *CDD*. The symbols represent yield anomaly predictions under the first quartile (green squares), the long-term average (blue diamonds) and the third quartile (red triangles) of *TDD*. The whiskers indicate the 95% confidence intervals.

largely unaffected by climatic conditions, also in contrast to our second hypothesis. However, the relative benefits, that is, the yield benefit divided by the average yield, were higher under detrimental compared with favourable conditions, as previously observed for maize in one of the sites (Gaudin et al., 2015).

The maximum attainable yield via diversification under detrimental conditions exceeded the average yield of monocultures under favourable conditions. In other words, increasing CRD can provide grain yield benefits comparable with improved climatic conditions, for example, decreasing temperature and length and temperature of dry spells for both small grains and maize, and increasing precipitation for maize. These results confirm that species-diverse and functionally rich rotations enhance grain yields under all growing conditions (Bowles et al., 2020; Gaudin et al., 2015; Marini et al., 2020; Smith et al., 2023). We expanded on this by explicitly considering climatic conditions and CRD levels, which allowed us to estimate the beneficial effects of an increase in CRD and the change in CRD needed to cope with a set change in climatic conditions.

Yields increased over time and more so at the CRD that maximized yields (Tables 1 and 3). These yield increases were the net result of changing climatic conditions, and technological and breeding improvements over time (Ortiz-Bobea & Tack, 2018). Disentangling the two effects would require manipulating the climatic conditions in experiments, which remains rare for arable crops (e.g., Renwick et al., 2021). We surmise that the benefit of increasing CRD could be even greater than observed in our data, because temperature has increased at all sites during the experiments (Figures S8 and S9) and warming generally has a negative effect on yields (Lobell et al., 2011).

The benefits of CRD for crop performance under low and high precipitation are likely mostly mediated by changes to soil properties and ecosystem functioning. Increasing CRD could improve soil structure and soil organic matter content, facilitating the retention of water and nutrients in several field experiments (Kremen & Miles, 2012; Schmer et al., 2020; Sprunger et al., 2020). Nevertheless, trade-offs might occur if the added crops increase water demands, as observed in some experiments (Blanchy et al., 2023), in the absence of sufficient soil water recharge outside the growing season. Improved soil water retention could reduce water stress under low precipitation and limit nutrient leaching under high precipitation (Renwick et al., 2019). Higher CRD also increased both the quantity and quality of carbon inputs in field experiments, promoting complexity in microbial communities, and in turn plant nutrient availability (Mooshammer et al., 2022; Zhang et al., 2021), even at reduced soil water content (Bowles et al., 2022). Plant nutrient availability further increased with increased soil moisture, allowing diverse rotations to increase crop productivity under low and high precipitation thanks to positive nitrogen and water use linkages (Renwick et al., 2019).

The benefits of CRD to grain yields under warming likely resulted from a combination of mechanisms. By enhancing soil structure and, hence, water availability (Blanchy et al., 2023; Kremen & Miles, 2012; Schmer et al., 2020; Sprunger et al., 2020), CRD might reduce water stress and increase evaporative cooling, which mitigates heat stress (Sadok et al., 2021). Similarly, preceding crops with large and deep rooting systems can create biopores, that is, pathways in the soil that facilitate root growth of the following crop, and hence deeper water uptake (Han et al., 2015), buffering against soil water fluctuations. Pest and pathogen pressure on staple grain crops increases with warming in temperate regions, based on observations and model analyses (Chaloner et al., 2021; Deutsch et al., 2018; Singh et al., 2023). Higher CRD might counteract this increase in pest pressure by enhancing the diversity and abundance of predators to crop pests in the field and in the cropped landscape (Aguilera et al., 2020; Heinen et al., 2023; Redlich et al., 2018; Rusch et al., 2013), reducing infestations (Wang et al., 2022). Crop diversity could also promote pathogen-suppressing microorganisms and reduce the presence of suitable hosts for pathogens (Peralta et al., 2018).

The statistical models had a low degree of explained variation (i.e., marginal R^2). This was expected given the large variation in experimental design, geographical location and variable treatment outcome from year to year. This prevents us from predicting future year-to-year yields, but the significant effects on yield anomalies of CRD and climatic conditions over the whole duration of the experiments allow for robust conclusions on CRD-yield responses to historical climatic conditions.

4.2 | Crop functional richness, not species diversity, was the main driver of yield benefits

Increasing crop functional richness enhanced yield anomalies, and hence yields, with no sign of decline, for all crops under high temperature and irrespective of precipitation. As such, functional richness steadily compensated yield reductions from detrimental climatic conditions occurring in monocultures and low diversity rotations.

Small grain yields were maximized at an intermediate species diversity of the crop rotation. At which CRD the maximum occurred depended on climatic conditions and indicator crop. For winter small grains, the yield-maximizing species diversity decreased in warmer and drier conditions. Spring small grains showed the opposite pattern. This suggests that less diverse rotations provide higher benefits to winter small grain yields under warming and low precipitation, compared with more diverse rotations. Winter small grains reach anthesis earlier than spring small grains and likely obtain a higher thermal optimum before the warmest period of the growing season begins (He et al., 2020). Furthermore, winter small grains have deeper root systems than spring grains, which can sustain biomass productivity even under water shortage (Kirkegaard et al., 2007). We speculate that winter small grains require a lower species diversity to maximize grain yield than spring small grains because they are relatively more productive under such conditions (Section 4.3). The diverging effect of CRD on small grain yield could also depend on the crop sequence (Reckling et al., 2022). We were not able to investigate this because crop sequences were heterogeneous across the LTEs. Full factorial designs would be needed to disentangle crop sequence effects from diversity effects.

The decline in small grain yields at high species diversity, but not at high functional richness, is likely the result of the choice of sown crops. The rotations included in our dataset are in line with typical local rotations. If the pool of crop species to choose from is small, just adding species might not provide the complementary functional traits that benefit cereal yield as diversity increases. Conversely, increasing CRD through functional richness might be more effective than species diversity in providing functional traits that promote climate change adaptation in cropping systems (Cadotte et al., 2011; Smith et al., 2023; Wright et al., 2021). It is possible that increased functional richness in particular promoted soil benefits due to complementarities in rooting depth, root density, and growing season period among the functional groups (Duchene et al., 2020; Griffiths et al., 2022). Moreover, crops with large and deep rooting systems facilitate a deep root growth of the following crop via biopores leading to deeper water and nutrient uptake (Han et al., 2015). However, trade-offs can occur, as investments in deeper roots can decrease yields when water is not limited. Also, biopores increase leaching under heavy rainfall (Wendel et al., 2022).

For maize, the species diversity that maximized yields did not change across climatic conditions and coincided with the highest level included in the data. However, the data on maize had a narrower range of species diversity compared with small grains. It is possible that extending the analysis to rotations with higher species diversity would show a shifting yield-maximizing diversity in response to climatic conditions. It remains to be explored whether a shift towards detrimental climatic conditions would require a species diversity higher than the highest diversities covered in our study to maximize maize yield.

4.3 | Yield response to climatic conditions and CRD depended on indicator crop

Warming reduced yields in all crops irrespective of CRD and precipitation. At higher than average precipitation, the yield reductions from warming were higher in winter small grains than in spring small grains and maize, irrespective of CRD. For a given temperature, increasing precipitation reduced yields in spring cereals, but increased them in maize and had no effect in winter small grains, irrespective of CRD. This partly contrasts the findings of Marini et al. (2020), where spring small grain yields increased with precipitation. A possible explanation is that our data have a wider geographic distribution, including cooler and wetter sites with spring grain cereals, such as the Tulloch and Woodside LTEs in Northern Scotland. Moreover, we considered a range of CRDs whereas Marini et al. (2020) focused on the monoculture-diverse rotation dichotomy, with the most diverse rotations corresponding to species diversity 4–6, that is, towards the right end of the parabola in our results (Figures 1 and 2; Figure S10). In line with our results for spring small grains, yields of spring and winter small grains in Finland declined with increasing precipitation occurring in late developmental stages due to lodging (Peltonen-Sainio et al., 2011). Winter wheat was not grown at such latitudes, so we were unable to assess whether winter and spring cereals react similarly to such conditions. The wide climatic gradient covered in our dataset might have contributed to the lack of response to precipitation for winter small grains. For example, in temperate LTEs such as in Broadbalk and Woburn, a decrease in precipitation had little impact on winter small grain yields, while in Mediterranean LTEs such as in El Encín and La Canaleja, it could lead to catastrophic yield losses (Figure S11).

Long and warm dry spells negatively affected winter small grains as expected (Brás et al., 2021), whereas the length and temperature of dry spells had negligible effects on spring small grain yields. The difference in response could be because the LTEs with spring small grains are located in cooler climates than for winter small grains, which included Mediterranean sites (Figures S1 and S3; Table S1). Lower temperature reduces evapotranspiration, and possibly the negative impact of dry spells on grain yields in temperate compared with Mediterranean climates. Moreover, dry spells were generally longer in LTEs with winter small grains than in LTEs with spring small grains (Figure S3; Table S1), likely exacerbating the impact of high temperatures on grain yields (Matiu et al., 2017).

Maize yields responded most negatively to co-occurring low cumulative precipitation and high average temperatures, and to long and warm dry spells, across all CRDs. These findings are in line with maize yield declines observed under combined warming and low precipitation, and under long dry spells (Lobell et al., 2014; Luan et al., 2021; Renwick et al., 2021).

5 | CONCLUSIONS

We showed that diversifying crop rotations can decrease the vulnerability of cereal yields to detrimental climatic conditions, based on primary data from 32 long-term experiments across Europe and North America. In these contexts, rotations including two to three species or at least two functionally different groups compensated for monoculture yield losses in small grains and maize occurring under detrimental climatic conditions. Climatic conditions such as anomalously warm and dry growing seasons and lengthy and warm dry spells are increasingly frequent due to climate change. Increasing CRD is thus an option for adapting cropping systems to climatic change. Further increasing functional richness can give added benefits, promoting grain yields beyond average levels achievable by monocultures also under beneficial climatic conditions. Growing several crop species also reduces risks through a rich portfolio of crops that are unequally affected by climatic disturbances (Cadotte et al., 2011; Loreau et al., 2021; Schindler et al., 2015). Increasing CRD provides insurance against more variable and uncertain climatic conditions.

AUTHOR CONTRIBUTIONS

Alessio Costa: Conceptualization; data curation; formal analysis; investigation; methodology; project administration; software; validation; visualization; writing – original draft; writing – review and editing. **Riccardo Bommarco:** Conceptualization; formal analysis; funding acquisition; supervision; writing – review and editing. **Monique E. Smith:** Data curation; investigation; supervision; writing – review and editing. **Timothy Bowles:** Data curation; investigation; writing – review and editing. **Amélie C. M. Gaudin:** Data curation; investigation; writing – review and editing. **Christine A. Watson:** Data curation; investigation; writing – review and editing. **Remedios Alarcón:** Data curation; investigation. **Antonio Berti:** Data curation; investigation. **Andrzej Blecharczyk:** Data curation; investigation. **Francisco J. Calderon:** Data curation; investigation. **Steve Culman:** Data curation; investigation. **William Deen:** Data curation; investigation. **Craig F. Drury:** Data curation; investigation. **Axel Garcia y Garcia:** Data curation; investigation. **Andrés García-Díaz:** Data curation; investigation. **Eva Hernández Plaza:** Data curation; investigation. **Krzysztof Jonczyk:** Data curation; investigation. **Ortrud Jäck:** Data curation; investigation. **Luis Navarrete Martínez:** Data curation; investigation. **Francesco Montemurro:** Data curation; investigation. **Francesco Morari:** Data curation; investigation. **Andrea Onofri:** Data curation; investigation. **Shannon L. Osborne:** Data curation; investigation. **José Luis Tenorio Pasamón:** Data curation; investigation. **Boël Sandström:** Data curation; investigation. **Inés Santín-Montanyá:** Data curation; investigation. **Zuzanna Sawinska:** Data curation; investigation. **Marty R. Schmer:** Data curation; investigation. **Jaroslaw Stalenga:** Data curation; investigation. **Jeffrey Strock:** Data curation; investigation. **Francesco Tei:** Data curation; investigation. **Cairistiona F. E. Topp:** Data curation; investigation; writing – review and editing. **Domenico Ventrella:** Data curation; investigation. **Robin L. Walker:** Data curation; investigation. **Giulia Vico:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; supervision; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The yield data that support the findings of this study are openly available in the Swedish National Data service at: https://doi.org/10.5878/8af1-0q60. The European climatic data that support the findings of this study are openly available in the E-OBS dataset at: https://www.ecad.eu and http://cds.climate.copernicus.eu. The North American climatic data that support the findings of this study are openly available in the Livneh daily CONUS near-surface gridded meteorological and derived hydrometeorological data at: https://psl.noaa.gov.

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