ORIGINAL ARTICLE

Crop Ecology, Management & Quality

Crop Science

Asynchrony is more important than genetic distance in driving yield stability in wheat variety mixtures

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Assigned to Associate Editor John Foulkes.

Abstract
In the face of climate change, improving yield stability is critical for food production systems. Increasing diversity in agricultural systems can be a way to stabilize yield across time and/or space. This can be done with mixtures of varieties, which represent a practical way to introduce diversity at the genotype level in agricultural fields. However, in Switzerland, wheat variety mixtures are still rarely used, due to a lack of understanding of the processes driving yield benefits and, consequently, no clear rules as to which varieties to combine. In this study, we used results from a Swiss wheat variety mixture trial to investigate the drivers of mixture productivity and stability. We hypothesized that mixtures composed of more different varieties—in terms of genetic distance but also of morphological, agronomic, or synchronicity aspects—would be more productive and/or stable. We did not find any effects of genetic distance on mixture productivity or stability, but we did observe an increase in mixture stability with reduced synchrony of the components, that is, when the components reacted differently to environmental conditions. This result was only significant in the first year of the trial, which was less productive due to more stressful conditions. This study shows that when combining asynchronous varieties, wheat variety mixtures have the potential to buffer possible yield losses due to external stressors during suboptimal years. While more research is needed to confirm this result, variety mixtures nonetheless represent a promising solution to sustainably increase the stability of wheat production in Switzerland.

1 | INTRODUCTION

Improving yield stability across time and space is critical for agroecosystems (Stomph et al., 2020); this is becoming particularly relevant given the global change that the planet is facing (Jägermeyr et al., 2021). Indeed, global change is predicted to increase the frequency and intensity of climate

Abbreviation: ACV, adjusted coefficient of variation.

hazards and extreme climatic events, such as droughts or heavy rainfalls (Ayanlade et al., 2018; IPCC, 2021; Philip et al., 2020). However, these changes in climate extreme events are rather unpredictable, which represents a serious threat to crop production in continental Europe (Congreves et al., 2016). In Switzerland, Swiss varieties have been bred and adapted for local Swiss conditions (Fossati & Brabant, 2003; Herrera et al., 2020), but recent increases in interannual weather variability have put this location-specific breeding

into question (Rogger et al., 2021). As a complement, farmers and breeders are now looking for ways to increase the crops' adaptability to climate change and increase yield stability over time (i.e., several years) but also space (i.e., across different sites in the country). To achieve these goals, agroecology has gained much attention over the past decades (Ratnadass et al., 2011). One key element of the transition to agroecology is to increase diversity, notably in terms of crops (Isbell et al., 2017). Crop diversification, whether at the level of species or variety, can indeed be a lever to possibly increase resilience to extreme climatic events (Caldeira et al., 2005; Hector et al., 2010; Prieto et al., 2015) as well as decrease the use of chemical inputs (Bedoussac et al., 2015). Diversified cropping systems are particularly relevant in organic or low-input production, as combining crop species or varieties with different resource needs or different susceptibilities to pests and diseases allows to reduce pesticides, fungicides, or chemical fertilization (Hauggaard-Nielsen et al., 2003; Jensen et al., 2020; Vidal et al., 2020).

Variety mixtures represent a practical way to diversify cropping systems, by enhancing genetic diversity at the field scale (Finckh et al., 2000; Kopp et al., 2023). For instance, variety mixtures could be particularly relevant for wheat production in Switzerland, since around 50% of the domestic production follows the *extenso* guidelines—proscribing the use of pesticides, fungicides, or plant growth regulators (Böcker et al., 2019; Finger & El Benni, 2013)—and 10% is organic (Swiss Granum, 2023). However, despite the potential benefits of variety mixtures, only 1.6% of the wheat area is currently cultivated with variety mixtures in Switzerland (according to seed sales statistics from Swisssem). The main barriers to the adoption of this practice include agronomic challenges and a lack of knowledge for farmers, as the success of a potential mixture is hard to predict (Finckh et al., 2000; Wuest et al., 2021). Indeed, variety mixtures have been shown to exhibit highly variable overyielding values, without clear reasons why (Borg et al., 2018); this can lead to struggles for farmers to ensure decent production and financial revenues (Finckh et al., 2000). Moreover, the mechanisms responsible for the potential stabilizing effect also remain unclear (Knapp et al., 2017; Ruijven & Berendse, 2007).

Understanding which varieties should be combined to ensure high productivity and stability is therefore essential and at the heart of current research in the field of agroecology (Cheriere et al., 2020; Engbersen et al., 2022). Ecological theory suggests that combining species or varieties with different genetic, functional, agronomic, or morphological characteristics would be more beneficial, as this would increase complementarity between the varieties/species (Evers et al., 2019; Kuebbing et al., 2017; Stomph et al., 2020). However, in practice, these rules do not necessarily hold true: within a given cropping system, experimental studies did not consistently find positive effects of increasing genetic or functional diversity on productivity (Bybee-Finley et al., 2017; Eng-

> ### Core Ideas
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> - Variety mixtures can improve the stability of wheat production in Switzerland.
> - Yield stability of the wheat variety mixtures was positively linked with the asynchrony of the components.
> - This result was especially significant during stressful environmental conditions.
> - Wheat variety mixtures have the potential to buffer possible yield losses due to external stressors during suboptimal years.

bersen et al., 2022; Stefan et al., 2022). Furthermore, the species or variety mixtures must remain workable by farmers: specifically, it is important to keep a certain level of uniformity in maturity, so that all the components can be harvested at the same time (Martin-Guay et al., 2018). In the case of wheat production in Switzerland, there are no simple, general criteria to combine varieties for increased stability and productivity; most variety mixtures come from trial-and-error processes or are chosen based on arbitrary criteria of agronomic or baking quality (IP-SUISSE, 2021). As wheat production represents 29.8% of the arable land in Switzerland (Federal Statistical Office) and in the face of changing climatic conditions in the future, understanding which wheat varieties to combine for stable and productive mixtures becomes crucial.

One of the proposed mechanisms explaining the positive diversity–stability relationship is compensation by different species or varieties (Weih et al., 2021), also called asynchrony (Egli et al., 2020). Asynchrony is an essential component of the insurance hypothesis (Yachi & Loreau, 1999) and is defined as species/variety-specific response to environmental fluctuations (St. Luce et al., 2020; Valencia et al., 2020), that is, negatively correlated responses to environmental drivers (Micheli et al., 1999). This means that when one variety is greatly suffering in response to a certain stressor, others will suffer less, or be less impacted by this stressor (Egli et al., 2020; Fletcher et al., 2019). This compensatory mechanism suggests that crop mixtures would benefit from choosing varieties or species that are more or less sensitive to different abiotic factors, such as rainfall or temperature. Yet, both theoretical and empirical evidence for a universal stabilizing effect of diverse plant communities is still inconclusive (Weih et al., 2021), thereby emphasizing the context dependence of these effects (Grman et al., 2010). Some studies indeed suggest that the mechanisms driving stability depend on the environmental conditions (Micheli et al., 1999; Ruijven & Berendse, 2007; Steiner et al., 2005). On the one side, increased compensatory dynamics could be expected in benign environments,

as the favorable growing conditions would make it easier for the stable, dominant species/variety to compensate (Grman et al., 2010). On the other side, one could also expect the stabilizing effect of diverse communities to be more pronounced in stressful, low-productivity environments, where some species/variety would suffer more than others (He et al., 2013; Mulder et al., 2001).

In this study, we are investigating the drivers of wheat variety mixture stability and productivity. More specifically, we examine whether the stability and productivity (in terms of grain yield and protein content) of variety mixtures can be linked to some genetic, morphological, or agronomic characteristics of the components, or to their asynchrony. We also investigate whether and how stressful climatic conditions affect these links. To do that, we performed a variety mixture trial in five sites in Switzerland for 2 years, with 23 different variety mixtures, and used data from the national variety testing program to compare the performance of the varieties when grown alone. We hypothesized that combining varieties with large differences in genetic, morphological, or agronomic characteristics—such as height, phenology, or yield—would lead to more stable and productive mixtures. We also suggested that combining asynchronous varieties would increase the stability of the mixture. Finally, we expected these effects to be more pronounced in stressful, less-productive environments.

2 | MATERIALS AND METHODS

2.1 | Experimental sites

The experiment took place in five sites across Switzerland, in 2019 and 2020. The sites were located in Nyon (1260), Delley (1567), Utzenstorf (3428), Zurich (8046), and Ellighausen (8566) and are characterized by the climatic conditions described in Figure S1.

2.2 | Experimental communities

2.2.1 | Mixtures

Experimental communities consisted of 32 different two-variety mixtures grown in 7.1-m^2 plots (1.5 × 4.7 m). The full list of variety mixtures is available in Table 1. Varieties were chosen from the current Swiss national breeding program, based on their morphological and agronomic characteristics to allow for a gradient of differences in height, heading dates, and foliage growth, while maintaining uniformity in maturity timing and baking quality (see Figure S2). We chose varieties that are currently in use by farmers, or that are being

developed, for the purpose of having applicable and usable results. We replicated the mixture experiment three times per site with the exact same variety composition. We used a randomized block design, with plots being randomized at each site within each block. Density of sowing was 350 seeds/m^2, and seeds were mixed beforehand at a 50:50 ratio in terms of mass. We used the 50:50 mass ratio as this is what is generally done in practice by farmers and seed suppliers. Plots were sown mechanically each autumn. The plots were mechanically fertilized according to the Principles of Agricultural Crop Fertilisation in Switzerland (Federal Office for Agriculture) with an average of 140 kg N/ha (ammonium nitrate), applied in three splits (40 at the tillering stage—60 at stem elongation stage—40 when the flag leaf is visible). The experimental trials were conducted following the *extenso* Swiss scheme, which means that there was no application of any fungicide, insecticide, or plant growth regulator (Böcker et al., 2019).

2.2.2 | Genetic similarity between varieties

All the varieties were genotyped using the 25K Infinium iSelected array. DNA extraction and SNP genotyping of all the varieties were performed by SGS Institut Fresenius GmbH TraitGenetics Section. The genetic similarity was evaluated by the percentage of pairwise common marker results between the varieties, after exclusion of failed markers.

2.2.3 | Single varieties

The performances of single varieties were obtained by going through the trials of the national variety testing program (Herrera et al., 2018). We gathered the data for the years 2018/2019 and 2019/2020. The data regarding single varieties could be obtained for three out of the five sites used for the mixtures: 1260, 1567, and 8566. Because there were no national variety trials at the two other sites (8046, 3428), we could not get any data for single varieties in these sites. Thus, all further analyses including single variety data were only done for the three sites mentioned above. At each of these sites, the variety trials were located on the same plot as the mixture trials, even though a little further apart. Therefore, soil parameters and crop precedents were the same between the mixture and variety testing trials. Furthermore, we only selected the national variety testing trials that respected the *extenso* conditions, that is, no fungicide, pesticide, or growth regulator application, and that received the same amount of fertilization as the mixture trials. In 8566 and 1567, sowing and harvesting dates were identical between the two trials; in 1260, sowing and harvesting dates could vary but remained within a week of each other.

TABLE 1 List of variety mixtures considered in 2019 and 2020.

Experimental year	Variety combinations
2019	**MOLINERA and CH COMBIN (ISUELA)**; **RASICA and CADLIMO**; RASICA and PIZNAIR; **AXEN and SCHILTHORN**; **SCHILTHORN and CAMPANILE**; FEDERIS and 111.15870; **BARETTA and MONTALBANO**; BARETTA and 111.15759; **RASICA and ALPVAL**; 111.15759 and PIZNAIR; **111.15759 and FALOTTA**; **AXEN and 211.14074**; **FALOTTA and CAMPANILE**; **ALPVAL and CADLIMO**; **ALPVAL and SCHILTHORN**; **ALPVAL and FALOTTA**; CAMINADA and CAMPANILE; **CAMINADA and 211.14074**; DIAVEL and CAMPANILE; **DIAVEL and CAMINADA**; **MOSSETTE and CAMPANILE**; MOSSETTE and ALPVAL
2020	**MOLINERA and CH COMBIN (ISUELA)**; **RASICA and CADLIMO**; **AXEN and SCHILTHORN**; **SCHILTHORN and CAMPANILE**; **BARETTA and MONTALBANO**; **RASICA and ALPVAL**; **111.15759 and FALOTTA**; **AXEN and 211.14074**; **FALOTTA and CAMPANILE**; **ALPVAL and CADLIMO**; **ALPVAL and SCHILTHORN**; **ALPVAL and FALOTTA**; **CAMINADA and 211.14074**; **DIAVEL and CAMINADA**; **MOSSETTE and CAMPANILE**; MONTALTO and 111.16291; COLMETTA and 111.16278; BONAVAU and BRAGA; BRAGA and PILATUS; 111.16041 and 111.16408; 111.16224 and 111.16278; FORTERESSE and BONAVAU

Note: Bold letters indicate variety combinations repeated in both seasons.

2.3 | Data collection

For each plot, heading dates were monitored, and average height at BBCH 59–75 was measured.

The prevalence of diseases was scored twice in the growing season. Specifically, the severity of brown rust, yellow rust, powdery mildew, and Septoria tritici blotch was assessed. This was performed by grading each individual plot from 1 to 9 for each disease, with 1 representing no disease and 9 a complete infection. The scoring scale follows a logistic progression based on the symptoms of the top three leaves (Michel, 2001; Moll et al., 1996). We used the data from the final scoring for statistical analysis, as the disease severity was usually more important then.

At maturity, we harvested each plot with a combine harvester. The harvested grains were dried when needed, weighed a first time, then sorted and cleaned by air and with a sieve cleaner, and subsequently weighted again. We measured specific weight and water content at the plot level using a Dickey-John machine (GAC 2100). Grain yield was subsequently standardized to 15% of humidity. Protein content was measured at the site level with a near-infrared instrument (ProxiMate; Büchi instruments).

2.4 | Data analyses

2.4.1 | Monoculture characteristics

For each mixture, we computed the absolute difference in yield, protein content, height, heading date, and hectoliter weight between the two components when grown as single varieties as: monoculture difference in parameter for the mixture (A,B) = absolute value (parameter of variety A when grown as single variety – parameter of variety B when grown

as single variety). This allows to see whether the two varieties constituting the mixture have different agronomic characteristics, and to quantify these differences. These differences were calculated per year and site, when the availability of data allowed us to do so, and subsequently averaged across sites and/or years.

2.4.2 | Productivity

Grain yield and protein content across mixtures and environments were assessed and described using basic R functions. Overyielding was calculated as the difference between observed and expected yield of the mixture, where expected yield is the sum of the yields in pure stands weighted by the relative abundance of each component (Loreau & Hector, 2001):

$$\text{Overyielding of mixture}(A, B) = \text{yield of mixture}(A, B)$$
$$- \left[r_A \times \text{yield of mono}(A) \right.$$
$$\left. + r_B \times \text{yield of mono}(B) \right],$$

where r_i indicates the relative abundance of the variety i in the mixture. The relative abundances were calculated based on the 50:50 mass ratio corrected with the thousand kernel weight values of the varieties at sowing.

2.4.3 | Stability

We assessed yield and protein stability of the mixtures across time and/or space using the adjusted coefficient of variation (ACV) (Döring & Reckling, 2018) from the package *metan* (Olivoto & Lúcio, 2020).
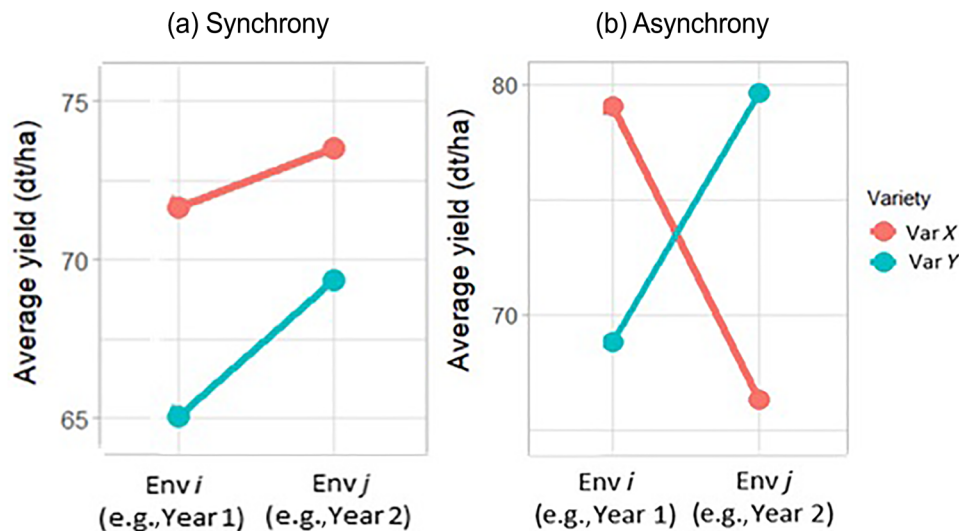
FIGURE 1 Schematic illustration of the concept of asynchrony. Dots indicate the yield of two varieties (*X* and *Y*) in two different environments (*i* and *j*). On the left plot, the two varieties follow the same trend across the two environments: this represents synchrony. On the right, the two varieties respond in opposite manners to the different environments, illustrating asynchrony.

We also compared the asynchrony in temporal and/or spatial fluctuations between varieties constituting the mixtures when grown alone and tested whether it was related to the temporal and/or spatial stability of the mixtures. We calculated the asynchrony metric according to Lepš et al. (2019), which is defined as the sum of all covariances (i.e., the difference between observed and expected variances of the total productivity) divided by the expected variance:

$$\text{Asynchrony} = -1 \times \frac{\text{var}(\sum_{i=1}^{S} \mathbf{x}_i) - \sum_{i=1}^{S} \text{var}(\mathbf{x}_i)}{\sum_{i=1}^{S} \text{var}(\mathbf{x}_i)}$$

$$= -1 \times \frac{2 \sum_{i,j>i}^{S} \text{covar}(\mathbf{x}_i, \mathbf{x}_j)}{\sum_{i=1}^{S} \text{var}(\mathbf{x}_i)},$$

where S is total number of varieties in the community, and $\mathbf{x}_i$ is the vector of productivity (grain yield or vegetative biomass) of the ith variety over time and/or space. Positive values indicate negative covariation between varieties (asynchrony), while values close to zero indicate a predominance of random fluctuations, and negative values indicate a common response of the varieties (synchrony; see the illustrated example in Figure 1). Asynchrony was first calculated across sites, per year (i.e., asynchrony in spatial fluctuations), and also across both site and year (asynchrony in spatial and temporal fluctuations; see Figure S3 for schematic illustration). The interaction between site and year will further be called "environment." The computation of asynchrony in temporal fluctuations (across years, per site) was only possible for two of our five sites, due to missing data in either 2019 or 2020 for some of the varieties in monocultures. Therefore,

due to insufficient sampling number, we could not further explore the site-specific behavior of temporal asynchrony (i.e., asynchrony between the two seasons of study).

The effects of differences in monoculture characteristics on productivity and stability of yield and protein content were investigated using linear mixed-effects models, with year interacted with site, monoculture differences in yield, protein content, heading date, and height as fixed factors, and variety composition as random factor, for example,

$$yield \sim year \times (site + mono\,culture\,difference\,in\,yield$$

$$+ mono\,culture\,difference\,in\,protein$$

$$+ mono\,culture\,difference\,in\,heading\,date$$

$$+ mono\,culture\,difference\,in\,height)$$

$$+ (1\,variety\,composition).$$

For analyses at the year level, the monoculture differences were averaged across sites. Links between productivity/stability of yield/protein content and genetic distance were investigated using a linear model, with genetic similarity interacted with year as factors, for example, $yield \sim genetic\,similarity \times year$. Links between asynchrony in yield/protein content and ACV in yield/protein content were investigated using a similar linear model, for example, $asynchrony \sim ACV \times year$. To check whether overyielding values were significantly different from 0, we used a t-test for each year. Homogeneity of variance and normality of residues were assessed visually and with Shapiro–Wilk tests (Royston, 1982).

2.4.4 | Disease prevalence in variety mixtures

In both years, the prevalence of yellow rust was very low, with no plots affected in 2019 and only 67 out of 330 in 2020. Therefore, we did not consider the results from yellow rust in our analyses. For the other diseases, to investigate the links between genetic similarity and disease prevalence, we used general linear mixed models with genetic similarity interacted with site and with year as fixed effects, and repetition as random factor, for example, $disease\ severity \sim genetic\ similarity \times (site + year) + (1|repetition)$. For Septoria tritici blotch, we used a standard negative binomial model with the function *glmer.nb*, while for mildew and brown rust, we had to correct for the zero inflation caused by many plots with no disease infection. For this, we used the function *glmmTMB* with a negative binomial family (Brooks et al., 2017).

3 | RESULTS

3.1 | Productivity—Yield and protein content

Across years and sites, grain yield of the mixtures reached an average of 77.91 dt/ha. In 2019, the average grain yield of the mixtures was 72 dt/ha across sites, while in 2020, it was 84 dt/ha (+17%) (Figure S4). Overyielding was significantly negative both years, with an average value of −1.6 dt/ha in 2019 (*t*-test *p*-value < 0.0001) and −7.3 dt/ha in 2020 (*t*-test *p*-value < 0.0001; Figure S5). Regarding protein content, we obtained an average value of 12.8% in 2019 and 13.4% in 2020 (Figure S4).

Grain yield of mixtures was significantly affected by site (postcode), year × site, and year × monoculture difference in protein content (Table 2). Notably, in 2019, yield was negatively correlated with the monoculture difference in protein content (Figure 2a; regression coefficient: −2.35; *p*-value: 0.021). This correlation was not present in 2020. When looking at the links between genetic similarity and yield of the mixtures, we did not observe any significant effects (*p*-value: 0.05597).

Protein content was significantly affected by site, year × site, year × monoculture difference in protein content, and year × monoculture difference in height (Table 3). More precisely, in 2020, protein content was positively correlated with monoculture difference in height (Figure 2b; regression coefficient: 0.48; *p*-value: 0.01) and negatively correlated with monoculture difference in protein content (Figure S6; regression coefficient: −0.685; *p*-value: 0.063). Furthermore, across both years, protein content was significantly negatively correlated with genetic similarity (coefficient: −0.111, *p*-value: 0.0118), meaning that mixtures composed of more genetically similar varieties tend to have a lower overall protein content.

3.2 | Stability—Yield and protein content

When looking at yearly scale, ACV of mixture yield was significantly affected by the interaction between year and monoculture difference in heading dates (Table S1): specifically, in 2019, ACV in mixture yield was positively correlated with difference in heading dates (Figure 3a; regression coefficient: 0.60; *p*-value: 0.019), meaning that mixture yield was more stable when the components reached the heading stage at the same time. Furthermore, the interaction between year and genetic similarity had a significant effect on ACV in yield (*F*-value: 6.3, *p*-value: 0.0167). In 2019, ACV in yield was negatively correlated with genetic similarity (Figure 3b; regression coefficient: −0.4, *p*-value: 0.00564), meaning that yield was more stable when the components of the mixtures were genetically closer. In 2020, there was no significant relationship (regression coefficient: 0.095, *p*-value: 0.51).

ACV in protein content of the mixtures was affected by year and by monoculture difference in yield (Table S2). In 2019, ACV in protein had an average of 16.05%, while in 2020, it had an average of 5.59% (−65%). Furthermore, ACV was negatively correlated with the monoculture difference in yield (Figure S7; regression coefficient: −0.36; *p*-value: 0.0498). Genetic similarity had no effects on ACV in protein content (*F*-value: 0.3366, *p*-value: 0.56).

When looking across environments, there were no significant effects of the monoculture characteristics or of genetic proximity on ACV in yield or protein content.

3.3 | Asynchrony—Yield and protein content

In 2019, ACV in yield of the mixtures was negatively correlated with the spatial asynchrony in yield of the mixture components when grown as monocultures (Figure 4; regression coefficient: −4.6, *p*-value: 0.036, *n* = 13), meaning that mixtures were more stable when the components were less synchronous. In 2020, there was no significant relationship between ACV in yield and asynchrony (regression coefficient: −1.29, *p*-value: 0.74, *n* = 13). Similarly, there was no significant correlation between ACV in mixture protein and asynchrony in protein content of the varieties (*p*-value: 0.83 in 2019 and 0.40 in 2020).

When looking across both years, there was no significant correlation between spatiotemporal ACV in yield or protein and spatiotemporal asynchrony in yield or protein of the mixture components (regression coefficient for yield: −0.35, *p*-value: 0.12; regression coefficient for protein: 0.09, *p*-value: 0.99).

TABLE 2 Type-III analysis of variance table of the response of mixture grain yield to the environmental parameters (year, site) and the corresponding monoculture characteristics.

	NumDF	DenDF	*F*-value	Pr (>*F*)
Year	1	43.427	0.0121	0.91295
Site	2	32.441	17.6995	**6.36 × 10⁻⁶*****
Monoculture difference in heading date	1	44.28	0.1762	0.67668
Monoculture difference in protein	1	38.828	0.0827	0.77525
Monoculture difference in height	1	42.258	0.3164	0.57674
Monoculture difference in yield	1	38.209	0.0014	0.97084
Year × site	2	31.569	32.6154	**2.09 × 10⁻⁸*****
Year × monoculture difference in heading date	1	43.446	2.8308	0.09965
Year × monoculture difference in protein	1	41.96	4.5117	**0.0396***
Year × monoculture difference in height	1	43.303	1.4123	0.24115
Year × monoculture difference in yield	1	31.626	0.2789	0.60109

Note: DenDF = degrees of freedom of error term; *F*-value = variance ratio; NumDF = degrees of freedom of term; Pr (>*F*) = error probability. Bold *p*-values are significant at $\alpha = 0.05$; $n = 59$.
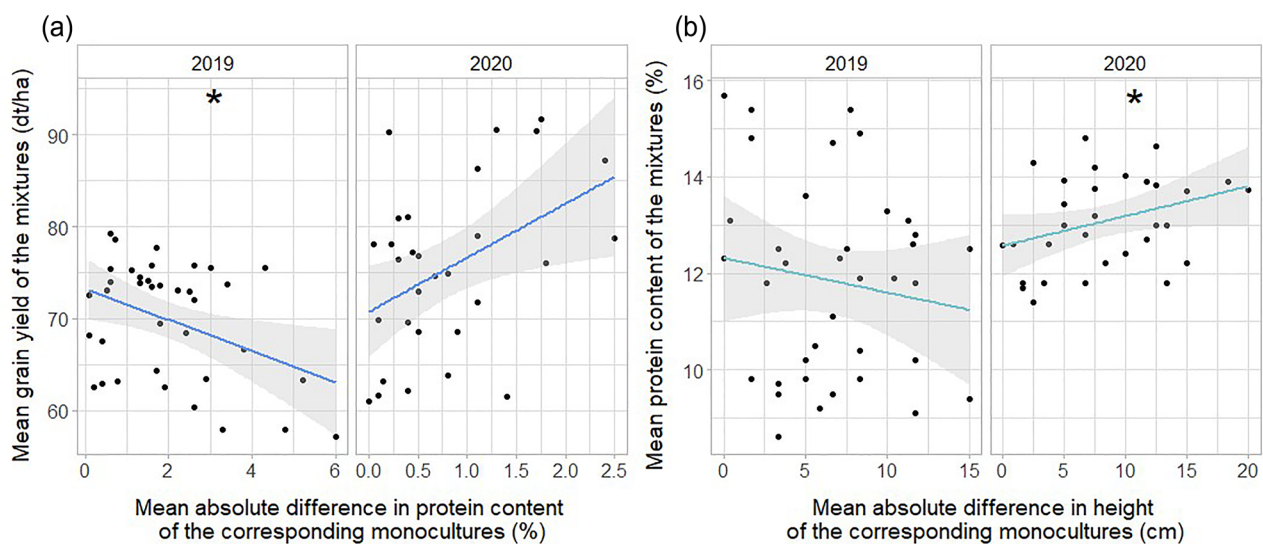*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

FIGURE 2 (a) Average grain yield (dt/ha) of the mixtures in relationship to the mean difference in protein content of the corresponding varieties when grown in monocultures (%), in 2019 and 2020. (b) Average protein content (%) of the mixtures in relationship to the mean difference in height of the corresponding varieties when grown in monocultures (cm), in 2019 and 2020. The lines represent linear regression fittings, with the gray area representing the 0.95 confidence interval. Stars represent significant relationships at $p < 0.05$.

3.4 | Disease prevalence in variety mixtures

Results from the three diseases investigated showed that disease prevalence and severity mainly depended on year and/or site, but did respond to genetic similarity (Table S3; Figure S8). Specifically, Septoria prevalence depended on site and year, with a higher severity in 2019, while brown rust and powdery mildew depended on site only.

4 | DISCUSSION

Our study investigated the links between productivity and stability of wheat variety mixtures and agronomic, morphological, or genetic characteristics of the mixture components. Specifically, we expected that combining varieties with highly different characteristics would increase productivity and/or stability. We found some evidence in this direction for protein content (but not for stability of protein content), which was

TABLE 3 Type-III analysis of variance table of the response of mixture protein content to the environmental parameters (year, site) and the corresponding monoculture characteristics.

	NumDF	DenDF	F-value	Pr (>F)
Year	1	43.454	0.4068	0.52695
Site	2	38.977	84.765	**6.40×10^{-15}***
Monoculture difference in heading date	1	44.629	0.1379	0.71213
Monoculture difference in protein	1	44.612	1.3443	0.25245
Monoculture difference in height	1	44.267	2.5754	0.11565
Monoculture difference in yield	1	44.99	3.6761	0.06156
Year × site	2	38.144	65.6635	**4.44×10^{-13}***
Year × monoculture difference in heading date	1	44.643	0.1302	0.71997
Year × monoculture difference in protein	1	44.972	5.323	**0.02571***
Year × monoculture difference in height	1	43.574	5.4015	**0.02485***
Year × monoculture difference in yield	1	40.443	0.9001	0.3484

Note: DenDF = degrees of freedom of error term; F-value = variance ratio; NumDF = degrees of freedom of term; Pr (>F) = error probability. Bold *p*-values are significant at $\alpha = 0.05$; $n = 59$.
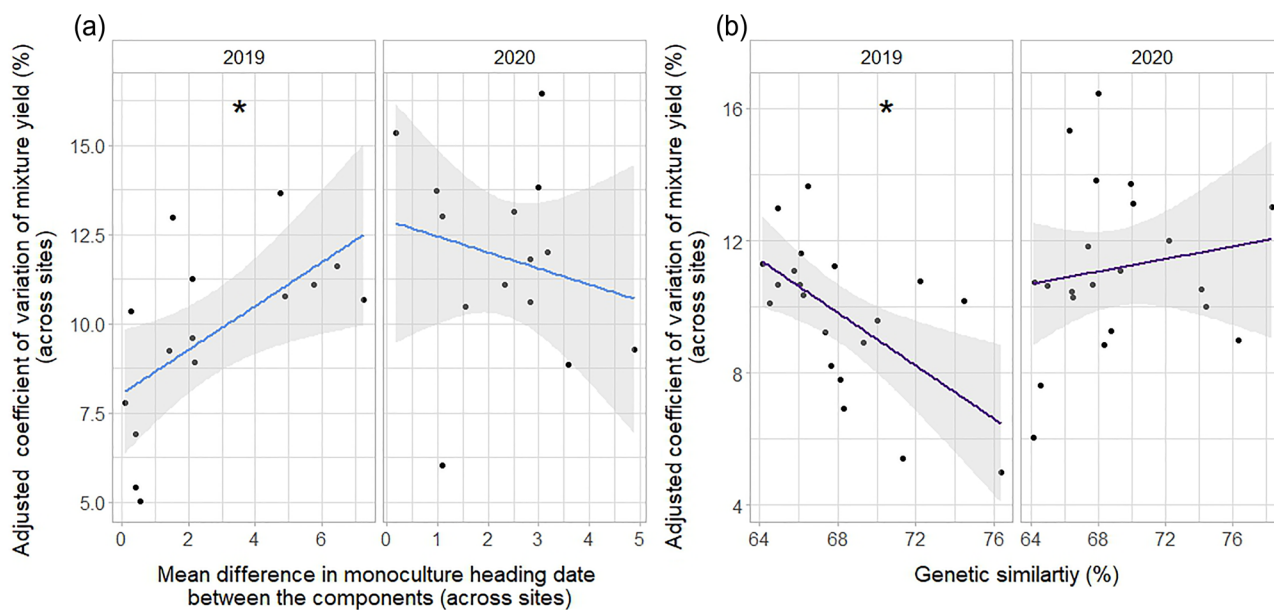*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

FIGURE 3 (a) Adjusted coefficient of variation of yield (%) of the mixtures in relationship to the mean difference in heading date of the corresponding varieties when grown in monocultures (day of year), in 2019 and 2020. (b) Adjusted coefficient of variation of yield (%) of the mixtures in relationship to the genetic similarity (%) between the varieties of the mixtures, in 2019 and 2020. The lines represent linear regression fittings, with the gray area representing the 0.95 confidence interval. Stars represent significant relationships at $p < 0.05$.

higher for mixtures combining varieties with lower genetic similarity and/or large differences in height. For yield on the contrary, we did not find results confirming our hypotheses: yield was, for instance, higher in mixtures combining varieties with similar baseline protein content. Also, yield was more stable for mixtures combining highly genetically similar varieties, varieties having similar phenologies, and/or varieties that respond less synchronously in different environments. However, in the case of yield, the significance of these links depended on the year.

4.1 | Mixing more genetically or agronomically different varieties does not necessarily increase productivity or stability

Our main hypothesis was that mixing varieties with larger differences in genetic, morphological, or agronomic traits would increase productivity and/or stability, in terms of grain yield and/or protein content. Indeed, ecological theory suggests that increasing diversity is beneficial for community productivity and stability (Bardgett & van der Putten, 2014; Borg et al.,
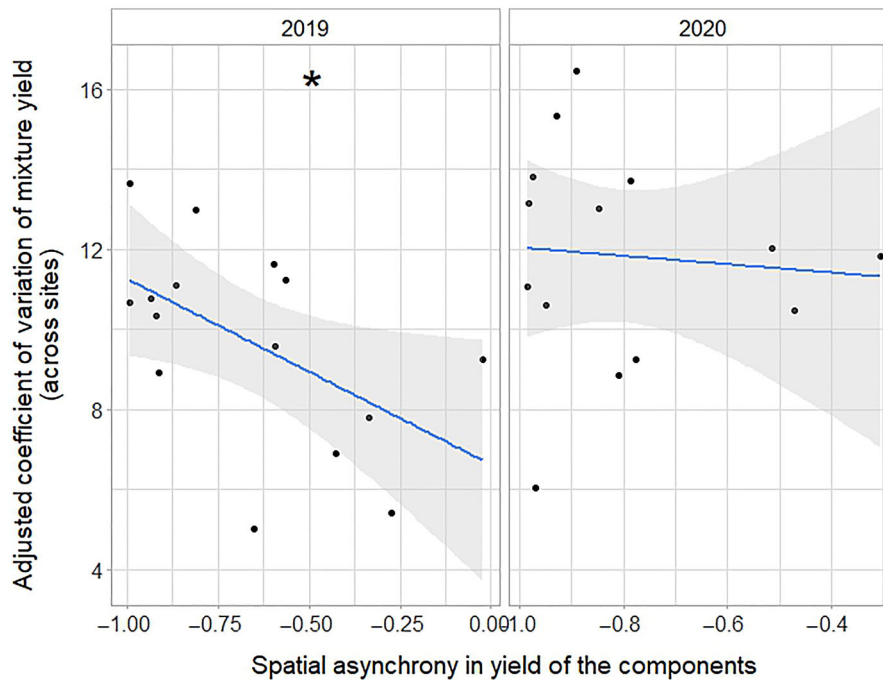
FIGURE 4 Adjusted coefficient of variation of yield (%) of the mixtures in relationship to the spatial asynchrony in yield of the corresponding varieties when grown in monocultures, in 2019 and 2020. The lines represent linear regression fittings, with the gray area representing the 0.95 confidence interval. Stars represent significant relationships at $p < 0.05$.

2018; Isbell et al., 2018; Tang et al., 2022). Furthermore, the higher the diversity in a system, the larger the benefits: very different species/varieties are more likely to use very different resources, thereby greatly increasing niche differentiation and, subsequently, community productivity (Flynn et al., 2011; Leduc et al., 2015; Tilman et al., 1997). In this study, we found evidence in that direction for protein content: protein content was higher in mixtures combining varieties with a higher genetic difference (both years), and/or with a higher difference in plant height when grown in monocultures (Figure 2b, only in 2020). Furthermore, protein content was more stable in mixtures with varieties showing larger differences in monoculture yield (Figure S6, both years). These results are consistent with several previous studies reporting a stabilizing effect of wheat cultivar mixtures on yield quality (Döring et al., 2015; Gallandt et al., 2001; Mundt, 2002) and emphasize the importance of intraspecific diversity for community-level benefits (Crutsinger et al., 2006; Fridley & Grime, 2010; Prieto et al., 2015). However, in the case of grain yield, we found the opposite results: in 2019, yield stability was notably higher when there was less genetic difference between the components, and/or when there was no difference in heading dates between the varieties when grown in monocultures (Figure 3). The absence of positive effect of genetic diversity on yield stability is surprising, but not unheard of; for instance, Döring et al. (2015) did not find any significant differences in yield stability between composite cross populations (i.e., mixtures with a high degree of genetic

diversity) and standard variety mixtures (i.e., with a lower degree of genetic diversity). Similarly, Li et al. (2023) showed that increasing the number of cultivars in wheat cultivar mixtures does not always promote productivity, while Schöb et al. (2015) only found a weak effect of barley genotype diversity on productivity benefits. In the field of intercropping research, it has sometimes been shown that species composition, rather than purely genetic diversity, matters for ecosystem functions (Finney et al., 2016; Isbell & Wilsey, 2011; Stefan, Engbersen, et al., 2021). In fact, kin selection theory even suggests that plant might experience weaker competition when grown with genetically closer neighbors, because plants may preferentially help their close relatives (Fréville et al., 2019, 2022). These contrasting results call for deeper, more detailed investigations in the processes governing plant–plant interactions between wheat varieties. Notably, functional diversity has, for instance, been suggested as the main mechanism driving complementarity between individuals (Kuebbing et al., 2017; Roscher et al., 2012; Leduc et al., 2015). Measuring more functional traits in both the variety mixtures and monocultures could therefore provide additional information regarding aboveground interactions. Specifically, plant height, plant width, as well as specific leaf area can provide information on competition for light (Engbersen et al., 2022; MacLaren et al., 2023), while leaf dry matter content can point toward competition for water and, more generally, can reflect ambient competition (Puy et al., 2020; Reich, 2014; Stefan et al., 2022). Belowground processes, such as interactions between

the roots or with the soil microbiome, may also play a role in shaping plant–plant interactions and complementarity (Fierer, 2017; Freschet et al., 2021; Stefan, Hartmann, et al., 2021). Finally, phenotypic plasticity also appears as an important mechanism influencing plant–plant interactions (Barot et al., 2017), which can explain why the behaviors of mixtures is hard to predict from their corresponding behaviors in pure stands (Dawson & Goldringer, 2011). For some traits, plants plastically respond to more diverse neighbors by diverging—that is, demonstrating more differences in these traits (Grime, 2006; Zuppinger-Dingley et al., 2014). Conversely, for other traits, cultivars can become more similar when grown in mixtures compared to pure stands, demonstrating adaptive similarity or trait convergence (Colom & Baucom, 2021; Dahlin et al., 2019; Stefan et al., 2022). Unfortunately, phenotypic plasticity could not be assessed in this study, as we were unable to distinguish the different varieties in the mixtures.

One limitation of our study was that the genetic differences between the chosen wheat varieties remained rather low (i.e., between 64% and 78%), which might explain the lack of strong effects of genetic diversity (Barot et al., 2017). Also, as these mixtures were tested in a perspective of practical application by farmers, we chose varieties so that the mixtures would remain easily harvestable—that is, not more than a week of difference in phenology or 15 cm in height, for instance. Moreover, the varieties were all coming from the Swiss breeding program of the recent years, and thus were developed to meet current standard cultivation practices. Therefore, our varieties might not have been functionally different enough to induce niche complementarity (Cantarel et al., 2021). Testing a wider range of genetic and functional differences, for instance, by including older varieties or landraces, would allow to better explore the roles of genetic and functional diversities (Vidal et al., 2020).

We also did not find any response of the prevalence of diseases to genetic diversity and propose several explanations for this: first, genetic proximity does not necessarily correlate with differences in specific disease susceptibility markers. Even if two varieties are very genetically different, it is possible that they have the same resistance genes for the considered diseases. Second, as we did not do artificial inoculations, the prevalence of diseases was rather low in general, and especially low in 2020. Therefore, it might well be that the disease pressure was too low to foster any response. Finally, our plots are 7 m^2 large only, which can be considered as rather small to observe disease propagation at the field scale, as it has been shown that disease prevalence is less severe in smaller plots (Burleigh, 1984; Conner et al., 2003).

4.2 | Mixing less synchronous varieties increases yield stability

In 2019, we found a positive correlation between yield stability and yield asynchrony of the mixture components (Figure 4); specifically, mixtures combining varieties that were less synchronous across sites—in terms of grain yield—had a more stable grain yield across these sites. This result is in line with both ecological theory—in particular, the insurance effects of biodiversity—and field trials (Blüthgen et al., 2016; Tilman & Downing, 1994; Wuest et al., 2021; López-Angulo et al., 2023). Insurance effects stem from differential varieties' responses to environmental variability, thereby leading to asynchronous dynamics: when the varieties' responses are not perfectly aligned, a reduction in performance of one variety is compensated by an increase in performance of another (Hector et al., 2010; Lukac et al., 2012). The importance of the insurance effects has been widely acknowledged in natural and agricultural systems. For example, in oilseed rape, variety mixtures performed better than varieties in pure stands only when these varieties in pure stands had different responses to the environments (Pellet et al., 2005). Some studies even suggest that asynchrony across species or varieties is more important for stability than mere species or variety diversity (Blüthgen et al., 2016). Therefore, it seems that stable variety mixtures would require to combine varieties that respond differently to environmental variations, for example, with different susceptibilities to abiotic stresses such as heat, water limitation, soil structure, solar radiation, and so forth. In practice, this requires to be able to properly characterize each environment and its limiting factors (Costa-Neto et al., 2020; Xu, 2016), but also to be able to predict how will each variety perform in that said environment (Costa-Neto et al., 2022; Herrera et al., 2018).

Stable variety mixtures do not necessarily imply productive variety mixtures: according to the overyielding results, which compare the performance of the mixtures to their corresponding pure stands, we could not observe any yield benefits. In fact, overyielding was significantly negative for both years, indicating yield losses (up to an average of −7 dt/ha across sites in 2020). This contrasting result of higher stability but lower productivity potential suggests the existence of a trade-off between stable yields and highest possible performances in particular locations or years (Wuest et al., 2021). Indeed, to be stable across environments, cultivars or mixtures must be adaptable genotypes showing a high degree of plasticity; this plasticity has, however, a cost in terms of energy and resource expenses, which may then impede the productivity of these cultivars (DeWitt, Sih, & Wilson, 1998).

4.3 | These effects were context dependent

The majority of the previously described links were context dependent; indeed, all the responses of yield to monoculture differences or asynchrony were only significant in 2019, but not in 2020. This suggests that the compensatory mechanisms observed between varieties were more important in 2019, which was a lower productive year than 2020 (Figure S1). In 2019, the average yield was 72 dt/ha, while in 2020, it reached an average of 84 dt/ha (+17%). This discrepancy can be explained by differences in climatic conditions between the years: 2019 was indeed a drier year, with fewer sunshine hours, and more extreme temperatures both in winter and summer (i.e., a colder winter but hotter summer; see Table 1). Furthermore, the prevalence of diseases such as Septoria tritici blotch was more important in 2019 compared to 2020. We therefore witnessed a higher compensation between varieties in the less productive, more stressful year, during which one variety was more likely to suffer substantial yield loss than during an optimal year. This is consistent with several previous findings showing that yield advantages of mixtures over monocultures were higher under low-yield conditions or in stressful environments (Döring et al., 2015; Ratcliffe et al., 2017; Steudel et al., 2012). When combining the proper varieties, wheat variety mixtures therefore allow to buffer stress that might arise during the growing season. Importantly, if the growing season happens to be optimal, and consequently no major stress is endured by the plants, yield stability across sites remains at similar levels. Hence, there is no loss in yield stability when using variety mixtures.

In conclusion, our study shows that combining varieties with a higher degree of genetic, morphological, or agronomic differences is beneficial for the amount and stability of grain protein content, but not for yield. The mechanisms governing what makes a highly productive mixture therefore remain elusive; further studies should investigate the functional aspects of the mixture components in more details. However, yield stability of variety mixtures was enhanced when mixing varieties with contrasting responses to different environments, that is, varieties that are asynchronous. This result was only valid in 2019, which was a lower productive year due to more tedious climatic and biotic pressure conditions. Therefore, this study shows that variety mixtures have the potential to buffer possible yield losses due to external stresses during suboptimal years. While more research is needed to confirm this result, notably across several years, variety mixtures nonetheless represent a promising solution to sustainably increase the stability of wheat production in Switzerland.

AUTHOR CONTRIBUTIONS
Laura Stefan: Data curation; formal analysis; validation; visualization; writing—original draft; writing—review and editing. **Dario Fossati**: Conceptualization; funding acquisition; methodology; supervision; validation; writing—review and editing. **Karl-Heinz Camp**: Conceptualization; data curation; resources; writing—review and editing. **Didier Pellet**: Formal analysis; supervision; validation; writing—review and editing. **Flavio Foiada**: Data curation; resources; writing––review and editing. **Lilia Levy**: Conceptualization; funding acquisition; methodology; project administration; resources; supervision; validation; writing—review and editing.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT
Data is available on Zenodo (https://zenodo.org/records/10209176).

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