

RESEARCH ARTICLE

Ecological and evolutionary effects of crop diversity decrease yield variability

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Abstract

1. Higher plant species diversity decreases variability of plant community productivity. The stabilizing effect of plant diversity can result from species-specific responses to environmental fluctuations and from shifts in competitive hierarchies. Evolutionary adaptation of species to surrounding plant diversity could further decrease productivity variability.
2. We used a three-year dataset from a crop diversity experiment with seven species to assess the effect of crop diversity and selection history on temporal variability of yield.
3. We found contrasting patterns of temporal variability: Yield of species varied more in mixtures than in monocultures over years. However, at community-level, we found lower yield variability in crop mixtures compared to monocultures, although only in combination with fertilizer application under Mediterranean climate. Furthermore, we found that a mixture selection history can increase yield productivity and decrease its variability, although only in monocultures. This suggests that the interspecific interactions among crops in mixtures act as an evolutionary selective force, promoting niche complementarity.
4. *Synthesis.* Our results highlight the ecological and evolutionary role of plant interactions in crop mixtures, which can affect yield stability, while also reflecting on the importance of climate and resource availability in modifying the diversity-stability relationship.

KEYWORDS

agroecology, asynchrony, crop, evolution, intercropping, productivity, species mixtures, stability, yield variability

1 | INTRODUCTION

Improving the year-to-year yield stability of agroecosystems is fundamental under ongoing global change. While weather variability is the main cause of variations in crop production (Osborne &

Wheeler, 2013; Ray et al., 2015), climate models anticipate an increment in the frequency and intensity of climate hazards (Pörtner et al., 2022). Furthermore, commercial crops are bred to optimize yield under current climatic conditions. Thus, these homogeneous varieties fail to cope with climate uncertainty and variability

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(Kahiluoto et al., 2019). Consequently, efforts are made to develop agricultural practices that strengthen the capacity for adaptation to climate change and decrease yield variability of crops over time. Increasing crop diversity through intercropping (i.e. the simultaneous cultivation of more than one species on the same field) has been suggested as an effective practice to sustainably promote yield stability (Gaudin et al., 2015; Li et al., 2021; Raseduzzaman & Jensen, 2017; Renard & Tilman, 2019; Ryan, 2021).

Theoretical and empirical work proposes that temporal stability of biomass production in plant communities increases with higher species richness (Tilman et al., 2006; Wagg et al., 2017). This suggests that species diversity acts as insurance against environmental changes and sustains more stable primary productivity over time (Isbell et al., 2017; Yachi & Loreau, 1999). The stabilizing effect can result from several ecological mechanisms, one being the asynchrony in temporal fluctuations between species (Valencia, de Bello, Galland, et al., 2020). Increased asynchrony means that year-to-year fluctuations in the abundance of some species are compensated by others. A pattern of species fluctuations associated with increased asynchrony among species could result from species-specific responses to environmental changes (Lepš et al., 2018). Therefore, in agricultural systems, diversification could potentially lead to an increased probability of including crops with different functional strategies or adapted to different environmental conditions—that is, increased asynchrony, maintaining yield production and compensating for the yield losses when others fail. Temporal asynchrony has been demonstrated to decrease the temporal variability of crop production at the national level (Egli et al., 2020). Also, at the field level, asynchrony of some combinations of cereals and legumes led to lower yield variability in intercropping than in sole crops (Weih et al., 2021). So, asynchrony between species can stabilize productivity even if the crops are not grown together in the same field, that is, this effect does not require the different species to interact.

Beyond the differences in environmental preferences among species, an additional driver of asynchrony is the variability in the frequency and intensity of plant–plant interactions (competition and facilitation) with changing environmental conditions (Bertness & Callaway, 1994; Callaway et al., 2002; He et al., 2013; Michalet et al., 2015). In this case, plant species do not fluctuate independently of each other as a result of the different responses to environmental changes, but compensatory dynamics arise from asymmetric competition (Lepš et al., 2018). For example, benign environmental conditions can trigger hierarchical competitive interactions between species thereby increasing temporal asynchrony (Tilman et al., 1998). Conversely, positive interactions such as facilitation can cause a decrease in asynchrony due to the existence of positive correlations in the temporal fluctuations between benefactors and beneficiaries. However, facilitation could also play a significant role in maintaining temporal stability by buffering extreme conditions (Mulder et al., 2001). Benefactor species that moderate the local environment (i.e. climate, soil, etc.) can be beneficial to many other species allowing their survival or higher performance across time (Mulder et al., 2001; Wilby & Shachak, 2004). Therefore, the shifts

in positive and negative plant interactions associated with variations in climate and resource availability can also affect yield variability by accentuating or reducing species'asynchrony (Butterfield, 2009). These stabilizing mechanisms require the different species to interact and so do not exist when the crops are grown in different fields.

Evolutionary processes have also been recognized as a factor playing a major role in ecosystem functioning, and particularly fomenting stabilizing effects. It is well known that using the local varieties of crop species decreases the temporal variability of productivity due to adaptation to the local abiotic and biotic stresses (Villa et al., 2005; Zeven, 1998). One of the main goals of current breeding programs is obtaining genotypes that are adapted to the local environmental conditions, but also more resilient to changing environmental conditions (Newton et al., 2011). In mixed cropping systems, it is also particularly relevant to find 'cooperative' varieties that reduce competition between species to decrease variability of crop yield (Wuest et al., 2021). This can become particularly critical when the changes in environmental conditions trigger asymmetry in the interactions between species. An evolutionary adaptation of species to mixtures could address this issue. Recent findings in experimental grassland communities showed a modification of species traits for species grown in mixtures after several generations (i.e. species with mixture history) (Zupping-Dingley et al., 2014). In line, van Moorsel et al. (2021) found in a long-term grassland biodiversity experiment that plant communities with joint co-occurrence history decreased ecosystem variability in comparison with naïve communities. Therefore, using crop species with a joint co-occurrence history (i.e. mixture selection history) could potentially lead to more stable yields (Wuest et al., 2021).

Understanding the ecological and evolutionary factors driving yield stability may help to design sustainable agricultural systems able to maintain stable production in a fluctuating environment. In this study, we evaluated the effect of crop diversity and the selection history of crop species in monocultures and mixtures on the primary productivity (yield and biomass), the year-to-year variability and the asynchrony of annual crops in mixtures. We hypothesized that: (1) productivity (yield and biomass) observed in mixtures is more stable and asynchronous compared to monocultures; (2) the mixture history decreases variability of productivity due to reduced competitive interactions between crop species both in mixtures and monocultures; and given that a higher stabilizing effect of facilitation is expected under more stressful conditions (3) yield variability is lower in unfertilized mixtures compared to fertilized mixtures and this pattern is more marked in Spain than in Switzerland due to the drier growth season.

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted a common garden experiment in Torrejón el Rubio (Cáceres, Spain) and Zurich (Switzerland) over three years (2018–2020). The gardens were located on the Irchel campus (University of

Zurich: 47° 23' 46"N, 8° 33' 03" E, 508 m a.s.l.) and at the experimental research station Aprisco (39° 48' 48"N, 6° 00' 01" W, 350 m a.s.l.). The two sites represent different climatic and soil conditions. Spain has a semi-arid Mediterranean climate, while Switzerland has a temperate climate. Mean annual temperature and total precipitation during the growing seasons varied from 14.5 to 16.7°C and from 63 to 326 mm in Spain and from 16.1 to 18.2°C and from 347 to 511 mm in Switzerland, respectively. The weather conditions in the first year were cooler and wetter in Spain, while in Switzerland it was warmer and drier compared to the second and third year (Figure S1). Climatic data from the period (2018–2020) were downloaded using the function `get_daily_climate()` from the `EASYCLIMATE` R package (Cruz-Alonso et al., 2023; Moreno & Hasenauer, 2016; Rammer et al., 2018).

The experimental plots were squares of 0.25 m² in raised beds of around 35 cm depth. The beds were placed on well drained local soil and open at the bottom to allow unlimited root growth. The plots were organized in 15 beds of 10 × 1 m in Spain and in 16 beds of 7 × 1 m in Switzerland. Plots were separated from each other by below-ground metal frames (35 cm deep). We filled the raised beds with standard, not enriched, agricultural soil coming from the local region. Spanish soil (78% sand, 20% silt, 2% clay; pH of 6.3; total C and N of 0.5% and 0.05%, respectively) was sandier and less fertile than the soil in Switzerland (45% sand, 45% silt, 10% clay; pH of 7.25; total C and N of 3.39% and 0.19%, respectively). The experimental gardens were irrigated to ensure survival of the crops during drought periods. In Spain, the automated irrigation system was configured for a dry threshold of soil moisture of 17% of field capacity, with a target of 25%. In Switzerland, the dry threshold was set at 50% of field capacity, with a target of 90%. Whenever dry thresholds were reached (measured through PlantCare soil moisture sensors (PlantCare Ltd., Switzerland)), irrigation was initiated until reaching the target value.

2.2 | Study species

We selected seven crop species: *Avena sativa* (oat), *Triticum aestivum* (wheat), *Lens culinaris* (lentil), *Lupinus angustifolius* (blue lupin), *Camelina sativa* (camelina), *Linum usitatissimum* (linseed) and *Coriandrum sativum* (coriander). These species were selected because they exhibit similar phenology, growth requirements and plant size, can easily be cultivated in Europe and present different phylogenetic or functional characteristics. We classified the selected species in four phylo-functional groups. Specifically, we selected two monocots (*A. sativa* and *T. aestivum* (Poaceae)); within the dicots, a superasterid (*C. sativum* (Apiaceae)) and among the superrosids, two legumes (*L. culinaris* and *L. angustifolius* (Fabaceae)) and two non-legumes (*C. sativa* (Brassicaceae) and *L. usitatissimum* (Linaceae)). We used different locally adapted crop varieties in each country (the list of cultivars and suppliers can be found in Table S1). Furthermore, whenever possible, we selected traditional or ancient open-pollinated varieties in order to maximize genetic variability needed for evolutionary processes to occur.

2.3 | Experimental design

We applied a plant diversity treatment with three levels: monocultures, two-species and four-species mixtures (Figure 1). The two-species mixtures include all combinations of two species from distinct phylo-functional groups, while the four-species mixtures include all combinations of four species including all four phylo-functional groups. Thus, this study included seven monocultures, 18 two-species mixtures and 8 four-species mixtures, with two replicates of all different species compositions. Several species mixtures resulting from all possible combinations are not currently used in intercropped systems, so they are experimental mixtures of crop species without an apparent economic interest. In 2019 and 2020, we additionally used a 'selection history' treatment with two levels: monoculture selection versus mixture selection. The monoculture history, sown as monoculture and mixture communities, consisted of communities assembled with offspring coming from plants that had grown in monocultures in the previous growing season. The mixture selection for mixtures consisted of communities assembled with offspring of plants that had grown in communities with the identical species composition (Figure 1). To grow the mixture selection in monocultures, we used seeds coming from a pool of all available four-species mixtures. Consequently, for the first year (2018), we used the original seeds provided by the seed suppliers, while for the second (2019) and third years (2020), we used seeds harvested in our own experiment during the previous year and the corresponding selection history. We replicated this set-up in Spain and Switzerland (factor 'country') at two soil fertility levels (non-fertilized control plots versus fertilized plots; factor 'fertilization') (Figure 1). We fertilized half of the beds with nitrogen (N), phosphorus (P) and potassium (K) at the concentration of 120 kg/ha N, 205 kg/ha P, and 120 kg/ha K (ORGAMAX 7-12-7, Productos Agrícolas MACASA S.L.): 41.5% of the fertilizer was applied before sowing, 41.5% when wheat was at the tillering stage, and the rest when wheat was flowering. The other half of the beds served as unfertilized controls. In 2018, we randomly allocated individual beds to a fertilized or non-fertilized control treatment. In the following years, we kept the initial fertilization treatment allocation. Monoculture and mixture plots were randomized among plots and beds each year, within each country and fertilization treatment. The combination of replicating the experiment in two countries with contrasting climatic conditions, along with the fertilizer treatment, allowed for testing how changes in climatic and soil conditions can shape the diversity-stability relationship.

2.4 | Experimental set-up

In Spain, we planted between the 2 and 5 of February, and in Switzerland between 1 and 7 of April, each year. In each plot, seeds were sown in four rows and a between-row distance of 12 cm. Each species was randomly assigned to a planting row in the plot. We sowed by hand following standard agricultural practices for sowing density and depth (see Table S1).

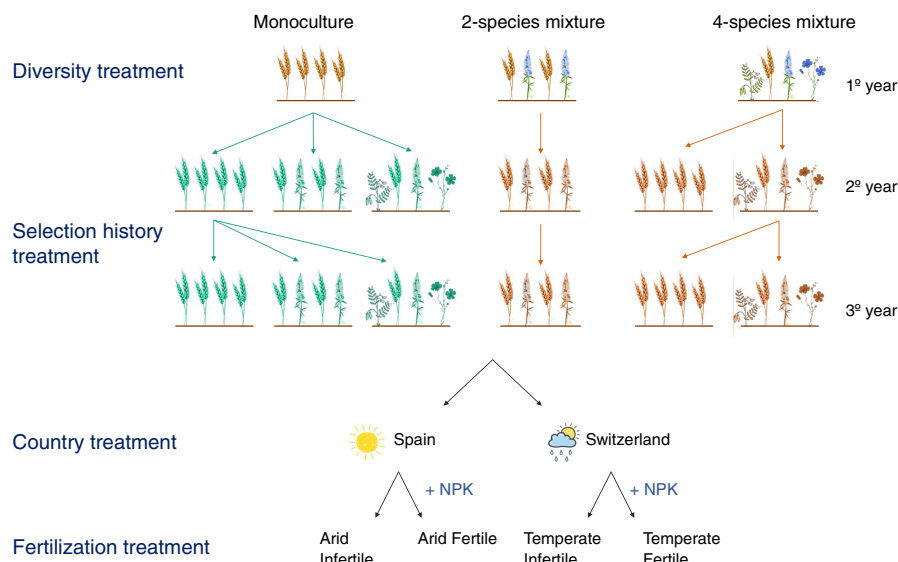


FIGURE 1 Experimental design. Seven species were grown in monocultures (7 different monocultures), 2-species mixtures (18 combinations) and 4-species mixtures (8 combinations) in 2018–2020. The monoculture selection history, sown as monoculture and mixture communities, consisted of communities assembled with offspring coming from plants that had grown in monocultures in the previous growing season. The mixture selection for mixtures consisted of communities assembled with offspring of plants that had grown in communities with the identical species composition. To grow the mixture selection in monocultures, we used seeds coming from a pool of all available four-species mixtures. The set-up was replicated in Spain and Switzerland, and with and without fertilizer (nitrogen, phosphorus and potassium) application in a factorial design. The green shades represent monoculture history selection, and the orange shades represent mixture history selection. See Methods section for details.

2.5 | Data collection

Harvest was conducted by hand when seeds reached maturity. Seeds were sun-dried for 5 days and weighed. To determine vegetative biomass, plants were clipped right above the soil surface. Vegetative biomass, including stems, leaves and chaff, was oven-dried at 80°C for 48h before weighing. We used both seed biomass (seed yield) and vegetative above-ground biomass as measures of productivity.

2.6 | Calculations

We tested the effect of species diversity on the productivity and variability at community- and species-level. At community-level, seed yield and vegetative biomass was the total seed mass and total vegetative biomass of all species cultivated in a community. At species-level, the seed yield and vegetative biomass of each species was multiplied by the number of species of the community to account for the fact that species were planted in different densities depending on the crop diversity treatment.

To compare the temporal variability in productivity of monocultures and mixtures at community-level, we calculated productivity of expected and observed mixtures. The productivity of expected mixtures is the productivity of mixtures generated using the productivity in monocultures. We first calculated the average of all replicates of the monocultures within the same treatment (same fertilization, year and country). We then summed the productivities divided by two or four for two-species and four-species mixtures,

respectively. The expected productivity variability was compared to the observed productivity variability in the mixture communities.

We calculated productivity variability over time as the adjusted coefficient of variation ($\text{variability}_{\text{acv}}$). $\text{variability}_{\text{acv}}$ is an adjusted coefficient of variation which removes the dependence of the variance from the mean. $\text{variability}_{\text{acv}}$ was calculated separately for each type of community, country, fertilization and species composition, and species combination following Döring and Reckling (2018) and using the function `acv` from the `METAN` R package (Olivoto & Lúcio, 2020). It is noteworthy that by comparing communities with the same species number (i.e. expected and observed mixtures), we can rule out the potential “portfolio effect” as mechanism responsible of the diversity-stability relationship (Doak et al., 1998; Mccann, 2000). Thus, yield-stabilizing effects would not be a mathematical artefact derived from the statistical averaging, which would predict that a sum of independent yields would be progressively more stable as more yields are summed. At species-level, we assessed the effect of the species diversity on productivity variability acv for each species in each treatment (crop diversity, species composition, country and fertilization level).

We also evaluated the response of the variability acv of expected and observed mixtures to the asynchrony in temporal fluctuations between species and compared the temporal asynchrony of expected and observed mixtures. We calculated the asynchrony metric according to Lepš et al. (2019):

$$\text{Asynchrony} = -1 * \frac{2 \sum_{i,j>i}^S \text{covar}(x_{ij})}{\sum_{i=1}^S \text{var}(x_i)},$$

where S is the total number of species in the community, X_{ij} is the productivity (yield or biomass) of the i -th and j -th species over time and X_i is the productivity (yield or biomass) of the i -th species over time. Positive values indicate negative covariation between species (asynchrony), while values close to zero indicate a predominance of random fluctuations, and negative values indicate a common response of the species (synchrony).

To evaluate the effect of selection history on the productivity variability, we calculated variability_{aCV} separately for each observed and expected mixture in each treatment (selection history, species composition, country, and fertilization level) for the 2 years in which there was selection history (2019 to 2020) and the year 2018. In this case, the data from the year 2018 was used to calculate the mean productivity of each observed and expected mixture for both levels of the selection history treatment.

2.7 | Data analyses

We evaluated the response of seed yield and vegetative biomass, and their variability_{aCV} (at community- and species-level) to the diversity and selection history treatment using linear mixed-effects models. We included crop diversity (one, two or four species), year (2018 to 2020), fertilization (yes, no) and their interactions as fixed effects. We also included country (Spain, Switzerland) and their interactions with the other factors as fixed effects due to the differences in the soil and climatic conditions, including soil moisture thresholds, and the starting seed material. To meet model assumptions of normality and homoscedasticity of errors, yield and vegetative biomass were root-transformed and coded to include heteroscedastic variance structure ('weights' argument in the 'lme' function). To evaluate variability_{aCV} at community-level, we included mixture type (expected versus observed), and the corresponding interactions as fixed effects, instead of crop diversity. At community-level, species composition was included as random effect, while at species-level, species composition and crop species were included as random effects.

We also evaluated the effect of the asynchrony in temporal fluctuations between species on the variability_{aCV} of the expected and observed mixtures using linear mixed-effects models. We compared the temporal asynchrony of expected and observed mixtures using linear mixed-effects models and including the type of mixture, country, fertilization and their interactions as fixed effects, and species composition as random effect.

We performed separate models to test the effect of the selection history (monoculture vs mixture) on the seed yield and its variability_{aCV}, because for this analysis we excluded the data from the first year (2018), when we used the original seeds from the seed suppliers. Besides the selection history, we included crop diversity (monoculture, mixture), year (2019, 2020), country (Spain, Switzerland), fertilization (yes, no) and their interactions as fixed effects. To evaluate variability_{aCV}, we included mixture type (expected versus observed), and the corresponding interactions as fixed

effects, instead of including crop diversity. Species composition was included as random effect.

Differences between treatments were analysed in more detail using Tukey's post-hoc comparisons. We removed all data, where at least one species within a plot had no biomass, because that means that the plot did not have the specified number of species in the community. However, data with zero values for yield were maintained as long as they had biomass, because that means that the plot had the specified number of species in the community. We excluded 101 (2,7%) from a total of 3697 species-level samples, and 59 (3,4%) from a total of 1671 plot-level samples.

3 | RESULTS

Increasing the number of crop species significantly increased primary productivity by 45.0% for seed yield and 51.5% for vegetative biomass but the intensity of this effect varied among years and between countries (Figure 2 and Figure S2; Table S2). Specifically, the marginal effect of crop diversity decreased over time in Switzerland (Figure 2), from 15.7% in 2018 over 9.6% in 2019 to 4.4% in 2020, while it increased in Spain from 4.7% in the first year to 19.1% in the third year. Furthermore, the effect of crop diversity on seed yield did not differ among the fertilizer treatments (Table S2).

We found that, at species-level, seed yield variability_{aCV} increased with crop diversity (Table S3, Figure 3). However, at community-level, seed yield variability_{aCV} was significantly affected by the interactions of the type of mixture with country and with fertilization treatment (Table S4). Post-hoc comparisons revealed that the yield variability_{aCV} was lower in observed mixtures than expected mixtures in Spain ($p = 0.002$), but not in Switzerland

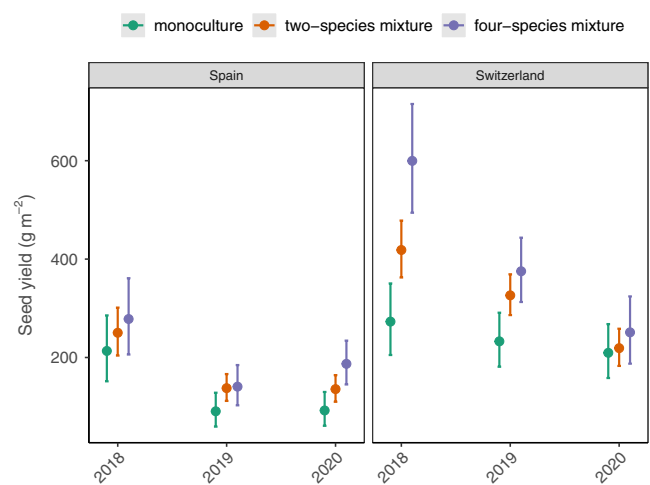


FIGURE 2 Seed yield (in g m^{-2}) of crop communities in response to plant diversity (monoculture, two-species mixture, and four-species mixture), year (2018, 2019 and 2020) and country (Spain and Switzerland). Points and error bars indicate marginal means and 95% confidence intervals, respectively. The results of ANOVAs are presented in Table S2.

($p = 0.363$; Figure 4A). Furthermore, on fertilized soils seed yield variability_{aCV} of the observed mixtures was significantly lower than expected (Figure 4B). Regarding the biomass variability, we did not find any difference between observed and expected mixtures (at the species- nor community-level) despite the biomass variability_{aCV} being affected by country and fertilization treatment (Figures S3 and S4).

As expected, yield asynchrony significantly decreased yield variability_{aCV} in the expected and observed mixtures (Figure 5A). We also found significant differences between the asynchrony of the expected and observed mixtures, but they were dependent on the country and the fertilization treatment, as indicated by the interaction of community type with country and fertilization treatment

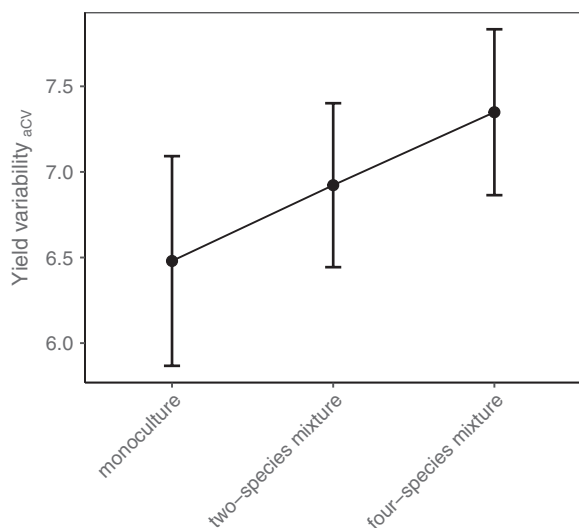
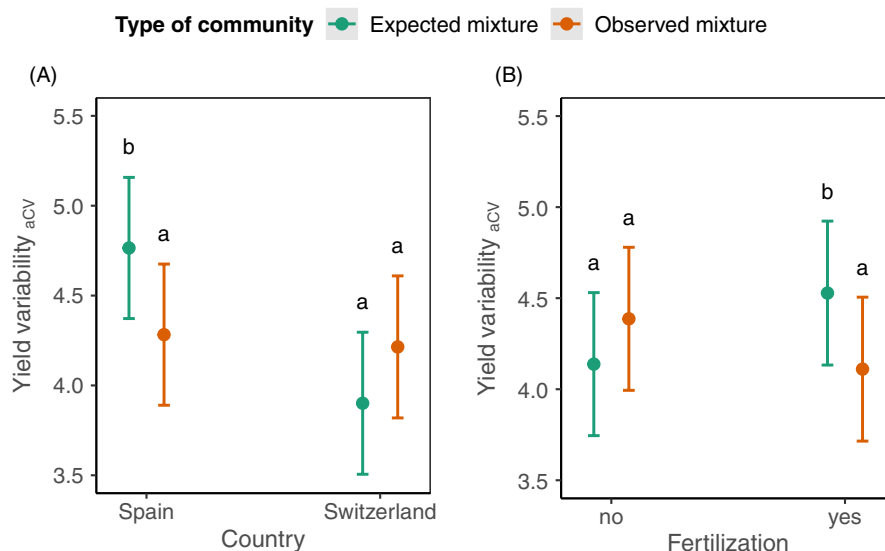


FIGURE 3 Seed yield variability_{aCV} at species-level in response to crop diversity. Points and error bars indicate marginal means and 95% confidence intervals which were calculated on the basis of the homogeneity of variances. The results of ANOVAs are presented in Table S3.

FIGURE 4 Seed yield variability_{aCV} of crop communities in response to mixture community (expected and observed mixtures), country (A; Spain and Switzerland) and fertilization (B; fertilized and unfertilized). Points and error bars indicate marginal means and 95% confidence intervals which were calculated on the basis of the homogeneity of variances. Shared letters indicate that means are not significantly different from each other (Tukey's post-hoc test, $\alpha = 0.05$). The results of ANOVAs are presented in Table S4.



(Table S5). Tukey's post-hoc tests revealed that under fertilized conditions and in Spain the observed mixtures exhibited higher yield asynchrony among species than expected (Figure 5B). Biomass asynchrony under fertilized conditions in Spain and also Switzerland was higher in the observed mixture communities than expected (Figure S5, Table S6).

Community-level seed yield and vegetative biomass were significantly affected by the selection history, but the effect varied depending on the community type (monocultures vs. mixtures; Table S6). Pairwise comparisons showed that both measures of productivity were significantly lower in monocultures with monoculture history than in mixtures, but monocultures with mixture history were no less productive than mixtures. In other words, using seeds with mixture history in monocultures increased seed yield by 22.2% ($p = 0.013$, Figure 6) and vegetative biomass by 15.5% ($p = 0.021$, Figure S6) compared to monocultures planted with plants from a monoculture history. We also found differences in yield and biomass variability_{aCV} between selection history treatments, but they were dependent on crop diversity, country, fertilization and years for the seed yield variability_{aCV}, and dependent on crop diversity and country for the vegetative biomass variability_{aCV} (Table S7). The pairwise comparisons showed that the monocultures composed of plants with a mixture history had more stable yields (and vegetative biomass) compared to monocultures planted with plants from a monoculture history, but these effects were only significant in Spain (Figure 7 and Figure S7).

4 | DISCUSSION

Our results provide evidence that: (i) crop species diversity decreases temporal yield variability at community-level through temporal asynchrony in the fluctuations of the productivity of crop species within mixtures, (ii) a mixture selection history can increase monoculture yield decreasing its variability, and (iii) positive biodiversity effects

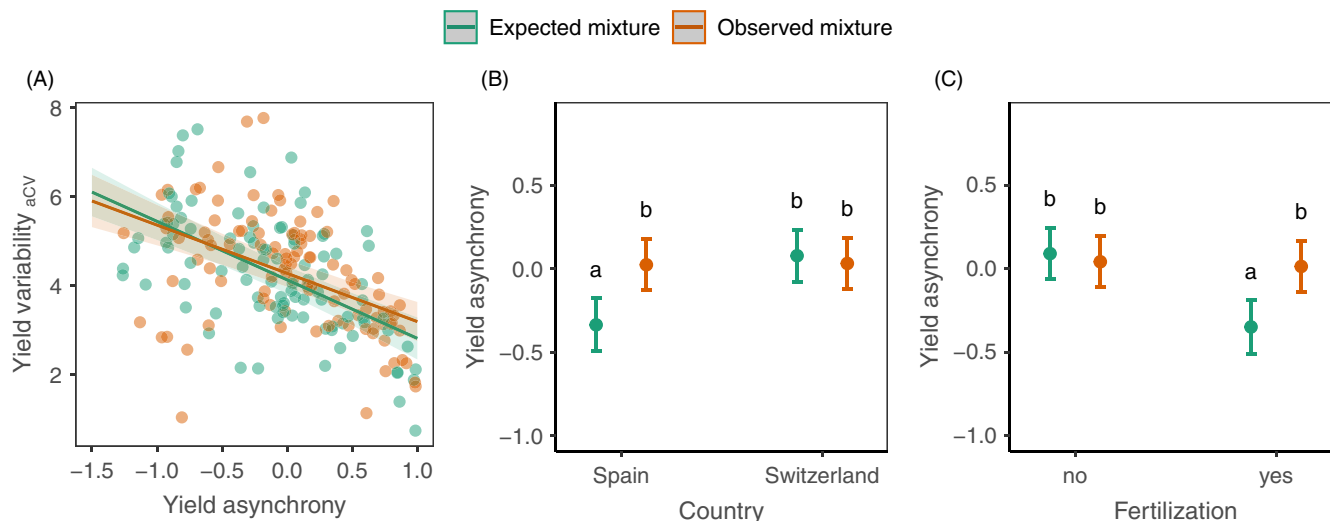


FIGURE 5 (A) Seed yield variability a_{CV} of crop communities in response to temporal asynchrony of seed yield and mixture community type and seed yield asynchrony in response to mixture community type (expected and observed mixtures), (B) country (Spain and Switzerland) and (C) fertilization (yes, fertilized; no, not fertilized). Points and error bars indicate marginal means and 95% confidence intervals, respectively. Shared letters indicate that means are not significantly different from each other (Tukey's post-hoc test, $\alpha = 0.05$). The results of ANOVAs are presented in Table S5.

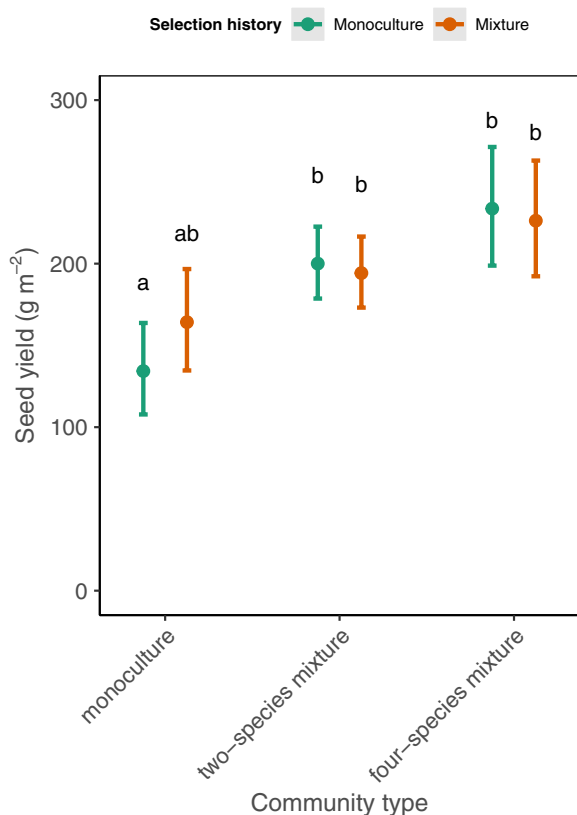


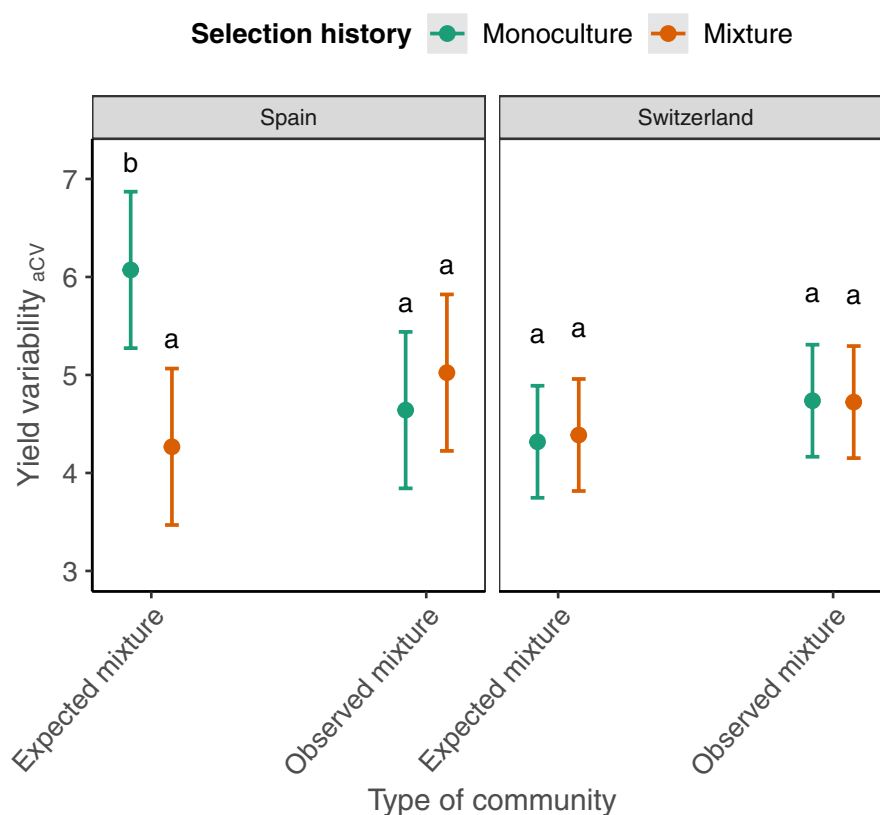
FIGURE 6 Seed yield (in $g\ m^{-2}$) of crop communities in response to crop diversity (monoculture and mixture) and selection history (monoculture and mixture). Points and error bars indicate marginal means and 95% confidence intervals, respectively. Shared letters indicate that means are not significantly different from each other (Tukey's post-hoc test, $\alpha = 0.05$). The results of ANOVAs are presented in Table S6.

of mixtures on yield and variability strongly varied depending on the country and fertilization conditions.

4.1 | Reduced yield variability in mixtures

The differences in seed yield variability between observed and expected mixtures (although under certain conditions) provides evidence of the stabilizing effect of crop diversity on yield. The positive diversity effects on seed yield variability could arise from facilitative interactions among species, which tends to stabilize community dynamics in more stressful environmental conditions (Butterfield, 2009; Mulder et al., 2001). However, we hypothesized a greater stabilizing effect of crop diversity under unfertilized conditions due to the hypothesized stronger influence of facilitation, but there were only significant differences in the yield variability of the observed and expected mixtures under fertilized conditions. As shown before in natural temperate grasslands (Lepš et al., 2018), our results indicate that the compensatory dynamics are more pronounced under fertilized conditions. Similarly, our results are in line with previous research showing that the year-to-year temporal stability of seed yield at field-level was higher in mixtures than in monocultures under fertilized conditions (Weih et al., 2021). The idea of intercrop mixtures exhibiting higher productivity stability than monocultures was also supported by the species asynchrony results, which reflect negative year-to-year covariation in temporal fluctuations between species with a similar pattern to the yield stability. Taken together, the results of yield variability and synchrony suggest that interspecific interactions in mixtures under fertilized conditions foster the asynchrony of productivity among species. Therefore, the compensatory dynamics in mixtures resulting from species-specific responses to

FIGURE 7 Seed yield variability_{aCV} at community-level in response to selection history (monoculture and mixture history), mixture community type (expected and observed mixtures) and fertilization treatment (yes and no). Points and error bars indicate marginal means and 95% confidence intervals, respectively. Shared letters indicate that means are not significantly different from each other (Tukey's post-hoc test, alpha = 0.05). The results of ANOVAs are presented in Table S7.



environmental changes are intensified by the competitive plant-plant interactions (Lepš et al., 2018; Tilman, 1996). Thus, our findings indicate that intercropping can help to decrease the yield variability in agricultural systems in which mineral fertilizers are used to intensify production.

4.2 | Increased monoculture yield and lower variability by mixture history

We found that in Spain the monocultures composed of plants with a mixture history were more productive and had more stable yields compared to monocultures planted with plants from a monoculture history. However, this effect was not apparent when plants were grown in mixture. This does not necessarily mean that the evolutionary mixture history effect is not there in mixtures. In fact, more likely is that the ecological processes on yield and stability have overrun these evolutionary processes in mixtures. The underlying rationale for the positive effects of the mixture selection on monocultures is that the mixture types of crop species grown in monocultures originating from all possible four-species mixtures potentially display higher functional diversity as a result of rapid transgenerational adaptation to surrounding plant diversity (Zupping-Dingley et al., 2014). Indeed, this statement is supported by Stefan et al. (2022) who found a higher coefficient of variation of leaf dry matter content and seed mass in monocultures planted with plants from a mixture history compared to monocultures composed of plants with a monoculture history. These results

are in accordance with previous studies which found that variety mixtures (i.e. high functional diversity) tend to be more productive than monocultures of the same varieties (Kjær et al., 2009; Reiss & Drinkwater, 2018; Wuest et al., 2021). Therefore, our results demonstrate that evolutionary breeding approaches that improve intraspecific niche complementarity in monocultures can reduce the yield difference with the mixtures which are usually more productive than monocultures (Chen et al., 2021; Isbell et al., 2017; Reiss & Drinkwater, 2018). Because the mechanism by which diversity stabilizes productivity is based on differences in the species responses to environmental changes (Tilman et al., 2006), our results suggest that the monocultures composed of plants with a mixture history could exhibit larger intraspecific differences compared to monocultures planted with plants from a monoculture history (Loreau & de Mazancourt, 2013; Prieto et al., 2015). This result, together with the effect of the selection history on yields, provides evidence that the interspecific interactions among crops in mixtures act as an evolutionary selective force which can lead to higher and more stable crop yields.

4.3 | Yield benefits of diversity are strongly context dependent

The positive effect of crop diversity on primary productivity found in this study is in line with previous evidence from agroecosystems (Chen et al., 2021; Isbell et al., 2017; Li et al., 2021; Stomph et al., 2020) supporting the general positive relationship between

biodiversity and productivity (Hector et al., 1999; Tilman et al., 1996). However, the intensity of this positive biodiversity effect strongly varied among years and between countries, indicating that the yield benefit of intercropping is strongly context dependent. Our results contrast with previous studies in which intercropping yields increased significantly through time in long-term field experiments based on maize (Li et al., 2021). This pattern can be due to the main mechanisms behind the positive biodiversity–productivity relationship, such as complementarity and sampling effects, being strongly affected by the interannual variability in environmental conditions (Barot et al., 2017; Engbersen et al., 2022). Annual climatic variability is a well-known global driver of primary productivity and therefore, a main determinant of the productivity stability in annual cropping systems (Moore & Lobell, 2015; Ray et al., 2015). The large intercropping benefits found in 2018 in Switzerland coincide with the high mean annual temperatures registered. However, in Spain, the positive diversity effects seem to be more coupled to the annual precipitation than to the mean annual temperatures (Figure S1), highlighting the environmental context-dependence of annual crop systems.

4.4 | Contrasting effects of diversity on the yield variability of species and communities

Despite the stabilizing effect of crop diversity on yield at community-level, yield of species varied more in mixtures than in monocultures among years. This result suggests that the fluctuations in yield of species are caused by changes in competitive interactions in mixtures across years (Lepš et al., 2018). Such temporal changes in competitive hierarchies are likely associated with year-to-year environmental variability. So, shifts in environmental conditions favouring a species' growth may also favour its competitive ability against a species growing under unfavourable conditions, thereby increasing the species yield variability. Our results are consistent with previous studies in different experimental grasslands which found that variability of primary productivity increased at species-level but decreased with increasing plant diversity at community-level (Tilman, 1996; van Moorsel et al., 2021; van Ruijven & Berendse, 2007). Compensatory dynamics between the species coexisting in mixtures are likely to explain the contrasting patterns of temporal yield variability at species and community-levels.

There are several caveats to this work that should be noted. First, we present data from only three years. A detailed analysis of yield variability with data from more years could influence the results. However, in this study, species richness and composition were maintained in both countries and under different fertilizer conditions. So, the observed changes were not due to shifts in species composition and species richness over time as is often the case in studies with grassland communities (Lepš et al., 2019; Valencia, de Bello, Lepš, et al., 2020). Here, we compared the productivity variability calculated for expected and observed mixtures with the same number of species and furthermore, the effect of the type of mixture was

tested within each species combination. Thus, the multifactorial design of our study offers several advantages that allow controlling for several factors that generally affect variability and that might compensate for the use of only 3 years to estimate the productivity variability. It is also important to note that only the last 2 years of the experiment were used for assessing the effect of selection history on productivity variability, since the first-year seeds were newly purchased from the seed suppliers and had no known selection history (although they were used to calculate the productivity variability). Therefore, it must be kept in mind that considering more years to estimate the productivity variability in annual cropping systems might likely intensify the evolutionary processes through which crop plants are adapted to crop diversity. Finally, the stabilizing effects of the crop diversity and selection history were context dependent, becoming most apparent in harsh and water-limited environments (i.e. Spain). This context-dependence may be explained by differences in abiotic factors between countries, but it is also important to keep in mind that different cultivars were used in Spain and Switzerland. It is probable that in Spain, where several wild types were used (Table S1), the cultivars were genetically more heterogeneous compared to the selected cultivars from Switzerland. This higher genetic diversity could allow the monoculture and mixture histories to exert different selective pressures, thereby increasing yield and stability by complementarity and compensatory dynamics between genotypes within species.

In summary, our findings provide evidence that mixture cropping can improve seed production and decrease yield variability, but the diversity benefits can strongly vary over the years depending on the environmental context. In our study, we found that the stabilizing benefits of diverse crop mixtures and mixture selection history were higher under harsher environmental conditions (i.e. Spain). Thus, these results may have important implications for enhancing the stability of cropping systems in the face of climate change and rising global temperatures. More research is needed to investigate the temporal factors affecting the variation in the effects of crop diversity on yield variability and productivity. We show that increasing the number of species through mixture cropping can decrease the temporal yield variability driven by asynchronous species dynamics, but the yield of particular crop species can be compromised. Thus, from a farmer's perspective, if stable yields of specific species are key, the use of monocultures might be favoured over intercrops, while intercrops provide benefits if different cash crops can be grown together. Our study also provides evidence for short-term evolutionary processes in annual crop communities. We found that a mixture selection history can increase yield productivity decreasing its variability, particularly in monocultures, suggesting that interspecific interactions among crops in mixtures act as an evolutionary selective force which promotes biodiversity effects. Current breeding programs are largely focused on monoculture cropping and breeding for monocultures, and crop seeds are multiplied in monocultures. However, our results suggest that the inclusion of plant diversity in breeding and seed multiplication schemes can lead to increased and more stable

yields, also in monocultures, through the selection of functional diversity and consequently intraspecific niche differentiation.

AUTHOR CONTRIBUTIONS

Christian Schöb conceived the study and designed the experiment together with Laura Stefan and Nadine Engbersen. All authors collected data. Jesús López-Angulo conceived the analytical framework, analysed the data and led the writing of the manuscript. All authors provided critical comments on the manuscript and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14092>.

DATA AVAILABILITY STATEMENT

Dataset and R code are available at the repository Zenodo <https://doi.org/10.5281/zenodo.7544811> (López-Angulo et al., 2022).

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SUPPORTING INFORMATION

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

Table S1. List of crop species, sowing density and depth, ecotypes and their suppliers in Switzerland and in Spain.

Table S2. Results of linear mixed effects model ANOVA (type II) for seed yield and vegetative biomass at community-level in response to crop diversity, country, year, fertilization and their interactions. NumDF, degrees of freedom of term; DenDF, degrees of freedom of error term; F-value, variance ratio; P, error probability. * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.001$).

Table S3. Results of linear mixed effects model ANOVA (type II) for variability_{aCV} of seed yield and vegetative biomass at species-level in response to crop diversity, country, fertilization and their interactions. NumDF, degrees of freedom of term; DenDF, degrees of freedom of error term; F-value, variance ratio; P, error probability. * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.001$).

Table S4. Results of linear mixed effects model ANOVA (type II) for variability_{aCV} of seed yield and vegetative biomass at community-level in response to community type (expected or observed mixture), country, year, fertilization and their interactions. NumDF, degrees of freedom of term; DenDF, degrees of freedom of error term; F-value, variance ratio; P, error probability. * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.001$).

Table S5. Results of linear mixed effects model ANOVA (type II) for asynchrony of seed yield and vegetative biomass in response to crop diversity, country, fertilization and their interactions. NumDF, degrees of freedom of term; DenDF, degrees of freedom of error term; F-value, variance ratio; P, error probability. * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.001$).

Table S6. Results of linear mixed effects model ANOVA (type II) for seed yield and vegetative biomass at community-level in response to crop diversity, selection history, year, country, fertilization and their interactions. NumDF, degrees of freedom of term; DenDF, degrees of freedom of error term; F-value, variance ratio; P, error probability. * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.001$).

Table S7. Results of linear mixed effects model ANOVA (type II) for variability_{aCV} of seed yield and vegetative biomass at community-level in response to crop diversity, selection history, country, fertilization and their interactions. NumDF, degrees of freedom of term; DenDF, degrees of freedom of error term; F-value, variance ratio; P, error probability. * ($P < 0.05$), ** ($P < 0.01$), *** ($P < 0.001$).

Figure S1. (a) Mean annual temperature (°C), (b) mean monthly temperature (°C) and (c) monthly total precipitation of the growing seasons in Spain and Switzerland. The growing seasons were between February and June in Spain and between April and August in Switzerland. Error bars indicate standard errors.

Figure S2. Vegetative biomass (in g m^{-2}) of crop communities in response to plant diversity (monoculture, two-species and four-species mixture), year (2018, 2019 and 2020) and country (Spain

and Switzerland). Points and error bars indicate marginal means and 95% confidence intervals, respectively. The results of ANOVAs are presented in Table S2.

Figure S3. Vegetative biomass variability_{aCV} at species-level in response to crop diversity. Points and error bars indicate marginal means and 95% confidence intervals, respectively. The results of ANOVAs are presented in Table S3.

Figure S4. Vegetative biomass variability_{aCV} at community-level in response to mixture community type (expected and observed mixtures), country (a; Spain and Switzerland), fertilization (b; yes, fertilized; no, not fertilized) and year (c; 2018, 2019, 2020). Points and error bars indicate marginal means and 95% confidence intervals, respectively. Shared letters indicate that means are not significantly different from each other (Tukey's post-hoc test, $\alpha = 0.05$). The results of ANOVAs are presented in Table S4.

Figure S5. Temporal asynchrony of vegetative biomass in response to mixture community type (expected and observed mixtures), country (a; Spain and Switzerland) and fertilization (b; yes, fertilized; no, not fertilized). Points and error bars indicate marginal means and 95% confidence intervals, respectively. Shared letters indicate that means are not significantly different from each other (Tukey's post-hoc test, $\alpha = 0.05$). The results of ANOVAs are presented in Table S5.

Figure S6. Vegetative biomass (in g m^{-2}) of crop communities in response to crop diversity (monoculture and mixture) and selection history (monoculture and mixture). Points and error bars indicate marginal means and 95% confidence intervals, respectively. Shared letters indicate that means are not significantly different from each other (Tukey's post-hoc test, $\alpha = 0.05$). The results of ANOVAs are presented in Table S6.

Figure S7. Vegetative biomass variability_{aCV} at community-level in response to selection history (monoculture and mixture history), mixture community type (expected and observed mixtures) and fertilization treatment (yes and no). Points and error bars indicate marginal means and 95% confidence intervals, respectively. Shared letters indicate that means are not significantly different from each other (Tukey's post-hoc test, $\alpha = 0.05$). The results of ANOVAs are presented in Table S7.

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