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ARTICLE

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Temporal stability of productivity is associated with complementarity and competitive intensities in intercropping

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Abstract

Year-to-year stability in crop production is a crucial aspect of feeding a growing global population. Evidence from natural ecosystems shows that increasing plant diversity generally increases the temporal stability of productivity; however, we have little knowledge of the mechanisms by which diversity affects stability. In fact, understanding the drivers of stability is a major knowledge gap in our understanding of biodiversity and ecosystem function in general. We varied resource inputs into crop monocultures and intercropping of maize/pea and maize/rapeseed for 3 years in field experiments to create a wide range of values for temporal stability, complementarity effects, selection effects, competition, and facilitation. We correlated whole-system temporal stability in productivity with these values and the stability of competitively subordinate species and competitively dominant species in the intercrops. We then used structural equation modeling (SEM), which combines complex path models with latent variables, to estimate how interspecific interactions for water, nitrogen, and phosphorus affected the relationships between stability and these values. Intercropping treatments did not increase stability, but the wide range of stability created by our experiments allowed us to explore the relationship of many factors with stability. Complementarity correlated positively with the temporal stability of grain yield and aboveground biomass, suggesting that either facilitative interactions or niche partitioning shifted over time in ways that promoted stability. Furthermore, the temporal stability of total productivity of intercropping relied most on the stability of more productive species. However, facilitation tested by relative interaction index independently did not correlate with stability, but the temporal stability of the whole system increased as the competitive effects of competitively dominant species (pea and rapeseed) on competitively subordinate species (maize) decreased and was highest when these competitive effects were virtually zero. SEM indicated that as competition for soil nitrogen from competitively dominant species on competitively subordinate species decreased, the overall temporal stability of whole-system aboveground biomass increased. This stability then led to greater stability in grain production. Our findings indicate that complex shifts in complementarity and competitive intensities are likely to be key mechanisms that maintain temporal stability in species-diverse agriculture and, potentially, in natural systems.

KEYWORDS
competition, complementarity, diversity effects, ecosystem function, facilitation, intercropping, productivity, temporal stability

INTRODUCTION

Feeding a growing global population requires increasing agricultural productivity and improving the temporal stability of productivity (Knapp & Van der Heijden, 2018; Renard & Tilman, 2019). In natural ecosystems, species diversity can substantially increase year-to-year stability (Loreau & De Mazancourt, 2013; Schnabel et al., 2019; Tilman et al., 1996). Agricultural practices that incorporate crop diversity can increase yields and resilience to environmental perturbations (Lin, 2011; Marcillo & Miguez, 2017; Snapp et al., 2010). One agricultural practice that utilizes crop diversity is intercropping, or growing at least two crop species in the same place at the same time (Li et al., 2007). Although two crop species are not highly diverse relative to natural systems, the modest diversity in intercropping can produce considerably different ecological processes, including increases in productivity, nutrient acquisition, and altered nutrient cycling, than single crop species (Li et al., 2016; Stefan et al., 2021). Moreover, intercropping can increase the stability of yields (Li et al., 2021; Snapp et al., 2010; Yang et al., 2021), but this depends on specific crop combinations (Raseduzzaman & Jensen, 2017). Despite the importance of species diversity for temporal stability in ecosystem functions, we know little about the roles of interspecific competition, facilitation, or complementarity as mechanisms of stability.

The conceptual and theoretical case for diversity producing ecosystem stability is foundational in ecology (Elton, 1958; May, 1973; Pimm, 1984). To our knowledge, Tilman and Downing (1994) conducted the first long-term field experiment to test this relationship and found that the productivity of more diverse plant communities was more resistant to drought than species-poor communities. Species dominance often reflects certain traits in a community, which in turn affects interspecific interactions (Hillebrand et al., 2008). As predicted by the mass ratio hypothesis (Grime, 1998; also see Sasaki & Lauenroth, 2011), species that dominate community biomass, which are also generally the most productive species, may regulate the temporal stability of plant communities more than diversity per se. For example, low community stability often occurs when a productive species, with lower tolerance to perturbations than other species, is included in the species pool (Wang et al., 2021). Yet current reports on how and which components of communities (dominant vs. subordinate) affect stability, especially in agroecosystems, are ambiguous. Furthermore, whether the effects of dominant species, based on biomass, on stability differ from the effects of species expressing different competitive intensities is unknown.

In natural and agricultural ecosystems, species diversity can also stabilize productivity by enhancing temporal niche complementarity between species (del Río et al., 2017; Isbell et al., 2009a; Raseduzzaman & Jensen, 2017). Complementarity provides insurance against poor performance of particular species when conditions vary (Lithourgidis et al., 2011; Tscharntke et al., 2012). In addition, temporal shifts in the intensity of interspecific competition and facilitation have the potential to affect the diversity–stability relationship (Douda et al., 2018; Isbell et al., 2009b; Lepš et al., 2018; Pennekamp et al., 2018). For instance, stronger competition between dominant and subordinate species in favorable times or stronger facilitative interactions in less favorable times (Douda et al., 2018) may determine diversity–stability relationships. Facilitative interactions can be strong in intercropped systems, with some crops enhancing the water-use efficiency (Franco et al., 2018) and nutrient acquisition (Li et al., 2007) of other crops and reducing the risk of crop failure (Rusinamhodzi et al., 2012). Competition can also be strong in intercropped systems, depending on the crop species combinations. Intercropping can reduce the nitrogen acquisition (Celette et al., 2009), nitrogen use efficiency (Neugschwandtner & Kaul, 2015), phosphorus acquisition, and phosphorus use efficiency (Gitari et al., 2018) of some crops through interspecific competition. Moreover, nutrient-induced shifts in interspecific interactions may affect ecosystem stability by mediating the synchrony in growth among species (Lepš et al., 2018; Liu et al., 2019). How such shifts in interactions might affect stability in the context of soil resources, such as water, nitrogen, phosphorus, and potassium, in diverse agroecosystems is unknown.

To explore the effects of interspecific complementarity, selection, competition, and facilitation on the temporal stability of productivity in diverse agroecosystems, we conducted a field experiment in which water, nitrogen, and phosphorus were manipulated experimentally. Our intent was to achieve a broad range of stability outcomes and gradients of net diversity effects, net competition, and facilitation in maize/pea and maize/rapeseed intercropping. We then correlated the strength of stability with these interaction gradients and other emergent factors from the experiments. We hypothesized that (1) the temporal stability of productivity was dependent on crop combinations, which mediate the intensity of interspecific interactions, and (2) the temporal stability of productivity would increase with increases in interspecific complementarity and with decreases in the intensity of interspecific competition for resources.

METHODS

Site description

We conducted a field experiment at the experimental station of the Institute of Soils, Fertilizers and Water-Saving Agriculture, Gansu Academy of Agricultural Sciences, at Baiyun in northwest China (38°37′ N, 102°40′ E; 1504 m above sea level). The soil is sandy loam—57% sand, 39% silt, and 4% clay. The physicochemical properties of the topsoil at depths of 0–20 cm and before the start of the experiment in 2014 are presented in Table 1. The soil type in this region is Orthic Antrosol (FAO/UNESCO, 1988). Most precipitation falls between May and September, and the total precipitation and potential evaporation are 124 and 2021 mm, respectively. The growing season is March through October. Average annual air temperature is 7.7°C. The frost-free period is 170–180 days, and total solar radiation is 5988 MJ m^{-2} $year^{-1}$. Agriculture in the area is dependent on irrigation. The experiment ran for 3 years, from 2015 to 2017.

Experimental design

The experiment was organized as a split-plot design with two factors and three replicates. Resource supply per different agricultural practices, Control 1 (no phosphorus fertilizer), Control 2 (no nitrogen fertilizer), conventional, and reduced resources, composed the main plots, and cropping systems, monocultures versus intercropping, were subplots to create the variation in stability required for an exploration of potential mechanisms. Resource supply for each main plot and cropping systems for each subplot are shown in Table 2. Fifteen subplots were watered and fertilized following conventional practices (Table 2) and 15 were watered and fertilized at "reduced" levels referenced and determined in other experiments to maximize yield per amount of water (Mao et al., 2012), nitrogen (Li et al., 2007), and phosphorus (Xia et al., 2013) used. The conventional treatment used levels of water, nitrogen, and phosphorus applied based on interviews with local farmers (Table 2). Additionally, two other main plots were established using resource supply, which was the same as the "reduced" level, but without phosphorus fertilizer (Control 1, 15 subplots) and without nitrogen fertilizer (Control 2, 15 subplots) applications (Table 2). There was a total of 60 subplots, including 12 subplots for maize/pea intercrops, 12 for maize/rapeseed intercrops, and 36 for monocultures of maize, pea, and rapeseed (see Appendix S1: Figure S1 for the field layout). Subplots were 5.5 × 4.2 m for all intercrop and monocultures of pea and rapeseed and 5.5 × 4.8 m for monocultures of maize due to the need to calibrate spacing with the intercropped subplots (12 rows, 40 cm between rows). This experiment compared monoculture stands of maize (*Zea mays* L. cv. Xianyu No. 335, $n = 12$ for each species) and pea (*Pisum sativum* L. cv. Longwan No. 2, $n = 12$ for each species), as well as monoculture stands of rapeseed (*Brassica campestris* L. cv. Gannan No. 4, $n = 12$ for each species) to intercropped stands of both species planted together (intercrops of maize and pea, $n = 12$; intercrops of maize and rapeseed, $n = 12$).

TABLE 1 Physicochemical properties of topsoil at depth of 0–20 cm before start of experiment.

Physicochemical property	Unit	Amount
Bulk density	g cm^{-3}	1.6
Soil organic matter	g kg^{-1}	14.8
Total N	g kg^{-1}	1.4
Olsen P	mg kg^{-1}	51.7
Available K	mg kg^{-1}	160.2
pH	1:2.5 soil:DI water	7.9

Maize, pea, and rapeseed were continuously and separately monocropped in plots over the duration of the experiment. For each maize/pea intercropping treatment plot, there were three intercropping combinations, and each intercropping combination included a 0.6-m pea strip (three rows of peas, with a 0.2-m interrow distance and 0.1-m interplant distance) and a 0.8-m maize strip (two rows of maize with a 0.4-m interrow distance and 0.24-m interplant distance). These two different crop strips within each individual intercropping combination

TABLE 2 Experimental factor settings.

Main plot	Subplot	Irrigation (mm)	Nitrogen (kg ha^{-1})	Phosphorus (kg ha^{-1})	Rhizobium inoculation
Control 1	Maize	600	300	0	No
	Pea	330	120	0	No
	Rapeseed	420	180	0	No
	Maize/Pea	600	300	0	No
	Maize/Rapeseed	780	300	0	No
Control 2	Maize	600	0	100	No
	Pea	330	0	100	No
	Rapeseed	420	0	100	No
	Maize/Pea	600	0	100	No
	Maize/Rapeseed	780	0	100	No
Conventional	Maize	750	400	150	No
	Pea	390	150	150	No
	Rapeseed	510	225	150	No
	Maize/Pea	750	400	150	No
	Maize/Rapeseed	990	400	150	No
Reduced	Maize	600	300	100	No
	Pea	330	120	100	Yes
	Rapeseed	420	180	100	No
	Maize/Pea	600	300	100	Yes
	Maize/Rapeseed	780	300	100	No

Note: Species with "/" are intercrops, and Controls 1 and 2 represent the treatments without phosphorus and nitrogen fertilizers, respectively. Winter irrigation was in the middle of November in each year. Conventional refers to resource inputs for water, nitrogen, and phosphorus as determined by local farmers. Reduced refers to the optimized resource inputs.

were rotated in planting position in each consecutive year. For each maize/rapeseed intercropping treatment plot, one intercropping combination included a 0.4-m rapeseed strip (four rows of rapeseed, with a 0.1-m interrow distance), and the two crop strips in each individual combination were rotated in the same way as maize/pea intercropping.

The same standards of interplant distance and interrow distance were used between intercropping and monoculture subplots, which made the planting density and corresponding aboveground biomass and grain yield in monoculture identical to intercropping in a comparable area. The total amount of nitrogen fertilizer (urea) was evenly divided into three equal portions and broadcasted by hand; the first portion as basal fertilizer was applied before sowing, the second portion was applied as topdressing at jointing stages (V6), and the third portion was only applied in the maize strips as topdressing before maize tasseling (V12) when the pea and rapeseed had been harvested. Triple superphosphate was applied as basal fertilizer. Pea and rapeseed were sown in late March and harvested in early July, and maize was sown in late April and harvested in early October. All sowing and harvesting processes were conducted by hand to avoid mechanical damage.

Productivity

Biomass and grain were collected manually. The entire central strip of maize (5.5 × 0.8 m), pea (5.5 × 0.6 m), and rapeseed (5.5 × 0.4 m) in intercropping plots, and an area of the same size in the middle of corresponding monocropped plots was sampled. Biomass and grain were air dried at room temperature for 30 days and converted to kilograms per hectare (kg ha^{-1}).

Resource capture

Water consumption

We evaluated the water consumption by evapotranspiration (ET) for each treatment in 0–120 cm soil depth. Water consumption was determined with the following equation (Hu et al., 2015):

$$\mathrm{ET} = P + I + \mathrm{WS}_S - \mathrm{WS}_h, \tag{1}$$

where P is the precipitation (mm) during the growing season (National Meteorological Information Center), I is the irrigation quota (mm), and WS_S and WS_h are the soil water storage (mm) at soil depths of 0–120 cm at sowing and harvest, respectively. Water storage was calculated from water moisture using measured soil bulk densities for each 0- to 20-cm soil layer for a total depth of 0–120 cm.

Nutrient acquisition

We randomly sampled 10 individual maize plants, 20 pea plants, and 20 rapeseed plants that neighbored the central biomass sampling strip. After harvesting, these plants were dried in an oven at 65°C for 72 h, and subsamples were separated into vegetative biomass and grain, then digested with H_2SO_4 and H_2O_2. Nitrogen, phosphorus, and potassium concentrations were measured using the micro-Kjeldahl procedure, the vanadomolybdate method, and flame photometry, respectively (Li et al., 2001a). Nitrogen, phosphorus, and potassium acquisition above ground was calculated as the product between aboveground vegetative biomass and corresponding nutrient concentrations of vegetative biomass, as well as grain yields and nutrient concentrations of grain. Total nutrient acquisition was the sum of nutrient acquisition in vegetative biomass and grain yield. Nutrient acquisition of intercropped systems was the sum of total nutrient acquisition for the two intercropped crops based on their own strip area in intercropping plot. Nutrient acquisition in the monoculture system was the sum of nutrient acquisition for the two monocropped crops in their own monocropped plot weighted by the proportion of area occupied by each corresponding crop in an intercropping plot; for example, for maize versus pea this was 6/8, and for maize versus rapeseed this was 4/8.

Temporal stability

We used the coefficient of variation (CV%) as an index of year-to-year variation in order to evaluate the temporal stability of aboveground biomass and grain yield by 1/CV% from 2015 to 2017, with a higher value indicating lower variability and, thus, higher stability, which is expressed as follows (Tilman et al., 1996):

$$\text{Temporal stability} = 1/\mathrm{CV}\% = \frac{\mu}{\sigma} \times 100, \tag{2}$$

where σ is the SD for aboveground biomass and grain yield, and μ is the mean values for aboveground biomass and grain yield across 3 years.

Competition and facilitation

We used the relative interaction index (RII) (Armas et al., 2004) as a metric to estimate the intensity of competition and facilitation between the intercropped species and to determine competitively dominant and subordinate species to categorize species in SEM, which may be different from productive and less productive species. RII is defined as

$$\mathrm{RII} = \frac{Y_I - Y_M}{Y_I + Y_M}, \tag{3}$$

where Y_I is the aboveground biomass or grain yield of an individual growing with another crop, and Y_M is the aboveground biomass or grain yield of monocropped crop of the same species. RII has defined limits from -1 to 1, with negative ratios indicating competition and positive numbers indicating facilitation. RIIs were also used to identify competitively dominant (less negative RIIs, indicating greater tolerance of competitors or benefiting more from facilitation) and competitively subordinate (more negative RIIs, indicating less tolerance of competitors) species in intercrops. However, it is important to note that a species that is more stable in a polyculture could also occur when the average strength of interspecific competition is weaker than the average strength of intraspecific competition (Turnbull et al., 2013).

Biodiversity effects

We measured the complementarity effect (CE) and selection effect (SE) following Loreau and Hector (2001):

$$\begin{aligned}\Delta Y = Y_O - Y_E &= \sum_i \mathrm{RY}_{O,i} M_i - \sum_i \mathrm{RY}_{E,i} M_i = \sum_i \Delta \mathrm{RY}_i M_i \\ &= N\overline{\Delta \mathrm{RY}}\,\overline{M} + N\mathrm{cov}(\Delta \mathrm{RY}, M).\end{aligned} \tag{4}$$

In this equation, M_i is the yield of species i in monoculture; $Y_{O,i}$ is the observed yield of species i in intercropping; $Y_O = \sum_i Y_{O,i}$ is the total observed yield of intercropping; $\mathrm{RY}_{E,i}$ is the expected relative yield of species i in intercropping, which is its proportion seeded or planted; $\mathrm{RY}_{O,i} = Y_{O,i}\ \mathrm{IM}_i$ is the observed relative yield of species i in intercropping; $Y_{E,i} = \mathrm{RY}_{E,i} M_i$ is the expected yield of species i in intercropping; $Y_E = \sum_i Y_{E,i}$ = total expected yield of intercropping; $\Delta Y = Y_O - Y_E$ is the deviation from total expected yield in intercropping; $\Delta \mathrm{RY}_i = \mathrm{RY}_{O,i} - \mathrm{RY}_{E,i}$ is the deviation from the expected relative yield of species i in intercropping; and N is the number of species in intercropping. Here, $N\overline{\Delta \mathrm{RY}}\,\overline{M}$ measures the CE, and $N\,\mathrm{cov}(\Delta \mathrm{RY}, M)$ measures the SE. A positive CE occurs when there is resource partitioning or facilitation between intercropped species. A positive SE occurs when species with higher-than-average monoculture yields dominate the intercrops.

Statistical analysis

To examine the effects of interspecific interactions on temporal stability (biomass and grain yield, μ/σ), we used linear mixed-effects models (LMMs) in R version 3.5.0 (R Foundation for Statistical Computing, Vienna, Austria, 2013), in the lmerTest R package (Kuznetsova et al., 2017). All repeated block and resource (water, nitrogen, and phosphorus) inputs were random factors in models that tested the effects of cropping system (intercropping vs. monoculture) and species combinations (maize/pea intercropping vs. maize/rapeseed intercropping) on the temporal stability of aboveground biomass and grain yield. When the main effects were significant, least significant difference (LSD) post hoc tests were used for pairwise comparisons. Student's *t*-test was performed to determine differences between maize/pea intercropping and maize/rapeseed intercropping systems for RII. We conducted linear regressions and nonlinear regressions to explore the relationships of temporal stability with RII and the stability of competitively dominant (pea and rapeseed) species, as well as competitively subordinate species (maize) with the R package basicTrendline (Mei & Yu, 2020) based on regression models with $p \leq 0.05$.

SEM was conducted using the lavaan package (Rosseel, 2012) in R to explore how the shifts of specific interactions affected stability via mediating resource acquisition. Thus, we separated the stability of the total intercropping system into two parts: the stability of competitively dominant species (pea and rapeseed, positive RIIs) and the stability of competitively subordinate species (maize, negative RIIs) in the structural equation models. First, we used SEM to explore the effects of CE and SE (Appendix S1: Figure S3a) and RII (Appendix S1: Figure S3c) for competitively dominant and competitively subordinate species on the final stability of grain yield; then we sequentially selected the corresponding final stable models (Appendix S1: Figures S3b,d, respectively) (Ma et al., 2017). Second, based on the results from the SEM for RII, we structured a full model that considered resource acquisition (water, nitrogen, phosphorus, and potassium) in subsequent SEMs as responders to competitive effects or facilitative effects measured by the RIIs (Figure 4). This examined the underpinning mechanisms of the final temporal stability of productivity more deeply. All models were evaluated by χ^2 tests ($p > 0.05$), Akaike information criterion (AIC), and root mean square error of approximation (RMSEA) (Ma et al., 2017). All significant differences among treatments were determined at $p \leq 0.05$, and standard errors of mean were calculated from the standard deviation of the data set from all replicates. All plots were mapped using the ggplot2 package (Wickham, 2009) in R.

RESULTS

Temporal stability of productivity in intercropping

Intercropping did not increase the temporal stability of biomass or grain yield production in comparison to monocultures (Figure 1d,e,j,k); however, our treatments created a wide range of temporal stability with which we could explore potential causal mechanisms. In fact, monocultures of maize and rapeseed were more stable, based on aboveground biomass ($p = 0.026$) and grain yield ($p < 0.001$), than intercropped maize and rapeseed (Figure 1e,k). Maize/pea intercrops were, as a system, more stable, in terms of grain yield, than maize/rapeseed intercrops ($p = 0.018$; Figure 1l). The stability of the aboveground biomass ($p = 0.025$; Figure 1c) and grain yield ($p = 0.021$; Figure 1i) of maize was lower when intercropped with rapeseed than in monocultures, and the stability of the biomass and grain yield of maize intercropped with rapeseed was also lower than the stability of the biomass and grain yield of maize intercropped with pea (Figure 1c,i). The stability of the aboveground biomass and grain yield of pea did not differ between intercropping and monocultures (Figure 1a,g); whereas the stability of the grain yield of rapeseed was higher in monocultures than in intercrops ($p = 0.002$; Figure 1h).

Temporal stability, dominance, and interspecific interactions

The RII calculated with grain yield or biomass showed pea and rapeseed to be the competitively dominant species with positive RIIs when intercropped with maize (Figure 2b,d). The intercropped maize was determined as

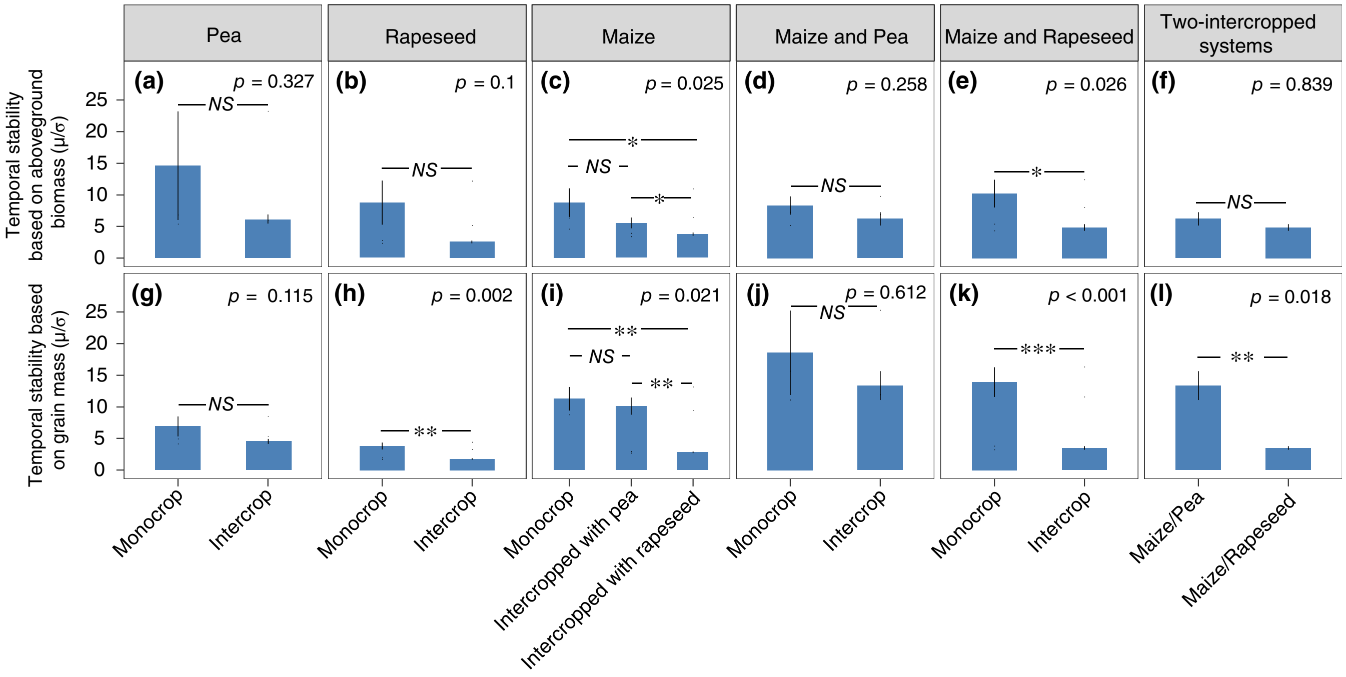

FIGURE 1 Bar plots of (a–f) temporal stability of productivity based on aboveground biomass (TSB) and (g–l) temporal stability of grain yield (TSG) for different crops, cropping systems, and cropping combinations. Here, panels (a–c) and (g–i) represent TSB and TSG sorted by crops of maize, pea, and rapeseed, respectively; panels (d, e) and (j, k) represent TSB and TSG, respectively, sorted by cropping systems (monocropping and intercropping), in which the "monocrop" is the mean temporal stability of the two corresponding monocropped crops; panels (f, l) represent TSB and TSG sorted by two intercropping systems or crop combinations (maize/pea intercropping and maize/rapeseed intercropping), respectively. "*", "**", and "***" above the bars indicate significant differences among different treatments at $p \leq 0.05$, $p \leq 0.01$, and $p \leq 0.001$ by least significant difference. Bar values are mean ± standard errors of mean.

competitively subordinate species with negative RIIs (Figure 2a,c). Intercropped pea had lower competitive effects on intercropped maize (increased values for RIIs calculated with maize grain yield), by an average of 66%, than rapeseed ($p = 0.014$; Figure 2c). The RIIs for the competitive effect of intercropped pea on intercropped maize, calculated with maize biomass, was marginally lower than that of rapeseed ($p = 0.085$; Figure 2a). Additionally, the CEs calculated with grain yield and aboveground biomass for pea/maize intercropping were significantly ($p = 0.017$) and marginally ($p = 0.093$) greater than those of rapeseed/maize intercropping, respectively (Appendix S1: Figure S2).

In addition to observing a wide range of temporal stability in total system aboveground biomass and grain yield, we found that species combinations produced gradients of complementarity and facilitation and competition. For instance, overyielding produced by intercropping was promoted by complementarity in six of eight experiments (Figure 3a). The CE ranged from −1.7 to 4.2 for total aboveground biomass (*x*-axis in Figure 3a) and −1.5 to 2.4 for grain yield (*x*-axis in Figure 3g). The SE were also common in our experiments, ranging from −4.5 to −1.2 for total aboveground biomass (*x*-axis in Figure 3b) and −2.6 to −0.8 for grain yield (*x*-axis in Figure 3h).

Complementarity was highly and positively correlated with temporal stability in total aboveground biomass ($R^2 = 0.69$; $p = 0.011$; Figure 3a) and grain yield ($R^2 = 0.73$, $p = 0.007$; Figure 3g). The SE was not correlated with stability for either measurement (Figure 3b,h). In addition to observing a wide range in temporal stability in total system aboveground biomass and grain yield, we found that different species and treatment combinations produced gradients of facilitative and competitive interactions measured by RII. We found that the RII for the competitively subordinate species (maize) was highly and positively correlated with stability in total aboveground biomass ($R^2 = 0.79$, $p = 0.013$; Figure 3c) and grain yield ($R^2 = 0.83$, $p = 0.002$; Figure 3i). In other words, as competitive intensity increased (more negative RIIs), temporal stability decreased. We found no relationship between the measure of stability and RII for competitively dominant species (pea and rapeseed), with either aboveground biomass (Figure 3d) or grain yield (Figure 3j).

The stability of both total biomass ($R^2 = 0.86$, $p = 0.001$) and grain yield ($R^2 = 0.99$, $p < 0.001$) of the

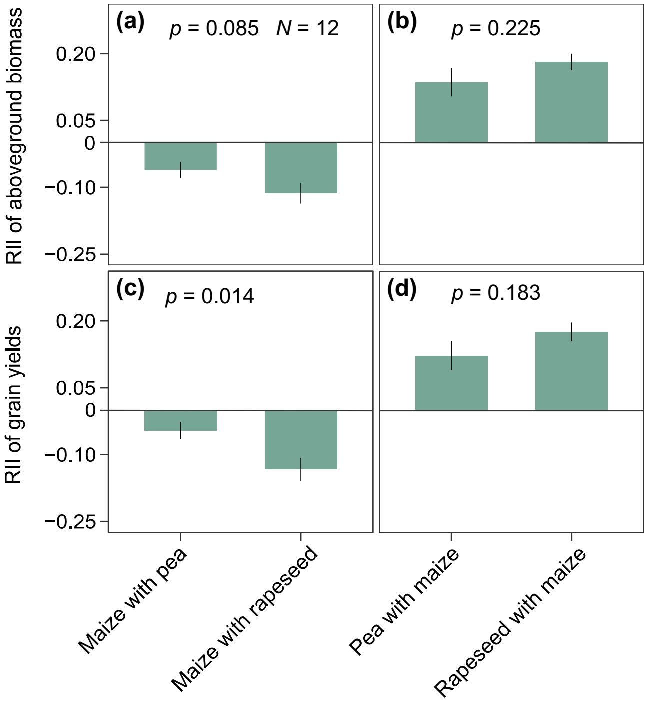

FIGURE 2 Mean relative interaction index (RII) based on (a, b) aboveground biomass and (c, d) grain yield for maize (a, c) and pea and rapeseed (b, d) in two intercropping systems. The p-value indicates the significant difference between two bars within a plot. Bar values are mean ± standard errors of mean.

competitively subordinate species of maize was highly correlated with whole-system stability for both metrics (Figure 3e,k). In contrast, the stability of the competitively dominant species, pea or rapeseed, was unrelated to the whole-system stability (Figure 3f,l).

Structural equation models

First, structural equation models indicated a path in which variation in the CE corresponded with the stability in biomass production of the competitively subordinate species (maize) (Appendix S1: Figures S3a,b). In other words, as the CE of intercropping increased, the temporal stability of the competitively subordinate species increased (standard path coefficient [SPC] = 0.43*, $R^2 = 0.2$). This stability then led to greater whole-system stability in biomass production (SPC = 0.9***, $R^2 = 0.8$), which in turn led to more stability in system grain yield production (SPC = 0.47*, $R^2 = 0.2$) (Appendix S1: Figure S3a,b). Similar mechanisms for biodiversity effects in the structural equation models also originated from the RII of competitively dominant and competitively subordinate species on final grain yield stability by SEM (see Appendix S1: Figure S3c,d).

Structural equation models further illustrated relationships between our two metrics of temporal stability and resource acquisition mediated by species interactions (Figure 4). As the competitive effects of the competitively dominant species (pea and rapeseed) on the competitively subordinate species (maize) for soil nitrogen decreased, but not that of soil water and soil phosphorus, this led to increased nitrogen acquisition for the system as a whole (SPC = 0.75***, $R^2 = 0.78$). But this also increased stability in productivity for competitively subordinate species (SPC = 0.57*, $R^2 = 0.29$). This stability then led to greater whole-system stability in biomass production (SPC = 0.91***, $R^2 = 0.91$; Figure 4).

DISCUSSION

Temporal stability of productivity depends on species combinations

As predicted by our first hypothesis, temporal stability was affected by particular species combinations. Grain yield in maize/pea intercrops, as a system, was more stable than that of maize/rapeseed intercrops. Specifically, the stability of maize intercropped with pea did not differ from that of monocropped maize, but the monocropped maize and monocropped rapeseed were more stable than the intercropped ones, all of which implied that the advantage of yield stability for intercropping over monoculture depend on crop combinations. This is consistent with a recent meta-analysis showing that legume and cereal grain combinations (e.g., faba bean/maize intercropping) improved yield stability more than intercrops of nonlegume and cereal grain combinations (e.g., rapeseed/maize intercropping) (Raseduzzaman & Jensen, 2017). In natural ecosystems, differences in plant species composition may have a large impact on ecosystem processes and in some cases can explain more variation in community production than diversity per se (Hooper & Vitousek, 1997; Jaillard et al., 2021; Lehman & Tilman, 2000; Loreau & Hector, 2001). For example, changes in plant species composition in response to climate may stabilize primary production in high-elevation ecosystems (Liu et al., 2018), and species composition contributed to the greater variance in temporal stability than diversity in temperate grasslands (Tilman et al., 1997).

An early review of previous studies indicated that greater improvements in the stability of intercrops can be realized via an interspecific compensation effect by maximizing the differences in functional traits between the two-crop combinations (Rao & Willey, 1980). Interestingly, in legume-based intercropping systems, competitive intensities might be reduced by the nitrogen supplied by the legumes

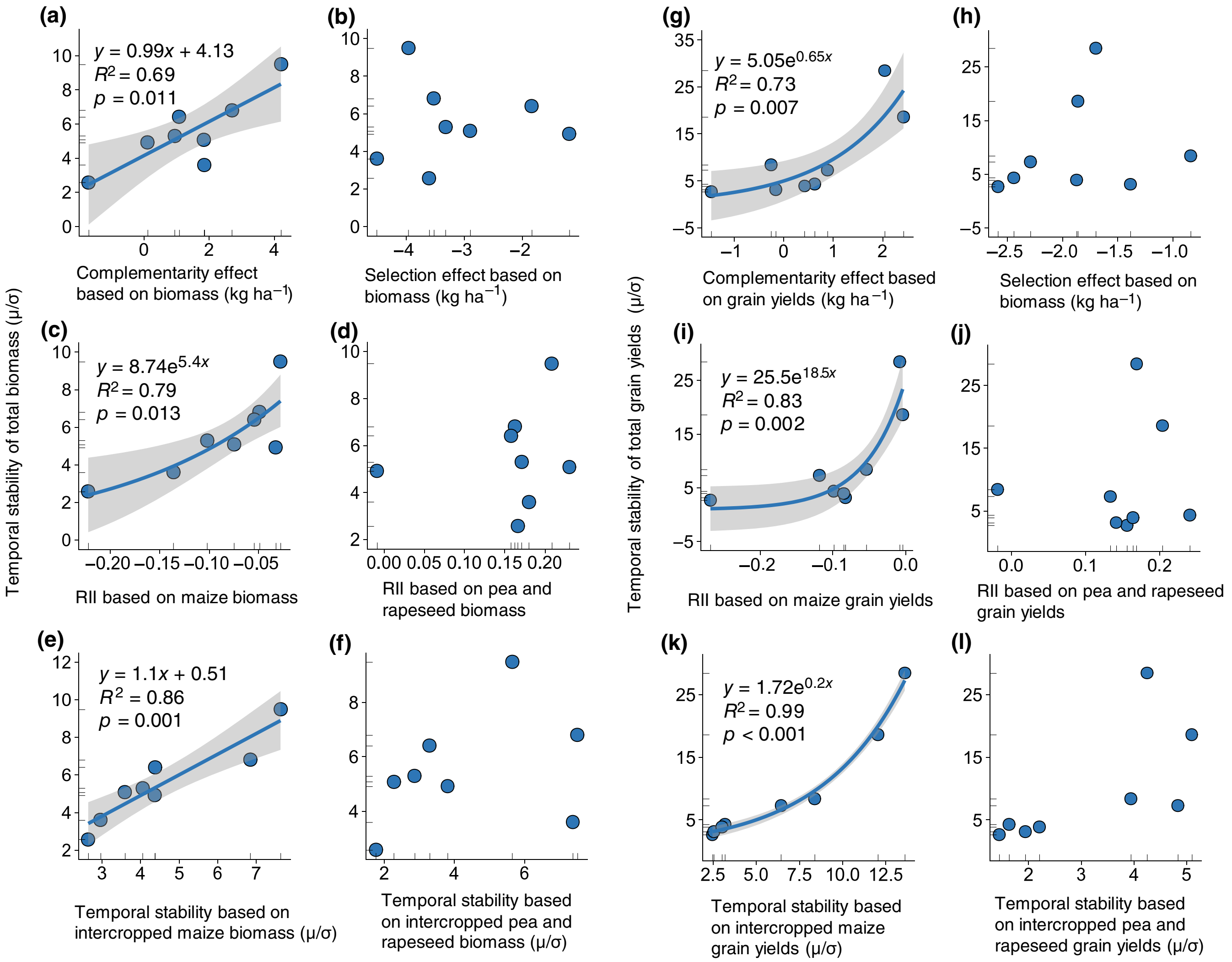

FIGURE 3 Relationships between the temporal stability of (a–f) aboveground biomass (TSB), (g–i) grain yield (TSG), and (a, g) the complementarity effect (CE), (b, h) selection effect (SE), (c, i) relative interaction index (RII) for maize, and (d, j) pea and rapeseed. Also presented is the temporal stability of maize (e, k) and (f, l) pea and rapeseed (RII), respectively. All points in plots are the average of three replicates. The lines fit the model equations and refer to a significant regression analysis, and shaded areas show 95% confidence intervals.

(Andersen et al., 2005). If so, perhaps the overall competitive effect from pea on maize in intercropping in our study was weaker when the underlying and simultaneous facilitative effects of N fixation by legumes on maize were high (Hu et al., 2016; Li et al., 2016). This would not be the case in rapeseed/maize intercropping.

Stability in different intercropping combinations relies on the most productive partner

In our experiment, the stability of biomass and grain yield of the productive maize was highly correlated with whole-system stability, but not the stability of the less productive pea and rapeseed in the intercropping systems. More specifically, maize is a productive species and generally produced more biomass and grain than pea or rapeseed. Thus, maize made a higher contribution to the total variation in productivity in whole intercropping systems. These results are consistent with the mass ratio hypothesis (Grime, 1998), which states that the extent to which a certain plant species affects ecosystem functions can be due to its contribution to the total community biomass. These results are also consistent with previous work showing that community biomass stability is largely determined by the temporal stability of the most productive species in grasslands (Ma et al., 2017; Sasaki & Lauenroth, 2011). In particular, increased community stability can be due to increases in community evenness as dominant species decrease in biomass (Zelikova et al., 2014) or as increased production by productive

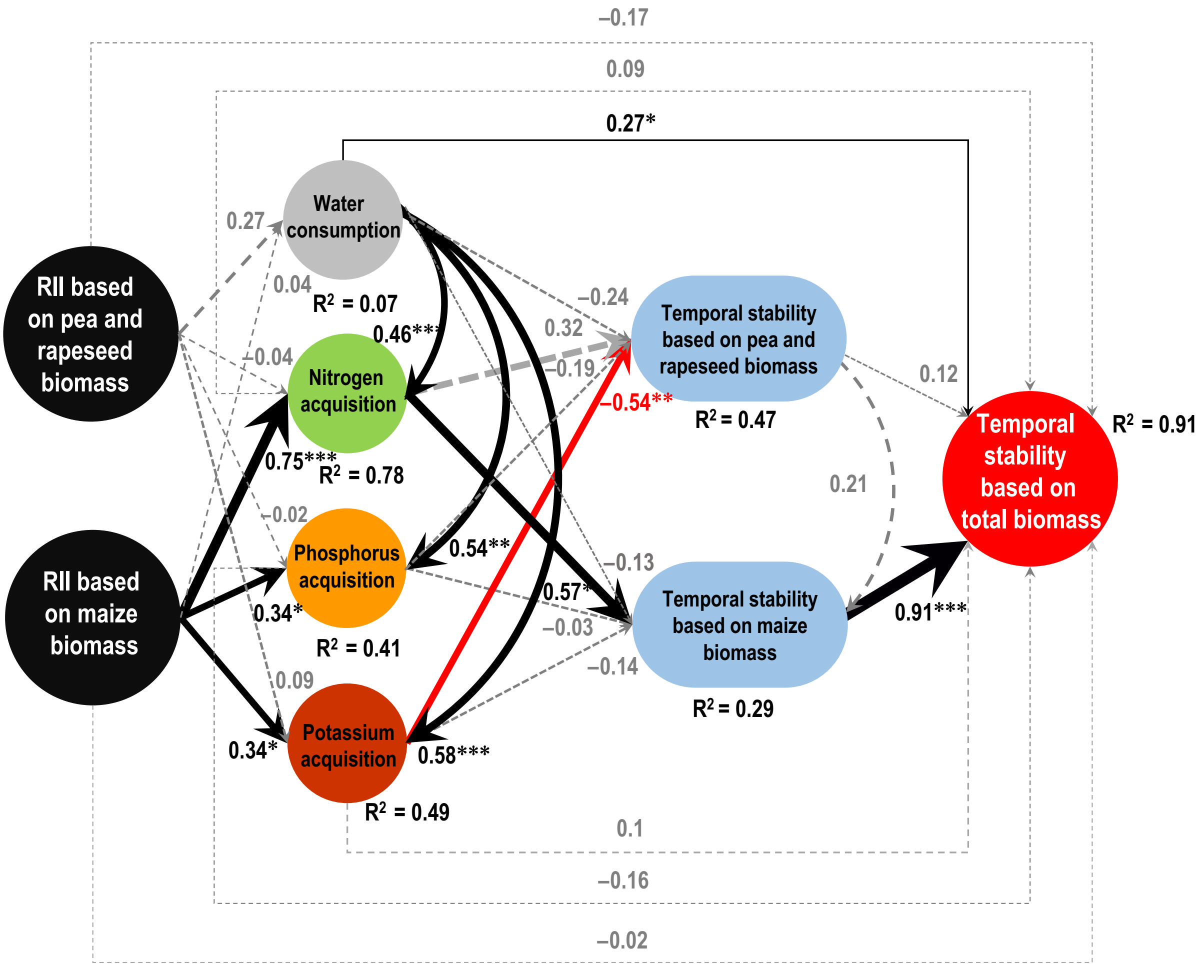

FIGURE 4 Structural equation modeling (SEM) originating from the effects of relative interaction index (RII) for the less productive pea and rapeseed and productive maize on the temporal stability of aboveground biomass of intercropping systems with all plausible pathways. The RII of less competitively dominant species (pea and rapeseed) based on aboveground biomass was associated with increased nitrogen acquisition at the whole intercropping system level. This indirectly enhanced the temporal stability of competitively subordinate species (maize) based on aboveground biomass and then finally promoted the temporal stability of the intercropping system. Black and red arrows represent significant positive and negative pathways, respectively, and gray dashed arrows indicate nonsignificant pathways. Bold numbers near each arrow indicate the standard path coefficients (SPCs). The arrow widths are proportional to the strength of the relationship. R^2 represents the proportion of variance explained for each dependent variable in the model. $*p \leq 0.05$; $**p \leq 0.01$; $***p \leq 0.001$. Statistical information for this model was as follows: $\chi^2 = 14$; df = 8; $p = 0.07$; root mean square error of approximation = 0.2; goodness-of-fit index = 0.9; Akaike information criteria = 88.

species offsets the negative effects of species loss (Smith & Knapp, 2003). Models also suggest that lower community stability can occur through the selection of species that are more productive but that have lower tolerance to perturbations (Wang et al., 2021).

The stability of productive species is mediated by interspecific interactions for soil resources and complementarity

Our results showed that stability was highly and positively correlated with complementarity, supporting our second hypothesis. In other studies, temporal stability in productivity was also strongly related to complementarity (Bai et al., 2004; Isbell et al., 2009a). Furthermore, we found no relationship between SE and the stability of either aboveground biomass or grain yields. Generally, positive complementarity indicates species interactions that result in niche partitioning or facilitation (Isbell et al., 2009a), and negative selection effects indicate that the least productive species in monoculture benefit the most from species interactions in mixture (Isbell et al., 2009b). In our case, the production for the less productive species of intercropped pea and rapeseed increased compared to monocultures, and this corresponded to interspecific facilitation, especially in pea/maize intercropping. This in turn favored the stability of the entire system (Isbell et al., 2009a). Other species, perhaps with higher complementarity among them, might produce different levels of stability than the species we used. Moreover, the production of maize significantly decreased in intercrops compared to monocultures, whereas the production of pea and rapeseed increased, which made the selection effect negative, and this weakened its effects on stability. In addition, resource complementarity minimizes niche overlap and competition between crop species (Lithourgidis et al., 2011).

As indicated by RIIs and structural equation models, the productive species, maize, was outcompeted by intercropped pea and rapeseed, and the suppression from intercropped rapeseed on maize was greater than that from intercropped pea. In natural systems, productive species may become competitively subordinate when abiotic conditions change, or the biomass dominance of species may not always reflect the strength of their competitive effects and responses (Besaw et al., 2011; Cahill & Casper, 2000; Weigelt et al., 2002). In our case, interspecific competition for resources in intercropping often occurs early in the growth of crops, during which maize appears to be outcompeted by pea and rapeseed. After pea or rapeseed harvesting, the suppressed growth of maize recovers to some extent, and it eventually shows greater biomass than pea or rapeseed (Li et al., 2001b). This is not conducive to the stability of maize intercropped with pea or rapeseed and puts the stability of intercropping at a disadvantage, relative to monocultures. Other studies also found competitive outcomes similar to those we measured in cereal/legume intercrops, including oat/pea intercropping (Neugschwandtner & Kaul, 2015) and wheat/faba bean intercropping (Xiao et al., 2018). In addition, Li et al. (1999) found that the leguminous faba bean was competitively dominant in maize/faba bean intercrops. In summary, our study led us to conclude that complementarity increased the temporal stability of productivity through reduced interspecific competition for resources.

One of the most interesting aspects of our regression and SEM analyses was a strong increase in the temporal stability of total grain and biomass with the decreasing competitive effects (negative RIIs) of competitively dominant species on competitively subordinate species. This is consistent with the results obtained by Douda et al. (2018), who found that the temporal stability of wetland species increased as the competitive effect of subordinate species decreased in high-stress conditions. In this context, facilitation can buffer competitive effects (Callaway & Pennings, 2000). If in the conditions that promoted weak competition peas increased their facilitative effects, perhaps these underlying facilitative effects promoted or maintained the stability of maize.

As noted, the temporal stability of whole-system productivity depended on the stability of the productive species of maize and increased in response to the reduced intensity of interspecific competition from pea or rapeseed on maize, or with an increasing CE of the whole system. Furthermore, this competition appeared to be for soil nitrogen, as indicated by the structural equation models. These results support our second hypothesis—that the temporal stability of productivity will increase with increases in interspecific complementarity and with decreases in the intensity of interspecific competition for resources. Others have found that intrinsic yield stability is driven by diversity via complementarity in resource use (Stomph et al., 2020) and by nutrient-induced shifts in interspecific interactions that increase species synchrony (Lepš et al., 2018; Liu et al., 2019). However, to our knowledge, we provide the first evidence of increased complementarity and attenuated competition as a potential mechanism for stabilizing productivity in diverse agroecosystems, which might shed light on similar processes in natural ecosystems.

Our results improve the mechanistic understanding of how plant or crop species diversity stabilizes community biomass over time and point to processes that might function in both natural and agricultural ecosystems. Our findings also indicate that complex shifts in competitive intensities are likely to be key mechanisms that maintain temporal stability in species-diverse agriculture. Understanding these mechanisms may contribute to the sustainable intensification of global food production and security. Furthermore, choosing optimal intercropping combinations may improve the stability of food production by minimizing interspecific competition or maximizing interspecific facilitation.

AUTHOR CONTRIBUTIONS

Jinpu Wu, Xingguo Bao, and Long Li designed the research. Jinpu Wu, Xingguo Bao, Jiudong Zhang, and Binglin Lu performed research. Jinpu Wu, Long Li, and Ragan M. Callaway analyzed the data. Jinpu Wu, Ragan M. Callaway, Weiping Zhang, and Long Li wrote the paper.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code (Wu et al., 2022) are available in Zenodo at https://doi.org/10.5281/zenodo.6837527.

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