



Triple cropping and diverse landscape enhance biological pest control and productivity in vegetable fields

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Abstract

Insect herbivores cause substantial economic loss to agricultural crops and insecticides are the foremost strategy in their management. Increasing crop diversity is expected to improve biological control services and primary productivity. However, the benefits of mixing more than two annual crop species remain poorly understood. Using okra (*Abelmoschus esculentus*), calabash (*Lagenaria siceraria*), and sponge gourd (*Luffa acutangula*), we compared the effect of double and triple cropping to monocropping on insect herbivore and predator abundance and diversity and the number of marketable fruits as yield in nine fields over 2022 and 2023 in Pakistan. We found 21 insect species, including 9 species of herbivores and 12 species of predators. Herbivore abundance of almost all species was significantly lower while predator abundance of all species was significantly higher in triple cropping. Herbivore richness was significantly and positively correlated with increasing vegetable diversity while a non-significant relation was noted for herbivore diversity and dominance. Predator diversity, richness and dominance were significantly and positively correlated with increasing crop diversity. Increasing landscape diversity (Shannon diversity) significantly reduced pest abundance and increased the diversity of pests and predators as well as predator abundance. Predator abundance and diversity matrices played a significant role in herbivore suppression suggesting a strong top-down effect. Number of fruits was higher in triple cropping. Path analyses proved that herbivore abundance affected the yield indirectly through predator diversity. Our results suggest that local and landscape diversity and complementarity among crop species and predator species are simultaneously regulating biological control and primary productivity in vegetable diversity gradient.

Keywords Plant diversity · Landscape diversity · Ecosystem functioning · Herbivores suppression · Biocontrol · Agricultural productivity

Introduction

Many of the sustainable development goals including Zero Hunger, Life on Land and Climate Action (*United Nations Sustainable Development*) directly or indirectly depends

on biodiversity in and around agricultural land and food production systems (Griggs et al. 2013). Conventional intensive food production systems aim to maximize yield and promote the use of agrochemicals and monoculture practices to meet the needs (Snapp 2020; Maggi et al. 2019). Though these strategies globally reduce the yield gaps in agricultural crops, benefits of extensive monoculture farming and chemical inputs are ambiguous (Rasmussen et al. 2018) and their efficacy in improving yields is saturating over time (Gaba et al. 2016; Ray et al. 2012). Farm intensification coupled with environmental degradation and destruction of natural ecosystems has jeopardized biodiversity in agroecosystems over the past 70 years (Raven and Wagner 2021). Agricultural productivity is continuously declining due to intensification of synthetic input use and these deficits in productivity will linger a century after agricultural abandonment (Isbell et al. 2019).

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Box 1 Explanation of different hypotheses predicting insect populations in diverse plant neighborhoods

Resource concentration hypothesis: “States that herbivores are more likely to find and remain on hosts that are growing in dense or nearly pure stands; that the most specialized species frequently attain higher relative densities in simple environments; and that, as a result, biomass tends to become concentrated in a few species, causing a decrease in the diversity of herbivores in pure stands” (Root 1973).

Associational susceptibility hypothesis: “The influence of one plant on another increases the likelihood of detection by, and/or vulnerability of a focal plant to, herbivores (above and beyond its innate ability to avoid detection or damage owing to herbivory)” (Barbosa et al. 2009).

Natural enemy hypothesis: “A greater diversity of prey/host species and microhabitats is available within complex environments, such as most natural, compound communities. As a result, relatively stable populations of generalized predators and parasites can persist in these habitats because they can exploit the wide variety of herbivores which become available at different times or in different microhabitats” (Root 1973).

Maintaining biodiversity while ensuring food security is becoming a crucial challenge of today’s agriculture while considering the global environmental changes (Butchart et al. 2010). To this end, ecological intensification aiming at maintaining crop productivity while increasing the environmental sustainability by harnessing the ecosystem functions with biodiversity need to be refined and appraised globally (Bommarco et al. 2013; Shah and Razaq 2020).

Biological pest control is a major ecosystem function that can enhance the sustainability of agroecosystems without sacrificing the economic yield and reducing the ecological footprints of agrochemicals on environments (Geiger et al. 2010; Rusch et al. 2017). To enhance biological control, plant diversification is pivotal because it can attenuate the herbivore populations by (1) supporting higher predator communities (the natural enemy hypothesis), (2) associational effects of neighboring plants (the associational susceptibility hypothesis) and (3) dilution of high-quality resource with increased heterogeneity (the resource concentration hypothesis) (Box 1). Diverse plant communities support a higher diversity of natural enemies in general by multiplying ecological niches favoring diverse resources (Koricheva et al. 2000; Haddad et al. 2009; Hertzog et al. 2017), which can lead to enhanced pest suppression via top-down control (Wan et al. 2020). However, increase in predation rate is not the only mechanism potentially constraining herbivore performances, as bottom-up effects via plant quantity and quality can also control herbivore densities. Associational susceptibility hypothesis suggests that neighboring plants in diverse ecosystems influence the plant phenology, i.e., plant size and quality (Kostenko et al. 2016) and by doing

so these can negatively affect the populations of specialist herbivores (Tahvanainen and Root 1972). Plant diversity contributes to herbivore suppression because energy gains of herbivores may decline from low plant diversity to higher plant diversity due to dilution of high quality resource with increased heterogeneity (Wetzel et al. 2016). It highlights the importance of the resource concentration hypothesis which states that increasing plant diversity reduces specific host plant concentration, thereby limiting performance of specialist herbivores (Root 1973). While these hypotheses have been widely applied in agronomic crops (Farooq et al. 2022), forests (Schuldt et al. 2018) and grasslands (Craven et al. 2016), empirical studies in vegetable-based systems remain limited. However, recent work demonstrated the biocontrol potential of increasing plant diversity by installing floral margins (Peris-Felipo et al. 2025; Li et al. 2020b) or through companion planting (Wang et al. 2025) in vegetable systems. Consequently, it is likely that both top-down and bottom-up approaches operate simultaneously to reduce the impact of herbivores in diverse agroecosystems (Hatt and Döring 2025).

Biocontrol services can be steered by management of arable lands from individual field scale and their surroundings to landscape scale (Petit et al. 2020). Homogeneous landscapes, characterized by large cropland with reduced crop diversity, fragmented natural habitats and increasingly homogenous land use types (Sirami et al. 2019), enhances cropping habitat connectivity, culminating into elevated pest densities (Rand et al. 2014) and reduced biocontrol services by natural enemies (Perović et al. 2010). Complex and heterogeneous landscapes, characterized by lower proportion of cropland with increased crop diversity and edge density between crop and non-crop habitat and high percentage of semi-natural habitats, typically sustain the source populations of natural enemies and encourage their dispersal in crops (Zhang et al. 2020; Martin et al. 2019; Dainese et al. 2019). Complex landscapes can strengthen the biocontrol services by providing overwintering refuges, undisturbed area that offers shelter from crop disruption, additional nectar resources and alternative hosts/prey to natural enemies (Balzan et al. 2015; Bianchi et al. 2006). For instances, landscape complexity has been shown to positively influence the populations of predators like Opiliones (Arachnida) (Gardiner et al. 2010) and coccinellids (Coleoptera: Coccinellidae) (Gardiner et al. 2009). Owing to this, pest suppression in an individual field is not only triggered by local diversity (plant and insect communities) but may also be augmented by landscape complexity (but see Karp et al. 2018).

Diverse plant communities often increase the overall productivity of agroecosystems (Tilman et al. 2001; Grace et al. 2016; Liang et al. 2016; Huang et al. 2018). It might be due to complementarity (i.e., the effective resource use of different species within a community to enhance ecosystem

functioning) effects or facilitation through niche differentiation or selection effect through more even productive species under polyculture cropping systems (Loreau and Hector 2001). Most studies on diversity-productivity relationships utilize artificial setups where plant diversity is maintained by selecting particular species from species pool and depict similar results (Liu et al. 2015; Huang et al. 2018). However, results from natural assemblages are contradicting, where diversity-productivity relationships are negative (Zhang et al. 2015), neutral (Assaf et al. 2011) and positive (Flombaum and Sala 2008). Meanwhile, this diversity-driven productivity, specifically for vegetable agroecosystems, remains poorly understood.

Vegetables are important group of crops that have been used for consumption as well as for their medical uses. Vegetables are often concurrently damaged by a variety of insect pests and their effects can be shaped by landscape composition (Paredes et al. 2022). Although some studies demonstrated positive (Cai et al. 2010) and neutral (Singh et al. 2017) effects of crop diversity on insect pests of different vegetables; however, the overall effect of specific combination of vegetables remains inconclusive. Here, we aimed to investigate how vegetable crop diversity and landscape heterogeneity influence arthropod communities and crop productivity. Specifically, we: (1) hypothesized that increasing vegetable crop and landscape diversity would reduce herbivore abundance and diversity through resource dilution and enhance predator abundance and diversity via improved habitat complexity and resource availability (Beaumelle et al. 2021); (2) assessed the role of predator diversity matrices (richness, evenness, and functional diversity) in suppressing herbivore populations; (3) quantified the relationship between vegetable crop diversity and crop yield, expecting higher diversity to improve productivity through enhanced biological control and reduced herbivory (Farooq et al. 2022); and (4) explored the ecological pathways by which crop diversity mediates yield outcomes, particularly through niche partitioning and plant-mediated indirect interactions (McArt et al. 2013).

Material and methods

Study area

The study was carried out in 2022 and 2023 in the district Multan of the southern Punjab, Pakistan. The river Chenab and its tributary canals are important to irrigate the study area making this region fertile for the production of cereals (Hamza et al. 2023), fiber crops (Shahid et al. 2023)

and vegetables (Akhter et al. 2023). The region is famous for mango orchards followed by citrus leading to mixed landscapes characterized by the growing of vegetables and agronomic crops in the orchards. Plant protection chemicals are routinely used on these crops as the sole measure to control pests. Climatically this region is characterized as subtropical, having semi-arid environment with an average annual rainfall of 186 mm. Three seasons dominates the region: the winter season extends from November to February during which temperature ranges from 4.5 to 34.6 °C, a very hot summer (April to June), and a wet season with precipitation (July–September) (Saeed et al. 2015).

We selected nine fields (with an area of 4046 m² for each) of vegetables at three locations (i.e., three fields per location; Location 1: 30°22'40.4"N 71°36'02.8"E, Location 2: 30°22'03.1"N 71°29'29.2"E, Location 3: 30°08'24.9"N 71°27'35.6"E; minimum distance between locations being 15 km, Fig. 1). Each field in each location has a different crop diversity (richness) level, i.e., the experimental treatments: monocropping (monoculture), double cropping (two crop combination), and triple cropping (three crop combination). Hence, each diversity treatment was replicated three times each year. We selected fields of okra *Abelmoschus esculentus* (L.) Moench (Malvaceae), calabash *Lagenaria siceraria* (Molina) Standley (Cucurbitaceae) and sponge gourd *Luffa acutangula* (L.) (Cucurbitaceae) sown in the last week of March in both the years. Incorporating okra, calabash, and sponge gourd into cropping systems not only adds structural diversity but also enhances chemical defenses i.e., phenols (Amirabbasi et al. 2020), cucurbitacins (Saeed et al. 2022), saponins (Eka et al. 2023), enriches resource diversity through varied flowering times and nutritional content, and creates complex habitat structures. All the fields were managed individually by the growers. As the benefits of crop richness, more than crop identity, was studied, crop identity was not necessarily similar among the three locations for the monocropping and double cropping fields, while triple cropping fields included all three crop species in all locations (Table S1). Farmers grow monocrops and double cropping as a matter of routine for economic purposes, and grew triple cropping upon our request for the experiment. To maintain consistent total crop density across treatments, we employed a substitutive design (i.e., double and triple cropping were formed by replacing a given number of plants of one species by the same number of the other species). Standard agronomic practices were adopted according to the local recommendations by the Punjab Government. No study field was exposed to any kind of agrochemicals during the course of data collection.

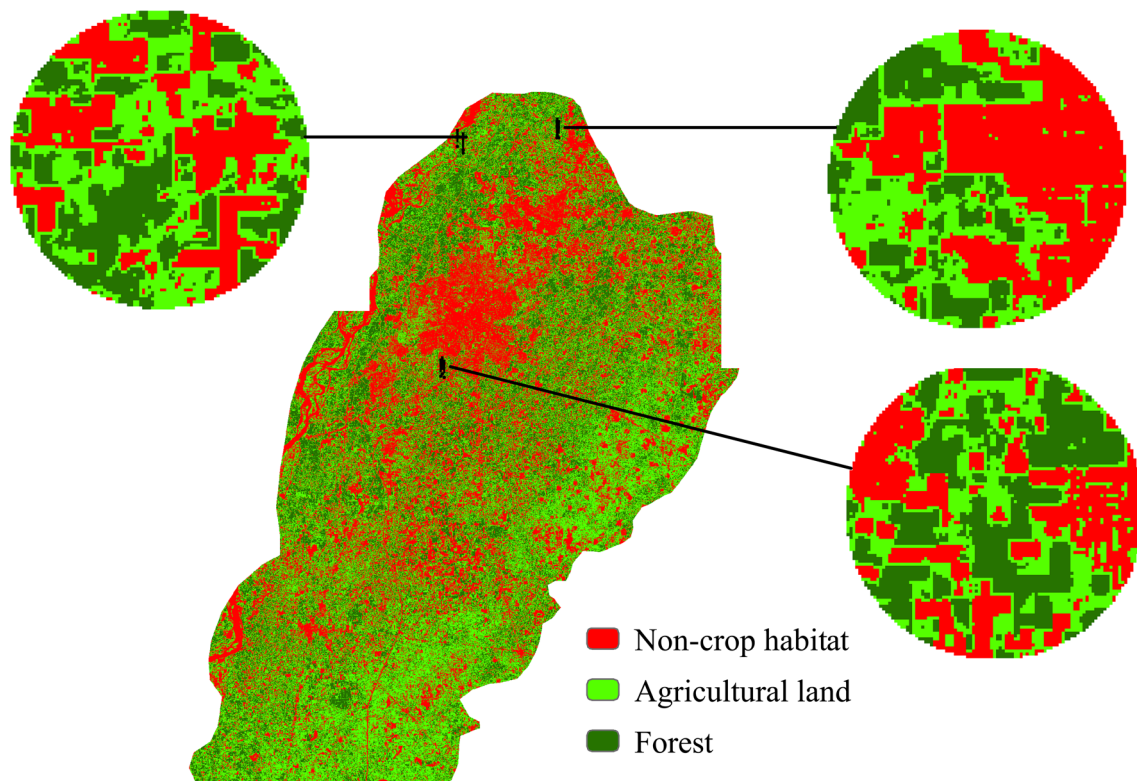


Fig. 1 Locations of the nine fields (black dots) sampled in Multan region during both 2022 and 2023. Inset map shows example of 500 m buffer around the sampling locations with corresponding land cover classes based on NDVI values

Landscape diversity

The selected locations were widely distant from one another, which led us to assume that landscape diversity might have an effect on arthropods. To address the effect of landscape diversity on the arthropod abundance and community composition, all the landscapes were quantified by considering all the land cover classes surrounding each field using Sentinel-2 imagery (<https://dataspace.copernicus.eu/>). Sentinel-2 bands 4 and band 8 have 10 m resolution and are the red ($R = 665$ nm) and near-infrared ($NIR = 842$ nm) channels of multispectral imager sensor. We uploaded the shape file of both bands in ArcGIS 10.8 (Esri 2011) and applied the formula of normalized difference vegetation index (NDVI) as,

$$NDVI = \frac{NIR - R}{NIR + R}$$

NDVI is a satellite-based vegetation index that depicts strong correlation with the above ground primary productivity (Pettorelli et al. 2005) and its value ranges from -1 to 1 . We quantified landscape elements embedded within circular buffer of 500 m from the center of each nine vegetable fields. Based on NDVI values all the landscape elements

were grouped into three landcover classes: non-crop habitat, agricultural land and forests (Fig. 1, Table S2). Shannon diversity index (SHDI) (proportional abundance of each landcover class (L_i) in each landscape) was used to characterize landscape diversity. SHDI was calculated using FRAGSTAT software (McGarigal et al. 2002) as:

$$SHDI = - \sum L_i \times \ln L_i$$

Insect sampling

In each field, insects were sampled from May 14 to July 9 in 2022 and from May 13 to July 8 in 2023 (i.e., nine times at weekly intervals each year). In each field, ten plants were randomly selected from the center and the whole plant was examined visually for insect counts. Each field was sampled for 30–40 min. In the monoculture plots, all ten plants were per definition of the same crop species; in the double cropping plots, we selected five plants from each of the two crop species; in the triple cropping plots, we selected three plants from each of the first two crop species (i.e., the two crops of the double cropping field in the same location) and four plants from the third crop species (see Table S1 for the crop species identity in each field). To ensure unbiased

sampling in the triple cropping plots, the crop plant selected four times in one location was not selected four times in the other locations. Insects observed were classified into different feeding guilds, i.e., herbivores and predators, based on their feeding behavior, trophic position and ecological role. We first visually observed the whole plant without disturbing it for counting the agile insects (e.g., whiteflies—Hemiptera: Aleyrodidae) and then we observed the upper and lower surface of leaves using magnifying glass to count insects having low mobility (e.g., aphids—Hemiptera: Aphididae; ladybird beetles—Coleoptera: Coccinellidae; green lacewings—Neuroptera: Chrysopidae and their larvae). Insects were identified morphologically (Pan and Bologna 2014; Ali et al. 2018; Asadi 2022; Gilligan and Passoa 2014; EPPO 2015), but some insects were sent to National Insect Museum, Islamabad, for identification. After sampling from each location, voucher specimens were deposited in IPM Laboratory at Department of Entomology, Bahauddin Zakariya University, Multan, Pakistan.

Yield determination

At the end of each season in 2022 and 2023, ten plants were selected, with the same sampling method described for insect sampling, from each field and the number of fruits were counted per plant (Mohammed et al. 2022). Fruits were collected from ten randomly selected plants per treatment at each location. In double cropping treatments, fruits were collected from ten plants per location, with five plants representing each crop species. In triple cropping treatments, fruits were collected from ten plants per location, with three fruits from two crop species and four fruits from the remaining crop species, ensuring that each crop species contributed four fruits per location once. For each cropping system, we calculated the average number of fruits per plant for each location and used these averages to standardize the yield data. This approach allowed us to account for the variability in fruit number between different crop species, ensuring a fair comparison of productivity across treatments. Additionally, reporting yield as fruit count allowed for consistent comparison across treatments, especially given the diversity of crop combinations and plant morphologies. Weight-based measurements would have introduced variability due to differences in fruit size, shape, and water content across species and cropping systems. Fruits were harvested based on marketability criteria aligned with international standards, like optimum size, uniform appearance, and absence of physical damage or scars, as outlined by the UNECE guidelines for fresh products (UNECE 2020).

Statistical analysis

Insect densities in each plot observed at weekly intervals were summed to obtain the seasonal totals in each year and these seasonal densities were pooled across the species in each diversity level. Effect of cropping diversity (i.e., monocropping, double cropping, and triple cropping) on the abundance of herbivores and predators were evaluated using generalized linear mixed model (GLMM) with a negative binomial distribution (to account for the overdispersion of the residuals when using a Poisson distribution), in which cropping diversity was fitted as fixed factor and fields were fitted as random factor. Herbivore abundances were significantly different among years, therefore we analyzed abundance of both years separately. In addition, insect abundance of each species separately was summed across years to assess the effect of cropping diversity on individual herbivore and predator species, by fitting similar GLMMs tested through *F*-test followed by LSD test for the pairwise comparison of treatments.

We used the raw number of insect species in each cropping diversity level as species richness and calculated species diversity and dominance indices according to the formulae of Shannon (1948) and Simpson (1949), respectively. Dominance refers to the exertion of a major controlling influence of one or more species upon all other species by virtue of their number, size, productivity or related activities. A Pearson's correlation was used to assess the associations among the plant species richness and insect diversity matrices (diversity, richness and dominance). A linear regression model was computed to assess the relationship between crop diversity and arthropod diversity matrices. Similarly, linear regression was also used to assess the effect of increasing landscape diversity on herbivore and predator abundance and diversity.

To assess the effect of increasing predator abundance, diversity, richness and dominance on the herbivore suppression, a linear regression model was computed. Herbivore abundance was tested for homogeneity of variance using Kolmogorov–Smirnov test and Shapiro–Wilk test and data were found to be typically non-normal. Hence, to increase compliance with assumptions of normality and homogeneity of error variance, these means were subjected to $\log(x + 1)$ transformation prior to analysis.

For yield data (number of fruits), we employed a separate analysis using ANOVA followed by *F*-tests to detect variation among diversity levels, and applied least significant difference (LSD) tests for pairwise comparisons.

We used structural equation modeling (SEM) in Analysis of Moment Structures (AMOS) to assess the direct and indirect effects of crop diversity on yield (Grace 2006). Path coefficients were calculated simultaneously within a unified SEM framework, rather than through independent

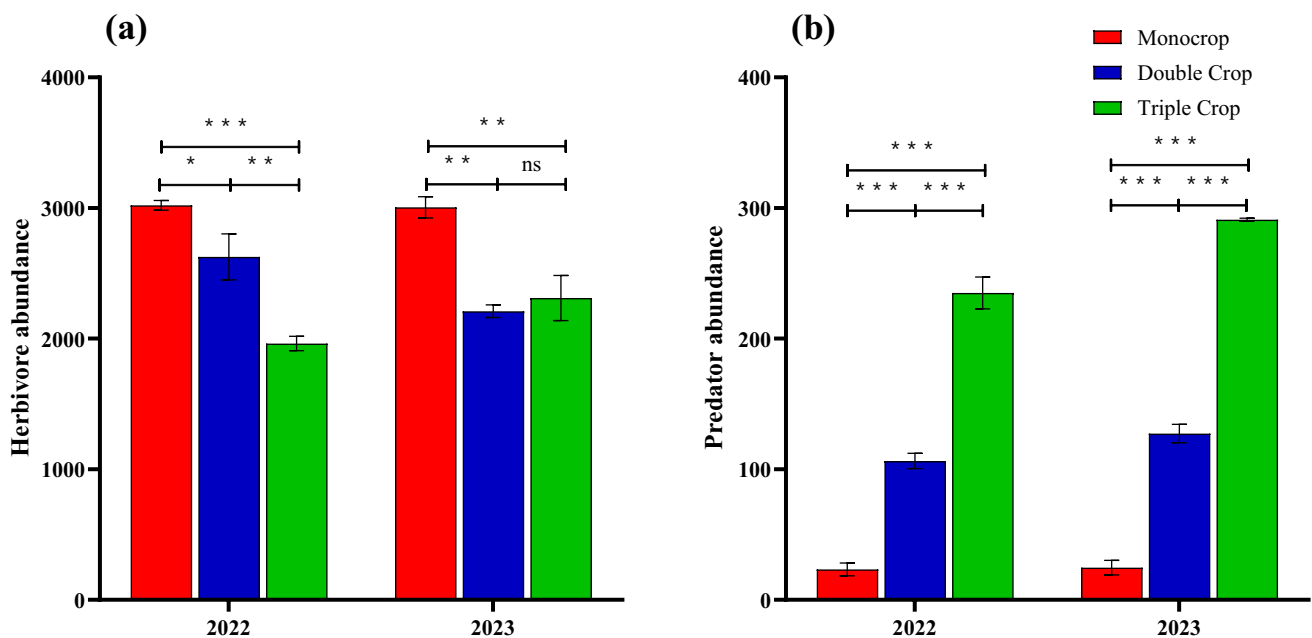


Fig. 2 Mean populations per treatment (+ SE) of **a** herbivores and **b** predators in monocropping, double and triple cropping fields in 2022 and 2023. Bars should be compared within each year and *, **, *** show significant difference at $p < 0.05$, $p < 0.01$ and $p < 0.001$

linear models. We used crop diversity as a potential predictor for altering yield. Moreover, predator abundance and diversity were considered as mediators to affect yield shaping herbivore population dynamics. This model was developed using AMOS software (Blunch 2012). All the statistical analysis were executed using Statistix 8.1 and SPSS (version 27).

Results

A total of 21 insect species (9 species of herbivores and 12 species of predators) were recorded during both years, i.e., 2022 and 2023 (Table S3). *Amrasca biguttula* (Distant) (Hemiptera: Cicadellidae) was the most abundant herbivore species (74% in 2022 and 68% in 2023). The most abundant predator species were *Brumoides suturalis* F. (Coleoptera: Coccinellidae) (18.28% in 2022 and 17% in 2023) followed by *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) (16.45% in 2022 and 15.43% in 2023).

Effect of crop diversity on insect abundance and diversity

Herbivore densities were significantly more abundant in monocrop in both years (2022: $F_{2,6} = 26.038$, $P = 0.001$, 2023: $F_{2,6} = 12.545$, $P = 0.007$, Fig. 2a) while predator densities were significantly higher in triple crop (2022: $F_{2,6} = 154.186$, $P < 0.001$; 2023: $F_{2,6} = 262.393$, $P < 0.001$, Fig. 2b). *Aphis gossypii* Glover (Hemiptera: Aphididae)

was not found in single crop while *Chaetocnema pulicaria* Melsheimer (Coleoptera: Chrysomelidae) only found in triple crop (Table S3). Densities of all individual herbivore species were significantly higher in monocrop fields except *Mylabris quadripunctata* Linnaeus (Coleoptera: Meloidae) (i.e., the least abundant species) for which no difference between cropping treatments was observed (Fig. 3a, Table S4). Conversely, densities of all predator species were significantly higher in triple cropping fields (Fig. 3b, Table S4).

Crop diversity was significantly and positively correlated with herbivore richness but correlations with herbivore diversity and dominance were non-significant (Table 1, Fig. 4). Predator diversity, richness and dominance were significantly and positively correlated with crop diversity (Table 1, Fig. 4).

Effect of landscape on consumer abundance and diversity.

Increasing landscape diversity reduced pest abundance ($F_{1,7} = 21.64$, $P = 0.002$, Fig. 5a), increased predator abundance ($F_{1,7} = 16.76$, $P = 0.004$, Fig. 5a), and increased the diversity of both pests ($F_{1,7} = 8.67$, $P = 0.021$, Fig. 5b) and predators ($F_{1,7} = 29.59$, $P = 0.001$, Fig. 5b). The different land cover classes (non-crop habitats, forests, agricultural land) taken separately did not significantly affect the abundance and diversity of the herbivores and predators (Table S5).

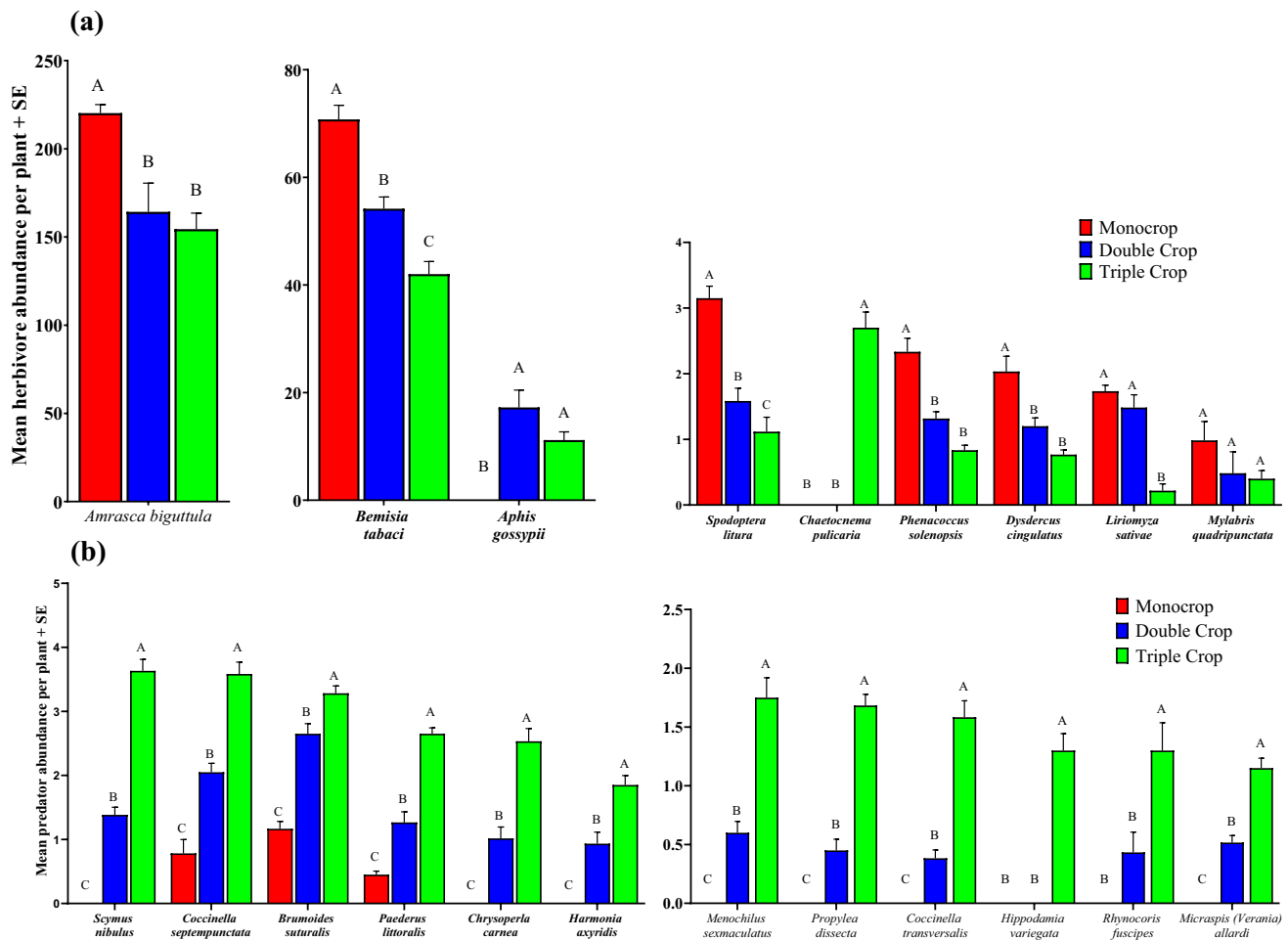


Fig. 3 Mean populations of individual herbivores (a) and predators (b) (+ SE) in monocropping, double and triple cropping fields in 2022 and 2023 (summed). Bars should be compared within each species

and different alphabets show significant difference at $\alpha < 95\%$ (see Table S4 for statistical results)

Table 1 Effect of vegetable crop diversity on diversity, richness and dominance of herbivores and predators in 2022 and 2023

Variables	Corr	F	P
Plant species richness			
Herbivore diversity	0.406	3.16	0.09
Herbivore richness	0.715	16.70	<0.001
Herbivore dominance	0.183	0.55	0.468
Predator diversity	0.930	102.00	<0.001
Predator richness	0.924	93.81	<0.001
Predator dominance	0.906	73.50	<0.001

Predator abundance and diversity effect on herbivore suppression

The abundance and diversity of predator communities was significantly related to reduced herbivore populations when taking all crop diversity levels together (Fig. 6).

Reduced herbivore abundance was significantly related to increasing predator abundance ($F_{1,16} = 13.95$; $p = 0.001$; Fig. 6a), predator richness ($F_{1,16} = 33.62$; $p < 0.001$; Fig. 6b), predator diversity ($F_{1,16} = 34.69$; $p < 0.001$; Fig. 6c) and predator dominance ($F_{1,16} = 31.06$; $p < 0.001$; Fig. 6d).

Yield

Number of fruits per plant was significantly higher in the triple crop ($F_{2,13} = 9.17$, $P = 0.003$, Fig. 7). Path analysis revealed the direct and indirect effects of crop diversity on herbivore abundance and crop yield (Fig. 8). Crop diversity increased the abundance and diversity of predator and decreased the diversity of herbivores while a non-significant effect was observed for herbivore abundance. Herbivore abundance significantly favored yield while a

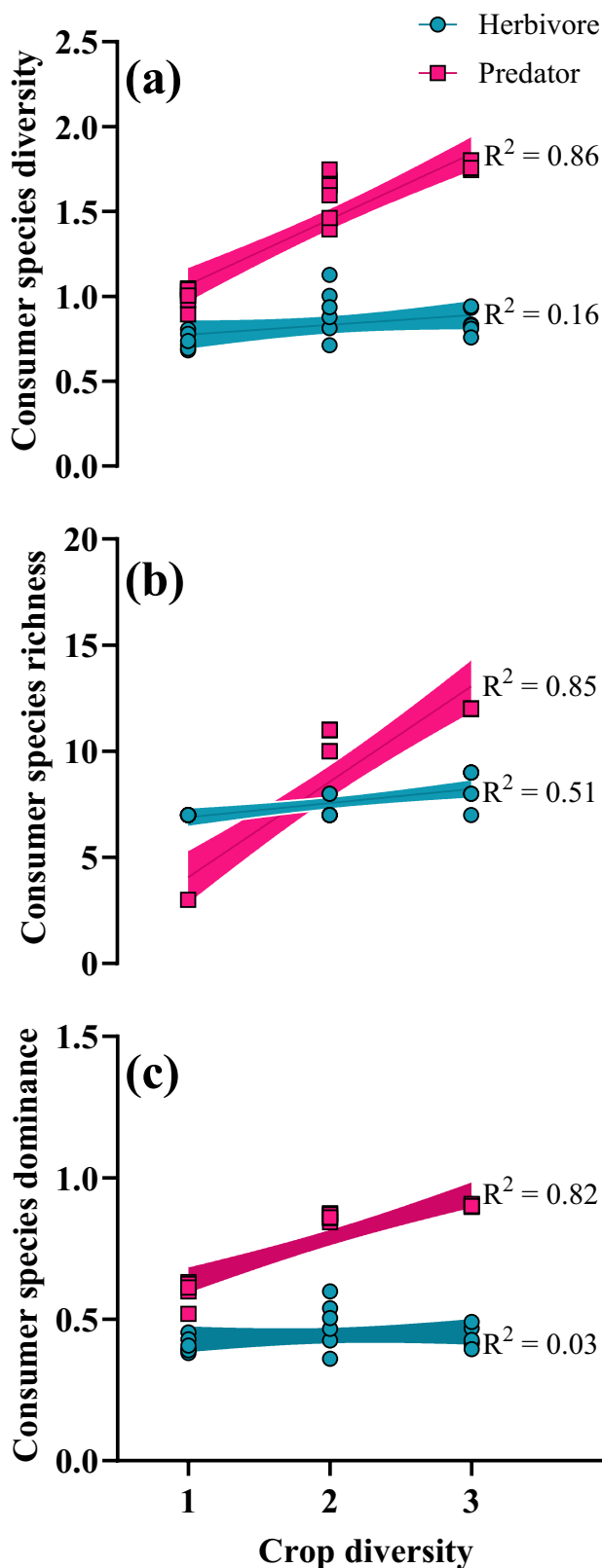


Fig. 4 Effect of vegetable crop diversity (richness) on **a** diversity, **b** richness and **c** dominance of herbivores and predators in 2022 and 2023. Solid lines represent the linear regression at 95% confidence level shown in shaded area (see Table 1 for statistical results)

non-significant effect was observed for herbivore diversity (Fig. 8).

Discussion

This study magnifies the importance of crop diversity in shaping multi-trophic interactions toward biological pest control in vegetable farming. The results highlight that all predator species were significantly more abundant in triple cropping while maximum herbivore species were significantly more abundant in monocrop fields. Herbivore richness, predator richness, diversity and dominance were significantly and positively correlated with increasing crop species richness while herbivore diversity and dominance were not affected by vegetable diversity. Furthermore, crop diversity promoted pest control services and improved productivity through effects mediated by pest and predator diversity and dominance.

Lower herbivore abundance might be due to higher natural enemy abundance in highly diverse plant composition (the natural enemy hypothesis). Higher plant diversity provides resources to natural enemies which can then indirectly suppress herbivore populations. Field plots that had a mixture of three crops likely resulted in increased resource availability including habitats, additional food resources, refuges and breeding sites than monocropping, which contributed to reduce herbivore abundance by escalating natural enemies abundance (Sanchez et al. 2018; Farooq et al. 2022; Beaumelle et al. 2021). In heterogeneous plant communities, herbivores are reported to exhibit negative density dependence response due to competition for more diverse but limited resources (Forrister et al. 2019). Higher herbivore population in single crop treatments might be explained by resource concentration hypothesis that posits isolated plants in monocultures lost much of their biomass to herbivory compared to the diverse plant communities (Root 1973). Moreover, plant-mediated indirect interactions also alter the herbivore species guilds. Plant chemical defense induction due to feeding of one herbivore influences the community structure (Van Zandt and Agrawal 2004) and reduces the attack by other herbivore guilds (McArt et al. 2013) in diverse plant communities. For example, *Popillia japonica* (Coleoptera: Scarabaeidae) feeding on leaves of *Oenothera biennis* (Onagraceae) accumulates the complex phenolic and jasmonic acid in the reproductive tissues which reduced the seed predation of three lepidopterans by 77% (McArt et al. 2013). In our diversified vegetable fields, the presence of multiple plant species likely contributes to a mosaic of chemical traits that interfere with herbivore host location and feeding behavior. This mechanism may reduce herbivore abundance in more diverse plots, suggesting that

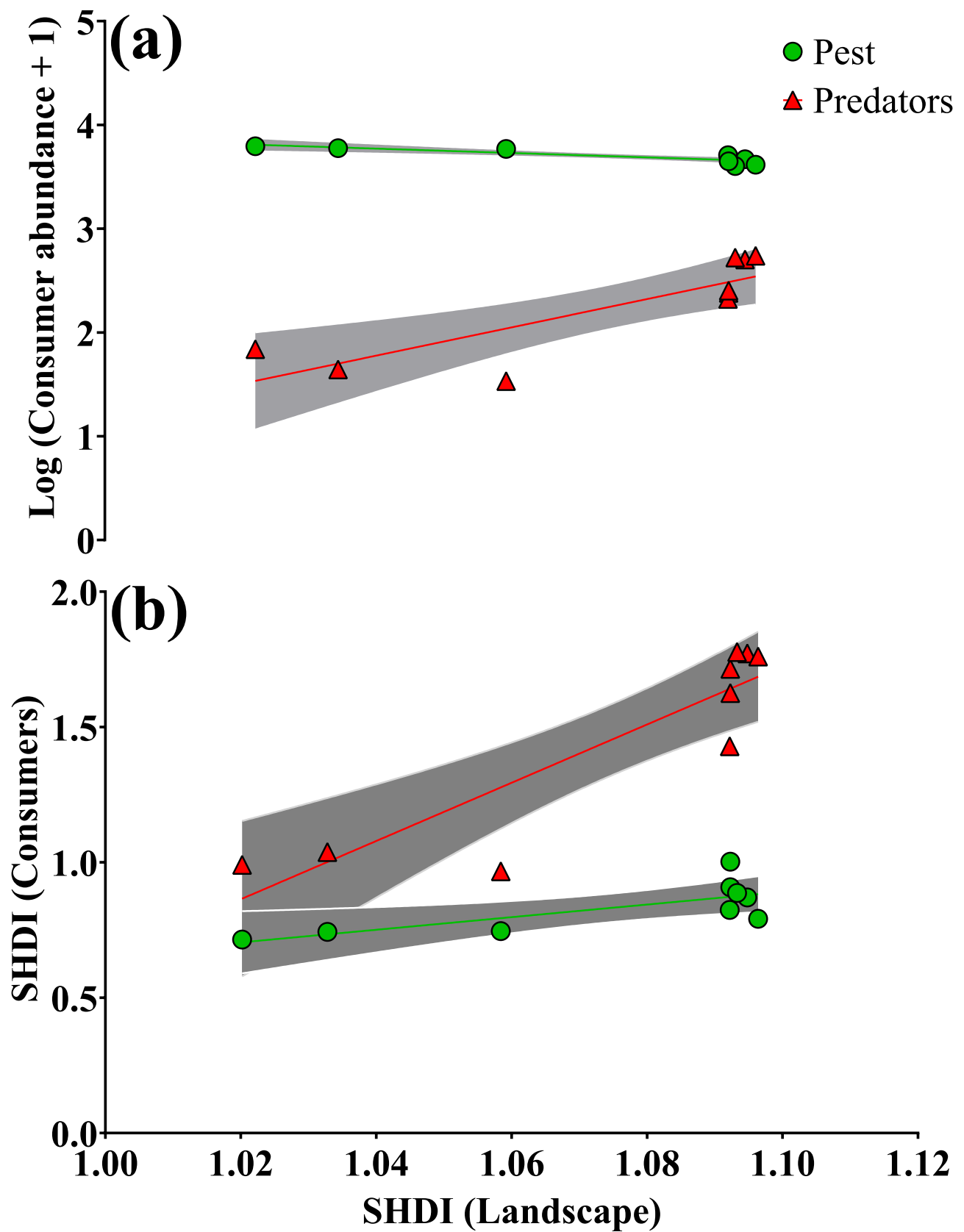


Fig. 5 Effect of landscape diversity on abundance **(a)** and diversity **(b)** of pests and predators

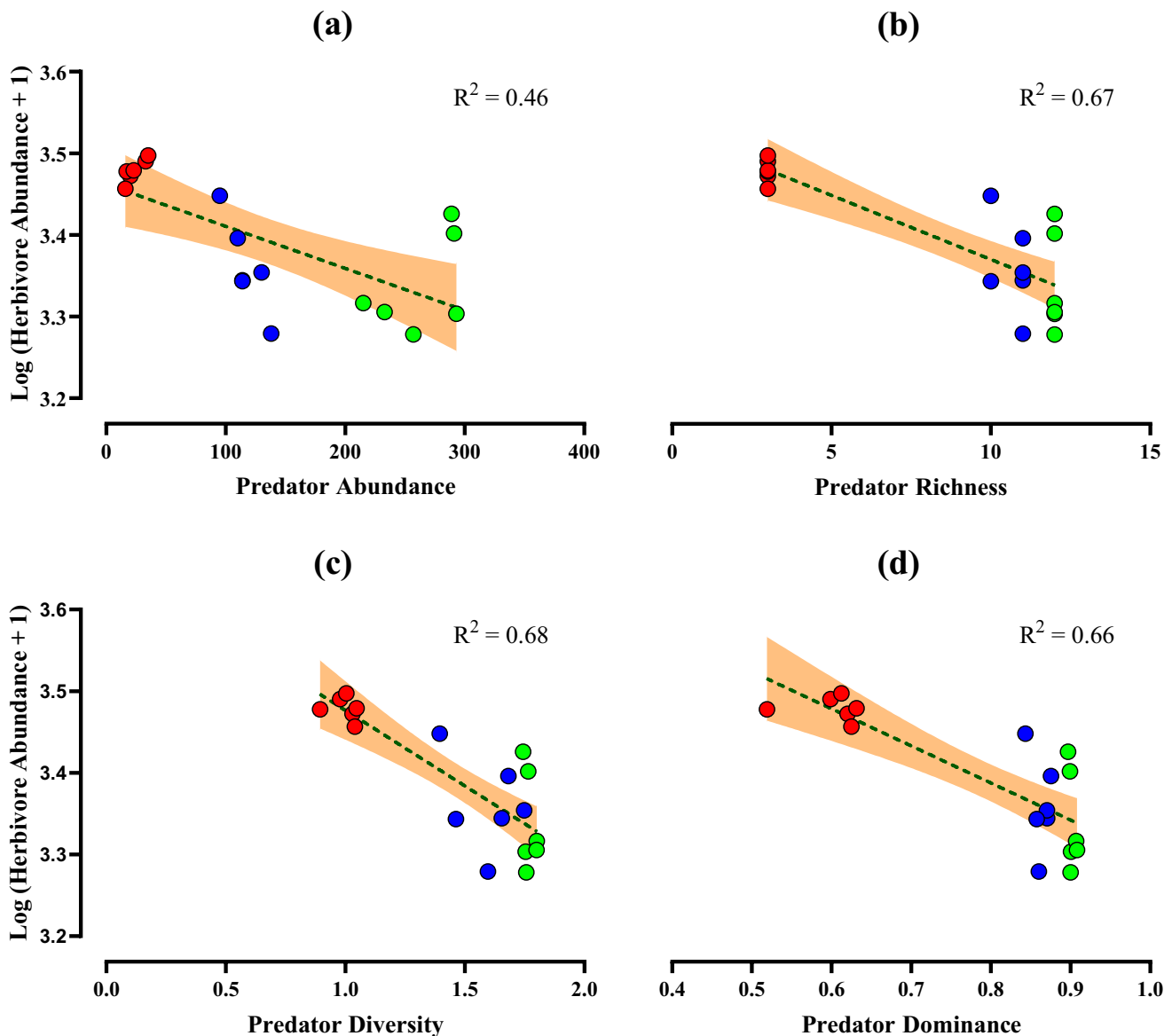


Fig. 6 Effect of predator **a** abundance, **b** richness, **c** diversity and **d** dominance on herbivore abundance in vegetable diversity field in 2022 and 2023. Herbivore abundance data was $\log (x+1)$ trans-

formed and pooled for both years in all panels. Red dots: monocropping, blue dots: double cropping, green dots: triple cropping

plant chemical diversity plays a role in pest suppression alongside habitat-mediated effects.

Agricultural biodiversity serves as cornerstone for ecosystem functioning and help in natural pest regulation to improve crop productivity (Cardinale et al. 2006). In our research increasing crop species richness increased the biodiversity of both herbivores and natural enemies which is consistent with previous studies (Rocher et al. 2024; Bischoff et al. 2016; Ebeling et al. 2018; Scherber et al. 2010). Agricultural landscape conversion from diverse cropping to monoculture of genetically uniform field crops is a major driver of biodiversity declines in agroecosystems (Outhwaite et al. 2022). Monocultures can

be truculent environment for predators, resulting in species poor communities of natural enemies mostly comprised of ruderal species, resistant to disturbance (Gurr et al. 2017). As per green world hypothesis, trophic cascades are central to biological pest control because natural enemies prevent herbivores from depleting terrestrial vegetation (Hairston et al. 1960). However, the role of biodiversity in shaping trophic cascades might be of much importance because addition or removal of a single species unlikely influences the cascades (Northfield et al. 2017). Biodiversity decline usually weakens biological pest control (Zhou et al. 2023) because effective pest regulation is maximized when various natural enemies co-occur and their complementarity in

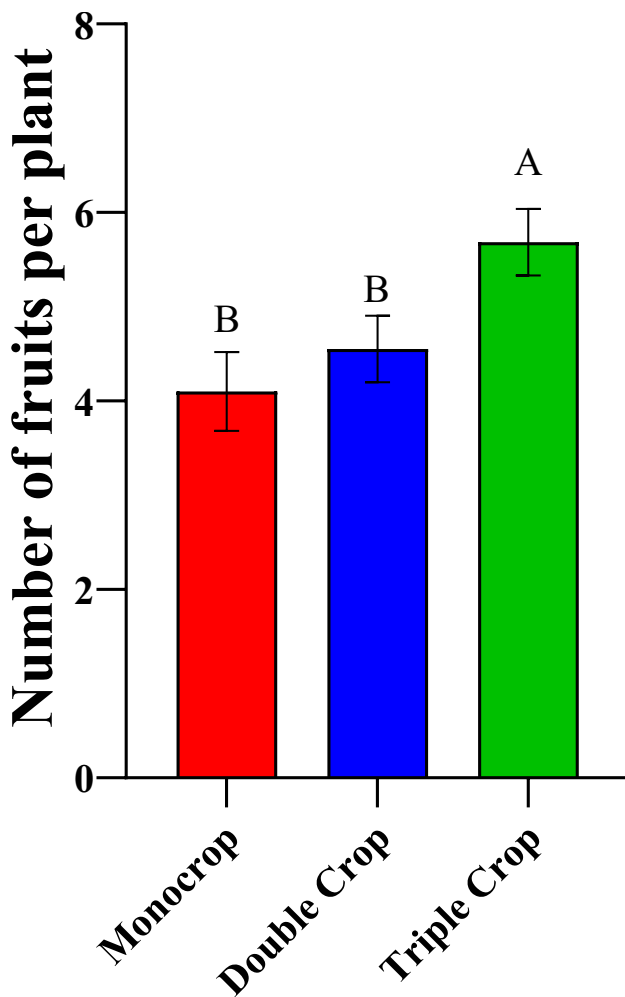


Fig. 7 Effect of vegetable crop diversity (i.e., richness) on number of fruits (yield) of all vegetables

resource acquisition strengthens the top-down functionality of diverse plant communities (Straub et al. 2008).

Species richness and evenness have long been envisioned as important components of biodiversity being critical natural pest regulators. Diversity at producer level (i.e., plants as first trophic level), complemented by positive interactions of neighbor plants, sets theoretical ground for consumer level effects on pest suppression. In upper trophic levels, species complementarity model suggests that pest mortality in highly diverse ecosystems might be a synergistic or additive action of various natural enemies, i.e., species richness (Dainese et al. 2017; Gagic et al. 2019; Jeavons et al. 2023; Michalko et al. 2019). Complementarity among natural enemies can be due to attacking herbivores of different life stages (Dainese et al. 2017) using diverse hunting strategies (Northfield et al. 2017). Moreover, foraging behavior that facilitate other natural enemies can also lead to positive predator complementarity, i.e., a facilitation among predators yielding synergistic impact

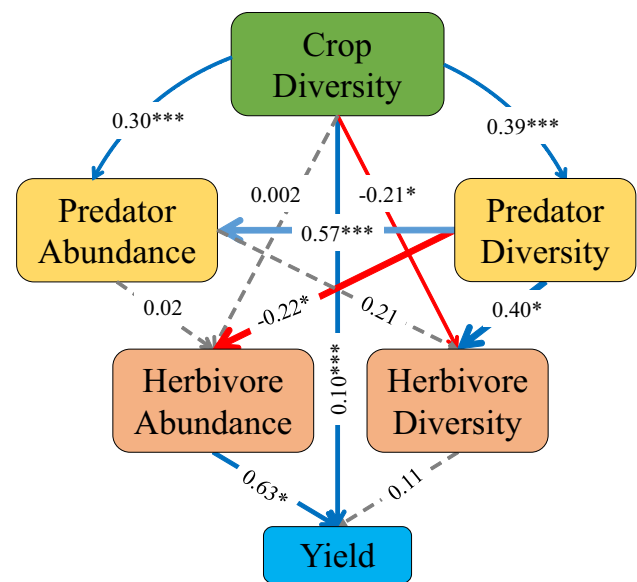


Fig. 8 Path model of effect of crop diversity on yield. Red arrows show significantly negative effects, blue arrows show significantly positive effects, and gray arrows indicate a non-significant effect. Estimates are provided, along with statistical significance: *, **, *** for $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively

(Northfield et al. 2017). Actively hunting predators chase herbivore into the waiting clutches of nearby ambush predators which would never encounter herbivores otherwise (Preisser et al. 2007). For instances, active ladybird beetle hunting for spider mite increased the risk of falling the prey to sit and wait spiders (Rosenheim et al. 2004). Furthermore, sampling effect increasing the probability of more influential natural enemy species yields stronger top-down control (Ives et al. 2004). Conclusively, the presence of superior natural enemy species and positive complementarity enhance the functional diversity, thereby improving biological control in a way that will not result from increasing species richness and evenness of functionally redundant species (Greenop et al. 2018).

At the landscape scale, increased landscape heterogeneity negatively affected herbivore populations and increased the abundance and diversity of natural enemies. Diverse landscapes are less prone to pest outbreaks (Paredes et al. 2021, 2022), support higher diversity of arthropod (Gallé et al. 2022), and enhance the potential of local natural enemies (Beaumelle et al. 2021). Landscape diversity, i.e., the proportion of land cover classes (grasslands, forests and non-crop areas), can benefit natural enemies by providing yearlong resources and facilitate species movements across different patches of landscapes (French et al. 2001). It can result in 46% increase in biological pest control as compared to homogeneous landscapes dominated by intensive cultivated areas (Rusch et al. 2016). Our findings contribute to underscore the critical role of landscape heterogeneity

in enhancing biological pest control by supporting natural enemies and reducing pest outbreaks. It is suggested that agricultural practices should incorporate and maintain landscape heterogeneity to harness the benefits of biological pest control, hence leading to more sustainable and resilient agricultural ecosystems.

We found a significantly higher marketable yield in triple crop. Such a positive effect is possible when diverse planting leads to niche complementarity (Li et al. 2023). These complementarity effects might be due to (1) resource partitioning, i.e., the different ways species acquire, capture and use common resources, (2) abiotic facilitation, i.e., the ability of species to alter their surroundings and to favor the fitness of neighboring species, or (3) multi-trophic plant interactions (Barry et al. 2019). Crops grown in mixtures tend to produce larger specific leaf area per unit leaf dry mass (Engbersen et al. 2022) enabling increased light capture leading to complete canopy cover (Williams et al. 2020). The positive relationship between fraction of photosynthetically active radiation (FPAR) and C:N ratio indicates that nitrogen use efficiency increases with increasing plant diversity (Engbersen et al. 2022). Moreover, diverse plant communities strongly affect above and below ground biomass due to positive complementarity (Mahaut et al. 2019; Cappelli et al. 2022). However, some studies have reported that increased plant diversity may also lead to yield trade-offs, particularly when interspecific competition for light, nutrients, or space outweighs facilitative interactions (López-Angulo et al. 2023; Li et al. 2010). These trade-offs highlight the importance of selecting compatible crop species and optimizing spatial arrangements to balance ecological benefits with agronomic performance. Yet, although the yield of each crop might be reduced in mixtures, the land-use efficiency (captured by the land-equivalent ratio, not measured here) is often higher with mixtures compared to monocrops (Li et al. 2020a). Interestingly, herbivores may be negatively affected by the shoot mass (proxy for resource quantity) indicating that herbivores are not necessarily controlled by resource quantity, while top-down control might be the foremost mechanism in suppressing pest populations in diverse plant communities (Dietrich et al. 2021).

The structural equation modeling (SEM) revealed several ecologically meaningful relationships among cropping system, insect communities, and yield. Crop diversity exerted a direct positive effect on both predator abundance and predator richness, as well as on overall yield, suggesting that diversified cropping systems enhance functional biodiversity and productivity simultaneously. Predator diversity positively influenced herbivore diversity, likely reflecting a more structurally complex and resource-rich environment that supports diverse trophic interactions, while exerting a negative effect on herbivore abundance, consistent

with top-down regulation. Notably, an unexpected positive correlation was observed between herbivore abundance and yield, a pattern that may reflect non-damaging herbivore presence, compensatory plant responses, or indirect ecological mechanisms. Mechanical injury due to insect herbivory can initiate physiological mechanism—e.g., increased branching and tillering, reallocation of resources, high rate of relative growth and increase in photosynthetic rate—that account for compensatory response after attack (Koch et al. 2016). Poveda et al. (2010) proved that potato tuber production increased after feeding of the Guatemalan potato moth, *Tecia solanivora* (Lepidoptera: Gelechiidae). Bustos-Segura et al. (2022) noted that injury at seedling stage of wild lima bean plant triggers higher compensatory growth and tolerance to insect herbivory in later growth stages compared to undamaged plants. It recalls that herbivores may not necessarily cause significant yield losses and can, in some cases, even benefits to yield (Gagic et al. 2016). More generally, negative impacts are usually observed when herbivore abundance exceeds a given abundance threshold (Ramsden et al. 2017) and in the presence of abundant natural enemies and effective biological control, i.e., as in the present study, economic thresholds for pests are increased (Zhang and Swinton 2009) resulting in less, if no, need of spraying insecticides.

The present study assessed pest and natural enemy abundances at the plot level; however, herbivore guilds are known to vary substantially across crop species, potentially influencing observed patterns in diversified systems. Okra and cucurbit crops, for example, host distinct herbivore communities due to differences in plant morphology, phenology, and chemical defenses (Gurr et al. 2017; Hooks and Johnson 2003). Yet, crop diversification can enhance biocontrol services even when herbivore assemblages differ (Letourneau et al. 2011).

One of the key considerations in this study is the replication structure within monocrop and double crop treatments. The lack of replication for specific crop combinations in monocrop and double crop treatments may influence species-specific insect interactions, though this design was intentional to focus on diversity effects rather than individual crop identities. However, the plantation of all three diversity levels on different locations leads to effective randomization of treatments and enable us to infer the impact of increasing vegetable diversity on insect populations. Additionally, differences in plant sampling across treatments, while structured within a substitutive design, could introduce minor variability in insect detection rates. Future studies could explore replicating specific crop combinations to further assess species-level interactions while maintaining diversity gradients.

Our findings on the impact of vegetable crop diversity on insect community structure and productivity align with and

extend the existing research on diversity effects in agronomic crops (Farooq et al. 2022), forests (Schuldt et al. 2018), and grasslands (Weisser et al. 2017). Our study confirms that vegetable diversity similarly enhances arthropod community structure and productivity, with higher diversity levels resulting in lower herbivore abundance and higher predator abundance due to increased resource availability and habitat complexity. While these results offer promising insights into biodiversity-function relationships in vegetable systems, they reflect context-specific patterns observed within a limited spatial and temporal scope. Future research should investigate the long-term impacts of vegetable diversity on arthropod dynamics and crop yield across different climatic regions and cropping systems. Additionally, exploring the specific mechanisms through which diversity influences predator–prey interactions in vegetable systems could provide deeper insights into sustainable pest management strategies. Understanding the economic and ecological implications of implementing diverse vegetable cropping systems will be crucial for developing comprehensive agricultural policies and practices.

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Author contributions The work was carried out in collaboration with all authors. MOF and MR: conceived the ideas and designed methodology. MOF: collected and analyzed the dataset and led the writing of the manuscript. FMS and SH: critically reviewed the final draft and edited it. All authors have approved the manuscript for publication.

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Declarations

Conflict of interest The authors have no conflict of interest to declare that are relevant to content of this article.

Ethical approval This article does not contain any studies with human or other animal subjects.

Consent to participate All the authors agree to participate.

Consent to publication All authors agree to publish.

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