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RECEIVED 11 November 2023

ACCEPTED 27 September 2024

PUBLISHED 24 October 2024

## CITATION

Lu A, Gonthier D, Sciligo A, Garcia K, Chiba T,  
Juárez G and Kremen C (2024) Arthropod  
arbiters: natural enemy communities mediate  
the effects of landscape and local-scale  
complexity on *Lygus*-induced crop loss in  
organic strawberries.  
*Front. Sustain. Food Syst.* 8:1336888.  
doi: 10.3389/fsufs.2024.1336888

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# Arthropod arbiters: natural enemy communities mediate the effects of landscape and local-scale complexity on *Lygus*-induced crop loss in organic strawberries

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Sustainable pest management requires growers and regional land managers to consider the relationships among pest management practices, pest and natural enemy communities, crop loss, and multi-scalar habitat complexity. However, the causal links among these variables, in particular potential interactions between landscape and local-scale habitat complexity, remain underexplored. In the context of organically managed strawberry crops in California's Central Coast, we tested the independent effects of landscape and local habitat complexity gradients on arthropod communities and crop loss using a piecewise structural equation model (PSEM). We found that landscape-scale woody habitat proportion indirectly decreased crop loss through its positive effect on natural enemy abundance, while grassland proportion had the opposite effect due to its association with an important strawberry pest (*Lygus* spp.). We detected a pattern suggesting that on-farm diversification practices are most effective at reducing crop loss at an intermediate level (26%) of woody habitat proportion. Both organic-compliant insecticide application and tractor vacuuming negatively impacted natural enemies, and therefore had qualified effects on crop loss. Our study shows the key roles of native woodlands and natural enemy communities in reducing crop loss and highlights the importance of managing habitat complexity at both landscape and local scales.

## KEYWORDS

habitat complexity, landscape composition, local diversification practices, crop diversity, pest management, pest control ecosystem services, crop loss, diversified agriculture

## 1 Introduction

Maintaining and restoring habitat complexity in agricultural landscapes to promote pest control services can lead to significant economic, ecological, and public health benefits (Kremen and Miles, 2012). Broadly, habitat complexity can be measured at different spatial scales and encompasses numerous land cover characteristics, including land cover diversity, crop and non-crop plant diversity, (semi)natural habitat proportion, and configuration. Habitat complexity in agricultural landscapes is generally associated with healthier (in terms

of abundance and diversity) communities of beneficial insects, including pollinators and natural enemies of agricultural pests (Dainese et al., 2019; Kremen et al., 2007; Sánchez et al., 2022; Sirami et al., 2019). Natural enemies provide pest control ecosystem services and theoretically reduce pest-induced crop loss in a process known as top-down control or the enemies hypothesis (Root, 1973). In contrast, landscapes dominated by crops, and especially monocultures, theoretically provide abundant resources for pests and increase pest pressure via the resource concentration hypothesis, also known as bottom-up effects (Gurr et al., 2017; Root, 1973). In practice, however, habitat complexity studies have shown highly variable effects on pest control and crop loss due to differences in spatial scale, types of habitat, crop types, arthropod traits, and farm management practices, among other factors (Karp et al., 2018; Tscharnkte et al., 2016). In order to design landscapes and manage farms that balance short-term productivity with long-term sustainability, policymakers and growers need to know the environmental conditions at landscape and farm scales that are most likely to enhance natural pest control and reduce pest-induced crop loss. Toward this end, we present a study to test the network of direct and indirect causal links among: (a) orthogonal (i.e., independent) gradients of landscape composition and local (farm-scale) diversification practices; (b) local pest management practices; (c) arthropod communities (pests and their natural enemies); and (d) crop loss, in a strawberry growing region of California's Central Coast.

Complexity at both local and landscape scales influences pest control ecosystem services. Several meta-analyses have concluded that local-scale plant diversity positively affects natural enemy communities, levels of pest control, and crop yield (Beillouin et al., 2021; Judt et al., 2023; Letourneau et al., 2011; Tamburini et al., 2020), but others show that these effects are inconsistent under different landscape contexts (Boetzel et al., 2020; Dassou and Tixier, 2016; Tscharnkte et al., 2012). At the landscape scale, meta-analysis reveals that complexity generally increases natural enemy abundance (Chaplin-Kramer et al., 2011b; Duarte et al., 2018), but effects on pest control services remain inconsistent and controversial (Karp et al., 2018; Rusch et al., 2016). A dominant source of variability among studies may be the interaction between different scales of complexity. For example, in landscapes with high proportions of natural habitat, colonization by low-mobility natural enemies may require local-scale features such as hedgerows to improve connectivity (Martin et al., 2016, 2019). Conversely, the effectiveness of local-scale diversification may also depend on landscape-scale complexity. Under the "intermediate landscape complexity hypothesis," simplified landscapes may contain insufficient habitat to sustain the natural enemy meta-populations needed to provide effective pest control even with ample local diversification, while in highly complex landscapes, pest control services may already be robust and thus adding local complexity may be redundant (Tscharnkte et al., 2012). Therefore, local diversification may have the highest impact at intermediate levels of landscape complexity. Despite the logical appeal of this hypothesis, few empirical studies have uncovered evidence of its operation (*but see* Beaumelle et al., 2021; Jonsson et al., 2015; Sánchez et al., 2022; Wilson et al., 2017).

Representing local-scale complexity is another challenge in multi-scale studies. Some studies investigating the interaction between habitat complexity at landscape and local scales have relied on the organic/conventional dichotomy as a proxy for local diversification (Martin et al., 2016; Saqib et al., 2020). Although organic management can increase

biodiversity relative to conventional management (Hole et al., 2005) and often relies on diversification practices to provide critical inputs to farming (Kremen and Miles, 2012), organically managed farms also include monocultures that employ ecologically disruptive pest control methods like organic-compliant insecticides and arthropod vacuuming (Guthman, 2000; Lu et al., 2022; Swezey et al., 2007; Tscharnkte et al., 2021). Thus, organic management does not reliably signify high on-farm complexity.

In Europe, where government-supported agri-environment schemes (AES) encourage growers to deploy specific non-crop diversification features such as flower strips, hedgerows, and fallow fields (Batáry et al., 2015), pest control researchers have studied multi-scale interactions by representing local complexity with presence/absence of an AES-compliant feature or comparisons between feature types (Beaumelle et al., 2021; Dainese et al., 2017). In the United States, pest control studies on specific feature types are less common (*but see* Wilson et al., 2017), perhaps because government incentives for local diversification are less accessible and consistent than in Europe, leading growers to use a patchwork of different diversification practices. A composite, continuous local diversification score comprising various practices is therefore a practical way to represent local complexity in our study region. A composite score also aligns with growing evidence that simultaneously deploying multiple diversification strategies, rather than individual ones alone, is more likely to generate positive social and environmental outcomes (Rasmussen et al., 2024). Despite the advantages of doing so, few studies have used continuous, orthogonal gradients to explore how interactions between multi-scale habitat complexity contribute to pest control services (*but see* Garcia et al., 2023).

Even fewer studies have measured crop yield (or loss), which is a crucial gap because it embodies the economic bottom line for growers (Chaplin-Kramer et al., 2011b; Kleijn et al., 2019), and it often does not correlate with measured levels of pest control, or even measured levels of herbivory (Iverson et al., 2014). Factors other than pest control can strongly affect yield, including management history, abiotic conditions, and soil quality (Liere et al., 2015; Schellhorn et al., 2015). The handful of studies that have investigated the interaction effect between landscape and local habitat complexity on crop yield have not revealed a consistent pattern. Some found evidence of an interaction effect with respect to pest control but not yield (Midega et al., 2014; Wilson et al., 2017), others have found no interaction effect on either (Albrecht et al., 2020), while others have found an effect on both (Gagic et al., 2021; Jonsson et al., 2015). All of these prior studies represent local diversification with an organic/conventional dichotomy or the presence of specific AES features. To our knowledge, this is the first study to explore the crop loss effect of a landscape by local-scale interaction using a composite continuous local diversification score.

Two additional hypotheses regarding the inconsistent effect of habitat complexity on pest control are the contrasting effects of different types of non-crop habitat (Karp et al., 2018), and the potentially confounding effect of local pest management practices such as insecticide application (Tscharnkte et al., 2016). We investigate non-crop differences by separating woody habitats from grasslands, which we expect to support different arthropod groups. We investigate local pest management practices by including covariates for two commonly used pest control practices in this region: frequency of tractor-mounted arthropod vacuuming and intensity of insecticide application.

We collected data for this study in the strawberry growing region of California’s Central Coast centered around Monterey Bay. Our study focused on the lygus bug, an economically important strawberry pest complex in this region, and its predator community. Absent pest management, an estimated 26–54% of strawberries grown in this region show signs of lygus-induced malformation resulting in crop losses (Pickel et al., 1995). Unlike crops whose yield is defined solely by harvested biomass, crop loss in strawberries can be estimated from crop damage surveys because yield is tracked by both weight and number of harvested (i.e., marketable) berries (Bolda et al., 2024). While the woody habitats in this region are generally perennial, native, and biodiverse, and are expected to provide resources for natural enemies, the grasslands are unmanaged and dominated by exotic grasses and annuals, many known to be lygus bug hosts (Fye, 1982; Scott, 1977). We sampled at sites located along orthogonal gradients of landscape composition and local diversification practices. At each site, we collected lygus bugs and natural enemies and surveyed strawberries to estimate lygus-caused crop loss. Our study addresses the following questions: (1) How do landscape-scale and local-scale habitat complexity interact to alter arthropod communities and crop loss, and how are those impacts influenced by pest management practices; and (2) What are the direct and indirect causal links among multi-scale habitat complexity, arthropod communities, and crop loss (Figure 1)?

## 2 Methods

### 2.1 Study system and site selection

The study was carried out in the Santa Cruz-Watsonville-Salinas area of California’s Central Coast, a region characterized by a mosaic landscape of natural habitat mixed with high agricultural productivity, heavy pesticide use, and unique biodiversity (Karp et al., 2016). The mean annual high and low daily temperatures are 20.1 and 8.9°C, respectively, and annual precipitation averages

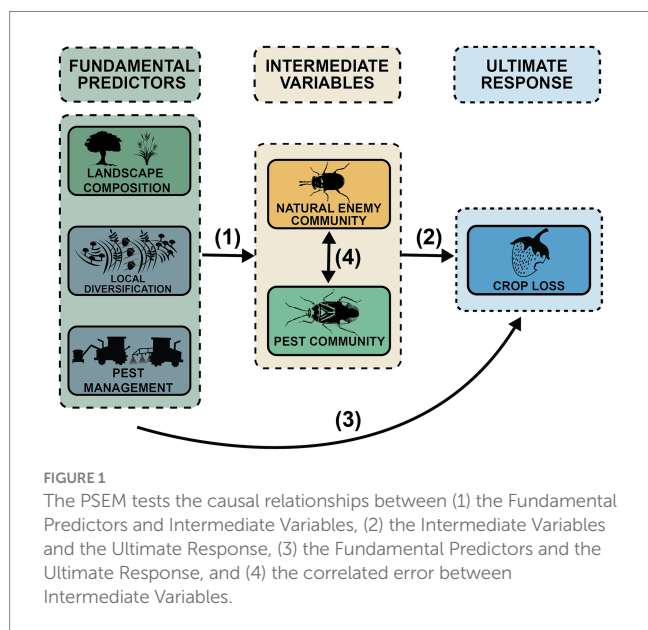
319.5 mm. During the peak strawberry harvest season of May–August when we sampled, the mean high and low daily temperatures are 21.3 and 11.9°C, respectively, and precipitation during those months averages 10.6 mm, of which 9.7 mm falls in May (NOAA, 2024a). The elevation at the Salinas Municipal Airport weather station is 22.3 m (NOAA, 2024b). To document the impact of local and landscape diversification on strawberry pests, their natural enemies, and crop damage, we sampled 27 organic strawberry farms from May–August in 2015 and 2016. Given that many organic strawberry farmers lease multiple spatially independent farms to accommodate crop rotation, some study sites were different between years. Thus, 17 sites were sampled in both years, 10 were unique to 2015, and another 10 were unique to 2016. Sites were selected along orthogonal gradients of landscape composition and local diversification practices, as described below. All sites were organically-managed farms containing strawberry as either the sole crop or as one of many types of crops, and were defined as contiguous cultivated areas under the same manager. Sites ranged in size from 0.88 to 100.3 hectares.

### 2.2 Local diversification score

A continuous, composite diversification score (hereafter, “diversification score”) was created by tallying on-farm diversification practices including four crop-related (crop diversity, crop rotational length, perennial crop structure, and cover crops) and three non-crop related elements (non-flowering non-crop plants, flowering non-crop plants, and water features). Water features were included in the score because they are accompanied by non-crop vegetation, increasing in diversity from sparsely vegetated sediment retention ponds to highly diverse riparian areas. After taking on-site observations, we scaled the observation states for each element at each site (unweighted) and then used Principal Components Analysis (PCA) to reduce the number of variables and create a composite score based on a site by score matrix (Supplementary Table S1). We used the function `prcomp` in the R package `stats` to perform the PCA. The first axis of the PCA, which accounted for 37% of the variance in our data, was used as a continuous variable representing local diversification (for further details, see Lu et al., 2022).

### 2.3 Landscape variables

The United States Geological Survey’s National Agriculture Imagery Program (NAIP) data was used to digitize landscape cover within 1,000 m buffers around each site (Earth Resources Observation and Science (EROS) Center, 2017). NAIP data is collected by aircraft at one meter spatial resolution. We used 2014 NAIP data and confirmed that the land cover in our buffers had not changed in the 2015 and 2016 data. Land cover categories were based on the Salinas-Pajaro Generalized Land Use / Land Cover Mapping and the Anderson Level II hierarchy (Karp et al., 2015). We reclassified the default land cover categories by placing native/riparian forest and woodland, exotic tree patches, chaparral and scrubland in the woody habitat category; and herbaceous vegetation, Mediterranean grasslands and forbs, and pasturelands in the grassland category. The grasslands in this region are not natural habitat; they are unmanaged or used as pasture, and are



dominated by exotic annual grasses and forbs. Proportions of woody habitat and grasslands were not correlated ( $\rho=0.11$ ,  $p=0.45$ ), largely due to a high proportion of cropland in the study region.

The most predictive buffer sizes for each response variable were determined by first regressing the response variable against each landscape proportion at buffer sizes ranging from 500 m to 1,000 m and then selecting the top-ranked (by AICc) buffer size for each response-landscape type combination (Jackson and Fahrig, 2012, 2015, Supplementary material). Neither of the landscape types was correlated with local diversification ( $|\rho|<0.21$ ;  $p>0.12$ ) at any of the selected buffer sizes, confirming the independence of the gradients (Supplementary Figure S1).

## 2.4 Pest management variables

While the premise of organic agriculture is fundamentally similar across the globe, variations in certification standards exist across countries. The growers in our study were certified to the standards set by the USDA National Organic Program (NOP) (National Organic Program, 2000) whose standards are outlined for growers in the NOP Handbook (USDA, 2024b). The USDA NOP Guidance on Natural Resources and Biodiversity Conservation adopted language in 2016 stating that “the [organic] producer must initiate practices to support biodiversity and avoid, to the extent practicable, any activities that would diminish it,” directing growers to use organic compliant pesticides only as a last resort (USDA, 2024a). The National List of Allowed and Prohibited Substances outlines the categories of substances in organic production (USDA, 2024c) and the Organic Materials Review Institute (OMRI) provides a list of USDA Organic compliant pesticides approved for use on our study sites (OMRI, 2024).

USDA organic compliant pesticides that are commonly applied in the study area were classified into one of three categories: targeting lepidopteran larvae (*Bacillus thuringiensis*-based (*Bt*)), broad spectrum (spinosad, pyrethrin, or *Chromobacterium subtsugae*-based), and targeting soft-bodied pests such as aphids, thrips, and whiteflies (*Beauveria bassiana* or azadirachtin-based). Insecticide intensity and tractor vacuum frequency were included as predictor variables to test their effects on arthropod communities and crop damage. In our study, insecticide intensity was assessed as an index from 0 to 3 indicating the number of insecticide categories applied; application frequency was not included in the index because farm managers seldom reported this information. The insecticide intensity variable is a proxy for the level of chemical management and does not directly link chemical modes of action with berry damage. For example, we do not expect *Bt* application to directly affect lygus damage; however, *Bt* may indirectly affect pest control and lygus damage by reducing alternative prey or imposing sub-lethal effects on natural enemies (De Bortoli et al., 2017). Tractor vacuum frequency ranged from 0 to 2 and indicates the number of times per week that the site was vacuumed during the growing season, as reported by farm managers.

## 2.5 Arthropod sampling

At each site, we sampled arthropod communities at three sampling stations located within the strawberry crop. Plants within an area of

approximately 10 m by 15 m were sampled at each site. To assess natural enemy and pest abundance and diversity, we sampled arthropods on 150 strawberry plants (50 per station) using a Stihl BG55 leaf blower in vacuum mode, directing the vacuum tube over each plant and holding for 1 s (method modified from Swezey et al., 2007). To reduce the effect of arthropods fleeing the sound of the vacuum, we sampled one of every five plants, skipping four plants between samples. Arthropods were trapped by a filter fabric bag attached to the vacuum tube entrance. To reduce bias caused by differences in arthropod activity under varying weather conditions, sampling occurred only under the following conditions: ambient temperature 20–28° C, average wind speed  $\leq 3.0$  m/s, and no fog or precipitation.

Natural enemy specimens were sorted into the following categories, all of which are known predators of lygus bugs: *Geocoris* spp. (Hemiptera), *Orius* spp. (Hemiptera), Coccinellidae (Coleoptera), *Nabis* spp. (Hemiptera), Neuroptera, Formicidae (Hymenoptera), and Araneae (Bolda et al., 2019; Hagler, 2011). The categories represent functional groups identified by previous lygus bug predation studies (Hagler et al., 2020a,b; Leigh and Gonzalez, 1976; Perkins and Watson, 1972; Wilson and Gutierrez, 1980; Zink and Rosenheim, 2008). The lygus bug complex in this region primarily comprises *Lygus hesperus*, and also includes small proportions of *L. elisus* and *L. lineolaris* (Hagler et al., 2020b). Individuals of all *Lygus* species were included in the lygus bug category.

Abundance measures are counts of individual specimens belonging to each order or finer classification. Shannon's diversity index  $H'$  was used to calculate natural enemy diversity (Magurran, 2013).

## 2.6 Strawberry damage survey

At each site, we surveyed 50 strawberry plants at each sampling station in 2015 (150 per site) and 20 strawberry plants at each station in 2016 (60 per site). Sampling effort in the second year was reduced following a power analysis indicating that the reduced sampling would suffice for this study's statistical analysis. For each plant, surveyors recorded the number of unripe ( $\geq 20\%$  white surface color) berries and ripe ( $<20\%$  white surface color) berries. Green berries were not included in the analysis because they are too small to consistently detect damage. All unripe and ripe berries were then classified according to the damage categories in Table 1. We performed a greenhouse study that compared the appearances of berries subjected to (1) lygus damage in the flower stage, (2) lygus damage in the berry stage, and (3) insufficient pollination (Sciligo et al., 2022) to determine characteristics of damage unequivocally attributed to lygus bugs. We found that berries subjected to lygus damage at the berry stage could be distinguished based on the formation of fully formed achenes within the puckered region. However, insufficient pollination alone could not be reliably distinguished from berries subjected to lygus damage at the flower stage (Figure 2). To isolate the effect of lygus bugs on crop damage, we included in this analysis only berries that, according to visual inspection, were damaged by lygus bugs at the berry stage and excluded those whose damage may have been caused by insufficient pollination. To estimate the crop loss, we categorized both unripe and ripe berries with damage levels 2 and 3 as damaged, representing berries that would be culled at harvest (Table 1).

## 2.7 Statistical methods

Statistical analyses were performed using the open source statistical programming language R (R Core Team, 2019). Piecewise structural equation modeling (PSEM) tests hypothesized causal links among predictor variables, response variables, and intermediate variables (variables acting as both predictors and responses) (J. S. Lefcheck, 2016). PSEM differs from traditional structural equation modeling (SEM) in that it represents a path diagram as a set of individually evaluated linear equations (i.e., pieces), whereas traditional SEM relies on global estimation from the observed variance–covariance matrix of the entire model. The piecewise approach enables the PSEM to fit

hierarchical data with non-normally distributed errors, which is typical of ecological data.

The predictor variables, response variables, and intermediate variables in the PSEM are depicted in the path diagram (Figure 1). The terminal response variable is crop damage odds (the ratio of the probabilities of a berry being damaged versus undamaged). Landscape composition, local diversification and pest management practices, interaction effects between landscape factors and local diversification, and interaction effects between landscape factors and time (days since rain, discussed below) are the hypothesized fundamental predictor variables. Lygus abundance, natural enemy abundance, and natural enemy diversity are the hypothesized intermediate variables. To test for parabolic changes in the effect of local diversification at different values of landscape composition (i.e., the intermediate landscape complexity hypothesis), we included linear and quadratic terms of both landscape composition factors (woody and grassland) in their respective interaction terms with local diversification.

The R package *piecewiseSEM* accepts pieces in the form of linear equations based on the causal paths represented in Figure 1 (Lefcheck et al., 2023). A multi-model inference process based on AICc ranking was used to select these linear models (Symonds and Moussalli, 2011; Supplementary material). The PSEM consists of three pieces – one equation for each of the response variables (crop damage odds, natural enemy abundance, and lygus abundance). We hypothesized natural

TABLE 1 Strawberry damage categories.

Damage category	Definition
Undamaged	No visible damage
Lygus damage	Puckered flesh with fully developed achenes
Level 1	≤10% of surface damaged
Level 2	11–25% of surface damaged
Level 3	>25% of surface damaged

Levels 2 and 3 are considered unmarketable by growers and are culled during harvest. In this study, berries that showed Lygus damage at Levels 2 and 3 were categorized as “damaged”.

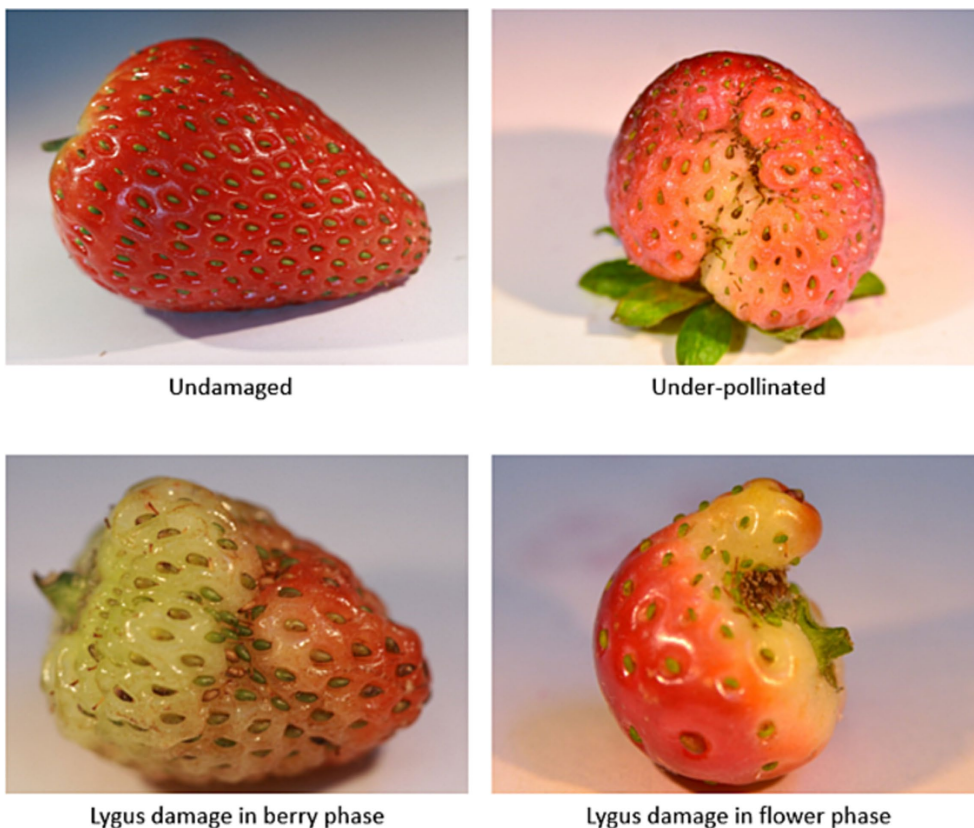


FIGURE 2 Representative strawberries showing the visual characteristics of different malformation types. Under-pollination and lygus damage in the flower phase show both puckered flesh (cat-facing) and under-developed achenes, while lygus damage in the berry phase shows puckered flesh with fully developed achenes. These characteristics were used to limit the category of damaged berries in this study to those that were damaged by lygus in the berry phase.

enemy diversity as a predictor variable of crop damage odds, but it was rejected in the model selection process and therefore not included in the PSEM. All three pieces were generalized linear mixed models. The crop damage odds response variable was modeled using the binomial error distribution with R package *lme4* and the two abundance response variables were modeled using the quadratic parameterization of the negative binomial error distribution with R package *glmmTMB* (Bates et al., 2015; Brooks et al., 2017). For each response variable, we began with a full model including all hypothesized predictors, as well as the covariates of site size in hectares, days since rain (DSR), and DSR<sup>2</sup>. DSR was used in lieu of Julian date (day of year), which is often included as a covariate to account for phenological changes in arthropod communities. A rain day is defined by the United States Geological Survey as 1 mm of rain within a 24-h period (United States Geological Survey, 2007). We opted to use DSR because it is a more accurate proxy of phenology than Julian date in our study area's Mediterranean climate. We included DSR<sup>2</sup> to account for potential non-linear patterns in arthropod phenology which have been detected across seasons in California (Leong et al., 2016). A random effect of site-year was included in all models to avoid pseudo-replication. The site-year random effect, rather than separate site and year effects, was used because a subset of sites (10 per year) was not sampled in both years. Based on the full model structures for each response variable, model structures containing all combinations of fixed effect terms were generated and ranked by AICc using the R package *MuMIn* (Barton, 2024). Three model structures corresponding to the three response variables (Table 2) were then chosen from the top-ranked structures (Supplementary Tables S3–S5) and entered into the PSEM.

Because we expected that natural enemy abundance and lygus abundance would be correlated, but we had no hypothesis regarding the causal relationship between them, we ran three versions of the PSEM. The first included a correlated error between natural enemy and lygus abundance, representing the hypothesis that their correlation is driven by additional, unmeasured predictor variables (Shipley, 2000). The second and third versions represented the hypotheses that natural enemy abundance drove lygus abundance and vice versa. We then selected the model with the best fit according to the Fisher's C statistic (Lefcheck, 2016; Shipley, 2009, 2013).

As commonly found with count data, the natural enemy and lygus abundance data were overdispersed; the negative binomial error distribution was used to account for overdispersion (Brooks et al., 2017; Hardin and Hilbe, 2007). No significant spatial autocorrelation was found in the residuals of the linear model pieces according to the Moran's I test in R package *ape* (Paradis and Schliep, 2019). We calculated variance inflation factors (VIF) for each linear model to confirm the absence of multicollinearity (all VIFs  $\leq 5.0$ ). Overdispersion, uniformity, outliers, and zero inflation for each of the linear models were tested using R package *DHARMA* (Hartig and Lohse, 2022).

### 3 Results

We collected 5,071 natural enemy specimens (total individuals across all natural enemy categories) and 1,347 lygus bugs. We surveyed a total of 32,706 berries, of which 3,518 (~11%) had level 2 or 3 lygus bug damage. The PSEM confirmed that landscape-scale habitats had both direct and indirect effects on crop damage odds (Figure 3; Supplementary material). At  $\alpha = 0.05$ , grassland proportion directly

influenced berry damage odds (linear component  $p = 0.03$  and quadratic component  $p < 0.001$ ; Figure 4A). Woody proportion had a direct positive effect on natural enemy abundance ( $0.7 \pm 0.3\%$ ,  $p = 0.05$ , Figure 4B), and grassland proportion had a similar, nearly significant effect ( $1.2 \pm 0.7\%$ ,  $p = 0.07$ ). The interaction between proportion grassland and the quadratic term of days since rain significantly influenced lygus abundance ( $p = 0.01$ , Figure 5A).

We detected a direct effect of the interaction between local diversification and woody proportion on berry damage odds ( $p = 0.04$ ). Logistic regression requires a transformation of the original response variable (expressed in probability or odds) into logit space (log odds) in order to linearize the regression equation. A consequence of this transformation is that significant interactions in logit space may not always reflect significant effects in probability space. The significance of interaction effects in probability space are calculated using simple slopes, which are the slopes of the predictor variable (here, local diversification) at specified values of the moderator variable (here, woody proportion). When berry damage odds are expressed as probabilities, the simple slopes of local diversification at  $\pm 1$  S.D. of woody proportion are not significantly different from zero ( $\beta = 0.04 \pm 0.22$ ,  $p = 0.87$  at  $+1$  S.D.;  $\beta = -0.05 \pm 0.20$ ,  $p = 0.82$  at  $-1$  S.D.). The simple slope of local diversification at mean woody proportion was also not significant ( $\beta = -0.24 \pm 0.16$ ,  $p = 0.13$ ), but we detected a pattern showing that the slope of local diversification is highest in magnitude at an intermediate value (26%) of woody proportion (Figure 5B).

Farm-scale pest management influenced berry damage odds directly as well as indirectly through its effects on arthropod communities. Both natural enemy ( $-19 \pm 8\%$ ,  $p = 0.007$ ) and lygus ( $-30 \pm 13\%$ ,  $p = 0.003$ ) abundance decreased with insecticide intensity (Figure 6A). Tractor vacuum frequency decreased natural enemy abundance ( $-19 \pm 9\%$ ,  $p = 0.028$ , Figure 6B), but had no effect on lygus abundance. Since higher lygus abundance directly increased berry damage odds ( $5.2 \pm 0.8\%$ ,  $p < 0.001$ ), while natural enemy abundance had the opposite effect ( $-1.5 \pm 0.4\%$ ,  $p < 0.001$ , Figure 7), pest management practices indirectly affected berry damage via effects on these arthropod groups. Insecticide intensity also directly reduced berry damage odds ( $-18 \pm 8\%$ ,  $p = 0.008$ ).

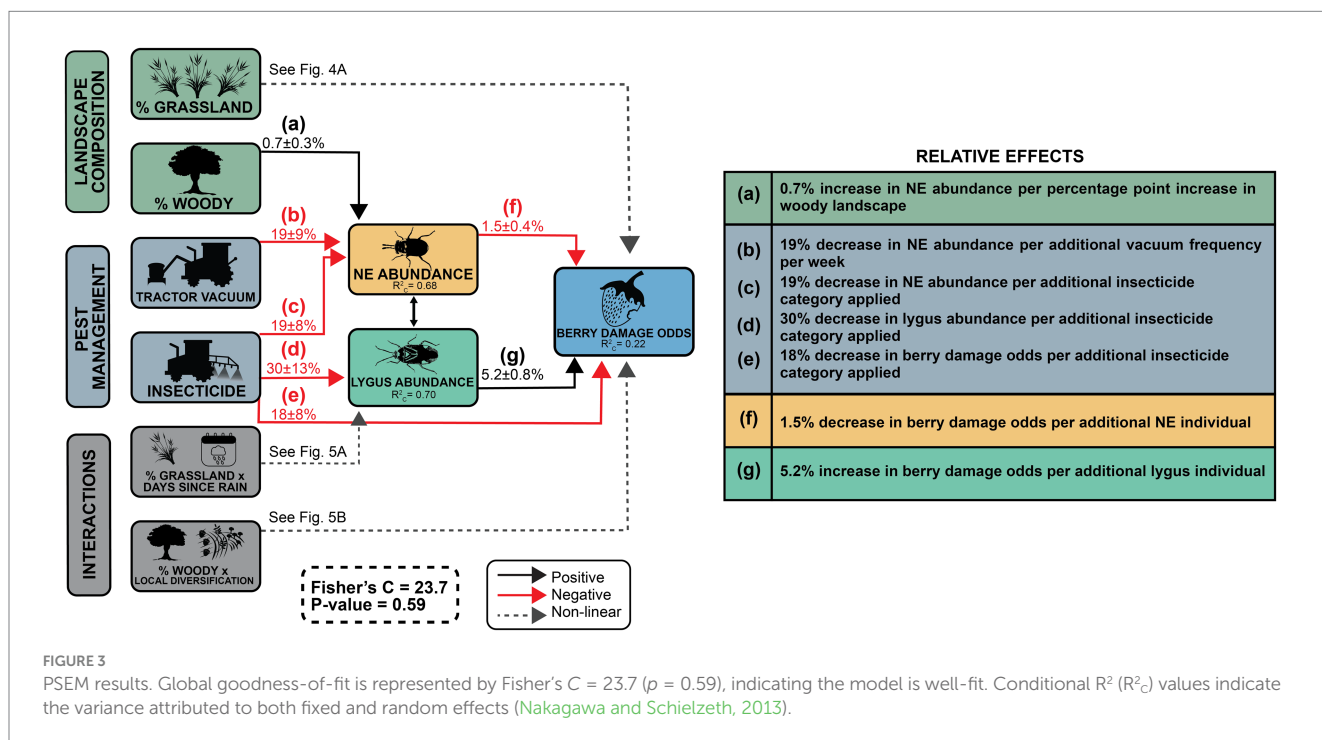
Of the three PSEM models, the correlated error model (Figure 3; Supplementary material) had the best fit, with Fisher's  $C = 23.7$  with  $p$ -value = 0.59, indicating that unmeasured factors drive both natural enemy abundance and lygus abundance more than they drive each other.

### 4 Discussion

Our results reveal that multi-scalar habitat complexity and local management practices influence crop loss directly as well as indirectly through their direct effects on arthropod communities. We found that natural enemy abundance decreased crop damage odds while lygus abundance had the opposite effect (Figure 7), evidence in support of the enemies hypothesis (top down control). Because our definition of berry damage aligns with the level of damage at which berries are culled at harvest, berry damage probability (Figures 4A, 5B, 7) can be interpreted as the estimated rate of crop loss. As we expected based on the contrasting plant communities between woody habitat and grasslands, natural enemy abundance, but not lygus abundance,

TABLE 2 Linear model PSEM pieces.

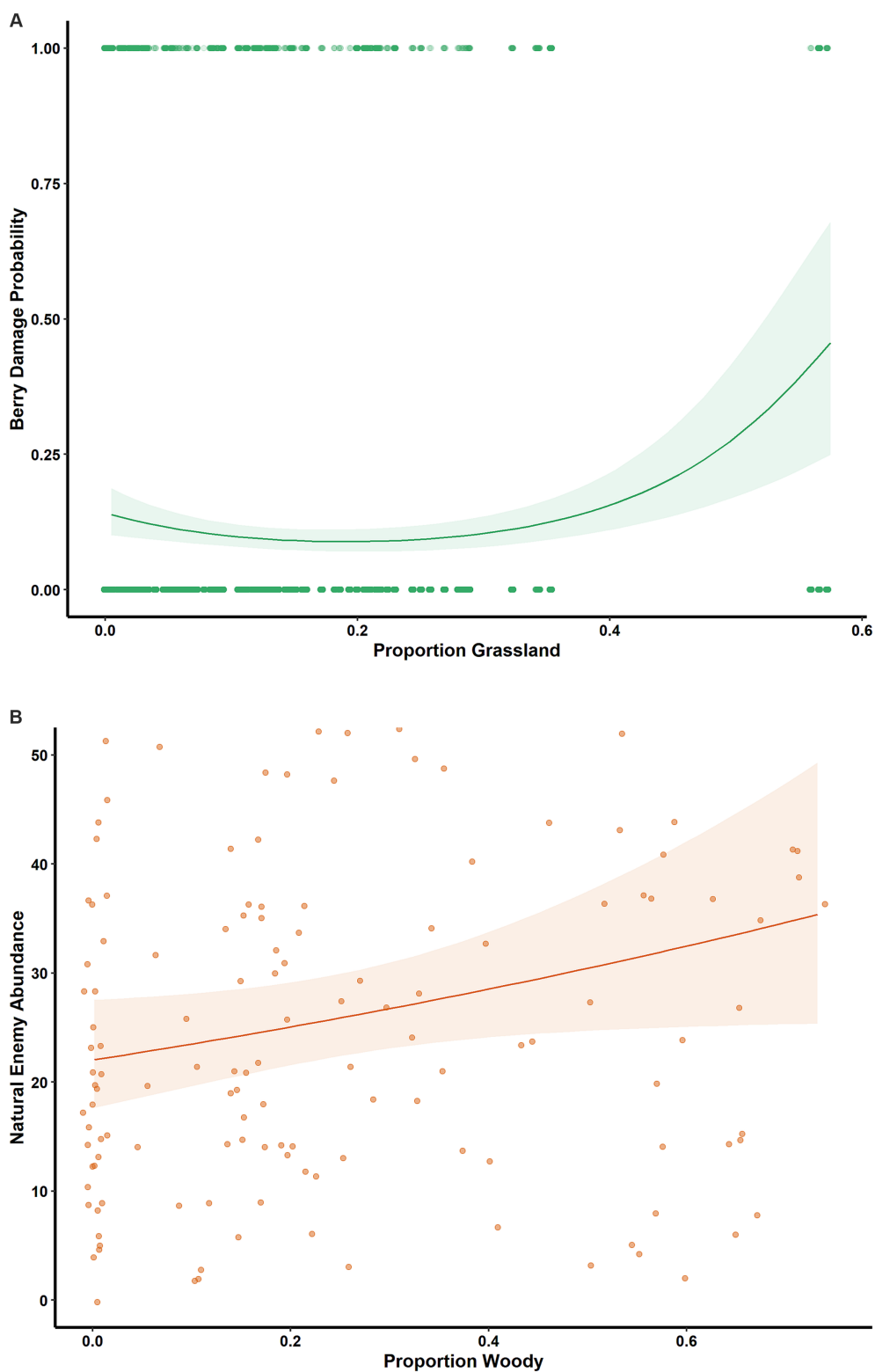
Response variable	Predictor variables (fixed effects)	Random effects	Error distribution
Crop damage odds	Natural enemy abundance, lygus abundance, proportion woody (linear and quadratic) X local diversification, proportion grassland (linear and quadratic), days since rain (linear and quadratic) X proportion woody, insecticide index	Sampling station nested within site_year	Binomial
Natural enemy abundance	Proportion woody, proportion grassland, tractor vacuum frequency, insecticide index	Site_year	Negative binomial (quadratic parameterization)
Lygus abundance	Proportion grassland (linear and quadratic), local diversification, days since rain (linear and quadratic) X proportion grassland, insecticide index, farm size	Site_year	Negative binomial (quadratic parameterization)



increased with woody proportion in the landscape (Figure 4B). A significant interaction effect with days since rain shows that varying levels of grassland proportion influence lygus abundance differently as the growing season progresses (Figure 5A). We uncovered evidence for the intermediate landscape complexity hypothesis in the form of an interaction effect between woody proportion and local diversification on crop loss, showing that the effect of local diversification on crop loss has highest magnitude at an intermediate value of woodland proportion (Figure 5B). Regarding pest management practices, insecticides decrease natural enemy and lygus abundance, while tractor vacuuming decreases only natural enemy abundance (Figure 6). These results illustrate the benefits of habitat complexity at landscape and local scales on pest control services, highlighting the importance of preserving and restoring native woody vegetation, managing exotic weeds, utilizing farm diversification practices and accounting for the ecological costs of pest management.

Based on our knowledge of lygus damage in strawberries and the focus among extension researchers and growers on lygus bugs as the primary cause of berry malformation in this region, we had

expected environmental effects on crop loss to be mediated entirely by lygus and natural enemy abundance. However, we found a direct effect of grassland proportion on crop loss (Figure 4A). We have two hypotheses regarding this unexpected direct effect. First, despite our best efforts, we may have included under-pollinated berries in our data. The results of the greenhouse experiment informed our protocol for visually distinguishing between malformation caused by under-pollination and lygus damage. Although we intended to limit our analysis to berries that were only lygus-damaged, our visual inspection could not have been perfect. Therefore, the changes in crop loss associated with grassland proportion may result in part from differences in pollination services. Prior work in this region has shown positive effects of landscape-scale forests and chaparral (i.e., woody habitat) on pollination services in crops, but these studies did not investigate the effects of pastures and non-native grasslands (Klein et al., 2012; Kremen et al., 2004). Studies on the interactions between pollinators, native plants, and invasive plants have shown that pollination of native plant species can be compromised in areas of high invasive density due to

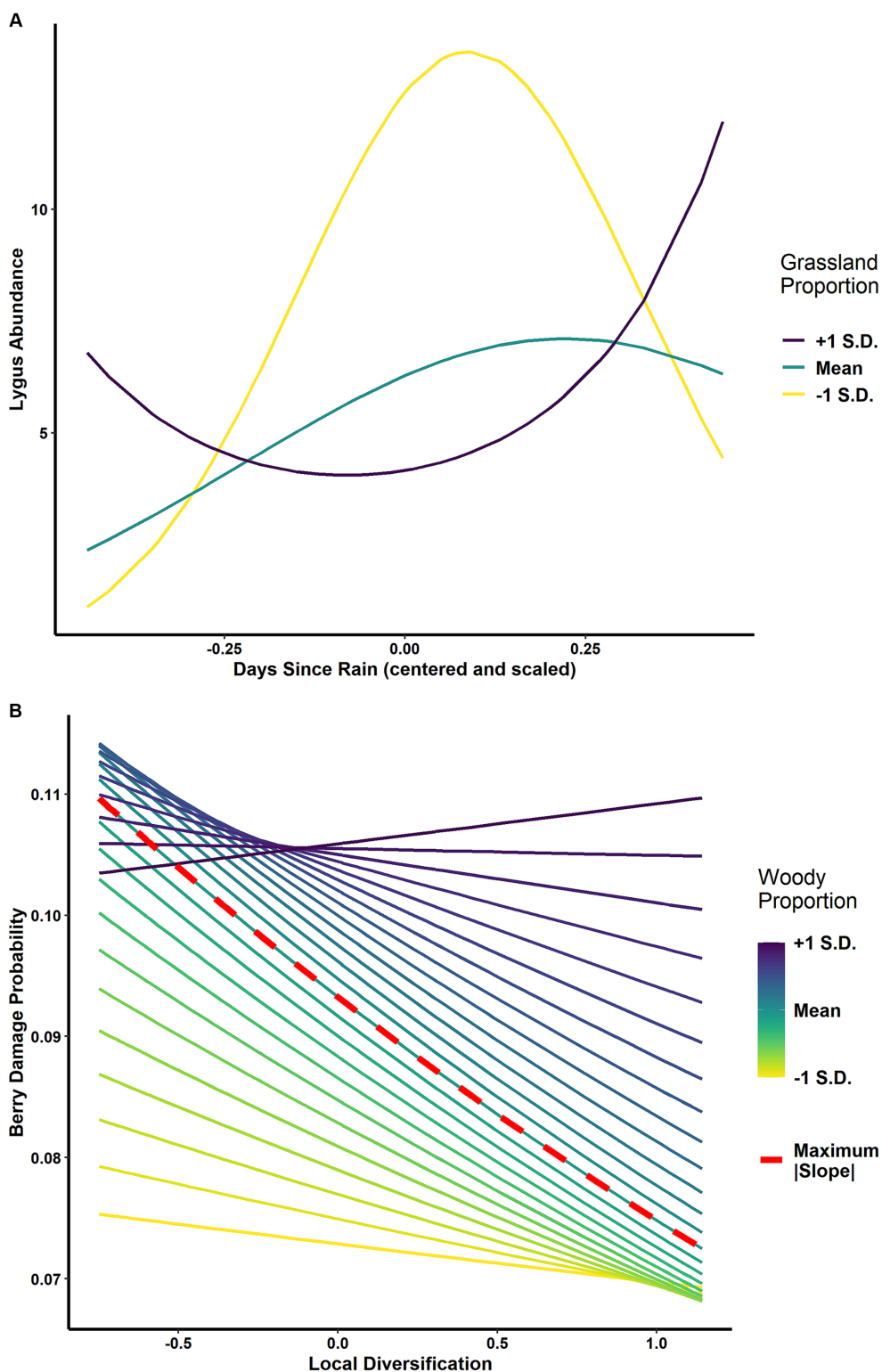


**FIGURE 4** Landscape-scale effects. **(A)** Estimated effect of grassland proportion on berry damage probability ( $p_{linear} = 0.03$ ;  $p_{quadratic} < 0.001$ ); generalized linear mixed model with binomial error distribution; **(B)** Estimated effect of woody proportion on natural enemy abundance ( $0.7 \pm 0.3\%$ ,  $p = 0.05$ ); generalized linear mixed model with negative binomial error distribution.

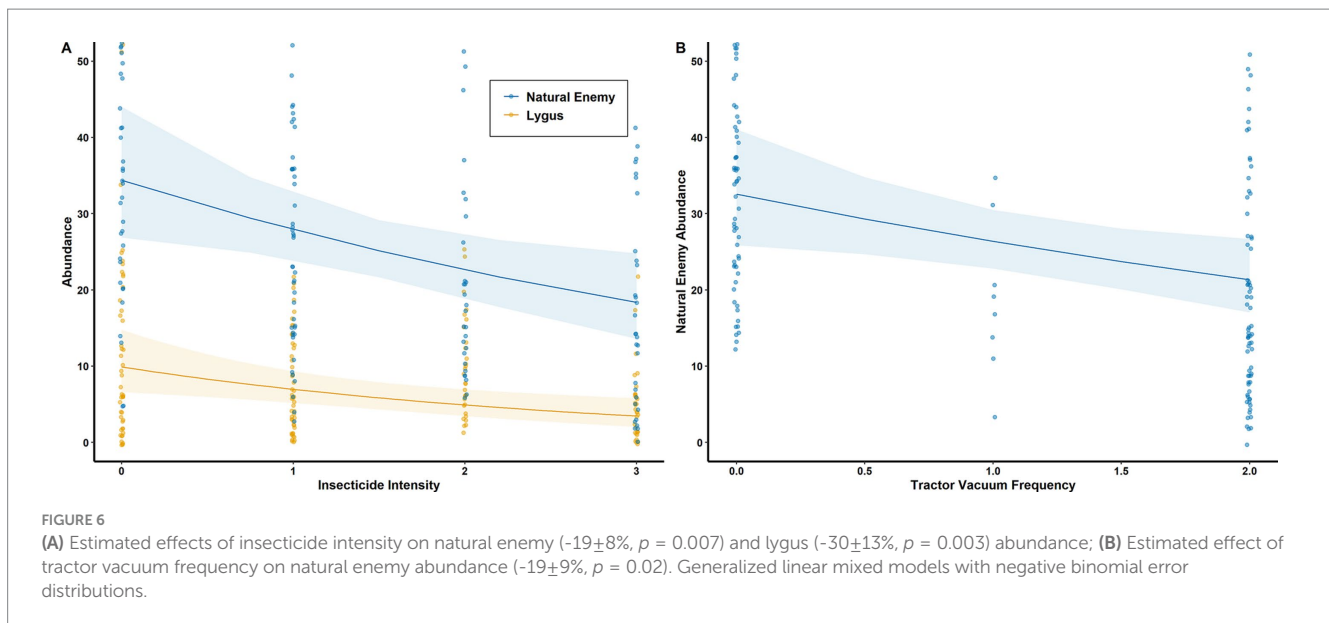
decreased flower visits and increased heterospecific pollen deposition (Bartomeus et al., 2008; Bruckman and Campbell, 2016; King and Sargent, 2012). Furthermore, species sensitive to pollen

limitation may be at higher risk of negative impacts from invasive plants (Dietzsch et al., 2011). In strawberry crops, excluding pollinators has been found to double the probability of berry





**FIGURE 5** Landscape-scale interaction effects. **(A)** Estimated interaction effect between grassland proportion and days since rain on lygus abundance ( $p_{quadratic}=0.01$ ), visualized as the effect of days since rain on lygus abundance at +/- 1 S.D. and mean values of grassland proportion; generalized linear mixed model with negative binomial error distribution; **(B)** Estimated interaction effect between woody proportion and local diversification on berry damage probability ( $p_{quadratic}=0.04$ ); generalized linear mixed model with binomial error distribution. Lines represent simple slopes (effect of local diversification on berry damage) at values of woody proportion from +1 S.D. to -1 S.D.; the dashed red line indicates the highest magnitude simple slope ( $\beta=-0.24\pm 0.16$ ,  $p=0.13$ ), which occurs at woody proportion=0.26; generalized linear mixed model with binomial error distribution.



malformation (Sciligo et al., 2022), and insect pollination can increase the average commercial value of marketable fruits by 92% over self-pollination (Wietzke et al., 2018). Future work in this region targeting the effect of non-native grasslands on native pollinators and pollination services may confirm that under-pollination decreases strawberry quality in landscapes dominated by exotic weeds and grasses.

Second, the direct effect of grasslands on berry damage odds may indicate that non-lygus species induce visually similar berry malformation. Researchers recently found that an “emerging pest” called the strawberry seed bug (*Neopamera bilobata*) causes cat-facing in Florida-grown strawberries, (Talton et al., 2020). Furthermore, the thrips species *Frankliniella occidentalis*, present in California, has recently been observed to cause similar malformations (Strzyzewski et al., 2021), a finding contrary to conventional wisdom in the Central Coast region (Allen and Douglas, 1974; Bolda, 2022). These studies imply that the economic importance and damage characteristics of pest species remain controversial and that relationships between arthropod pests and crops are dynamic. The direct effect of insecticide on berry damage odds lends further support to this hypothesis, suggesting that insecticides negatively impact non-lygus pests that cause visually similar damage. While researchers and growers have historically focused on lygus bugs as the primary cause of berry malformation in this region, further experiments that expose strawberry flowers and fruit to understudied pest species may reveal additional economically important strawberry pests.

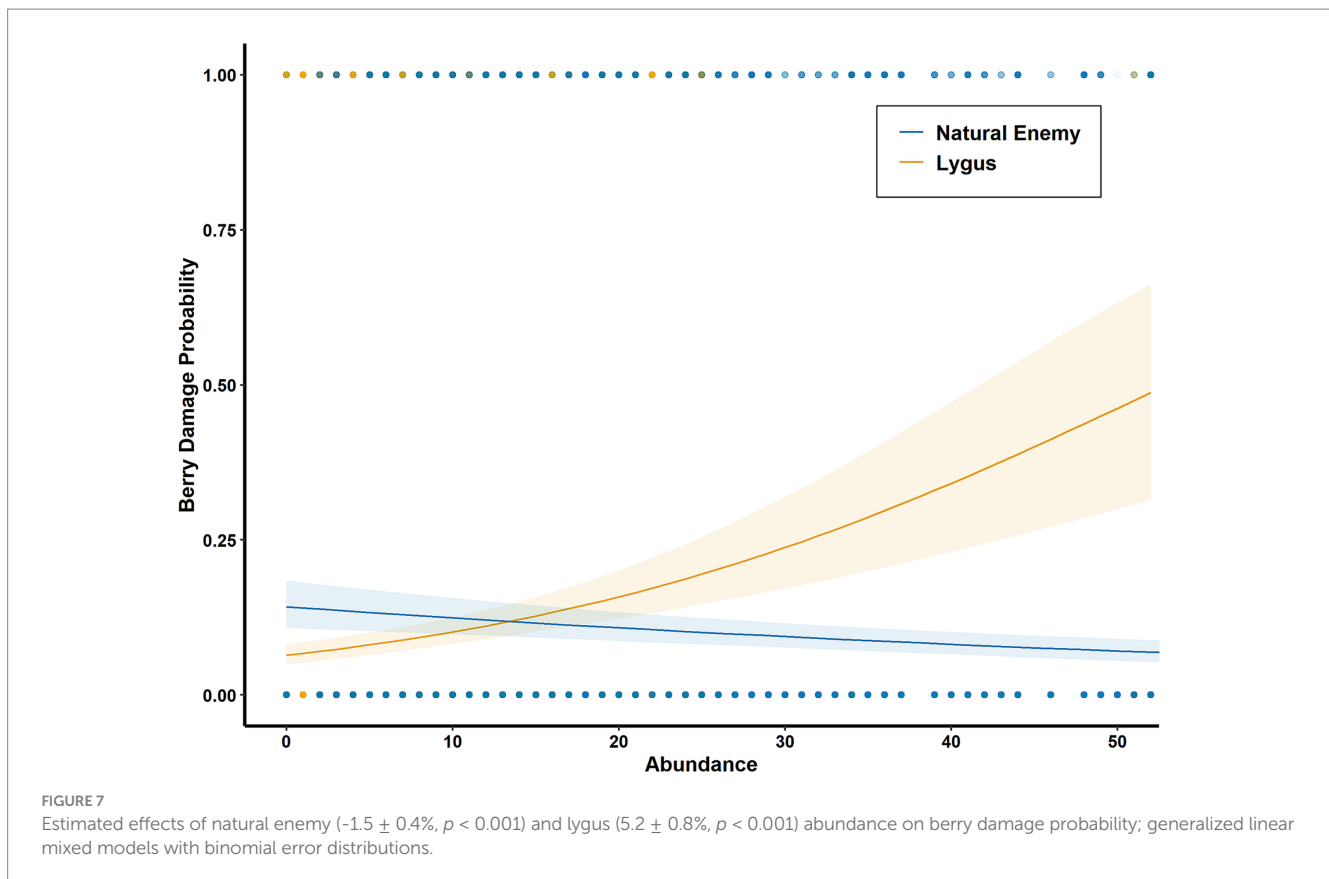
Grasslands in this region are dominated by exotic forbs and grasses known to be lygus hosts and were hypothesized to increase lygus abundance in nearby fields via bottom-up effects (i.e., the resource concentration hypothesis). Furthermore, we expected these effects to strengthen as weeds desiccated during the dry season, inducing more lygus bugs to seek the greener pastures of irrigated strawberry crops. The interaction between days since rain and grassland on lygus abundance supports the hypothesis that high grassland proportion promotes early lygus colonization of strawberry

fields and feeds population growth throughout peak harvest season (Figure 5A). In contrast, at mean and low levels of grassland proportion, lygus abundance starts low but increases through mid-season before decreasing into late season.

The different effects of high and low grassland proportion in mid-season may be related to the role of grasslands as sources of natural enemies and the dynamic interactions between natural enemies and lygus. We detected a relatively strong, nearly significant positive effect of grassland proportion on natural enemy abundance, consistent with a previous study suggesting that grasslands may be a source of natural enemies as well as lygus bugs (Nieto et al., 2023). In general, natural enemies are attracted to sites with high food resources, commonly resulting in positive correlations between natural enemy and pest abundance (Eubanks, 2001; Lundgren et al., 2015). Here, natural enemies may follow lygus bugs into crop fields and eventually suppress lygus abundance where grassland proportion is relatively low. However, at high levels of grassland, where early-season lygus abundance is high and substantial lygus migration into crops continues as weeds desiccate, natural enemy suppression may never overcome lygus population growth. In agreement with previous studies in this region (Morandin et al., 2014; Nieto et al., 2023), our results reinforce the benefits of preserving and restoring native woods and shrubs while controlling invasive grasses and flowering weeds; relative to each other, woody habitats tend to support beneficial insects while grasslands tend to be sources of pests.

We wish to highlight here the importance of pest and natural enemy population dynamics in the investigation of pest control services (Costamagna et al., 2015; Gardiner et al., 2009). In particular, future work should examine the environmental factors and grower actions that would delay pest establishment and facilitate earlier colonization of crops by natural enemies, reducing the risk of lygus outbreaks (Le Gal et al., 2020). Studying the arthropod population dynamics associated with native plant species that support natural enemies in this region could be a fruitful starting point (Lundin et al., 2019).

In addition to the effects of landscape composition, we aimed to explore the relative contribution of local diversification to



changes in arthropod communities and crop loss. The interaction between local diversification and woodland proportion exhibits evidence of the intermediate landscape complexity hypothesis with respect to crop loss (Figure 5B). Recently, systematic reviews and meta-analyses have found that it is critical to maintain 20–25% or more of natural and semi-natural habitats within agricultural working landscapes to maintain a wide variety of ecosystem services, including, but not limited to pest control (Garibaldi et al., 2021; Mohamed et al., 2024). Interestingly, our finding that diversification practices enhanced pest control at approximately the same proportion of natural/semi-natural habitat provides additional evidence for multi-scalar synergies (Estrada-Carmona et al., 2022) and reinforces both the policy goal of retaining or restoring ~20% of natural habitat within working lands and promoting on-farm diversification practices.

Despite the interaction effect between woody landscape and local diversification, we found no main effect of local diversification on either natural enemy or lygus abundance. These effects may have been obscured by the effect of small-scale weedy refuges, such as ditches, field edges, and roadside vegetation common in the region. These features are largely populated by exotic annual plants such as wild mustard (*Brassica* spp.), wild radish (*Raphanus raphanistrum*), and shepherd's purse (*Capsella bursa-pastoris*), all known to be favored hosts of lygus bugs as well as other hemipteran pests (Fye, 1982; Malcolm, 1953). In some cases, these plants even provide enemy-free spaces for certain pest species (Chaplin-Kramer et al., 2011a). Although their surface area is miniscule, the ubiquity and linear configuration of these weedy strips may create a highly

connected habitat across the landscape for certain organisms, generating outsized impacts on arthropod abundance and diversity that obscure the effects of local diversification (Haan et al., 2020; Thiele et al., 2018). Landscape configuration is relatively understudied in comparison to landscape composition, but recent studies have shown its influence on pest control services, and future work in this region controlling for linear weedy features may uncover relationships between local diversification and arthropod communities (Ali et al., 2023; Martin et al., 2016, 2019).

Local pest management techniques (insecticide application and tractor vacuuming) were included as covariates to address our primary research questions, but they also produced notable effects on arthropods (Figure 6) and berry damage odds (Figure 3). Despite the putative efficacy of insecticides in reducing crop loss, the goal of pest management is not merely to reduce pest abundance but to enhance pest control, and the effectiveness of insecticide application must be qualified by its negative impact on natural enemy communities. Insecticide use may have depressed natural enemy populations over a long time period, reducing their current contributions to pest control. Even when toxicology studies indicate similar insecticide impacts on natural enemy and pest species, natural enemies are generally more severely impacted due to population characteristics such as longer generation times and lower fecundity (Roubos et al., 2014; Stark et al., 2004). Sub-lethal effects of insecticides, including behavioral changes, can also impose greater harm on natural enemy populations than toxicological results suggest (Desneux et al., 2007). The contributions of insecticides to pest control must therefore

be qualified by the possibility of past, cumulative impacts on natural enemy populations. These ecological costs must not be neglected when calculating the total cost of organic-compliant insecticide application.

We found no evidence that tractor vacuuming decreases lygus bug abundance or crop loss, but its negative effect on natural enemies is clear (Figure 6B). Organic strawberry growers may resist the idea that tractor vacuuming does more harm than good because it is touted as one of their few tools against lygus bugs (Wells et al., 2020). According to a number of studies from the preceding decades, the efficacy of tractor vacuuming is limited at best, and has never been shown to conclusively reduce lygus damage under an economically acceptable level (Joseph and Bolda, 2018; Pickel et al., 1994; Rancourt et al., 2003; Vincent and Lachance, 1993). Although we cannot unequivocally state that tractor vacuuming is ineffective, our results reinforce the importance of accounting for negative ecological impacts such as removal of natural enemies and pollinators (Chiasson et al., 1997) in the costs of tractor vacuuming, along with the economic costs of fuel, labor, maintenance (\$1,351 per acre per year) and equipment (\$12,937 per tractor per year) (Bolda et al., 2024). To put these costs in context, organic strawberry growers in this region earn an average of \$8,555 in profit per acre per year, on \$112,000 of revenue (Supplementary material).

## 5 Conclusion

Our results offer many considerations for pest management in strawberry production. First, habitat complexity in the farming landscape, which is out of most individual growers' control, has a large influence on crop loss. In our study system, woody habitats and grasslands had opposite effects on crop loss. Second, local diversification, within the purview of some growers, may reduce crop loss, but this effect is highest near intermediate amounts of woody habitat, which are beneficial in their own right for maintaining a wide variety of critical ecosystem services. Third, on-farm pest management practices that are commonly used in this study system such as organic-compliant insecticides and tractor vacuuming may cause more harm than good, particularly over the long term, due to their negative impacts on natural enemies.

For regional land managers, our study provides evidence that preserving and promoting native woodlands, shrubs, and chaparral can be beneficial for natural pest control. Because they tend to be sources of pests, grasslands dominated by exotic annuals may be fertile ground for replacement with native flora.

As of 2016, organic certification in the United States charges growers with specific mandates to conserve and maintain natural resources, including biodiversity. The USDA National Organic Program sets rules for organic certification compliance and requires use of pest control methods that maintain or improve on-farm biodiversity to the greatest extent possible. Our results show that growers can adhere more closely to these rules by implementing pest control strategies that focus on building natural enemy populations rather than single-mindedly targeting pests. We hope that our results will advance advocacy for enhancing the U.S. Farm Bill's conservation programs, including the Environmental Quality Incentives Program, The Regional Conservation and Partnership Program, and the Conservation Reserve Program. These programs

help growers and regional land managers maintain and restore multi-scalar natural habitats and biodiversity that will bolster our efforts in creating a healthy, sustainable, and productive agricultural system.

## Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

## Author contributions

AL: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Supervision, Validation, Visualization, Writing – original draft. DG: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing – review & editing. AS: Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing – review & editing. KG: Data curation, Investigation, Methodology, Visualization, Writing – review & editing. TC: Data curation, Investigation, Methodology, Writing – review & editing. GJ: Investigation, Writing – review & editing. CK: Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing – review & editing.

## Funding

The author(s) declare that financial support was received for the research, authorship, and/or publication of this article. The United States Department of Agriculture (NIFA Project # 2015–67019–23147/ 1005662), the CS Fund, the Robert and Peggy van den Bosch Memorial Scholarship, the Berkeley Fellowship for Graduate Study, and the Margaret C. Walker Fund provided funding for this study.

## Acknowledgments

Erin Berg, Maggie Deng, David Hung, Elizabeth Ordeman, Shuhan Song, and Candace Yee contributed their efforts toward categorizing, counting, and storing specimens. Sara Winsemius deserves special thanks for her multiple roles as lab manager, keeper of specimens, and invaluable field team member. We appreciate Michael Seagraves, Ryan Kennedy, and Diego Nieto at Driscoll's in Watsonville, California for their help in contacting growers and providing comments on preliminary results. Finally, we express our

sincere gratitude to all of the growers in the Santa Cruz -Watsonville-Salinas area who shared their expertise, allowed our field teams to collect data on their farms, and offered their time to coordinate our field visits. Their participation and dedication to science made this work possible.

## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) declared that they were an editorial board member of *Frontiers*, at the time of submission. This had no impact on the peer review process and the final decision.

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## Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fsufs.2024.1336888/full#supplementary-material>

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