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RESEARCH ARTICLE

Changes in arthropod communities mediate the effects of landscape composition and farm management on pest control ecosystem services in organically managed strawberry crops

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Abstract

1. Landscape composition and local diversification practices such as polyculture, cover cropping and hedgerows may promote natural pest control by benefiting natural enemy communities on farms. Our study employs piecewise structural equation modelling (PSEM) to test causal hypotheses regarding the effects of landscape composition and local diversification practices on arthropod communities and pest control ecosystem services.
2. We sampled 27 organic strawberry fields in California's Central Coast region in 2015 and 2016 (17 repeated between years) for a total of 37 distinct sites across years. The sites were selected along orthogonal gradients of landscape composition and local diversification practices. We also investigated the effects of two common pest management practices. At each site, we sampled arthropod communities using a handheld vacuum and performed sentinel prey experiments using the pest species *Lygus hesperus* to estimate pest control levels.
3. At the landscape scale, proportion of woody habitat increased natural enemy abundance; at the local scale, on-farm diversification practices increased natural enemy diversity.
4. Insecticides and tractor vacuuming, aimed at controlling pests, were indirectly detrimental to pest control services. Both practices decreased natural enemy abundance, and while insecticides also decreased pest abundance, vacuuming did not.
5. Natural enemy abundance and diversity increased pest control levels, while pest abundance had the opposite effect. The PSEM results confirmed our hypotheses that landscape and local effects on pest control are mediated through changes in arthropod communities.
6. *Synthesis and applications*. At the landscape scale, higher proportions of woody habitat are associated with greater natural enemy abundance, which increases pest control levels in organic strawberry crops. When promoting pest control ecosystem services is a policy goal, regional planners should prioritize the conservation and restoration of woodlands in agricultural landscapes. At the local scale, actions by individual growers *can* impact pest control services. For many growers,

adopting practices that promote on-farm plant diversity may be a feasible solution for increasing pest control levels while avoiding the environmental and economic costs imposed by insecticide application and tractor vacuuming.

KEYWORDS

agroecology, biodiversity, conservation biological control, diversification practices, lygus, organic strawberry, pest management, piecewise structural equation modelling

1 | INTRODUCTION

Biological pest control is an ecosystem service critical to cultivating more sustainable agricultural production (Kremen & Miles, 2012). The risks to ecosystems and human health imposed by chemical insecticides can be mitigated by expanding the role of biological pest control (Bale et al., 2008; Gill & Garg, 2014; Rosa-Schleich et al., 2019). Arthropod communities in agricultural landscapes, including agricultural pests and their natural enemies (predators and parasitoids), are key to understanding the effectiveness of biological pest control (Dainese et al., 2019; Gurr et al., 2019). Both landscape composition and local, farm-level plant diversity affect these communities, but general patterns remain elusive for landscape and local effects on pests and pest control (Chaplin-Kramer, O'Rourke, et al., 2011). Rarely explored interactions between landscape composition and local practices may explain the inconsistencies among existing studies (Karp et al., 2018). Here, we present a study that quantifies the simultaneous effects of landscape composition, a local gradient in farm-scale diversification and local pest management practices on arthropod communities (the lygus bug and its predators) and pest control services, using piecewise structural equation modelling (PSEM) to test the causal inferences among these variables.

Within agricultural landscapes, larger amounts of natural habitat are hypothesized to support larger natural enemy meta-populations and reduce negative impacts caused by agricultural disturbances such as mechanized tilling, chemical fertilization and chemical pesticide application (Begg et al., 2017). Meta-analyses have shown that natural enemy populations (abundance and/or diversity) and predation/parasitism rates consistently benefit from higher landscape complexity (Chaplin-Kramer, O'Rourke, et al., 2011; Veres et al., 2013), and conversely that landscape simplification tends to reduce top-down pest control (Rusch et al., 2016). Natural enemy activity generally responds positively to both woody and herbaceous habitats (Alignier et al., 2014; Bianchi et al., 2006; Gardiner et al., 2009). However, in some cases landscape-scale woody habitat increases predator abundance while grassland proportion has no effect (Janković et al., 2017). Furthermore, studies exploring the effects of landscape complexity on pest populations remain inconsistent (Karp et al., 2018), likely due to broad natural habitat categories that ignore the different effects of distinct habitat types on various trophic levels (Martin et al., 2013; Redlich et al., 2018; Veres et al., 2013). In a study where semi-natural habitats were categorized as woods, grasslands and hedges, the authors noted that even finer classifications would be needed to improve the analysis because the ecological effects of different types of grasslands may have confounded the results (Alignier et al., 2014). Moreover, in Australia, studies have consistently shown that the quality of non-crop habitats is important; native plants are associated with lower pest abundance and higher natural enemy abundance, while exotic weeds are associated with more pests (Gagic et al., 2018). Perhaps more importantly, most landscape-scale pest control studies neglect the local factors that may also drive changes in arthropod communities and ecosystem services (Karp et al., 2018; Tscharntke et al., 2012; but see Jonsson et al., 2015; Wilson et al., 2017). At local scales, monocultures tend to increase pest abundance (Root, 1973) while polycultures generally suppress herbivores, enhance natural enemy populations and suppress crop damage (Letourneau et al., 2011). However, many locally focused studies failed to account for surrounding landscape composition.

Beyond polyculture, crop and non-crop diversification on farms can include a wide array of practices over space and time, such as crop rotation, cover cropping, hedgerow addition and others, that may influence pest control (Kremen & Miles, 2012). Most studies testing the effects of local diversification on pest control are limited to one practice such as floral strips, beetle banks or hedgerows (Balmer et al., 2014; Balzan & Moonen, 2014; Midega et al., 2014; Tschumi et al., 2015, 2016). Studying a single practice can be valuable when specific practices are incentivized by regional policies such as Europe's agro-environment schemes (AES), but in many jurisdictions, including much of the United States, growers may implement various combinations of practices. We found no studies that explored how pest control is affected by a gradient of on-farm plant diversity created by differential adoption of diversification practices. One study that explored the interaction between local practices and landscape composition, for example, used only a binary category for local practices—AES versus no AES (Concepción et al., 2012). Further, studies that tested the effect of local factors on pest control often classify farm sites with a simple organic/conventional dichotomy (Letourneau & Goldstein, 2001; Martin et al., 2016), obscuring the reality that local diversification levels can vary widely within these categories. On one end of the organically managed spectrum are monocultures at industrial scales, using organic-certified inputs perceived to maximize production and minimize risk. At the other end are diversified farms that reach beyond organic certification baselines, using a wide variety of practices to promote biodiversity and sustainable land use (Guthman, 2014). Our study was restricted to

organic-certified farms, and accounted for the range of diversification practices among them by characterizing farms along a gradient of local diversification. This gradient is a more accurate proxy than the organic/conventional distinction because it is a continuous variable reflecting a spectrum of on-farm plant diversity.

Local practices on these farms also include pest management through insecticide application and physical pest removal. Although perceived as relatively benign, organic-certified insecticides acutely harm important natural enemy species (Biondi et al., 2012, 2013; Biondi, Mommaerts, et al., 2012). In organic strawberry fields, growers are limited to a short list of organic compliant insecticides, leading many farmers to complement insecticides with tractor-mounted vacuums that aspirate and destroy the arthropods that pass through the vacuum blades. Tractor vacuuming is a commonly used pest control method in California and some other strawberry-growing regions (Pickel et al., 1994, 1995; Swezey et al., 2007). Although perceived by growers as effective, tractor vacuuming may not prevent pest abundances from reaching economic thresholds (Pickel et al., 1994), and effects on pest abundance and crop damage are inconsistent (Rancourt et al., 2003; Vincent & Lachance, 1993). Moreover, tractor vacuums have been shown to negatively impact beneficial insects (Chiasson et al., 1997). Despite its costs (both economic and ecological) and equivocal efficacy, tractor vacuuming continues to be recommended by the California Strawberry Commission (2019).

Most previous work on pest control services has been limited by the difficulty of testing causal hypotheses. Correlative methods such as linear regression are unable to disentangle causal relationships when predictor variables are correlated. However, testing hypotheses about direct and indirect correlations among variables may enable researchers to make stronger causal inferences, leading to more specific guidance for farmers and regional planners. Towards this end, a recently developed statistical method called PSEM (Lefcheck, 2016) has been applied to investigate the cascading effects of landscape and local effects on arthropod communities and pest damage (Flores-Gutierrez et al., 2020; González et al., 2020). Piecewise SEM provides important advantages over the traditional, well-established structural equation modelling (SEM) method, including the ability to analyse data with hierarchical structure and non-normal error distributions (Lefcheck, 2016). One study found that native forest cover directly increased natural enemy abundance which directly increased soya bean yield (González et al., 2020); another found that intensive farm management directly decreased natural enemy abundance, and that natural enemy abundance directly increased papaya yield (Flores-Gutierrez et al., 2020). Our study uses PSEM to explore the effects of orthogonal landscape and local diversification gradients on arthropod communities and an indicator of pest control (Figure 1).

The primary objective of this study was to explore the relative importance of landscape and local factors, particularly diversification, on arthropod communities and pest control. We examined arthropod communities and conducted a sentinel prey experiment (as an indicator of pest control) at sites that were selected across orthogonal landscape composition and local diversification gradients. The sentinel prey experiment utilized the principal pest of organically grown strawberries in California's Central Coast, the lygus bug *Lygus hesperus*, which was shown to cause malformation in 26%–54% of berries in this region when pests management was not applied (Pickel et al., 1995). Generalist predators including *Geocoris* spp., *Nabis* spp. and *Orius* spp. are known to be important natural enemies of lygus bugs (Hagler et al., 2018; Leigh & Gonzalez, 1976; Perkins & Watson, 1972; Zink & Rosenheim, 2008). Other studies have shown that neuropterans, coccinellids, ants and spiders also prey upon lygus bugs (Hagler, 2011; Hagler & Blackmer, 2013; Young, 1989). Two species of specialist parasitoids have been studied in this region, but their pest control impact has not been comprehensively measured and our study does not examine parasitism (Norton & Welter, 1996; Pickett et al., 2009; Swezey et al., 2014). Biological control by

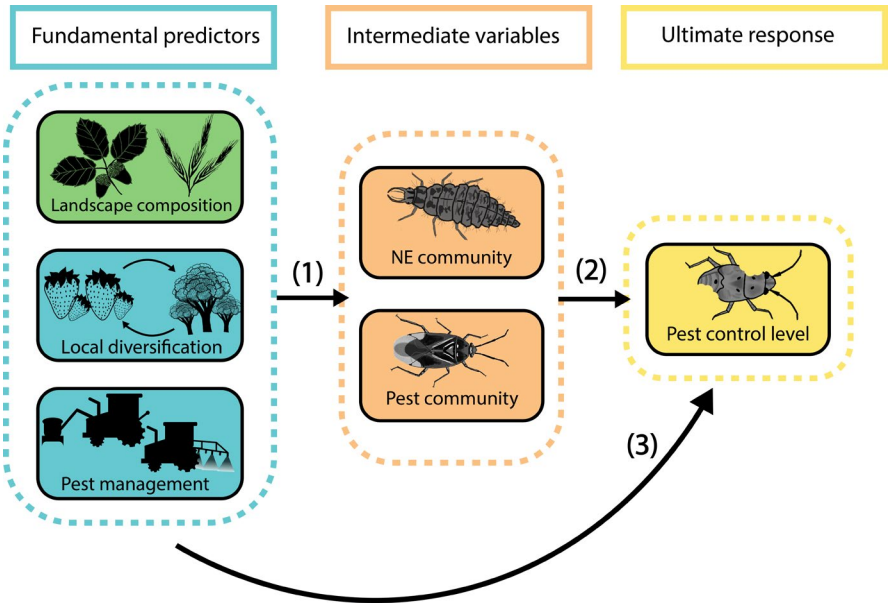

FIGURE 1 The piecewise structural equation modelling tests the causal paths between (1) the fundamental predictors and the intermediate variables; (2) the intermediate variables and the ultimate response; and (3) the fundamental predictors and the ultimate response

natural enemies contributes significantly to regulating pest damage in organic strawberry fields (Jacobsen et al., 2019; Kovanci et al., 2007; Krey et al., 2020).

We also analysed the effects of two farm-scale pest management practices employed by growers in the region, insecticide application and tractor-mounted vacuuming. At the landscape scale, we tested both proportion of woody habitat and proportion of grasslands to account for the potentially differential effects of these two natural habitats on the lygus bug and its arthropod predators. In our study system, neither woods nor grasslands are irrigated or otherwise managed. Woody habitats are remnants of native shrub and forest that provide diverse shelter and food resources. Grasslands are dominated by non-native annuals, many of which are known to be favoured hosts of lygus bugs (Fye, 1982; Scott, 1977); local farmers believe that lygus bugs migrate from grasslands into crops as the dry season progresses.

The second objective of this study was to test causal paths among landscape and local factors, arthropod communities and pest control. Specifically, we tested the extent to which landscape and local effects on lygus bug control are mediated through its arthropod predators. Because the grasslands in our system are low diversity and dominated by non-native annuals, we expected higher grassland proportions to provide relatively more resources to lygus bugs than natural enemies, hence increasing pest abundance by a greater factor than natural enemy abundance. Due to woody habitats being perennial, native and biodiverse, we expected higher woody proportions to have a relatively higher direct positive effect on natural enemies than on lygus bugs, resulting in higher levels of pest control. We expected higher local diversification to benefit natural enemy communities through the provision of diverse on-farm resources while providing relatively less benefit to lygus bugs, thus enhancing pest control levels. We expected both insecticides and vacuuming to reduce lygus bug and natural enemy populations. Because sentinel predation depends directly on the presence of ambient predators, we expected pest management practices to reduce pest control levels.

2 | MATERIALS AND 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 geographically diverse region characterized by high agricultural productivity, heavy pesticide use and unique biodiversity (Karp, Baur, et al., 2015; Karp, Gennet, et al., 2015; Karp et al., 2016). To document the impact of local and landscape factors on strawberry pests, their natural enemies and levels of biological pest control, we sampled 27 different fields in 2015 and 2016 (17 repeated between years) for a total of 37 different sites across 2 years. In both years, sampling took place between May and August, the peak harvest season for strawberries in this region. Local management practices tend to be consistent during these months. Although strawberries are perennial plants, growers manage them as annual crops in California's Central Coast (Samtani et al., 2019). Strawberries are often rotated with row crops, with the fields undergoing high-intensity ploughing each year. All sites were organically managed farms containing strawberry crops and were defined as contiguous cultivated areas under the same management. We obtained permission from each farm's respective owner/operator to sample on their sites. Sites ranged in size from 0.88 to 100.3 ha. Ethical approval was not required for this study.

2.2 | Local diversification index

A diversification index was created by scoring diversification practices comprising four crop-related and three non-crop-related elements (Table 1). Each of these diversification practices increased on-farm plant diversity. For each element, we scaled the observation state on each site, created a site by score matrix and entered this matrix into a principle component analysis (PCA) using function prcomp in the R package *stats* to create a composite index which was then used as a predictor variable in the PSEM (Armengot et al., 2011)

TABLE 1 Local diversification practices at each farm site were scored according to these values. Higher scores indicate greater plant diversity

Diversification practice	Description	Score
Crop diversity	Shannon diversity weighted by crop area	[0,1]
Crop rotational length	Continuous crop	0
	Two crops (short)	0.17
	Three crops (medium)	0.33
	≥Four crops (long)	0.5
	Prior long-term fallow	1.0
Perennial crop structure	None	0
	Shrubs only	0.33
	Trees only	0.66
	Both shrubs and trees	1.0
Cover crops	Absent (prior to strawberry)	0
	Present	1.0
Non-flowering non-crop plants	None	0
	Annuals	0.25
	Perennials	0.75
	Both annuals and perennials	1.0
Flowering non-crop plants	None	0
	Annuals	0.25
	Perennials	0.75
	Both annuals and perennials	1.0
Water features (defined as permanent water sources, which are generally accompanied by non-crop vegetation)	None	0
	Sediment retention ponds	0.25
	Wetlands	0.5
	Riparian conservation areas	0.75
	Multiple water features	1.0

(Supporting Information Section A, Table S1). The composite index allowed us to explore the effect of local diversification without including a variable for each practice. The local diversification elements were not weighted.

The first principal component represents the linear combination of variables that accounts for the greatest variance contained in the original variables, which was 37% in our case (Supporting Information Section A). As a confirmatory analysis, we processed the same linear models and PSEM using a sum of z-scores for all seven diversification practices in place of the first principal component (Song et al., 2013; Ward et al., 2009). The results from this analysis were functionally equivalent to the original results (Supporting Information Section G).

2.3 | Landscape variables

National Agriculture Imagery Program data were used to digitize landscape cover within 1,000-m radius buffers of each site (EROS Center, 2014). Land cover categories were based on the Salinas-Pajaro Generalized Land Use/Land Cover Mapping and the Anderson Level II hierarchy (Karp, Baur, et al., 2015; Karp, Gennet, et al., 2015). The woody habitat category included forest and riparian woodland, chaparral, scrubland and exotic tree patches; the grasslands category included grassland and pasture. The proportions of woody habitat and grasslands were not correlated ($\rho = 0.11$, $p = 0.45$).

The most predictive buffer sizes, ranging from 50 to 1,000 m in 50 m increments, for each response variable were determined using a ΔAICc ranking method (Jackson & Fahrig, 2012, 2015, Supporting Information Section B, Table S2). At each of the selected buffer sizes, neither of the landscape variables (woody and grassland) was correlated with local diversification ($|\rho| < 0.21$; $p > 0.12$), confirming the orthogonal nature of the gradients across local diversification and landscape composition depicted in Figure 2.

2.4 | Pest management variables

Certified organic compliant insecticides that are commonly applied in the study area were classified into one of the three categories: targeting lepidopteran larvae (*Bacillus thuringiensis*-based), broad spectrum (spinosad, pyrethrin or *Chromobacterium subtsugae*-based) or targeting soft-bodied pests such as aphids, thrips and whiteflies (*Beauveria bassiana* or azadirachtin-based). Insecticide intensity was defined as an index from 0 to 3 indicating the number of insecticide categories applied; application frequency was not included because farm managers seldom reported this information. Tractor vacuum frequency ranges from 0 to 2 and indicates the number of times per week that each site was vacuumed during the growing season, as reported by farm managers.

Landscape composition measures at selected buffer sizes were uncorrelated with tractor vacuum frequency ($|\rho| < 0.20$, $p > 0.15$) and insecticide intensity ($|\rho| < 0.14$, $p > 0.36$), suggesting that the intensity of pest management was uncorrelated with landscape factors.

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 station. 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 and directing the vacuum tube over each plant and holding for 1 s (method modified from Swezey et al., 2007). Arthropods were trapped by a filter bag attached to the vacuum tube entrance. To control for differences in arthropod activity under extreme weather conditions, sampling occurred only

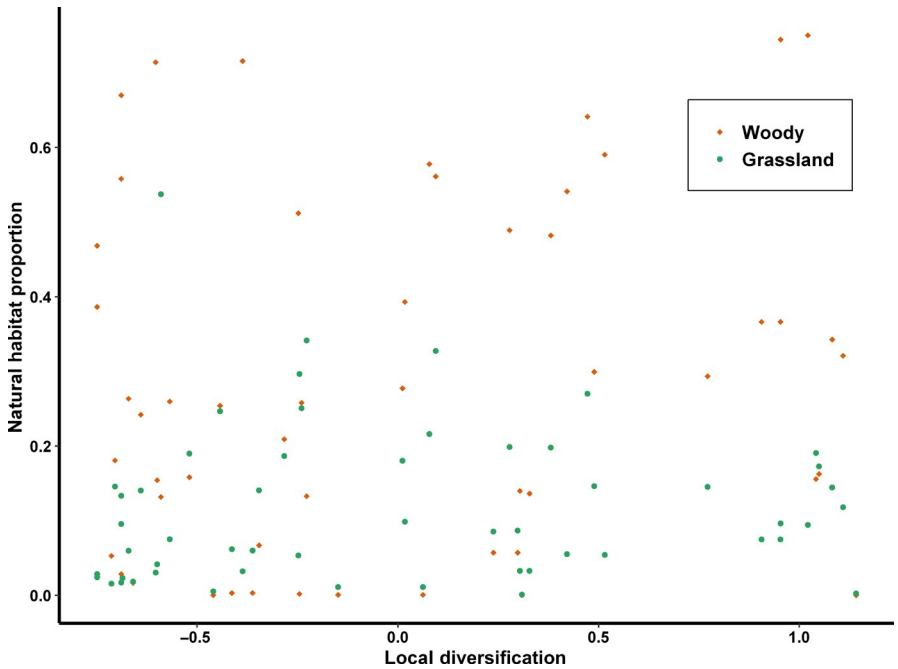

FIGURE 2 Study sites were selected along orthogonal gradients of landscape composition and local diversification. This figure visualizes the distribution of sites across these gradients within 1-km radius buffers of each site

under the following conditions: ambient temperature 20–28°C, average wind speed ≤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., 2020; Hagler et al., 2020; Leigh & Gonzalez, 1976; Perkins & Watson, 1972; Wilson & Gutierrez, 1980; Zink & Rosenheim, 2008). The lygus bug complex in this region primarily consists of *Lygus hesperus*, and also includes small proportions of *L. elisus* and *L. lineolaris* (Hagler, Nieto, et al., 2020). Individuals of all *Lygus* species were included in our lygus bug category.

Abundance measures are counts of individual specimens belonging to each category. Shannon's diversity index H' was used to calculate natural enemy diversity based on the categories listed above (Magurran, 2013).

2.6 | Pest control levels

We performed a sentinel experiment to estimate pest control levels (Lövei & Ferrante, 2017). The lygus bug was used in this experiment due to its importance as a strawberry pest in this region (Bolda et al., 2019). To ensure a steady supply of sentinel specimens, we maintained a lygus bug colony started using individuals collected from wild mustard plants in the Salinas/Watsonville region. Sentinel cards were fabricated by affixing live third to fifth instar nymphs onto 1.5 cm by 4 cm pieces of waterproof paper using double-sided tape. At each site, three sentinel cards (one per station) containing five nymphs each were deployed by attaching them on the underside of strawberry leaves to minimize sun exposure. After 24 hr, the cards were collected and the nymphs were scored as damaged (missing body parts), removed (missing entirely) or undamaged. An inherent limitation of this method is that it only detects predation by natural enemies with chewing mouthparts. Despite our efforts to minimize sun exposure, hemipteran (sucking) predation could not be reliably distinguished from ambient desiccation. Both damaged and removed nymphs were considered predation successes, and undamaged nymphs were considered predation failures. The probability of predation was calculated by dividing the number of predated nymphs by the total number deployed at each station. Predation odds, defined as p/(1-p) where p is the probability of predation, were then calculated for each station.

2.7 | Statistical methods

Statistical analyses were performed using R (R Core Team, 2019) and the packages LME4 (Bates et al., 2015) and PIECEWISESEM (Lefcheck, 2016).

First, we identified the predictor, response and intermediate (both predictor and response) variables in the path diagram (Figure 1). The terminal response variable is predation odds, representing pest control level. Landscape composition and local practices, the interaction effects between landscape and local factors and the interaction effects between landscape factors and days since rain (DSR; a measure of time within the growing season) are the hypothesized fundamental predictor variables, and lygus bug and natural enemy community measures are the hypothesized intermediate variables. The PSEM consists of four pieces—one equation for each of the response variables (predation odds, natural enemy abundance, natural enemy diversity and lygus bug abundance). The predation odds response variable was modelled with the binomial distribution, the two abundance response variables were modelled with the Poisson distribution and natural enemy diversity was modelled with the normal distribution. For each response variable, we began with a full model including all hypothesized predictors, as well as the covariates of field size in hectares, DSR and DSR^2. A rain day is defined by the US Geological Survey as 1 mm of rain within a 24-hr period, and we opted to use DSR because in the Mediterranean climate of our study area, progression into the dry season may be a more accurate proxy of phenology than day of year (United States Geological Survey, 2007). We included DSR^2 to account for potential nonlinear patterns in insect phenology that 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 is appropriate for our data because a subset of sites (10 per year) was not sampled in both years. Based on the full models, reduced model structures containing all combinations of fixed effect terms were generated and ranked by AICc (Symonds & Moussalli, 2011; Supporting Information Section C) using the R package MuMIn (Barton, 2019). Four models (corresponding to the four response variables) were then chosen from the top-ranked models (Supporting Information Section C; Tables S3–S7) and entered into the PSEM.

As commonly occurs with count data, the natural enemy and pest abundance data were overdispersed. An observation-level random effect was included in these response models to address the overdispersion (Harrison, 2014).

The tests of uniformity and dispersion for the linear model residuals were confirmed to be non-significant using R package DHARMA (Hartig, 2020). No significant spatial autocorrelation was found in the linear model residuals according to the Moran's *I* test in R package APE (Paradis & Schliep, 2019). The PSEM's fit with the data was quantified using the Fisher's *C* statistic (Lefcheck, 2016; Shipley, 2009, 2013).

3 | RESULTS

We collected 1,954 *Lygus* individuals, 1,465 *Orius* individuals, 1,770 *Geocoris* individuals, 469 coccinellids, 348 *Nabis* individuals, 157 neuropterans, 265 ants and 3,163 spiders. We deployed a total of 802 sentinel nymphs. The mean rate of predation was 18.1% (SD = 23.2%). Natural enemy abundance increased with proportion of woody habitat in the landscape (p = 0.02). *Lygus* abundance (p = 0.02) and natural enemy diversity (p = 0.002) increased with DSR.

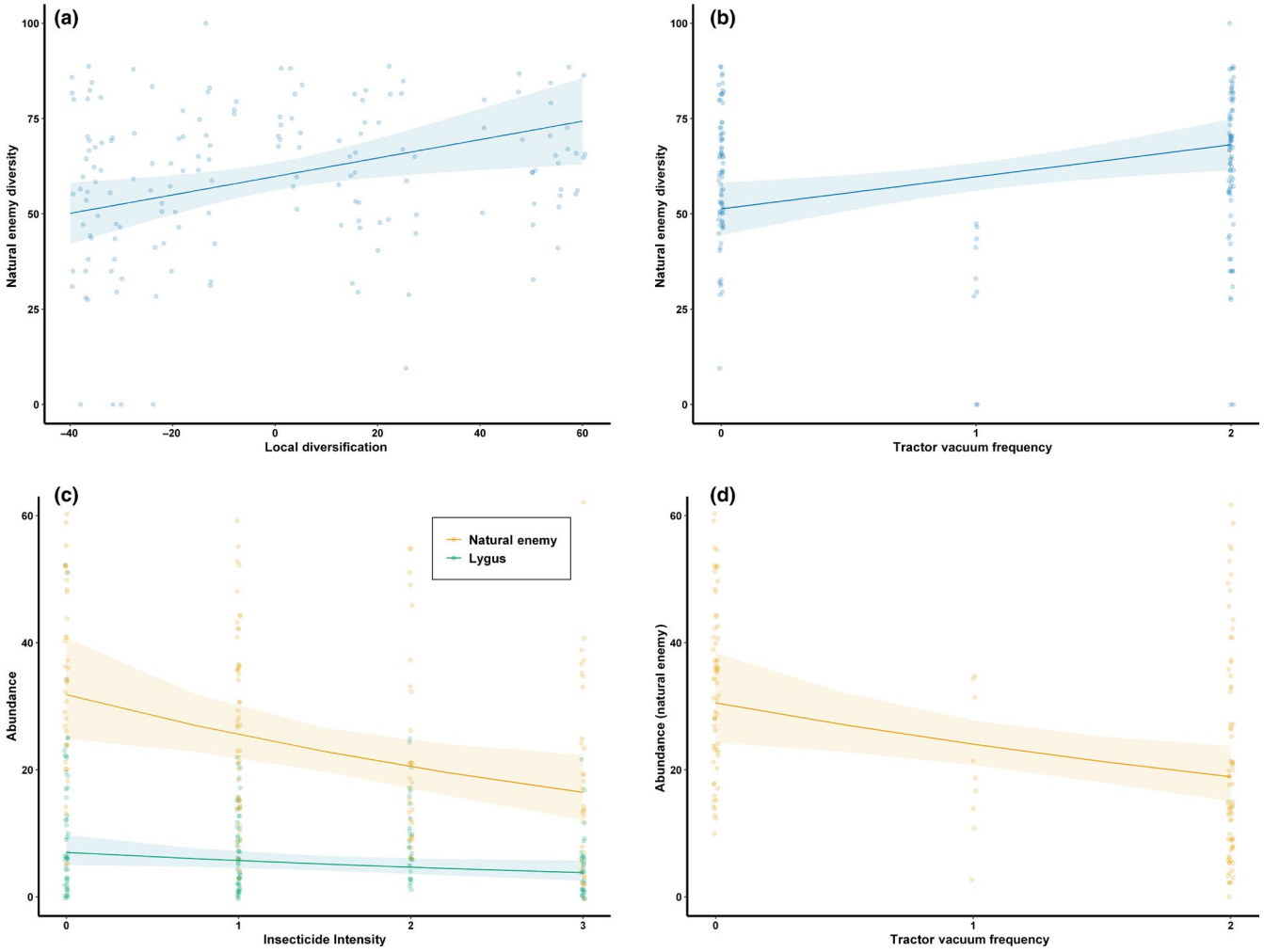

FIGURE 3 (a) Estimated effect of local diversification on natural enemy diversity ($p = 0.01$); (b) estimated effect of tractor vacuum frequency on natural enemy diversity ($p = 0.006$); (c) estimated effect of insecticide intensity on natural enemy ($p = 0.006$) and pest abundance ($p = 0.006$); and (d) estimated effect of tractor vacuum frequency on natural enemy abundance ($p = 0.008$)

Local diversification increased enemy diversity ($p = 0.01$, Figure 3a), but had no significant effect on any other response variable. Enemy diversity increased with tractor vacuum frequency ($p = 0.006$, Figure 3b). Both enemy ($p = 0.006$) and lygus bug ($p = 0.006$) abundance decreased with insecticide intensity (Figure 3c). Tractor vacuum frequency decreased enemy abundance ($p = 0.008$, Figure 3d), but had no significant effect on lygus bug abundance.

We detected no significant interaction effects between either of the landscape composition measures and local diversification on any of the response variables.

The probability of predation increased with both enemy abundance ($p = 0.004$, Figure 4a) and enemy diversity ($p = 0.01$, Figure 4b), and decreased with pest abundance ($p = 0.01$, Figure 4a).

The PSEM results confirmed that all landscape and local effects on pest control levels were indirect and mediated through changes in arthropod communities (Figure 5; Supporting Information Section D). The proportion of woody habitat indirectly increased predation odds by increasing enemy abundance and local diversification indirectly increased predation odds by increasing enemy diversity. Tractor vacuum frequency indirectly decreased predation odds by decreasing enemy abundance, but also indirectly increased predation odds by increasing enemy diversity. Insecticide intensity indirectly decreased predation odds by decreasing enemy abundance, but also indirectly increased predation odds by decreasing pest abundance.

4 | DISCUSSION

Our study shows that larger proportions of landscape-scale woody habitat and higher local diversification increased natural enemy abundance and diversity, respectively, which in turn increased the pest control levels. In line with our expectations, proportion of woody habitat in the landscape increased natural enemy abundance. The proportion of woody habitat had a nearly significant ($p = 0.06$) negative effect on lygus abundance, and grassland proportion had no effect on either natural enemies or lygus abundance. Lygus response to grassland proportion may have been obscured by the

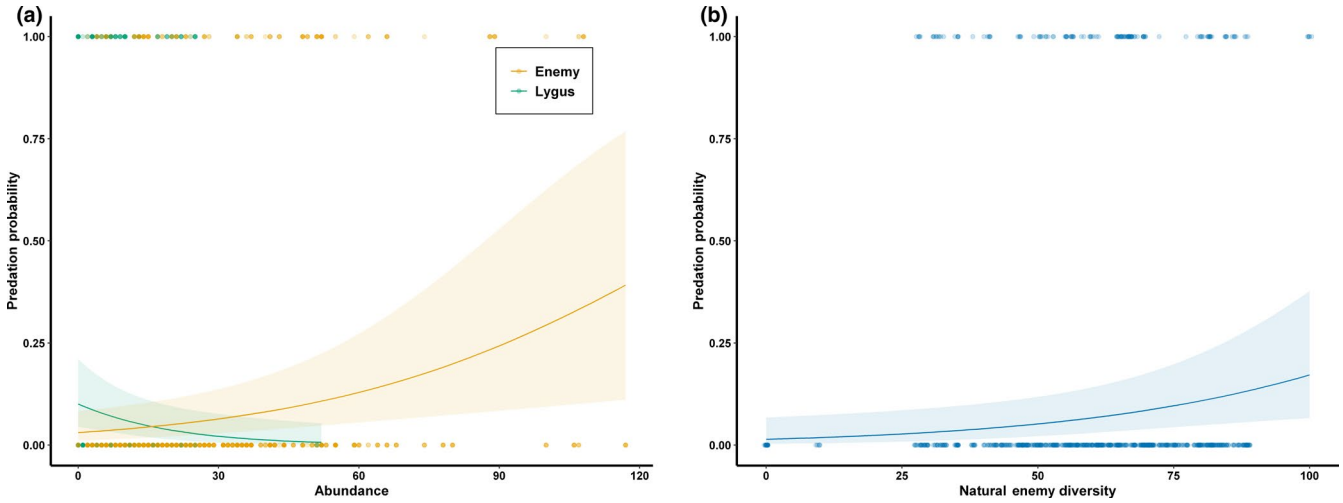

FIGURE 4 (a) Estimated effects of lygus ($p = 0.01$) and natural enemy ($p = 0.004$) abundance on predation probability and (b) estimated effect of natural enemy diversity on predation probability ($p = 0.01$). Predation probability was calculated from the predation odds response variable used in the statistical models

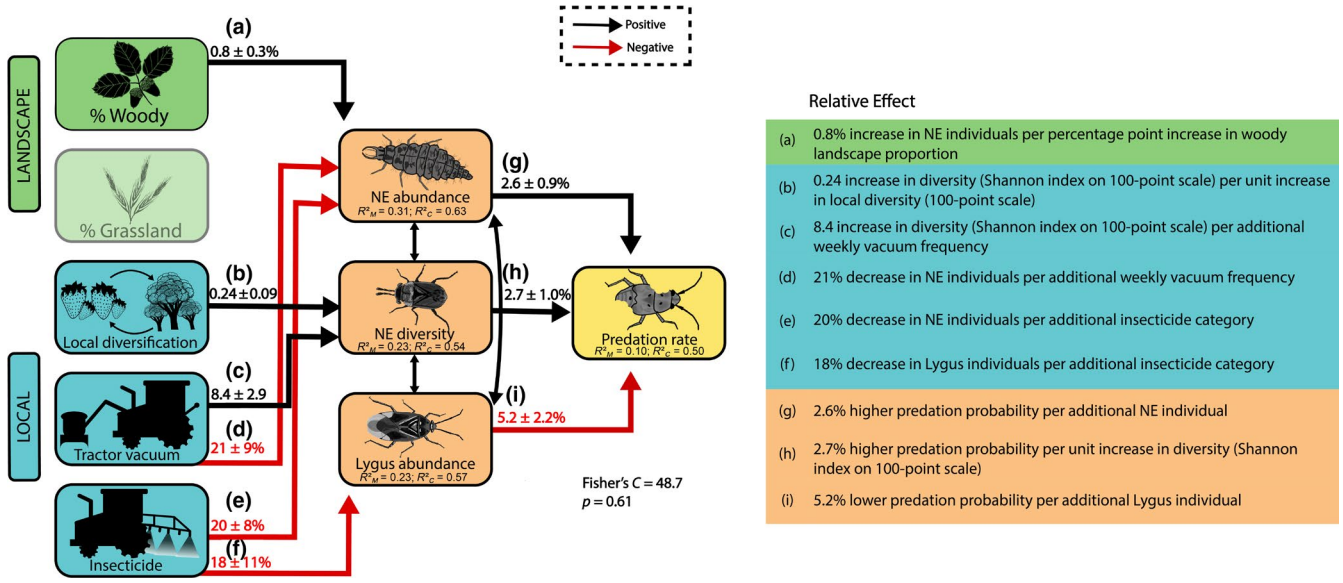

FIGURE 5 Piecewise structural equation modelling results. Global goodness-of-fit is represented by Fisher's $C = 48.7$ ($p = 0.61$), indicating the model is well-fit. Marginal R^2 (R^2_M) values indicate the variance attributed to fixed effects, and conditional R^2 (R^2_C) values indicate the variance attributed to both fixed and random effects (Nakagawa & Schielzeth, 2013). Letters (a) through (i) represent model estimates and standard errors and are further explained in the accompanying table. Double-headed arrows represent correlated errors

occurrence of small-scale, weedy refuges found commonly within this agricultural landscape, including ditches, field edges and roadside vegetation that contain exotic annual plants such as wild mustard *Brassica* spp., wild radish *Raphanus raphanistrum* and shepherd's purse *Capsella bursa-pastoris*. These weeds are known to be favoured hosts of lygus bugs as well as other pests (Fye, 1982; Malcolm, 1953), in some cases providing enemy-free spaces for certain pest species (Chaplin-Kramer, Kliebenstein, et al., 2011). In a follow-up study to this one, we explored the roles of these weedy refuges as sources or sinks of pest species (Lu, 2020). The widespread application of conventional pesticides in our study region may also have obscured landscape effects on lygus bugs. The positive effect of woody habitat proportion on natural enemy abundance further suggests and supports other studies that more woody habitat within agricultural landscapes may promote pest control services (Chaplin-Kramer et al., 2013; Karp et al., 2016). Our results, which indicate no significant interaction effects between DSR and either landscape type, do not support the common belief among growers that lygus bugs migrate to agricultural fields from semi-natural grassland as the dry season progresses; some hypothesize that this may happen because irrigated crops become more favourable as unmanaged annuals desiccate. However, the positive effect of DSR on lygus abundance

accords with the observation that lygus bug populations build up over the growing season.

Local diversification increased natural enemy diversity. Diverse plant communities, both crop and non-crop, have been shown in past studies to support more diverse assemblages of beneficial insects due to the provision of a variety of resources and ecological niches (Landis et al., 2005; Letourneau et al., 2011; Lichtenberg et al., 2017; Siemann et al., 1998). Among the diversification practices we studied, perennial crop structure, followed closely by crop diversity and flowering non-crop plants, were most closely correlated with the first principal component in our PCA (Table S1). Our study provides further evidence that higher plant diversity (both crop and non-crop) at the farm scale facilitates more diverse natural enemy communities.

Natural enemy abundance and diversity increased sentinel predation odds. While theory and evidence indicate that higher natural enemy abundance generally increases pest control (Gurr et al., 2019), the effect of natural enemy diversity is less clear (Roubinet et al., 2015). Some studies find positive effects of diversity such as resource partitioning (Northfield et al., 2010) and facilitation (Prasad & Snyder, 2010), while others indicate that enemy diversity may decrease pest control due to negative intra-guild interactions (Vance-Chalcraft et al., 2007). Here, the positive effects of natural enemy diversity appear to overshadow the negative interactions. Pest abundance had a negative effect on sentinel predation odds, possibly due to a dilution effect by which a greater number of ambient prey reduced the predation odds of each sentinel individual.

As expected, insecticide application indiscriminately reduced arthropod abundance, with similar effect sizes and significance levels for natural enemies and lygus bugs. Insecticides' efficacy must be qualified by their concomitant impacts on pest control services. Insecticide application may do more harm than good if the goal is to promote pest control and not merely to reduce pest abundance. Our finding provides further support for the USDA's National Organic Program regulation requiring that insecticides be used as a last resort, only after all other cultural, mechanical and ecological methods are found to be insufficient (Crop Pest, Weed, and Disease Management Practice Standard, 2000).

We found that vacuuming frequency had no effect on pest abundance but had a strong negative effect on natural enemy abundance. In our study region, tractor vacuuming is perceived to effectively control lygus bugs in organic strawberries. This perception may arise from recommendations by the California Strawberry Commission, which promotes the use of ever more powerful (and energy-intensive) tractor vacuums (California Strawberry Commission, 2019). We performed an additional analysis (Supporting Information Section E) and found that tractor vacuuming was uncorrelated with maintaining lygus abundance below the treatment threshold (University of California Agriculture & Natural Resources, 2018). However, factors other than vacuum inefficacy may explain this lack of correlation. Farms with small ambient lygus populations most likely do not run tractor vacuums as often (or at all) compared with farms suffering outbreaks. Factors that we did not explore, such as proximity to fields suffering outbreaks, may drive ambient lygus populations. Therefore, we cannot assert that tractor vacuums are ineffective but only that we found no evidence of their effectiveness. Our results clearly show, however, that vacuuming shrinks natural enemy abundance, which reduces that community's capacity to control pests. When developing pest management plans, this ecological cost should be considered along with the equipment, fuel and labour costs of tractor vacuuming.

Because we detected an unexpected positive effect of vacuum frequency on enemy diversity, we conducted a post hoc linear mixed model analysis to explore the implications of this result. We found that the negative effect of vacuuming on natural enemy abundance would likely negate any potential benefit of increased diversity (Supporting Information Section F, Tables S9 and S10). These results are further evidence that growers aiming to increase biological pest control may find greater success by employing local diversification rather than tractor vacuuming, while also avoiding the ecological and economic costs of vacuuming.

The PSEM results confirm that local and landscape factors indirectly drive changes in pest control through their direct effects on the lygus bug and its natural enemies. The lack of direct correlations between the fundamental predictors and predation odds reflects this result, and indicates that our causal hypotheses are supported by the data. Specifically, the PSEM results show that all effects of landscape composition, local diversification and local pest management practices on predation odds were mediated through natural enemy abundance, natural enemy diversity and lygus bug abundance. Our study provides evidence that landscape composition and local diversification effects on pest and natural enemy communities determine the levels of biological pest control in agricultural fields.

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CONFLICT OF INTEREST

None of the authors have a conflict of interest.

AUTHORS' CONTRIBUTIONS

C.K., D.J.G., A.R.S. and A.L. conceived the ideas and designed the methodology; A.L., D.J.G., A.R.S., T.C., K.G. and G.J. collected the data; A.L. analysed the data; A.L. led the writing of the manuscript; K.G. illustrated the Graphical Abstract and Figures 1 and 5. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.tht76hf0v (Lu et al., 2021).

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