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Diet specialization mediates drivers of *Cucurbita* herbivory in a semi-arid agroecosystem

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ABSTRACT

Herbivory is a major fitness pressure for plants and a key driver of crop losses in agroecosystems. Dense monocultures are expected to favor specialist herbivorous insects, particularly those who primarily consume crop species; yet, levels and types of herbivory are not uniform within regional cropping systems. It is essential to determine which local and regional ecological factors drive variation in herbivory in order to support functional agroecosystems that rely less on chemical inputs. Crops in the genus *Cucurbita* host a suite of both generalist and specialist herbivores that inflict significant damage, yet little is known about the relative contribution of these herbivores to variation in herbivory and how local- and landscape-scale *Cucurbita* resource concentrations, management practices, and natural enemies mediate this relationship. In this study, we tested whether three foundational ecological hypotheses influenced *Cucurbita* herbivory across 20 pumpkin fields in the semi-arid Southern High Plains Region of Texas. We used generalized linear mixed models and confirmatory path analysis to assess whether the Density-dependent Herbivory Hypothesis, Resource Concentration Hypothesis, or the Natural Enemies Hypothesis, could explain variation in *Cucurbita* herbivory and insect dynamics in the context of conventional agronomic practices. We found that herbivory increased over time, indicating that herbivores were causing sustained damage throughout the growing season. We also found that fields with higher local *Cucurbita* resources had lower herbivory, suggesting a resource dilution effect. Natural enemy communities were more abundant and taxonomically rich in sites with greater generalist herbivore abundance, though predator abundance declined over time, indicating that late-season crop fields are most at risk given high herbivory and low natural enemy-based control. Our findings also suggest that while local resource availability may drive the abundance and richness of arthropod communities, additional agronomic and phenological information is needed to anticipate herbivory risk in an agriculturally dominated landscape.

1. Introduction

Damage from herbivorous insects is among the top fitness pressures shaping plant communities, specifically in agroecosystems where 8–20% of yield losses can be attributable to herbivory (Oerke, 2006; Sharma et al., 2017). The combined conditions of modern crop production, including extensive monocultures, irrigated fields, and domesticated plant species with lower defensive qualities may act in concert to attract and retain distinct arthropod communities as compared to nearby natural ecosystems (Atwood et al., 2008). Dense and highly concentrated crop monocultures at the local and landscape scale can support higher abundances of both specialist and generalist herbivore populations (Altieri et al., 1984; Andow, 1991; Bernal and Medina, 2018). Conversely, in agriculturally dominated landscapes with limited natural habitat availability, natural enemies may have relatively low abundances and richness due to the lack of alternative plant and prey resources required to support natural enemy populations (Rand et al., 2006; Galloway et al., 2021). This is particularly important given

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the critical role natural enemies can play in managing herbivorous pests (Gurr et al., 2017). Therefore, it is crucial to identify the factors that lead to declines in herbivores and increases in natural enemies in order to minimize herbivory and protect sustained crop production in agroecosystems.

Local crop density and the proportion of a landscape under cultivation represent two scales at which plant resource concentration can influence herbivores and herbivory. In annual cropping systems, herbivores typically immigrate from overwintering habitats within the field or surrounding natural habitats into the newly planted fields. In agriculturally dominated monoculture landscapes, both specialist and generalist herbivores must exert little effort to find a field containing host plant monocultures (O'Rourke and Petersen, 2017). For example, Gagic et al. (2021) found that larger cotton fields located in landscapes with <10% semi-natural habitat experienced the earliest immigration and highest abundances of small, piercing-sucking arthropod pests. Once in a field, areas of high crop density can be more vulnerable to herbivory as specialist herbivores concentrate on that preferred resource at the local scale (a.k.a Resource Concentration Hypothesis; Root, 1973; Feeny, 1976). On the other hand, resource dilution effects can occur when high local crop density outstrips the ability of an herbivore population to take advantage of that resource, as seen in the declines of pollen beetles with increasing densities of oil rape seed plants (a.k.a Resource Dilution Hypothesis; Schneider et al., 2015). Resource dilution effects may be more common in landscapes containing a higher proportion of acceptable host-plants in both natural and agricultural areas, as reliable and abundant preferred resources remove food limitation as a driver of herbivore populations (Schneider and Martin, 2020). Yet, the effects of crop resource concentration on herbivory inflicted by herbivore communities often depends upon the crop system, landscape, and regional context, making it difficult to anticipate effects in understudied environments.

In contrast to herbivores, natural enemy groups often require alternative plant and prey resources to persist within agricultural fields. These alternative plant resources are important to consider in land management given that natural enemies can often control overall herbivory through predation of herbivores (Root, 1973; Landis et al., 2000; Wilby and Thomas, 2002). Specifically, increases in the density of crop plants at the local and landscape scales often decreases the availability of alternative plant resources, supporting fewer, less diverse natural enemies (Dassou and Tixier, 2016; Beaumelle et al., 2021). Evidence suggests that practices which increase in-field plant diversity, including polyculture and higher weed tolerance, support higher natural enemy abundances and taxonomic richness. However, the strength of these relationships depends on the landscape context (Licthenberg et al., 2017). Specifically, local plant resource diversification is likely most beneficial to natural enemies in simpler landscape configurations where increases in plant diversity at the local level offer more varied resources than the surrounding monoculture fields (Tscharntke et al., 2012; Sanchez et al., 2022). Understanding how landscape context mediates the effect of plant diversity on natural enemies and herbivory is particularly relevant given economic and social costs of changing crop management methods (Piñeiro et al., 2020).

Beyond crop resources, differences in agronomic practices and planting schedules can also influence how herbivores and natural enemies respond to plant resource concentration. At the local field scale, management choices including tillage regimes, irrigation methods, and chemical input standards can alter the level of disturbance, microclimates, and mortality experienced by arthropods (Puech et al., 2015; Han et al., 2022). Specifically, by retaining >30% of previous crop plant residues, reduced tillage methods increase habitat complexity for herbivores and natural enemies and may increase or decrease herbivory intensity depending on how arthropods respond to these undisturbed areas (Buchanan and Hooks, 2018; Appenfeller et al., 2022). Further, distance to field edge can influence the abundance and spatial distribution of both herbivores and natural enemies, particularly for

organisms that are satiated by the level of resources provisioned by crop planting density, uniformly implemented across a field (Nguyen and Nansen, 2018). Finally, arthropods also respond to crop plant maturity, with herbivores often preferring young seedlings over older plant stages (Quintero and Bowers, 2018). Understanding how these agronomic and temporal factors alter how arthropods respond to resource concentration could aid in identifying methods to mitigate crop losses to herbivory.

Finally, intrinsic biological factors such as diet breadth, specifically degree of diet specialization, could be a key functional trait modulating the effect of resource availability (Moreira et al., 2016) for both herbivores and natural enemies (Root 1973). Specialist herbivores are expected to be most sensitive to temporal changes in resource concentration as their development and reproduction is dependent upon a narrow range of host plants (Doublet et al., 2019). Generalist herbivores are likely less sensitive to crop plant concentration as they can switch to alternative host plants more nimbly. For example, the polyphagous pest *Apolygus lucorum* can use >200 host plants over a single year in Northern China (Pan et al., 2015). Similarly, among natural enemies, predators often have wider diet breadths than parasitoids, which must evolve strategies to overcome host prey defenses and thus often specialize within a genus or family of prey (Vorburger 2022). A recent global meta-analysis found that the decline of generalist herbivore abundance in response to crop resource dilution in bicultures was stronger than the decline in specialist herbivore abundance (Hahn and Cammarano, 2023), and numerous other studies have observed variable responses to landscape-level resource concentration among herbivores and natural enemies with varying diet breadths (Egerer et al., 2017; Perez-Alvarez et al., 2019). While general patterns emerge from a global perspective, regional variation in arthropod responses to local and landscape-level resource availability underscores the need for regional and crop-specific studies to understand herbivory risks within a given production system.

Crops in the genus *Cucurbita*, including pumpkins and squashes, offer an economically and ecologically important system to examine the modulating effect of diet specialization on drivers of herbivory including local plant resources, landscape context, and crop management. *Cucurbita* production in the United States is valued at over $480 million annually, with top producing states including three Midwestern states, two Mid-Atlantic states, California, and Texas (USDA 2022). Wild relatives of *Cucurbita* crops produce high levels of the feeding deterrent cucurbitacin, which has resulted in the co-evolution of specialist herbivores (Metcalf 1989). Domesticated *Cucurbita* crops produce much less of these bitter compounds and are more palatable to both generalist and co-evolved specialist herbivores, making these crops uniquely vulnerable to both groups of herbivores (Brzozowski et al., 2019). In humid regions, some specialist herbivores also vector highly lethal bacterial wilt diseases to *Cucurbita* crops (Rojas et al., 2015), thus previous ecological studies have overwhelmingly focused on this sub-set of herbivores (Mabin et al., 2020; Buchanan and Hooks, 2018). Little is known about the combined contribution of both specialist and generalist herbivores to *Cucurbita* herbivory.

Studies from Midwestern, Mid-Atlantic and Central American regions, reveal that specialist herbivores vary in their response to *Cucurbita* resource concentration by location, herbivore species, and type of resource dilution. Specifically, research in Turrialba, Costa Rica has found support for a resource concentration effect whereby specialized cucumber beetles are less abundant in polyculture and more likely to emigrate from polycultures than monocultures of *Cucurbita* (Risch 1981). In small-holder farms in Cárdenas, Tabasco, MX, *Cucurbita* resources diluted by polyculture additions of maize and cowpea had divergent effects (Letourneau 1986). Specifically, the melonworm moth, *Diaphania hylinata* (Family: Crambidae) was generally less abundant in polyculture, suggesting a resource dilution effect, while, squash bugs, *Anasa tristis* (Family: Coreidae), were more abundant in polycultures, suggesting a resource concentration effect. A similar study in Ithaca, NY,

USA further examined the effect of polyculture on squash bugs and concluded that neither the Resource Concentration Hypothesis nor presence of natural enemies was sufficient to explain squash bug population dynamics (Harmon et al., 2003). Further, studies of biocontrol by natural enemies in Ohio *Cucurbita* production found that predators were not influenced by the availability of alternative host plants and that control of target specialist herbivores was higher in sites with greater predator richness and in landscapes with more agriculture (Phillips and Gardiner, 2016; Mabin et al., 2020). These and an additional three studies (Lawrence and Bach 1989; Hooks et al., 1998, and Frank and Liburd, 2005) included in a recent meta-analysis (Hahn and Cammarano, 2023) all utilized additive polycultures to examine variation in the relative density of *Cucurbita* plants and test the Resource Concentration Hypothesis as a frequency-dependent process (Kim and Underwood, 2015). Much less is known about how absolute density-dependent processes, derived from variation in local-level *Cucurbita* establishment and landscape-level *Cucurbita* production, influence herbivory. Further, few studies examine resource concentration effects at production scale within the monoculture-dominated landscapes characteristic of agriculture in much of the United States.

In this study, we examine the drivers of herbivory, herbivore community composition, and natural enemy community composition across a series of large-scale *Cucurbita* agroecosystems. We ask 1) *does resource availability and degree of diet specialization influence herbivore and natural enemy community composition* and 2) *do herbivore and natural enemy abundances drive herbivory?* Specifically, we test the Resource Concentration Hypothesis, which states that herbivore populations are limited by availability of preferred plant resources (Root, 1973). Thus, we predict that herbivores will be more abundant in fields with higher concentrations of *Cucurbita* plants at the local and landscape level, and that this will be strongest for specialist herbivores (Fig. 1 arrows A, B). We also test the Density-dependent Herbivory Hypothesis that plant damage from herbivory is directly correlated with herbivore density (as in Rusch et al., 2013) and we predict to find greater leaf damage in fields with greater densities of herbivores (Fig. 1 arrow C). Finally, we examine evidence for the Natural Enemies Hypothesis, which states that plants will be protected from herbivory by natural enemies of herbivores where their required alternative plant and prey resources are abundant (Root 1973). We predict that natural enemies will be more abundant and diverse where the shelter, nectar, alternative prey, and pollen resources required are more accessible, particularly for predators with a more generalized diet (Fig. 1 arrows D-F). We would expect herbivory to be lowest in areas with lower crop resource concentration at the local and landscape scale, due to higher natural enemy abundance and diversity and lower specialist herbivore abundance.
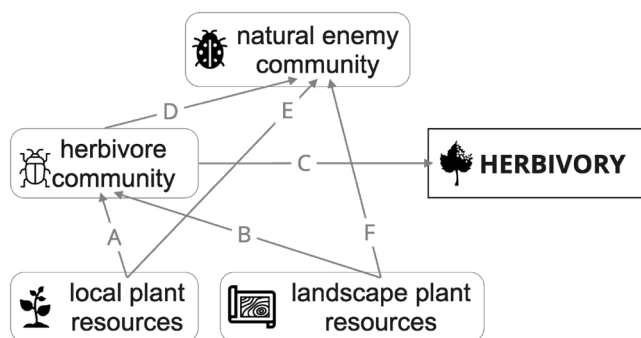
2. Methods

2.1. Site selection and characterization

We conducted this study during the 2021 vegetative and flowering phase of *Cucurbita* pumpkin crops (July 2nd to August 13th) in the Southern High Plains Region of Texas (33.98, -101.34) (Fig. 2). This region is characterized by a cold, semi-arid climate, remnant short-grass prairies, ephemeral playa lakes, and extensive (~30% of total land area) cotton cultivation, whose irrigated acres depend entirely on the High Plains Aquifer (Qi, 2009; Begosh et al., 2022; Pathak et al., 2022) (Fig. 2). This region is within the native range of the wild buffalo gourd, *Cucurbita foetidissima*, an alternative host of specialist cucurbit herbivores (Jenny et al., 2023), however pre-season field surveys found only a few sparse, low-density aggregations of this plant. *Cucurbita* cultivation began at production scale in the 1960s but remains a minor specialty crop which covers less than 1% of the total land area in the few counties where its produced (USDA, 2019; Tomascik, 2020).

We established a 150 × 3 m sampling transect in each of the 20 *Cucurbita* production fields selected for this study out of the 29 *Cucurbita* fields present. The remaining 9 fields did not meet our inclusion criteria of ≥ 2 km between fields with an aim to increase the heterogeneity of our sampling and ≥ 12 contiguous rows planted in common field pumpkin (*Cucurbita pepo* spp. *pepo*) to control for variation in specialist herbivore preference among *Cucurbita* species (Jaccard et al., 2021). In this region, farmers rotate from pumpkin to cotton or other row-crop (sorghum, maize, wheat) production so that our focal fields had 1–3 (mean = 2.35, sd = 0.75) years between the current pumpkin crop and the last time the field had been planted in pumpkin. We placed transects in two adjacent rows of the *C. pepo* spp. *pepo* block so that the transect lay at least 2 rows away from the parallel field edge (14 m) and was equidistant from the start of the production rows (Artz et al., 2011). We subdivided the 150 m long transect into 8 sub-transects, each measuring 10 × 3 m with a 10 m buffer between each sub-transect.

For all sites, we obtained field maps and management plans to verify field coordinates, area, distance to nearest pumpkin field, and years since pumpkin production. While we located our selected block of *C. pepo* within all sites, full field planting plans were only available for 18 of the 20 fields. In this system, all fields were managed under similar agronomic practices including a combination of drip-tape and pivot irrigation, IPM-driven chemical pest control through aerial sprays, and conventional soil amendments. Fields received 1–2 insecticide and 3–4 fungicide treatments over the course of this study, with specific chemical agents, rates of application, and timing between applications consistent across fields. More detailed pesticide information cannot be reported due to privacy concerns. Data was not collected within 24 hours of a pesticide application or pivot irrigation to avoid displacement of arthropods. Fifty percent of fields had been 100% full-tilled prior to planting and 50% of fields had been 50% strip-tilled, leaving remnant
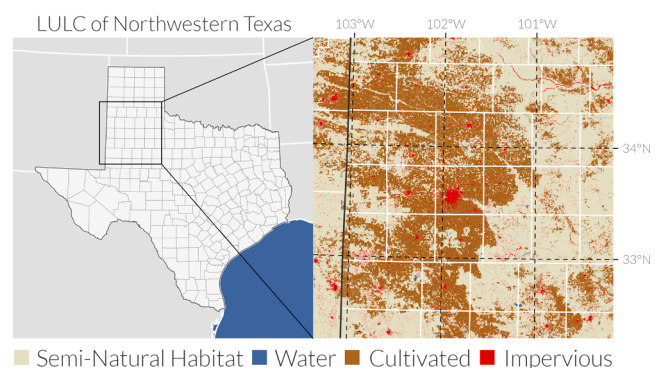

Fig. 1. Conceptual path diagram depicting relationships examined in this study. Arrows A and B examine the Resource Concentration Hypothesis through the effect of local and landscape plant resources on the herbivore community. Arrow C examines the hypothesis of Density-dependent Herbivory. Arrows D, E, and F examine the Natural Enemies Hypothesis through the effect of alternative resources on natural enemies.

Fig. 2. Map of the a) Southern High Plains Region of Texas and b) land-use/land-cover (LULC) data for the study system.

cotton or wheat stubble between *Cucurbita* rows. Farmworkers inter-mittently removed non-*Cucurbita* plants with hoes during the first half of the study, after which fields were dominated by crop plants, but main-tained some non-*Cucurbita* weed or volunteer cotton plants.

2.2. Field methods

2.2.1. Vegetation surveys

Beginning on July 2nd, we conducted three, biweekly visual surveys of the arthropod and plant communities within the 8 sub-transects at each of the 20 field sites. These surveys were conducted between 0600 and 1300, in parallel with pollinator surveys conducted during the daily flowering window (Nepi et al., 2001). We assessed initial *Cucurbita* plant abundance across the entire area of each sub-transect (total of 30 m^2 per site) and then we sub-sampled each sub-transect to assess *Cucurbita* and non-*Cucurbita* plant cover, richness, and max height. All values were corrected for unit area before analyses. Specifically, within each of the 8 sub-transects, we identified and recorded the density (percent cover) of *Cucurbita* and non-*Cucurbita* plants and measured mean vegetation height within two 1 m^2 quadrats randomly placed within the two pro-duction rows in each sub-transect. Each sub-transect measured 30 m^2, therefore the two 1 m^2 quadrats represent ~10% of the sub-transect vegetation and 6% of the total sub-transect area, exceeding previous plant sampling efforts in *Cucurbita* agroecosystems (Buchanan and Hooks, 2018; Testani et al., 2019). In the first survey, we assessed seedling and young *C. pepo* ssp. *pepo* health and growth stage by recording foliar herbivory (% of leaf area removed or damaged by herbivores) for each *Cucurbita* plant within the sub-transect via visual assessment with an experienced observer trained on a digitally-verified greenhouse dataset (Johnson et al., 2016; Getman-Pickering et al., 2020). In the second and third surveys, *Cucurbita* plant density had increased to the extent that individual *Cucurbita* plants could not be visually separated, therefore we estimated foliar herbivory as the average of all the *Cucurbita* leaves within the same 1 m^2 quadrats used to estimate non-*Cucurbita* measurements (Johnson et al., 2016). From these measurements we calculated average plant richness, non-*Cucurbita* density, *Cucurbita* density, plant height, and herbivory per m^2 for each sub-transect for each survey round.

2.2.2. Arthropod visual surveys

During each survey round, we conducted 10-minute visual surveys spanning the entire sub-transect area in which we searched pumpkin plants for arthropods, starting at the crown of the plant and working our way to cover the base (as per Blubaugh, 2023) and the surrounding 0.5 m radius of vegetation. All arthropods encountered during this survey were counted and noted as egg, larvae, or adult, and were identified to the lowest taxonomic level possible in field conditions (most often family) and assigned a morphospecies name. Whenever possible, we collected representative morphospecies samples for later identification to finer taxonomic resolution.

2.2.3. Arthropod traps

To sample small and/or highly mobile herbivores and parasitoids that may otherwise be missed by visual surveys (Dreistadt et al., 1998), we deployed sticky card traps on alternating weeks from the visual surveys (as per Egerer et al., 2017). We used a 7.62 × 12.7 cm double-sided sticky card trap (Catch Master Bayonne, NJ, USA) secured to an orchid stake located above the leafy canopy in the middle of each sub-transect, and ensured all sticky cards were located between two pumpkin plants that were separated by less than one meter. Traps were left in the field for 24 hours, collected in clear plastic bags to prevent traps sticking to one another, and stored at -20 °C prior to identification.

2.3. Post-field methods

2.3.1. Arthropod IDs

We focus on herbivore and natural enemy trophic levels in this study, and in order to identify arthropods in our field survey, we identified all hand-collected representative arthropods under a stereomicroscope using various identification keys (McAlpine, 1981; Goulet and Huber, 1993; Arnett and Thomas, 2000; Arnett et al., 2002), BugGuide (2023), GLOBI database (Poelen et al., 2014), and iNaturalist (https://www.inaturalist.org/). Based on these taxonomic assignments, we updated identifications in the visual survey data with individuals identified to family: 92.2%, genus: 35.9%, and species: 36.1% (similar resolution as past studies, Egerer et al., 2017; Lowenstein and Minor, 2018; Mabin et al., 2020). We identified arthropods on the sticky traps by first identifying all large and medium (> 5 mm in length) arthropods on the front and back of the card. For small arthropods (< 5 mm), we identified arthropods within a 1 × 5 in vertical strip in the middle of the trap on both the front and back of the card and extrapolated counts for the total card by multiplying by 3 (Dreistadt 1998). Individuals identified to family: 98.5%, genus: 48.0%, and species: 48.0% (similar resolution as past studies, Musser and Nyrop, 2004; Gardiner et al., 2010; Bennett and Gratton, 2012). After identification, we assigned a trophic level (her-bivore, predator, parasitoid, pollinator, detritivore, other) based on ecological information from Triplehorn et al. (2005), BugGuide (Bug-Guide 2023), a cotton IPM extension document created for our study region (Vyavhare and Kerns, 2022) or from primary literature. PER-MANOVA indicated that the visual sampling and trap sampling methods characterized significantly distinct subsets of the herbivore ($p < 0.001$, $F = 237.76$, $R^2 = 0.21$) and natural enemy ($p < 0.001$, $F = 251.67$, $R^2 = 0.21$) communities, suggesting little resampling between the two methods and justifying combining the two sampling methods (as per Egerer et al., 2017) per sampling round. For the herbivore taxa, we then noted whether it specialized on *Cucurbita* or Cucurbitaceae and used this information to classify the herbivores as either generalist or specialist (as per Jonsen and Fahrig 1997). We divided natural enemies into 'generalist predators' and 'specialist parasitoids' and hereafter describe them as such due to the fact that parasitoids tend to be specialized on narrow taxonomic groups of host prey (Strand and Obrycki 1996). We then used the *vegan* package (v.2.6–4)(Oksanen 2022) to calculate abundance and family level richness of generalist herbivores, specialist herbivores, generalist predators, specialist parasitoids. Family-level richness was calculated for the entire herbivore community (including generalist and specialist taxa) and used in subsequent analyses, as specialist herbivore richness had little variability and were represented in only two of the 39 total herbivore families identified in our system. A summary of the herbivore community can be found in Table S1 and a summary of the natural enemy community in Table S2.

2.4. Landscape data

To characterize herbivore resources at the landscape level, we combined data from the 2019 National Land Cover Database (Dewitz and USGS, 2021) and the 2019 National Agricultural Statistical Service (NASS) Cropland Data Layer (USDA 2019), both of which have a 30-m spatial resolution, as well as the county-level pumpkin production maps within buffers relevant to herbivores present (50 m, 100 m, 250 m, 500 m, 1 km, 2 km, 5 km) (Table S3). Buffers were measured from the center coordinate of the full transect at each site. Land-use/land-cover (LULC) data were summarized for each buffer zone and buffer radius by calculating the relative area of each category. Data were collected and processed using Google Earth Engine (GEE, Gorelick et al., 2017) and the code used for pulling multi-scale LULC data is available via Harvard Dataverse (Peter et al., 2021). Ground-truthing cropland cate-gories revealed that the USDA NASS data source was accurate for delineating row crops (i.e., cotton, sorghum, maize, and wheat); how-ever, it did not accurately detect *Cucurbita* crops within our landscape.

Therefore, we obtained field coordinates for all *Cucurbita* acreage within our two study counties from local partners. We then created two variables, *Cucurbita* cropland, and non-*Cucurbita* cropland. With the remaining LULC classes from the NLCD data, we created the combined categories of semi-natural habitat, impervious, and water (Table S4) (as per Cusser et al., 2018). Both NLCD and NASS data were converted from area units to proportion cover within a given buffer (expressed as a percentage).

At the100 m scale *Cucurbita* production covered the greatest proportion of the landscape (mean = 0.70, sd = 0.12), followed by production of non-*Cucurbita* crops (mean = 0.24, sd = 0.14), semi-natural habitat (mean = 0.03, sd = 0.07), impervious surface (mean = 0.03, sd = 0.05), and no water was present. At the 2 km scale, non-*Cucurbita* production covered the greatest proportion of the landscape (mean = 0.80, sd = 0.09), followed by semi-natural habitat (mean = 0.14, sd = 0.09), impervious surfaces (mean = 0.03, sd = 0.01), and *Cucurbita* production covered the same area as water (both mean = 0.02, sd = 0.01). While initial analyses considered various landscape scales (Table S3), we focus our analyses on the effects of *Cucurbita* and semi-natural habitat at the 2 km landscape scale as this scale is often relevant for both herbivores and natural enemy communities (Thies et al., 2003; Mitchell et al., 2014; Philpott et al., 2020).

2.5. Agronomic data

To control for differences in agronomic practices across sites, we gathered agronomic data relevant to insect-plant interactions for each field site. These included planting date, tillage practice (50% strip till or 100% full till), years since the field was planted in *Cucurbita*, and distance to the in-row field edge for each sub-transect to capture any edge effects. Field sites contained other pumpkin species outside of our *C. pepo* spp. *pepo* transect area including *C. argyrosperma, C. moschata, C. maxima,* and one site had a small area planted in *Lagenaria siceraria* (Calabash gourd) for a mean of 2.56 (sd = 0.90) *Cucurbita* species per site. For the 18 fields for which we had full-field planting data, we calculated the proportion of a field planted in *C. maxima* (mean = 0.20, sd = 0.15) to assess trap-crop effects (Andersen and Metcalf, 1987) However, as preliminary analyses did not find it to be a significant predictor of specialist herbivore abundance or herbivory, we removed it from our analysis given that two of our sites lacked this information.

2.6. Statistical analysis

To understand the drivers of herbivory, we took a two-phase analysis approach (as per González et al., 2020). First, we used generalized linear mixed models (GLMM) to test specific direct hypotheses about the relationships between herbivores, plant resources, and natural enemies. Then, we conducted a confirmatory path analysis by building piecewise structural equation models (piecewiseSEM) based on the significant predictors in our GLMMs to examine the whole system of interacting organisms in the landscape. All data analysis was carried out in R version 4.2.2 (2022–10–31).

2.6.1. GLMM

To analyze direct relationships between landscape/local site factors and resulting arthropod community characteristics and herbivory levels, we constructed generalized linear mixed effect models (GLMM) (*glmmTMB* and *lme4* packages; Bates et al., 2014; Brooks et al., 2017) for 8 sets of response variables: herbivore richness, generalist herbivore abundance, specialist herbivore abundance, generalist predator abundance, generalist predator richness, specialist parasitoid abundance, specialist parasitoid richness, and herbivory. Prior to model construction, we examined all pairwise Pearson's correlations among potential predictor variables. If variables were significantly and strongly correlated ($p \leq 0.05$, Pearson's r ≥ 0.70), we chose the most biologically relevant variable to include in a model (Table S5). This resulted in nine

possible fixed predictor variables: *Cucurbita* density, non-*Cucurbita* density, plant richness, and distance to in-row field edge, days after planting, tillage practice (50% strip or 100% full), years since *Cucurbita* cultivation, proportion *Cucurbita* cultivation, and proportion semi-natural habitat in a 2 km radius. Additionally, specialist herbivore abundance and generalist herbivore abundance were used as predictor variables in models with natural enemy responses. We provide a summary of variables used in this analysis in Table 1. For each model, we accounted for repeated measures of field sites (1|site) as a random effect. We standardized all continuous predictors using the 'scale' function in R and tested for multicollinearity using variance inflation factor scores and the function 'check_collinearity' in the *performance* package (Fox and Weisberg 2014, Lüdecke et al., 2021), confirming that all models had VIF > 3 (Variance Inflation Factor; James et al., 2013; Craney and Surles, 2002).

We then explored using an informatic theory model selection and averaging ($\Delta AIC_c \leq 2$ from top model) approach to address overfitting and sorting models based on efficacy and parsimony, however in all models the significant predictors were the same across saturated, top, and averaged model. Therefore, we present results from the saturated models given limitations in reporting random effects on averaged models. We report the adjusted interclass correlation coefficient as a measure of the proportion of the total response variance accounted for by the random effect of site ('icc' function in the *performance* package (Lüdecke et al., 2021) and R^2_{GLMM} as a measure of the proportion of variance explained by the model fixed effects ($R^2_{marginal}$) or in conjunction with the random effect of site ($R^2_{conditional}$) ('r.squaredGLMM' in the *MuMIn* package) (Barton et al., 2023; Nakagawa et al., 2017). We visualized significant fixed effects with observed data with the *Effects* and *ggplot2* package (Fox and Hong, 2009; Wickham, 2016).

2.6.1.1. Resource concentration hypothesis (Fig 1 arrows A & B). Next, to test the resource concentration hypothesis, we used the 'glmmTMB'

Table 1
Summary of variables included in statistical analysis.

Scale	Data source	Variable	Mean	SD
sub-transect	mid sub-transect measurement	distance to field row edge	88.50	45.86
	vegetation survey	plant species richness	2.51	0.94
		non-*Cucurbita* density	4.29	10.02
		Cucurbita flower abundance	1.54	1.94
		Cucurbita density	49.35	31.31
		herbivory	5.15	6.14
	arthropod visual survey & traps	specialist herbivore abundance	8.16	48.42
		generalist herbivore abundance	57.39	56.72
		herbivore family richness	6.92	2.56
		generalist predator abundance	37.45	30.18
		specialist parasitoid abundance	7.96	7.01
		generalist predator family richness	3.86	1.44
		specialist parasitoid family richness	2.18	1.44
site	agronomic survey	days after planting	46.69	13.72
		years since pumpkin cultivation	2.42	0.67
		tillage (1 = 100% conventional, 0 = 50% strip)	0.48	0.50
landscape	National Land Cover Database	semi-natural habitat in 2 km radius	0.14	0.09
	agronomic survey & groundtruthing	*Cucurbita* in 2 km radius	0.02	0.01

function to construct GLMMs modeling the abundance of herbivores as a function of the eight predictor variables; proportion *Cucurbita* and proportion semi-natural habitat at the 2 km scale, *Cucurbita* density, plant richness, years since pumpkin cultivation, distance to in-row field edge, tillage practice (50% strip, 100% full), and days after planting. These variables were chosen as measures of plant resource availability and agronomic management choices that can influence herbivore populations. We constructed separate models for generalist herbivore abundance and specialist herbivore abundance using a negative binomial distribution to account for overdispersed count data (as per Grimm and Stegmann, 2019). We tested the effect of the same predictors on herbivore family level richness using the 'lmer' function given the normal distribution of this response variable. We explored using diet breadth (generalist herbivore vs specialist herbivore) as an interaction rather than fitting two separate models, however we could not resolve issues of model fit and convergence after including the interaction, likely due to the stark differences in abundances between the two groups (see Table 1).

2.6.1.2. Natural enemies hypothesis (Fig 1 arrow D, E, F). To examine the effects of resource availability and concentration on natural enemies, we constructed GLMMs modeling the abundance and richness of predators and parasitoids. For all four models we examined natural enemy response as a function of generalist herbivore abundance and specialist herbivore abundance as measures of prey resource availability, as well as proportion semi-natural habitat at the 2 km scale, *Cucurbita* density, non-*Cucurbita* density, plant richness, distance to in-row field edge, and days after planting. Tillage was considered as an additional predictor variable, however we could not resolve issues of model fit and convergence and include both tillage and measures of herbivore prey abundance. We used a negative binomial distribution to model predator and parasitoid abundance to account for overdispersed count data (Grimm and Stegmann, 2019). Predator and parasitoid richness models used a normal distribution.

2.6.1.3. Density-dependent herbivory (Fig 1 arrow C). Finally, to test for evidence of a direct effect of herbivore density on herbivory damage, we modeled herbivory (log transformed to meet assumptions of gaussian distribution) as a function of generalist herbivore abundance and specialist herbivore abundance (cucumber beetles: *Acalymma vittatum, Acalymma trivitattum, Diabrotica undecimpunctata,* and *Paranapiacaba tricincta* and squash bugs: *Anasa tristis*), and days after planting.

2.6.2. piecewiseSEM confirmatory path analysis

To understand the interplay between landscape and local factors, arthropod communities, and herbivory in our *Cucurbita* agroecosystem (Fig. 1), we conducted a confirmatory path analysis based on the results of our hypothesis-driven GLMMs. We chose piecewiseSEM over a more traditional structural equation modeling technique as it can accommodate random effects (Lefcheck, 2016). Using the 'psem' function in the *piecewiseSEM* package (Lefcheck, 2016) we constructed an initial global model including all significant direct interactions from the GLMM models. We standardized all quantitative variables to a mean of zero and a standard deviation of one to obtain comparable estimators as in (González et al., 2020). We included site as a random variable for all component models and checked for model fit and assessed independence claims with Fisher's C and AIC metrics (Shipley 2013). Pairwise variables that were flagged as non-independent based on Fisher's C test were incorporated in the next iteration of the model either as a correlation if the two variables were from the same data category (e.g., generalist herbivore abundance and herbivore richness) or as a missing path to be added as a variable if the parameters were in different categories (e.g., plant richness and natural enemy richness). We refit the model and examined Fisher's C and AIC values again as in past studies (Sudnick et al., 2021; González et al., 2020). To simplify the model and aid in

interpretation, we then removed any variables that were not part of any significant paths and removed any remaining non-significant paths until model fit metrics indicated worse fit than a more complex model (Heckman et al., 2020).

3. Results

3.1. Arthropod communities in Cucurbita fields

We observed 53,150 arthropods across our two sampling methods, of which 47.8% were herbivores and 34.8% were natural enemies. The remaining 17.4% of arthropods were detritivores, fungivores, or pollinators not relevant to this analysis. The herbivore community was dominated by generalists (83.2%), with the most abundant being thrips (Thysanoptera, 47.8%), leafhoppers (Hemiptera: Cicadellidae, 11.8%), and cecidomyiid flies (Diptera: Cecidomyiidae,11.3%). Specialists made up a smaller fraction of the herbivore community (16.8%), comprised of squash bugs (Hemiptera: Coreidae: *Anasa tristis,* 2.8%) and cucumber beetles (Coleoptera: Chrysomelidae: Diabroticites, 1.9%), where cucumber beetles were observed in all 20 field sites and squash bugs were observed in 11 field sites (Table S1). The natural enemy community was dominated by generalist predators (84.8%), with the most abundant being hybotid dance flies (Diptera: Hybotidae, 61.1%), ants (Hymenoptera: Formicidae, 24.0%), and coccinellid beetles (Coleoptera: Coccinellidae, 4.8%). Specialist parasitoids made up a smaller fraction of the community (15.2%), the most abundant of which were mymarid wasps (Hymenoptera: Mymaridae, 25.0%), trichogrammatid wasps (Hymenoptera: Trichogrammatidae,18.6%), and braconid wasps (Hymenoptera: Braconidae,10.5%) (Table S2).

Landscape-level plant resources were not predictive of any measure of the arthropod community (Table S6). Herbivore richness increased significantly with increasing days after planting and *Cucurbita* density (Fig. 3, Table S6). Generalist herbivore abundance increased significantly with increasing days after planting and plant richness (Fig. 4, Table S6). Specialist herbivore abundance was significantly higher in 100% vs 50% tillage, and decreased significantly with increasing distance from the in-row edge (Fig. 5, Table S6). Generalist predator and specialist parasitoid abundance and richness all increased significantly with increasing generalist herbivore abundance (Fig. 6b,d, Fig. 7b,d, Table S6). Generalist predator abundance also decreased significantly with increasing days after planting (Fig. 6a, Table S6). Both generalist predator richness and specialist parasitoid abundance also increased significantly with increasing *Cucurbita* density (Fig. 6c, Fig. 7a; Table S6), while specialist parasitoid richness also increased with increasing plant richness (Fig. 7c, Table S6). The site-level random effect explained 4–35% variation in arthropod responses across models (see ICCs, Table S6). Site explained the most amount of variation in specialist herbivore abundance (ICC = 35%), therefore we added a post-hoc examination of the distribution of specialist herbivores among sites that varied in tillage treatment. We found that squash bugs, but not cucumber beetles were present in a disproportionate number of 100% full till sites (χ^2 test = 15.43, p < 0.001; χ^2 test = 0.74, p = 0.388 respectively).

3.2. Cucurbita herbivory

Herbivory increased significantly over the growing season from an average of 0.69% (SE = 0.06%) 23 days after planting to 15.24% (SE = 4.30%) at 73 days after planting (Fig. 8, Table S6). However, herbivory was not predicted by generalist herbivore nor specialist herbivore abundances (Table S6), nor did analyses find an effect of combined generalist and specialist abundance on herbivory (z-value = -1.572, p = 0.116).

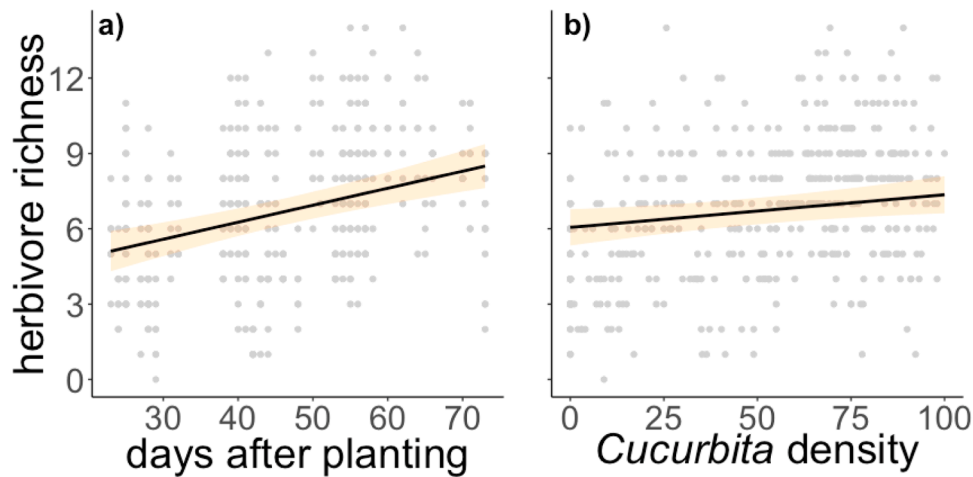**Fig. 3.** Estimated effect of a) days after planting ($z = 4.39$, $p < 0.001$) and b) *Cucurbita* density ($z = 2.83$, $p = 0.005$) on herbivore richness (S). Shaded area around the solid line indicates 95% CI predicted by GLMM. Gray dots show data points for all sites and sampling rounds.
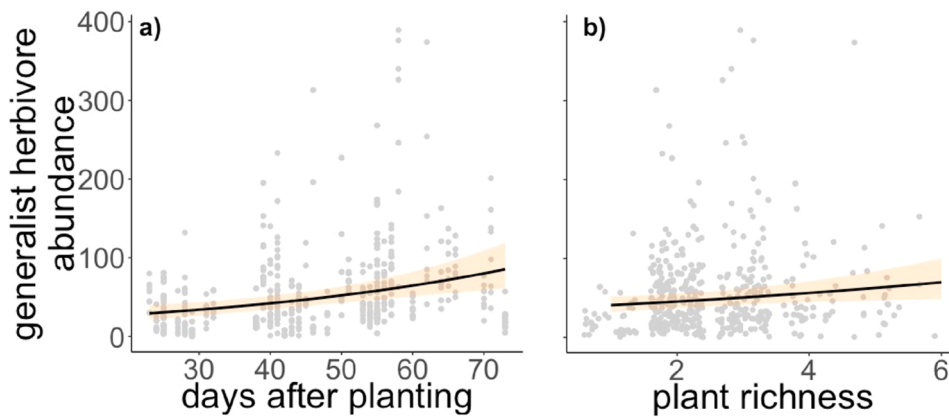

Fig. 4. Estimated effects of a) days after planting ($z = 4.08$, $p < 0.001$) and b) plant richness ($z = 3.04$, $p = 0.002$) on generalist herbivore abundance. Shaded area around the solid line indicates 95% CI predicted by GLMM. Gray dots show data points (panel b) jittered) for all sites and sampling rounds.
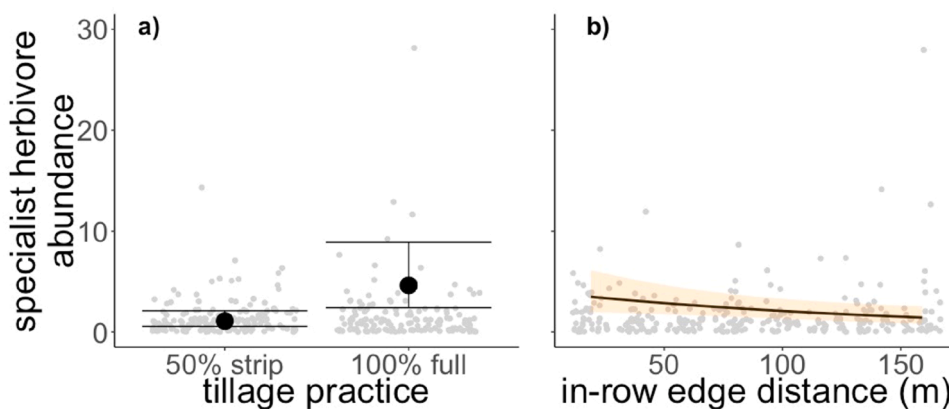

Fig. 5. Estimated effects of a) tillage practice ($z = 2.84$, $p = 0.005$) and b) distance to in-row edge ($z = -2.46$, $p = 0.014$) on specialist herbivore abundance. Shaded area around the solid line and error bars in panel b indicates 95% CI predicted by GLMM. Gray dots show data points (jittered).

3.3. Direct and indirect effects on herbivory (piecewiseSEM)

Confirmatory path analysis of GLMM model results found that a model which included missing paths and correlations and removed all non-significantly-interacting variables fit the data best, as indicated by balancing AIC and Fisher's C fit statistics (Table S7). This model explained 15% marginal and 38% conditional variation in herbivory and indicated that time since planting drove an increase in herbivory, herbivore richness, and generalist herbivore abundance, and a decrease in predator (generalist) abundance (Table 2, Fig. 9). Increases in *Cucurbita* density drove an increase in herbivore, generalist predator, and specialist parasitoid richness but a decline in herbivory, though no direct
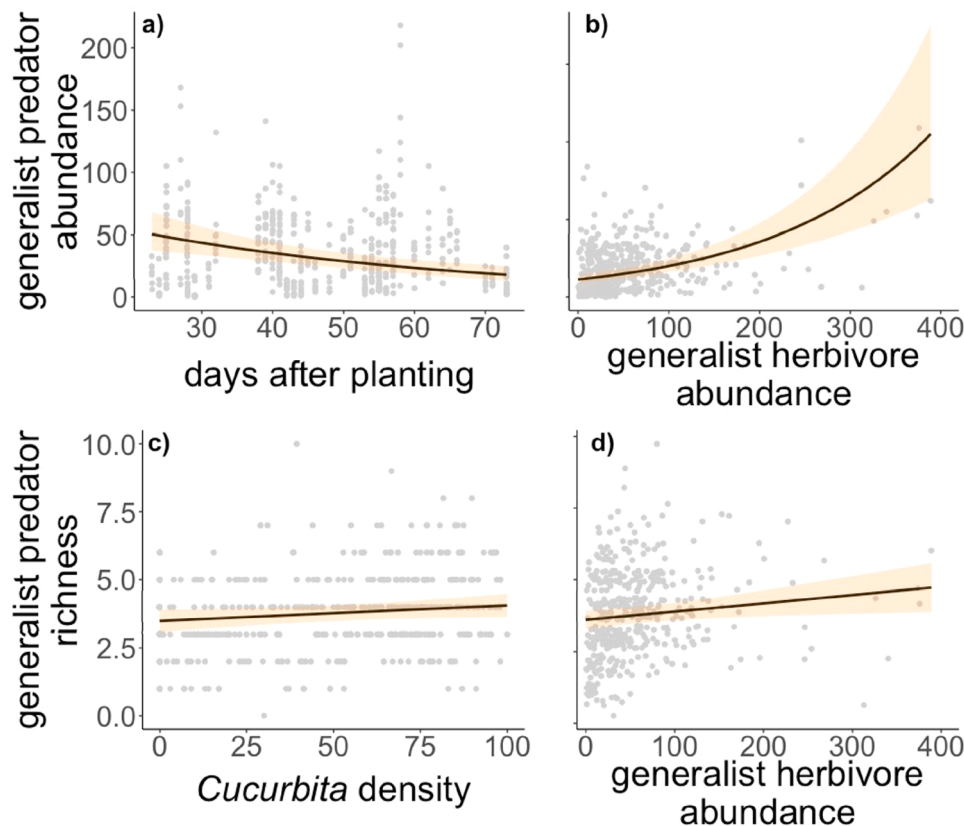
Fig. 6. Estimated effects of a) days after planting ($z = 4.76$, $p < 0.001$) and b) generalist herbivore abundance($z = 7.99$, $p < 0.001$) on generalist predator abundance and effects of c) *Cucurbita* density ($z = 2.21$, $p = 0.027$) and d) generalist herbivore abundance ($z = 2.24$, $p < 0.001$) on generalist predator richness. Shaded area around the solid line indicates 95% CI predicted by GLMM. Gray dots show data points for all sites and sampling rounds.

links were found between the herbivore community and herbivory (Table 2; Fig. 9). Increases in plant richness drove increases in generalist herbivore abundance, herbivore richness, and specialist parasitoid richness (Table 2; Fig. 9). Increased generalist herbivore abundance drove increases in generalist predator and specialist parasitoid abundance and richness (Table 2; Fig. 9). Finally increased herbivore richness drove both generalist predator and specialist parasitoid richness (Table 2; Fig. 9). Significant effects of tillage practice and distance to the in-row edge on specialist herbivore abundance did not persist in the global piecewiseSEM model, nor was the component model predicting specialist herbivore abundance retained in the final model (Table 2; Fig. 9).

4. Discussion

Our study found mixed support for the Resource Concentration Hypothesis for herbivores, and little support for both the Density-dependent Herbivory and Natural Enemies Hypotheses within our agriculturally dominated study-region. Instead, our results suggest an indirect effect of natural enemies on herbivory, mediated by a concentrating effect of local *Cucurbita* resources on both generalist predators and specialist parasitoids with an associated decline in herbivory. Overall herbivore richness increased with local *Cucurbita* density, though specialist and generalist herbivores were neither concentrated nor diluted in areas of higher *Cucurbita* density. While herbivory was not driven by the abundance of herbivores or natural enemies, generalist herbivore abundance was positively impacted by plant richness and both generalist predators and specialist parasitoids were more abundant in the presence of generalist herbivore prey. We found low abundances of specialist herbivores, yet we documented a significant association of the specialist squash bug abundance and 100% tillage. Taken together,

these results demonstrate that *Cucurbita* herbivory levels in agriculturally-dominated, semi-arid landscapes depend primarily on a combination of local crop plant resources and land management.

Our finding of strong *Cucurbita* density effects on overall herbivory levels resonates with past work exploring the role of plant density on herbivory risk, but also provides new insight for an understudied species and region. Previous work has shown that striped cucumber beetles (*Acalymma vittatum*) emigrate less from patches with lower densities of Cucurbitaceae plants, leading to higher beetle densities, but that these specialist beetles are also more abundant where non-*Cucurbita* plants act as a barrier to emigration at field edges (Bach 1988; Andow 2023). In our study system, field edges were extensively managed to remove vegetation to allow transportation of agronomic vehicles, therefore there were few vegetative barriers to herbivore movement at field edges. In contrast to previous work focusing on the role of crop density on herbivores and herbivory, our work documents how variation in monoculture fields under putatively identical planting schemes can give rise to variation in herbivory. Though *Cucurbita* spacing at time of planting was uniform, variation in emergence success, soil quality, and localized rainfall led to sub-transects with a range of *Cucurbita* densities at a given plant age. Interestingly, the lack of a direct link between herbivore community composition and herbivory within *Cucurbita* fields was surprising but is not uncommon in the agroecological literature. Feeding trials by Brzozowski et al. (2019) showed that *Cucurbita* herbivory induces volatile deterrent production that slows the growth of generalist herbivores, which they suggest could lead to an uncoupling of herbivory from generalist herbivore abundance under field conditions (Brzozowski et al., 2019). In our system, we found that specialist herbivores were much less abundant than in previously studied *Cucurbita* systems within the United States, indicating that they were not the primary drivers of herbivore damage. This pattern and mechanism have
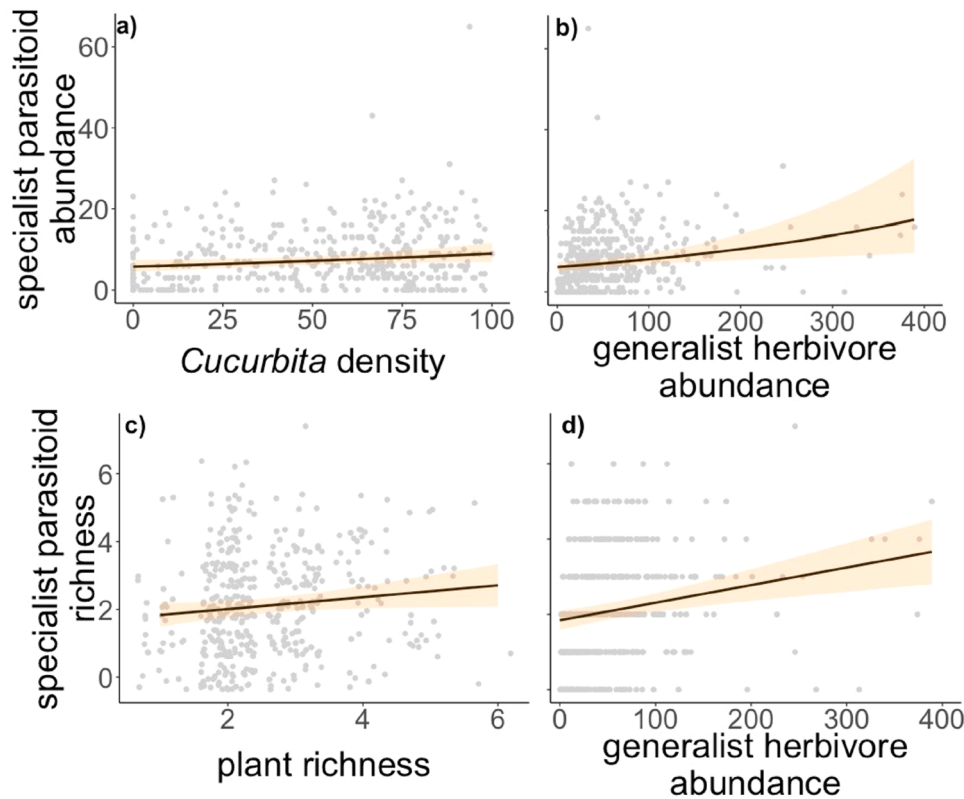
Fig. 7. Estimated effects of a) *Cucurbita* density ($z = 2.07$, $p = 0.039$) and b) generalist herbivore abundance ($z = 2.82$, $p = 0.005$) on parasitoid (specialist) abundance and effects of c) plant richness ($z = 2.50$, $p = 0.012$) and d) generalist herbivore abundance ($z = 3.43$, $p = 0.001$) on parasitoid richness. Shaded area around the solid line indicates 95% CI predicted by GLMM. Gray dots show data points for all sites and sampling rounds.
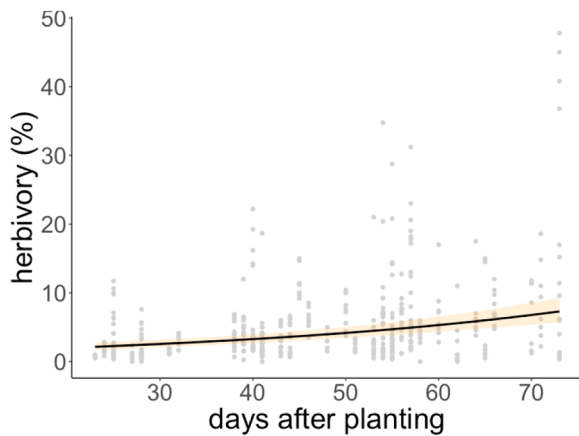

Fig. 8. Estimated effects of days after planting on percent herbivory ($z = 7.99$, $p < 0.001$). Shaded area around the solid line indicates 95% CI predicted by GLMM. Gray dots show data points for all sites and sampling rounds.

been proposed in other systems, where generalist herbivores inflicted more damage than specialists on less defended species within the genus *Penstemon* (Kelly and Bowers, 2016) and where abundant small-bodied aphids inflict more economic damage than larger-bodied beetles in soybean production (Lundgren et al., 2013). Indeed, in our study, the generalist herbivore community was diverse and included many small-bodied herbivores whose individual contribution to herbivory levels may be smaller as compared to large-bodied herbivores.

Local but not landscape level plant resource variation influenced both herbivore and natural enemy communities in our study system. Our results are consistent with the Uhl et al. (2020) study of moth species in

Italy, which found no correlation among landscape-scale attributes and species diversity but found that local factors did influence local arthropod species diversity. Compared to previous studies exploring landscape impacts on *Cucurbita* herbivory dynamics, which occurred in Midwestern and Central Californian landscapes (Phillips and Gardiner, 2016; Egerer et al., 2020), our study system was embedded in an agriculturally dominated landscape with >80% row crop cultivation (56% cotton) at the 2 km scale. In highly simplified landscapes, effects of in-field diversification are theorized to have minimal effect on arthropod communities given a limited regional species pool (Tscharntke et al., 2012). Instead, we found that parasitoid and herbivore richness as well as generalist herbivore abundance were higher in sites with higher levels of local plant richness. Plant richness in our system was related to the management intensity of our fields, where less intensively weeded fields had more weed species and volunteer cotton plants intermixed with the focal *Cucurbita* crop.

Further, our finding that herbivory declined with increasing *Cucurbita* density while accounting for plant age, provides some evidence for a resource dilution effect for herbivore abundance, as documented for many other herbivores within large-scale cropping systems (Power 1987; Parsa et al., 2011; Rosenheim et al., 2022). The vast scale of *Cucurbita* production in our study system was markedly larger than in previous research on *Cucurbita* agroecosystems. Farmers in our study region often used entire quarter sections of fields, instead of narrow strips, to produce pumpkins, with average field size around 16.6 hectares as opposed to an average of 6.75 hectares in temperate region studies (Petersen et al., 2013, personal communication). With reliably abundant *Cucurbita* resources in the landscape each year, herbivores are likely not as limited by these food resources and may instead be constrained by environmental variables related to overwintering habitat or mortality from management actions (as in Lawton et al., 2022) rather than food resource availability.

Table 2

PiecewiseSEM model of factors influencing herbivore richness, generalist herbivore abundance, generalist predator abundance and richness, specialist parasitoid abundance and richness and herbivory with site as a random effect. Modeled correlations indicated by (~~) below dashed line.

| Response	Predictor	Est.	SE	p	Std.Est	$R^2_{marginal}$	$R^2_{conditional}$
herbivore richness	days after planting	0.33	0.07	0.000	0.33	0.23	0.35
	Cucurbita density	0.17	0.06	0.006	0.17		
	plant richness	0.10	0.05	0.035	0.10		
generalist herbivore abundance	days after planting	0.25	0.05	0.000	0.25	0.09	0.18
	plant richness	0.10	0.05	0.035	0.10		
generalist predator abundance	days after planting	-0.26	0.05	0.000	-0.26	0.18	0.31
	generalist herbivore abundance	0.41	0.04	0.000	0.41		
generalist predator richness	Cucurbita density	0.15	0.05	0.003	0.15	0.10	0.18
	herbivore richness	0.22	0.05	0.000	0.22		
specialist parasitoid abundance	Cucurbita density	0.16	0.05	0.001	0.16	0.07	0.10
	generalist herbivore abundance	0.19	0.05	0.000	0.19		
specialist parasitoid richness	generalist herbivore abundance	0.11	0.05	0.045	0.11	0.09	0.11
	plant richness	0.10	0.05	0.035	0.10		
	herbivore richness	0.18	0.05	0.001	0.18		
herbivory	days after planting	0.02	0.00	0.000	0.46	0.15	0.38
	Cucurbita density	-0.01	0.00	0.042	-0.13		
~~generalist herbivore abundance	~~herbivore richness	0.45	–	0.000	0.45		
~~ specialist parasitoid richness	~~ generalist predator richness	0.20	–	0.000	0.20		
~~ specialist parasitoid abundance	~~ specialist parasitoid richness	0.73	–	0.000	0.73		
~~ specialist parasitoid abundance	~~ generalist predator richness	0.13	–	0.003	0.13		
~~ generalist predator richness	~~ generalist predator abundance	0.14	–	0.001	0.14		
~~ specialist parasitoid abundance	~~ generalist predator abundance	0.14	–	0.002	0.14		
~~ generalist predator richness	~~ specialist parasitoid richness	0.12	–	0.008	0.12		
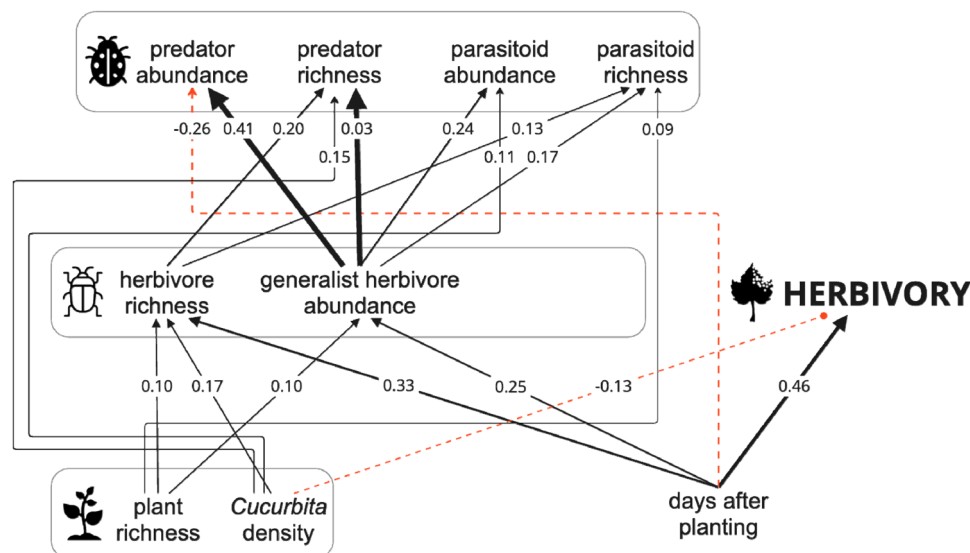
Fig. 9. Visual summary of piecewiseSEM confirmatory path analysis of drivers of herbivory in semi-arid *Cucurbita* agroecosystems based on results by GLMM analysis. Dashed red lines indicate negative paths, black lines indicate positive paths. Grey boxes around variables indicate variables belonging to the same trophic level (plant, herbivore, natural enemy). Weight of lines between variables indicates strength of estimated coefficient.

Our study was also the first to document land-management effects on High Plains herbivores outside of the dominant cotton production systems, specifically the impact of tillage intensity and distance to in-row edge on specialist herbivore abundance. Though tillage intensity has historically been thought to disproportionately harm soil-associated herbivore populations, a recent meta-analysis found that foliar, but not soil associated herbivores were influenced by tillage with greater abundances in more intensively tilled fields (Rowen et al., 2020). The authors of this meta-analysis posit that tillage effects on foliar herbivores are likely due to complex changes in bottom-up plant resources and top-down natural enemy forces in response to tillage. Our findings align with this global pattern, given that specialist herbivore abundances were higher in full (100%) tilled fields and that foliar squash bugs, but not soil-associated cucumber beetles, were the specialist species more likely to be found in full tillage fields. Previous examinations of tillage effects

on *Cucurbita* herbivores have either grouped all herbivores together (Quinn et al. 2016) or have reported effects of strip tillage compared to mulch or row covers without a full tillage control (Appenfeller et al., 2022; Buchanan and Hooks, 2018; Skidmore et al., 2019). Within our Southern High Plains study region, Parajulee et al. (2006) found that foliar thrips and cotton fleahoppers were also more abundant in full tillage than strip tilled cotton. No effect of tillage on the natural enemy community in our confirmatory path analysis suggests that bottom-up changes in plant quality are more likely driving shifts in foliar herbivore abundance. Our finding that specialist herbivores were most abundant at field edges also suggests that host plant locating behavior may play a large role in determining herbivore densities across the landscape, as has been found in other *Cucurbita* systems (Bach 1988, and Xue, 2009). Taken together, these results suggest that larger fields with less intensive tillage could help suppress specialist herbivore

populations, though these decisions would have to be balanced with goals related to soil health and production within a region.

Phenological differences in arthropod and crop dynamics have long been incorporated into pest management programs, but rarely do studies examine how regional production context may change which factors drive arthropod dynamics. In our semi-arid agroecosystem, we found a decline in predator abundance over time while generalist herbivore abundance, herbivore richness, and herbivory increased. Previous work in humid Appalachia found that predator abundance increased mid-season, matching the phenology of squash bugs, and declined again as *Cucurbita* plants reached maturity (Decker and Yeargan, 2008). Though we did not find a significant effect of days after planting on specialist herbivore abundance, their abundance was highest in the earliest sampling round. Additionally, in our cotton-dominated landscape, *Cucurbita* crops were the first to emerge during the growing season and few other host plants and prey were available. Cotton emerged as the dominant crop in the landscape midway through our fieldwork and has been shown to significantly support populations of coccinellid predators, whose movement is known to track aphid prey in an adjacent region (Osawa 2000; Parajulee and Slosser, 2003). Declines in predator abundance in our *Cucurbita* fields, as cotton increased in adjacent fields, suggests that mobile predators may have emigrated in search of alternative prey. The decline in predator abundance with time, but increase in both generalist herbivore abundance and richness, suggests that a decline in top-down herbivore control could have contributed to the higher herbivory observed later in the season, shedding light on the important ecological role of predators in herbivore control.

Overall, our study found that herbivory in semi-arid *Cucurbita* agroecosystems was driven by an indirect effect of natural enemies, mediated by a concentrating effect of local *Cucurbita* resources on natural enemies. However, we did not find a direct density-dependent relationship between herbivores and herbivory. Measurements of predation intensity on sentinel prey could clarify if release from top-down control contributes to herbivore dynamics in this system. Our findings also highlight the need to consider both in-field and landscape-scale contexts to anticipate herbivory levels, and a critical need for future work that tracks emigration and immigration of both herbivores and natural enemies to understand the effects of regional crop phenology on local insect-plant interactions.

Author Contributions

H. Gray conceptualized field studies with support from M. López-Uribe and S. Jha. H. Gray and S. Longing selected field sites and established collaborator networks. N. Ivers, E. Lopez, and H. Gray collected field data. E. Lopez and H. Gray identified all arthropod herbivore samples. B. Peter curated landscape data and provided context on geographic scale. H. Gray performed data analysis with guidance from S. Jha and N. Ivers. First draft written by H. Gray and S. Jha. Edits and improvements on subsequent drafts by all authors.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data associated with this manuscript can be found at doi:10.17605/OSF.IO/VFYW9.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.cris.2024.100087.

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