

**DIET BREADTH MEDIATES ARTHROPOD RESPONSES TO
NUTRIENT AVAILABILITY ACROSS TROPHIC LEVELS**

by

JULIA BERLINER

(Under the Direction of Carmen Blubaugh)

ABSTRACT

Nutrients mediate a sprawl of ecological interactions, challenging our ability to predict basal trophic cascades. Diet breadth determines unique consequences of nutrients for herbivorous insects, with specialists less tied to plant quality than generalists. Predator responses also vary by diet breadth; foliar-feeding omnivores respond to plant quality, while generalist predators may lack direct links to nutrient availability. Here, we manipulate a gradient of soil fertility in a field of two model host plants, zucchini and tomato, and measure responses of herbivores and predators that vary in diet breadth. Diet breadth mediated responses to fertility across trophic levels, with specialist and generalist herbivores exhibiting unique responses to fertility on zucchini. Foliar-feeding omnivores had positive responses fertility on both host plants, while generalist predators had a neutral response. Rather than promoting herbivore outbreaks, our results suggest that bottom-up effects of nutrient availability might come back around as top-down control via omnivore recruitment.

INDEX WORDS: diet breadth, nutrient availability, bottom-up cascade, tri-trophic interactions, omnivores

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

If trophic interactions are an intricate game of “Chutes and Ladders,” then nitrogen sets the rules of the game (Vitousek and Howarth 1991, Hunter and Price 1992). However, diverse and dynamic responses to nutrient availability at each trophic level challenge our ability to predict the ecological consequences of nitrogen. Along a gradient of soil fertility, plants strategically invest in toxic chemical defense against herbivores under low-nitrogen conditions and prioritize growth under high-nitrogen conditions (Herms and Mattson 1992, Mur et al. 2017). In simple bi-trophic systems, nitrogen-rich plants attract and support higher abundances of generalist herbivores (Price 1991, Herms and Mattson 1992, Cornelissen et al. 2008). However, specialist herbivores have an enhanced ability to locate their host plant via its defenses and detoxify, sequester, or sometimes incorporate those defenses to defend themselves from predators (Dyer 1995, Reudler Talsma et al. 2008, Ali and Agrawal 2012). These adaptations may allow specialists to outcompete generalist herbivores on low-nitrogen plants (Mooney et al. 2012). Thus, specialist herbivores may have muted positive, or even negative, responses to nitrogen availability (Staley et al. 2010, Blubaugh et al. 2021). Diet breadth is clearly an important source of nuance in herbivore responses to fertility, with yet unknown consequences at higher trophic levels (Rowen et al. 2019).

Predators also mount unique responses to fertility depending on their diet breadth. For example, foliar-feeding omnivores tend to increase in abundance (Eubanks and Denno 2000, Liman et al. 2017) and preferentially oviposit (Seagraves and Lundgren 2010, Vankosky and

VanLaerhoven 2017) on nitrogen-rich plants, subsequently suppressing more herbivores (Eubanks and Denno 2000, Seagraves and Lundgren 2010, Liman et al. 2017, Rinehart and Long 2022). In contrast, predators that do not feed on foliar tissue, henceforth “generalist predators,” respond to fertility via indirect pathways. For example, predators may respond to fertility-mediated increases in herbivore density and quality (Ives et al. 1993, Chaplin-Kramer et al. 2011, Alkherb et al. 2016, Bijleveld et al. 2016). Low-nitrogen plants can also reduce prey nutritional quality, which may lead predators to compensate by either consuming more prey per-capita (Denno et al. 2002, Couture et al. 2010, Aqueel and Leather 2012, Schmidt et al. 2012) or eating other predators to meet their nitrogen requirements (Denno and Fagan 2003, Matsumura et al. 2004, Kagata and Katayama 2006). Increased fertility can also attenuate prey toxicity (Nishida et al. 1992, Malcolm 1992, Couture et al. 2010, Chaplin-Kramer et al. 2011), with implications for predator performance (Kos et al. 2011, 2012) and mortality (Banfield-Zanin et al. 2012). Fertility can also affect predators by modulating plants’ defenses such as glandular trichomes and herbivore-induced volatile compounds (Han et al. 2022). For example, as plants increase trichome density under low-fertility conditions (Barbour et al. 1991, Lynn and Fridley 2019), predators not adapted to navigating trichome-dense plants may experience reduced mobility and survival (Riddick and Simmons 2014). On the other hand, decreased fertility might increase attraction of natural enemies by enhancing emissions of herbivore-induced volatiles that predators exploit to locate prey (Schmelz 2003, Burney 2012, De Lange and Rodriguez-Saona 2019, but see Gouinguéné and Turlings 2002, Lou and Baldwin 2004, Olson et al. 2009), (Vet and Dicke 1992, Chen et al. 2008, Mumm and Dicke 2010). Linking predator responses to soil fertility is a dizzying game of “Chutes and Ladders,” but examining tri-trophic interactions through the lens of diet breadth may clarify context-dependent outcomes of nutrient availability.

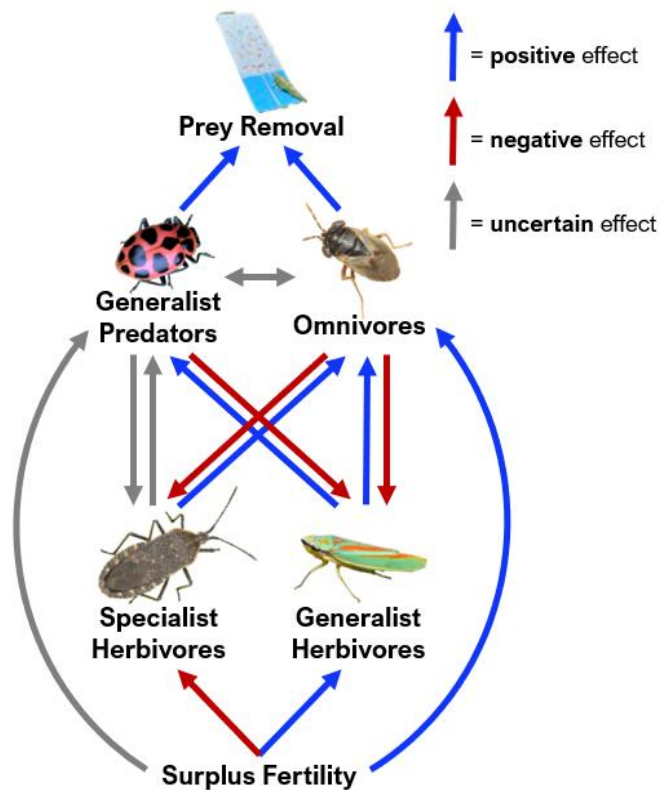


Figure 1. Hypothesized trophic cascades induced by surplus fertility. The direction of the hypothesized effect is indicated by the color of the arrow. Functional groups are represented by the most abundant taxa found on zucchini during our study.

To examine how diet breadth mediates arthropod responses to soil nutrients across trophic levels, we manipulate a gradient of fertility and measure the abundances of herbivores and predators that vary in diet breadth. Because plant chemistry and insect communities vary by host plant, we examine two model systems: zucchini, *Cucurbita pepo* var. *cylindrica*, and tomato, *Solanum lycopersicum*. We predicted that generalist herbivores and foliar-feeding omnivores would increase in abundance in response to surplus fertility (Cornelissen et al. 2008, Liman et al. 2017). Specialist herbivores,

reliant on cues from host-specific defenses, may increase to a lesser degree than generalists or even decrease in abundance in response to surplus fertility (Nishida et al. 1992, Staley et al. 2010, Blubaugh et al. 2021). Generalist predators may not exhibit a clear response to fertility, as they are linked to nitrogen by a suite of indirect mechanisms which have contrasting consequences for predator abundance (Chen et al. 2010). To assess how predator responses to nutrient availability impact predation rate, we measure the removal of immobile prey. Because we expect to see more omnivores on nitrogen-rich plants, we expect higher rates of prey removal (Liman et al. 2017, Rinehart and Long 2022). By examining the ecological consequences of nitrogen on arthropods

that vary in their diet breadth across trophic levels, we increase the resolution with which we can trace the effects of nitrogen in food webs.

CHAPTER 2

METHODS AND RESULTS

Methods

Study System

The study took place in a certified organic field of zucchini (*Cucurbita pepo* cvs. Yellow Fin) and tomatoes (*Solanum lycopersicum* cvs. Celebrity) at the University of Georgia Durham Horticulture Research Farm, Watkinsville, GA, USA (33.887110, -83.420523, elevation ~220 m). The soil was mainly Georgia clay with low organic content (%N<0.2, Supplementary Table 1).

The zucchini herbivore community is dominated by the squash bug, *Anasa tristis*, a specialist (Schmidt et al. 2014). Other prominent specialist herbivores of zucchini are the striped cucumber beetle, *Acalymma vittatum*, the squash beetle, *Epilachna borealis*, and the squash vine borer, *Melittia cucurbitae* (Hinds and Hooks 2013). Generalist herbivores of zucchini include the spotted cucumber beetle (*Diabrotica undecimpunctata*), leafhoppers including Hemiptera: Cicadellidae and Hemiptera: Delphacidae, the garden fleahopper (*Microtechnites bractatus*) the tarnished plant bug (*Lygus lineolaris*) flea beetles (tribe Alticini) Eastern leaf-footed bugs (*Leptoglossus phyllopus*), and melon aphids (*Aphis gossypii*). Important predators in our zucchini food web are the big-eyed bugs (*Geocoris* sp.), minute pirate bugs (*Orius* sp.), damsel bugs (*Nabis* sp.), the pink spotted lady beetle (*Coleomegilla maculate*), the Asian lady beetle (*Harmonia axyridis*), dusky lady beetles (tribe Scymnini), long-legged flies (Diptera: Dolichopodidae), lacewings (Neuroptera: Chrysopidae and Neuroptera: Hemerobiidae), long-jawed orbweavers

(Araneae: Tetragnathidae), and the green lynx spider (*Peucetia viridans*) (Schmidt et al. 2014). *Geocoris* sp., *Orius* sp., and *Nabis* sp. are omnivorous predators (Zhang 2021, Eubanks and Denno 2000), while the other listed predators do not foliar-feed.

Our tomato herbivore community consists of one specialist, the tobacco hornworm (*Manduca sexta*) and two generalist herbivores, the potato aphid (*Macrosiphum persicae*) and Western flower thrips (*Frankliniella occidentalis*) (Letourneau and Goldstein 2001). The predator community consists of stilt bugs (Hemiptera: Berytidae), big-eyed bugs (*Geocoris* sp.), minute pirate bugs (*Orius* sp.), damsel bugs (*Nabis* sp.), the yellow garden spider (*Argiope aurantia*), the pink spotted lady beetle (*Coleomegilla maculate*), the Asian lady beetle (*Harmonia axyridis*), long-legged flies (Diptera: Dolichopodidae), and lacewings (Neuroptera: Chrysopidae). *Geocoris* sp., *Orius* sp., *Nabis* sp., and Berytids are omnivorous (Wheeler and Schaefer 1982, Eubanks and Denno 2000, Zhang et al. 2021), while the other listed predators do not foliar-feed.

Experimental Design

Five replicates of each fertility treatment were distributed across a field of twenty 7.32 x 7.32 m plots separated by 1.83 m buffers. Within each plot, we planted two rows of zucchini (*Cucurbita pepo* cvs. Yellow Fin) and two rows of tomatoes (*Solanum lycopersicum* cvs. Celebrity). The rows, all on raised beds, were 7.32 m long separated by 1.83 m. Tomatoes were spaced 0.3 m apart with 25 plants per row, and zucchini were spaced 0.6 m apart with 13 plants per row.

Tomatoes were seeded in Pro-Mix® organic mycorrhizal potting soil on March 26th and watered every 2-3 days in a greenhouse maintained with 16:8 light/dark cycles at approximately

26°C. Tomatoes were transplanted and zucchini were direct-seeded on May 8th.

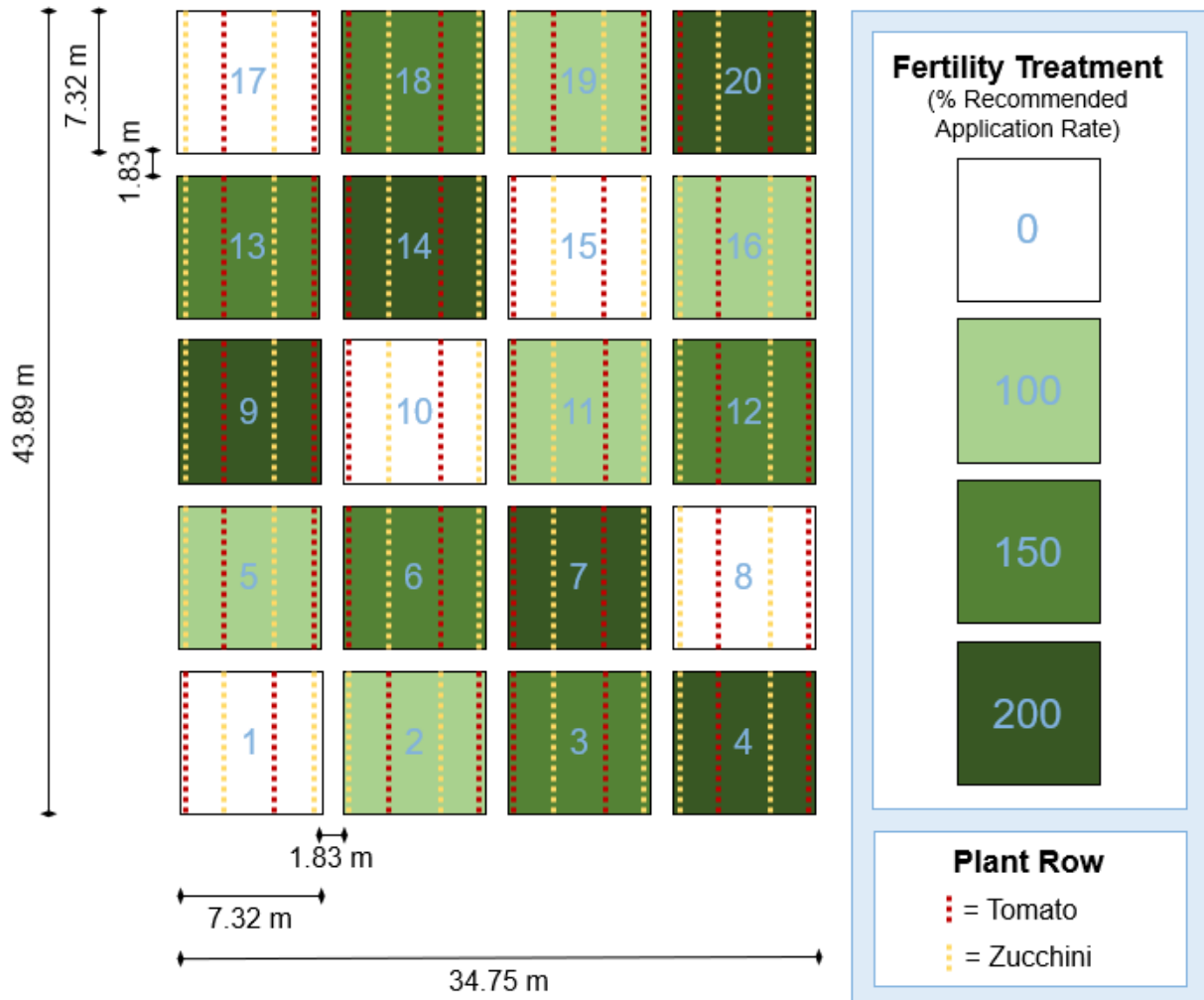


Figure 2. Five replicated fertility treatments in randomized blocks. Treatments 0, 100, 150, and 200 % recommended fertility are represented by a gradient from white to dark green.

Symphony® 5-4-3 organic composted chicken manure fertilizer was applied to the raised beds on April 27th at four rates in relation to the recommendation on the bag: 0% (0 kg/ha), 100% (3906 kg/ha), 150% (5859 kg/ha), and 200% (7812 kg/ha) of the recommended application rate. The beds were tractor-tilled on April 29th, and drip tape irrigation was installed in the middle of each bed. On June 15th, crops were side-dressed by hand with half the initial weights of fertilizer.

Fertility treatments were applied in a randomized complete block design, and zucchini and tomato plants were randomly assigned to alternating rows within each plot.

Sampling

All data were collected in the two middle rows of each plot, one row of tomato and one row of zucchini.

Visual Arthropod Surveys

After 5 weeks of growth, we visually surveyed arthropods weekly on June 16th, June 23rd, June 30th, July 14th, and July 28th (zucchini plants were not surveyed on the final date due to pathogen-related mortality). In each plot, three zucchini and three tomato plants were haphazardly selected each week to be surveyed. For each plant surveyed, the total number of leaves, number of herbivore damaged leaves, number of fruit, and number of flowers were counted. We surveyed two blooming flowers, or all flowers if the plant had fewer than two flowers, inside, outside, and down the stem. For each zucchini plant, we surveyed six leaves and their petioles: two young leaves near the top of the plant, two leaves of medium age and height, and two older leaves near the bottom of the plant. For each tomato plant, three leaves and their petioles coming from the central stem were surveyed: one near the top of the plant, one in the middle, and one toward the bottom.

Vacuum Sampling

Vacuum samples were collected weekly on June 17th, June 24th, and June 30th. We vacuumed 13 zucchini plants and 25 tomato plants for 10 seconds each and collected the arthropod samples in one mesh bag per plot for each host plant.

Arthropod Identification and Assignment to Functional Groups

Arthropods were counted and identified to the most specific taxonomic level possible on sight. All herbivorous or predacious insects were identified at least to family, while spiders were identified at the order level. We excluded microhymenoptera, as it is challenging to distinguish between primary and secondary parasitoids. We categorized arthropods as herbivores or predators and then assigned them to functional groups based on diet breadth; herbivores were categorized as generalists or specialists, and predators were categorized as generalist predators (non foliar-feeding) or omnivores (foliar-feeding).

Sentinel Prey Removal Assays

To assess how predation rate varies across fertility treatments, we used sentinel prey assays. We attached 25 *Drosophila melanogaster* pupae to pieces of cardstock approximately 2x4 cm with Duck® brand double-sided carpet tape. The remaining exposed tape was covered with sand. These cards were secured with paperclips to two plants approximately a third from the end of each middle row and retrieved after about 24 hours. We deployed sentinel prey cards once weekly from mid-June through July. The number of pupae removed from each card was recorded and converted to a proportion.

Statistical Analyses

Analysis 1: Does diet breadth mediate arthropod responses to fertility?

For herbivores and predators, Poisson generalized linear mixed-effects models tested whether annual sums of arthropods observed per plot varied with fertility and diet breadth (main effects and interactions were tested) with plot included as a random effect. We ran separate models for each host plant (tomato and zucchini) and trophic level (herbivores and predators). Posthoc Tukey pairwise comparisons were made within functional groups.

Analysis 2: Does predator removal of sentinel prey vary with fertility?

Mean proportions of prey removed from sentinel prey cards were calculated across all collection dates. Logistic models for each host plant tested whether mean proportions of prey removed varied with fertility treatments.

Results

Herbivore Responses to Fertility

On zucchini, diet breadth mediated complex herbivore responses to fertility (Table 1), with significant decreases in generalists in the 100% recommended fertility treatment relative to the control (Figure 3a), and increases of both generalists and specialists at 150% the recommended application rate (Figure 3a). Fertility treatments had variable effects on tomato herbivores (which were nearly all generalists), increasing their abundance at the recommended rate, while decreasing their abundance at 150% the recommended rate (Figure 3b).

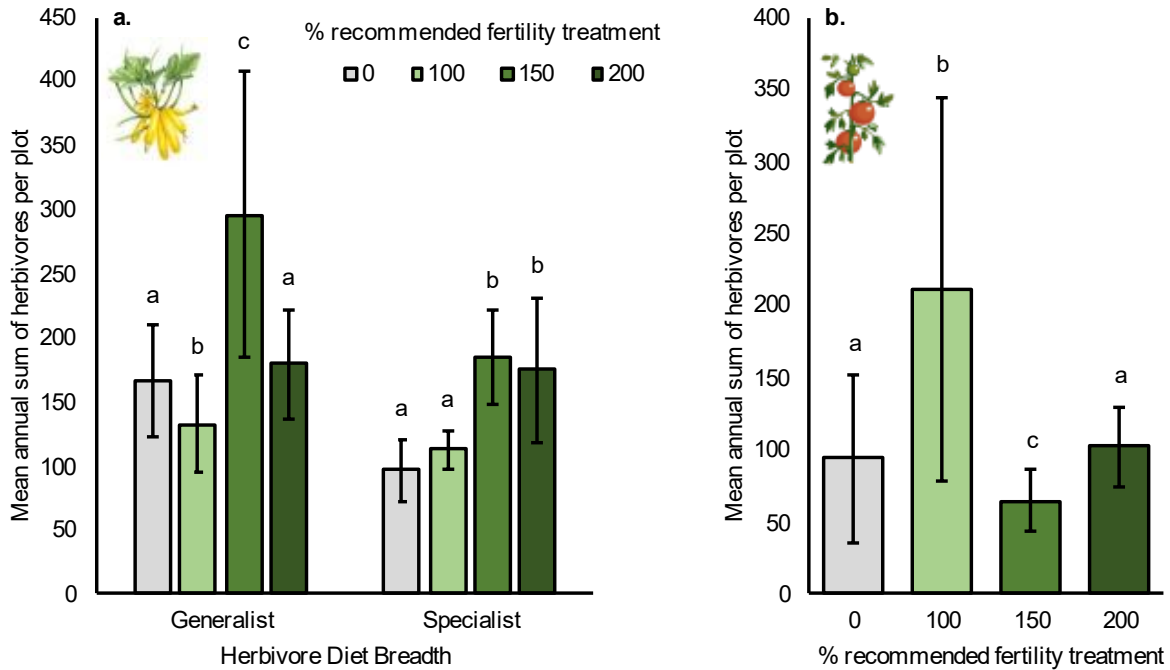


Figure 3. Effects of fertility treatment on annual sums per plot of herbivores counted on zucchini (a) and tomato (b). Left to right, bars represent 0, 100, 150, and 200% recommended application rate of organic poultry fertilizer. Herbivores on zucchini were categorized by diet breadth. Herbivores on tomato were summed across functional groups because few specialists were observed on tomato. Error bars indicate standard error about the mean ($N=$ five replicates per treatment for both models). Groups with different lowercase letters were significantly different. For ease of interpretation, pairwise contrasts were made within each functional group (specialists and generalists).

Table 1. Output from Poisson generalized linear mixed models evaluating how annual sums of herbivore counts on zucchini (a) and tomato (b) vary across a gradient of fertility. Because few specialist herbivores were counted on tomato, all herbivores were binned together. Fertility parameters are in reference to the 0% control. Parameter estimates for fertility treatments are calculated relative to the unfertilized control. $N=$ five replicates for both models.

a. Zucchini				
	Estimate	S.E.	Z	P
(Intercept)	5.155	0.152	33.833	< 0.001
Fertility (100%)	-0.233	0.216	-1.078	0.281
Fertility (150%)	0.425	0.215	1.983	0.047
Fertility (200%)	0.038	0.215	0.175	0.861
Diet Breadth (Specialist)	0.181	0.045	4.017	< 0.001
Fertility (100%) x Diet Breadth	0.197	0.067	2.959	0.003
Fertility (150%) x Diet Breadth	-0.346	0.059	-5.869	< 0.001
Fertility (200%) x Diet Breadth	0.036	0.063	0.573	0.566
b. Tomato				
	Estimate	S.E.	Z	P
(Intercept)	4.537	0.046	98.046	< 0.001
Fertility (100%)	0.814	0.056	14.644	< 0.001
Fertility (150%)	-0.375	0.073	-5.171	< 0.001

Fertility (200%)	0.084	0.064	1.313	0.189
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Predator Responses to Fertility

On zucchini, predator responses to fertility varied across diet breadth, with increased abundance of omnivores by ~50% in fertilized treatments, while generalist predators exhibited a neutral response to fertility (Table 2, Figure 4). On tomato, predator responses to fertility also varied by their diet breadth with foliar-feeding omnivores increasing in fertilized treatments by ~25%, and generalist predators exhibiting a neutral response to fertility (Table 2, Figure 4). Neither generalist predators nor omnivores correlated with herbivore densities (Estimate = 0.0001, SE = 0.0003, Z = 0.463, P = 0.643).

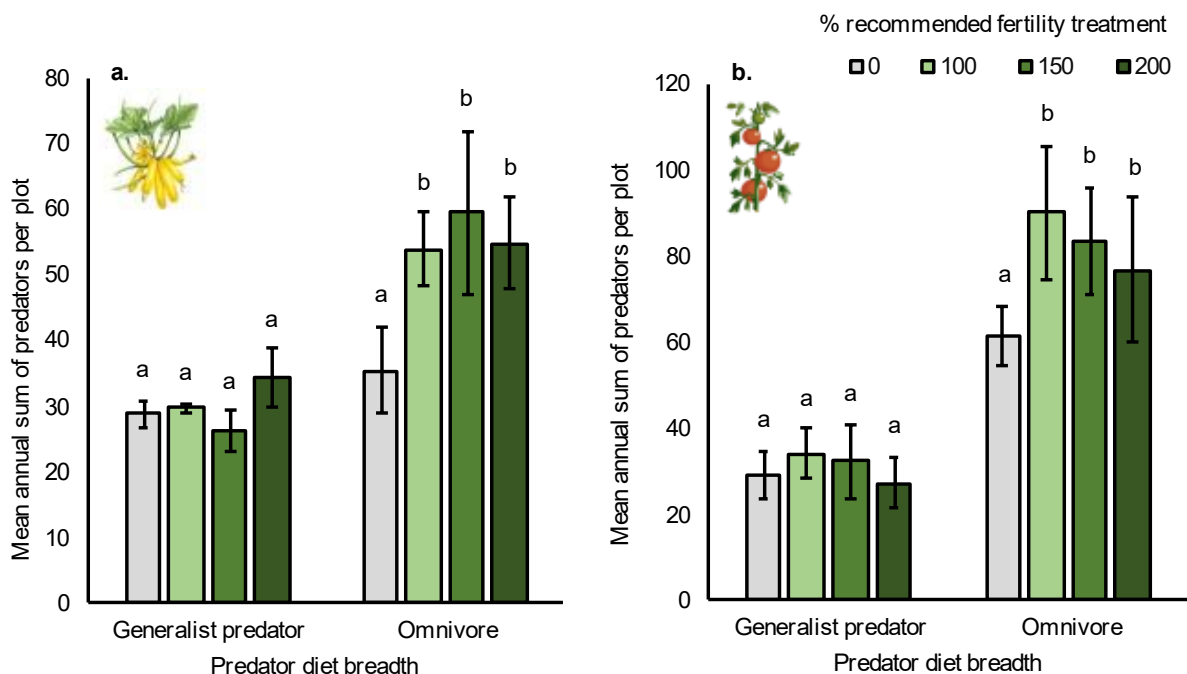


Figure 4. Effects of fertility treatments on annual sums per plot of predators vacuum sampled on zucchini (a) and tomato (b) plants, categorized by their diet breadth. Left to right, bars represent 0, 100, 150, and 200% the recommended fertility rate. Error bars indicate standard error. N= five replicates per treatment for both models. Groups with different lowercase letters were significantly different. For ease of interpretation, pairwise contrasts were made within each functional group (generalist predators and omnivores).

Table 2. Output from Poisson generalized linear mixed models evaluating how annual sums of predator counts vary by diet breadth across a gradient of fertility on zucchini (a) and tomato (b). Parameter estimates for fertility treatments are calculated relative to the unfertilized control (0%). N=five replicates per treatment for both models.

a. Zucchini	Estimate	S.E.	Z	P
(Intercept)	3.339	0.126	26.523	< 0.001
Fertility (100%)	0.039	0.177	0.223	0.824
Fertility (150%)	-0.107	0.180	-0.592	0.554
Fertility (200%)	0.176	0.175	1.008	0.313
Diet Breadth Omnivore	0.206	0.112	1.842	0.065
Fertility (100%) x Diet Breadth	0.391	0.152	2.581	0.010
Fertility (150%) x Diet Breadth	0.612	0.153	3.994	< 0.001
Fertility (200%) x Diet Breadth	0.259	0.148	1.749	0.080
b. Tomato	Estimate	S.E.	Z	P
(Intercept)	3.332	0.188	17.733	< 0.001
Fertility (100%)	0.122	0.264	0.462	0.644
Fertility (150%)	0.085	0.265	0.320	0.749
Fertility (200%)	-0.123	0.267	-0.461	0.645
Diet Breadth Omnivore	0.753	0.101	7.498	< 0.001
Fertility (100%) x Diet Breadth	0.225	0.135	1.666	0.096
Fertility (150%) x Diet Breadth	0.201	0.137	1.469	0.142
Fertility (200%) x Diet Breadth	0.285	0.142	2.012	0.044

Sentinel Prey Removal in Response to Fertility

Mean proportions of sentinel prey removed did not vary across fertility treatments on either crop (Table 3, Figure 5).

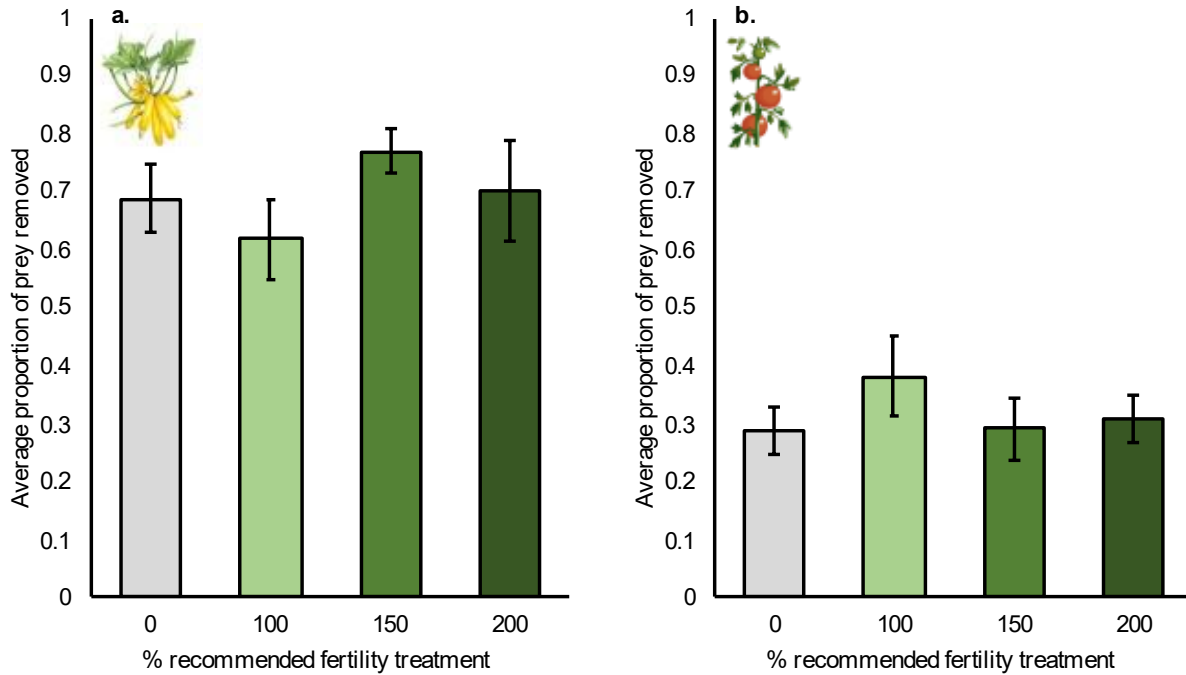


Figure 5. Effects of fertility treatment on annual mean proportion of sentinel fly pupae removed on zucchini (a) and tomato plants (b) N=Five replicates per treatment. Error bars indicate standard error.

Table 4. Output from logistic regressions evaluating how annual mean proportions of sentinel prey removed vary across a gradient of fertility on zucchini (a) and tomatoes (b). N=5 for both models.

a. Zucchini	Estimate	S.E.	Z	P
(Intercept)	0.791	0.965	0.819	0.413
Fertility (100%)	-0.313	1.334	-0.234	0.815
Fertility (150%)	0.410	1.434	0.286	0.775
Fertility (200%)	0.063	1.373	0.046	0.964
b. Tomato	Estimate	S.E.	Z	P
(Intercept)	-0.912	0.989	-0.922	0.357
Fertility (100%)	0.424	1.352	0.314	0.754
Fertility (150%)	0.018	1.396	0.013	0.990
Fertility (200%)	0.102	1.384	0.074	0.941

CHAPTER 3

DISCUSSION

In simple bi-trophic systems, herbivores generally thrive in response to nutrient inputs (Price 1991, Cornelissen et al. 2008, Butler et al. 2012). Yet in our complex tri-trophic field study, fertility treatments had unique effects at each trophic level that depended on arthropod diet breadth (Table 1, Table 2). While generalist and specialist herbivores each had varied responses to fertility, diet breadth was consistently a robust predictor of responses to fertility at the third trophic level; foliar-feeding omnivores mounted strong positive responses to fertility, while generalist predators had neutral responses, across two unique host plants.

As predicted, diet breadth mediated herbivore responses to fertility, but not consistently across levels of fertility (Table 1, Figure 3). With surplus fertility, plant quality tends to boost generalist herbivore preference (Cornelissen et al. 2008) and performance (Awmack and Leather 2002). Specialist herbivores, however, often exploit more specialized plant volatiles specific to their host plant as olfactory cues for feeding and oviposition (Bowers and Puttick 1988, Leimu et al. 2005). Because plants generally increase biosynthesis of secondary metabolites and indirect defenses under low-nutrient conditions (Schmelz et al. 2003, Burney et al. 2012, De Lange and Rodriguez-Saona 2019), we predicted specialist herbivores to be more attracted to low-nitrogen plants, as has been demonstrated in *Brassica* systems (Staley et al. 2010, Blubaugh et al. 2021). However, we did not see the expected overall muted response of specialists compared to generalists in our cucurbit system (Table 1, Figure 3). This system's most abundant specialist

herbivore, the squash bug (*Anasa tristis*), depends on short-range contact cues to identify host plants (Cook and Neal 1999), so the strength of fertility-mediated volatile cues may be less important. Low-nitrogen plants can elevate prey toxicity among specialist herbivores that exploit secondary metabolites for protection from predators (Staley et al. 2010, Ali and Agrawal 2012, Blubaugh et al. 2021), however, zucchini specialists may not benefit from such protection (Tallamy 1985, Pratt et al. 2008, Bruno et al. 2022). In a cucurbit food web, plant quality may surmount plant defense as a cue for specialist herbivores (Reudler Talsma et al. 2008). As the evolutionary ecology of defense varies across plant taxa, so may the role of diet breadth in mediating herbivore responses to fertility.

Foliar-feeding omnivores responded positively to fertility (Table 2, Figure 4), consistent with our predictions. Plant quality may be the cardinal determinant of omnivore preference, as omnivores prefer environments with nitrogen-rich plants (Vankosky and VanLaerhoven 2017, Liman et al. 2017, Rinehart and Long 2022) and will choose them over environments with abundant prey (Seagraves and Lundgren 2010). Generalist predators (non-foliar feeders), by contrast, did not respond to fertility nor to prey density. Predators can respond to fertility-mediated indirect plant defenses like trichomes (Riddick and Simmons 2014, Yao et al. 2021) and herbivore-induced plant volatiles (Vet and Dicke 1992, Mumm and Dicke 2010), which are generally heightened under low-nitrogen conditions (Schmelz 2003, Burney 2012, De Lange and Rodriguez-Saona 2019, but see Gouinguéné and Turlings 2002, Lou and Baldwin 2004, Olson et al. 2009). Fertility-mediated changes in prey nutritional quality (Couture et al. 2010, Aqueel and Leather 2012) and toxicity (Chaplin-Kramer et al. 2011) may also shape indirect predator responses to fertility, but resource-mediated bottom-up effects appeared to have little influence over generalist predators in our system.

Top-down suppression by natural enemies may be more important in shaping herbivore communities than bottom-up resource-mediated effects (Vidal and Murphy 2018), and here we clarify that bottom-up effects of nutrients can have tri-trophic consequences that might neutralize herbivore growth in environments where omnivores thrive (Eubanks and Denno 2000, Liman et al. 2017, Rinehart and Long 2022). Herbivores are well known to prefer well-fertilized host plants (Price 1991, Cornelissen et al. 2008, Butler et al. 2012) and grow more rapidly in high-fertility environments (Bi et al. 2001, Awmack and Leather 2002). The varying herbivore responses to fertility we observed may be the result of enhanced predation by omnivores in fertilized treatments. Indeed, omnivores appeared to be the predominant predators in this system, as removal of sentinel prey correlated with omnivore abundance (Supplementary Figure 1, Supplementary Table 2), even though fertility treatments had non-significant effects on prey removal (Figure 5).

Neutral patterns of prey removal could be the result of combined action of omnivores and generalist predators that had contrasting responses to fertility. Along a gradient of plant quality, diet-mediated niche partitioning among diverse predators could potentially give rise to such neutral effects (Finke and Snyder 2008) and stabilize herbivore growth over time (Tylianakis et al. 2008, Peralta et al. 2014, Gonzalez et al. 2020). Alternatively, this neutral outcome may have arisen from reduced per-capita predation in high fertility treatments, where omnivores may have been ‘distracted’ from prey by high-quality plant-based food (Eubanks and Denno 2000, Liman et al. 2017, Rinehart and Long 2022). Future research must quantify predation rates of specialist and generalist prey and herbivore/predator population growth to clarify the tri-trophic consequences of nutrient availability over longer timescales.

On two distinct host plants, we reveal that diet breadth explains nuanced effects of nutrient availability across trophic levels. Rather than predicting herbivore outbreaks, soil nutrients had

inconsistent effects on specialist and generalists, with consistent, robust, positive effects on omnivorous predators. Diverging multi-trophic responses to fertility along the lines of diet breadth suggest that soil nutrition will determine unique outcomes in food webs depending on the composition and functional roles of the resident arthropod taxa. For example, trophic cascades can be dampened when herbivore communities are dominated by specialists (Singer et al. 2014), yet basal resource heterogeneity determines whether specialists or generalists are favored (Staley et al. 2010) and strengthens complementarity among functionally diverse natural enemies (Tylianakis et al. 2008). Our study lays the framework to unite diet-mediated responses to nutrient availability in an interconnected multi-trophic approach that will allow us to trace bottom-up trophic cascades with more precision and appreciate that, when nitrogen sets the rules of the game of “Chutes and Ladders,” omnivores may be key players that make-or-break how herbivores fare.

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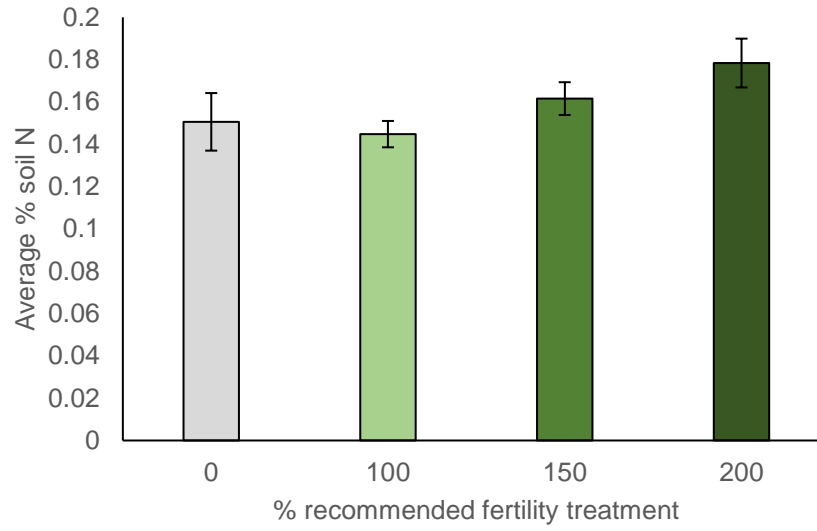
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APPENDIX A

MEASUREMENTS OF SOIL FERTILITY

Supplementary Table 1. Soil test results for samples from each plot

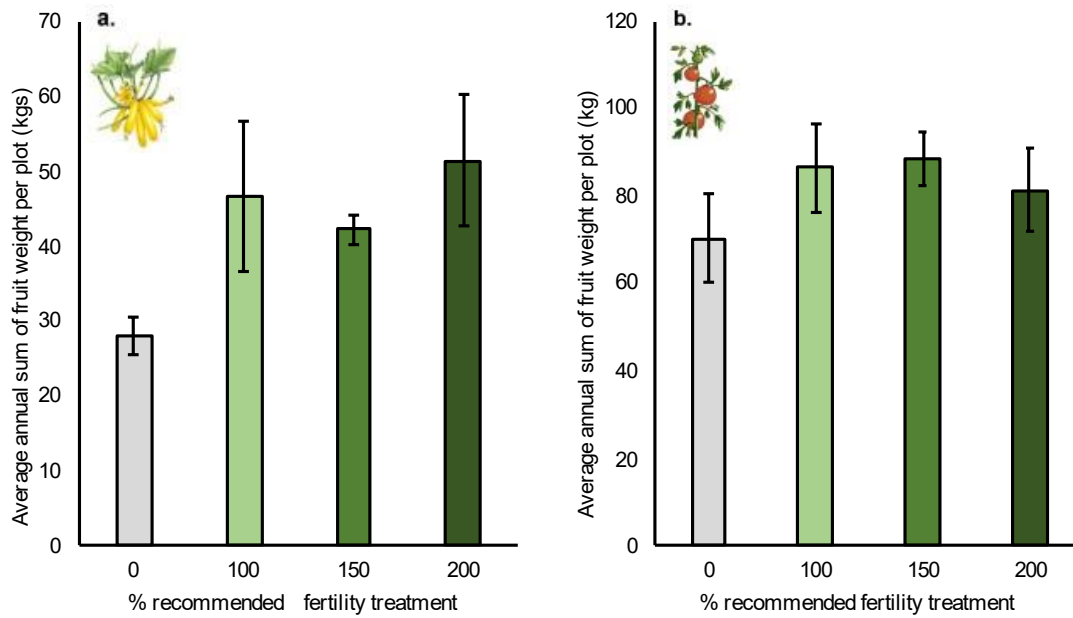
Plot	% rec. fertility	%	ppm CaCO ₃ /pH		pH ²	Mehlich 1 mg/kg (ppm)					
	Treatment	N	LBC ¹	LBCeq		Ca	K	Mg	Mn	P	Zn
1	0	0.181	318	922	6.62	655	78.2	44.6	22.9	36.9	3.37
2	100	0.126	343	995	6.71	1237	173.9	98.4	28.5	143.6	5.81
3	150	0.185	414	1201	7.10	1550	317.9	122.1	32.4	125.8	5.88
4	200	0.189	324	940	6.52	1944	282.4	140.3	39.6	193.3	7.41
5	100	0.142	301	873	6.64	1273	260.1	102.4	30.5	138.2	7.44
6	150	0.168	352	1021	6.79	1666	280.3	126.9	33.2	169.5	6.37
7	200	0.207	365	1059	6.20	1827	252.8	143.9	29.7	207.1	6.89
8	0	0.118	394	1143	6.98	961	49.2	70.2	16.8	53.2	1.63
9	200	0.182	317	919	6.41	2024	658.6	187.8	55.6	288.1	12.07
10	0	0.176	415	1204	6.78	1168	72.1	92.5	25.7	76.3	2.79
11	100	0.160	312	905	6.54	1432	192.5	104.8	26.0	112.8	4.17
12	150	0.139	349	1012	6.35	1340	177.3	96.7	25.6	132.0	4.97
13	150	0.164	425	1233	6.93	1171	225.4	98.0	31.4	90.7	6.54
14	200	0.177	271	786	6.13	1945	352.3	160.2	41.3	175.6	7.59
15	0	0.119	262	760	6.20	903	59.4	61.8	22.6	70.5	1.77
16	100	0.157	303	879	6.10	1390	139.6	70.2	25.7	68.3	3.69
17	0	0.159	346	1003	6.57	856	73.4	75.6	21.2	19.3	3.17
18	150	0.152	339	983	6.67	1326	164.5	113.3	27.1	61.2	5.01
19	100	0.139	275	798	5.73	1315	348.2	109.8	38.1	178.9	6.01
20	200	0.137	408	1183	7.75	550	84.0	48.4	22.1	60.7	3.09



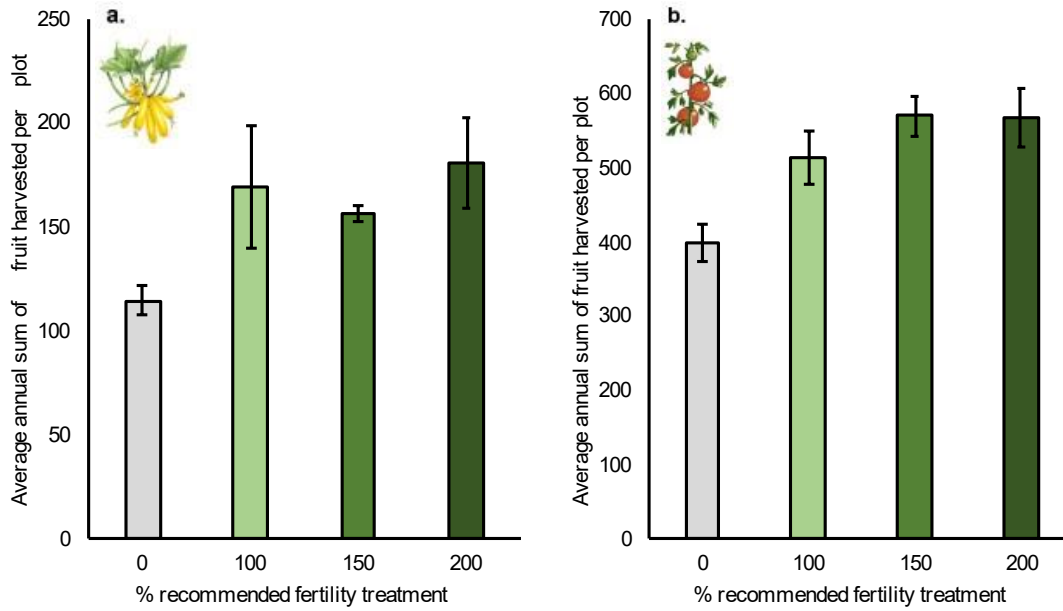
Supplementary Figure 1. Average % Nitrogen of soil samples taken from every plot of each fertility treatment (N=5).

APPENDIX B

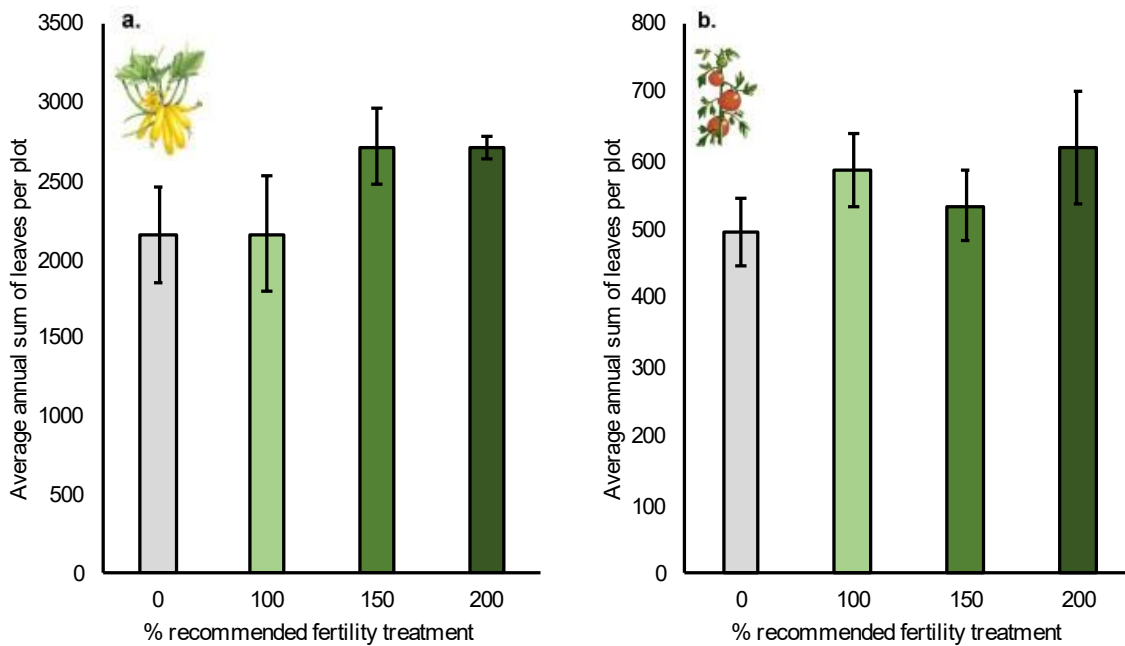
MEASUREMENTS OF PLANT QUALITY



Supplementary Figure 2. Effects of fertility treatments on average annual sum of fruit weight (kgs) harvested per plot from (a) zucchini and (b) tomato (N=5).



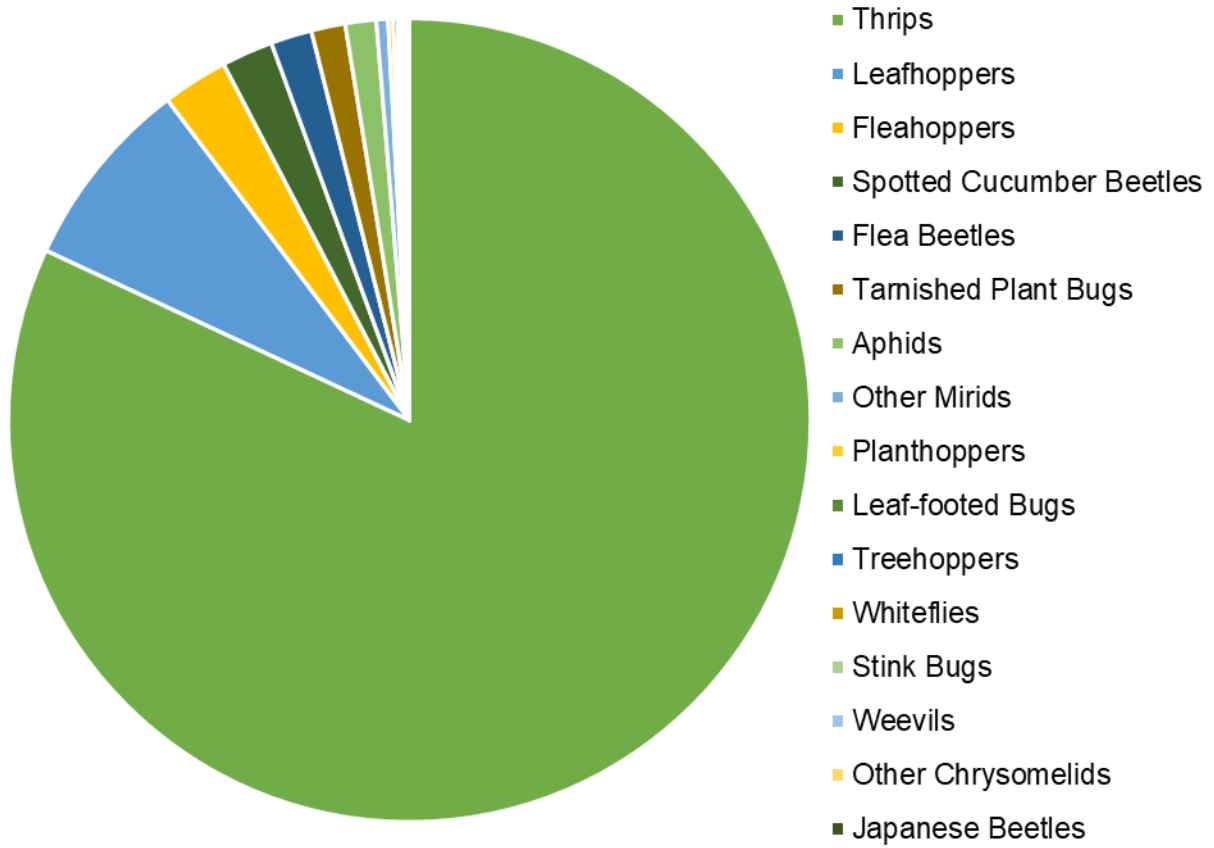
Supplementary Figure 3. Effects of fertility treatments on average annual sum of fruit count harvested per plot from (a) zucchini and (b) tomato ($N=5$).



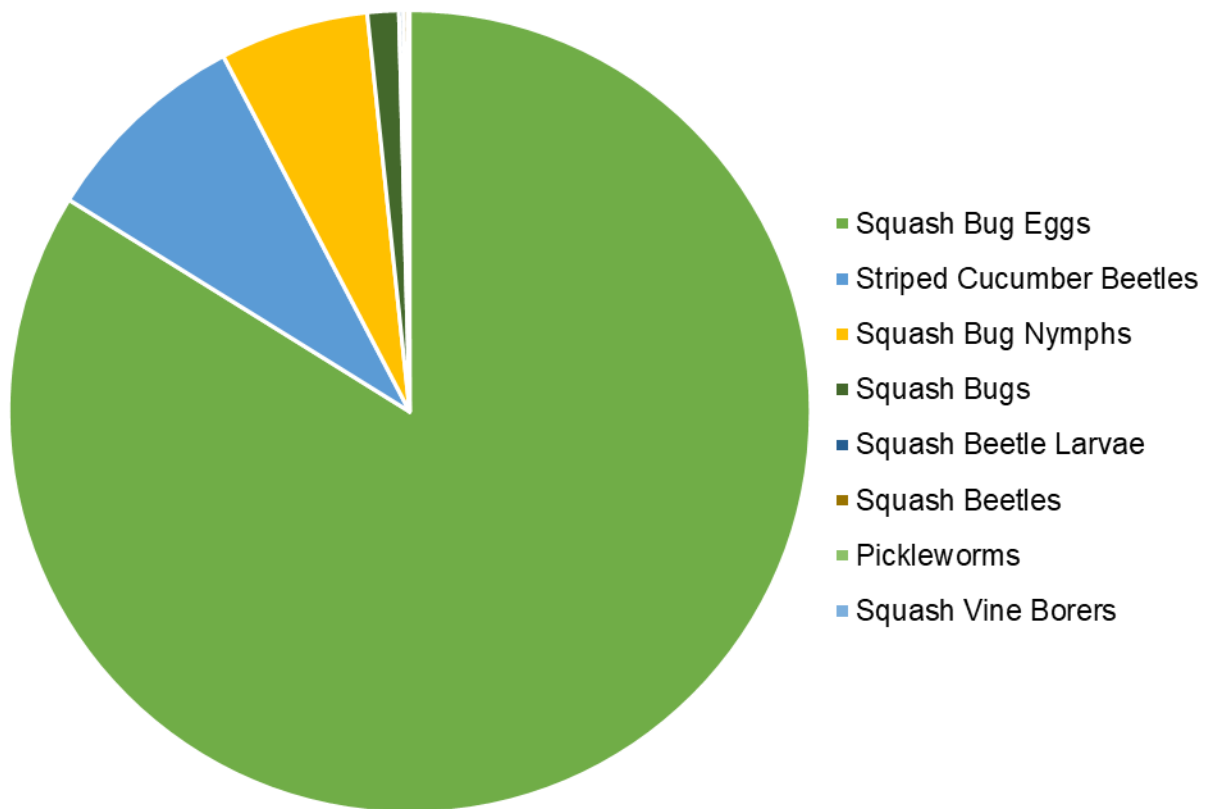
Supplementary Figure 4. Effects of fertility treatments on average annual sum of leaves counted on three plants per plot during visual surveys of (a) zucchini and (b) tomato ($N=5$).

APPENDIX C

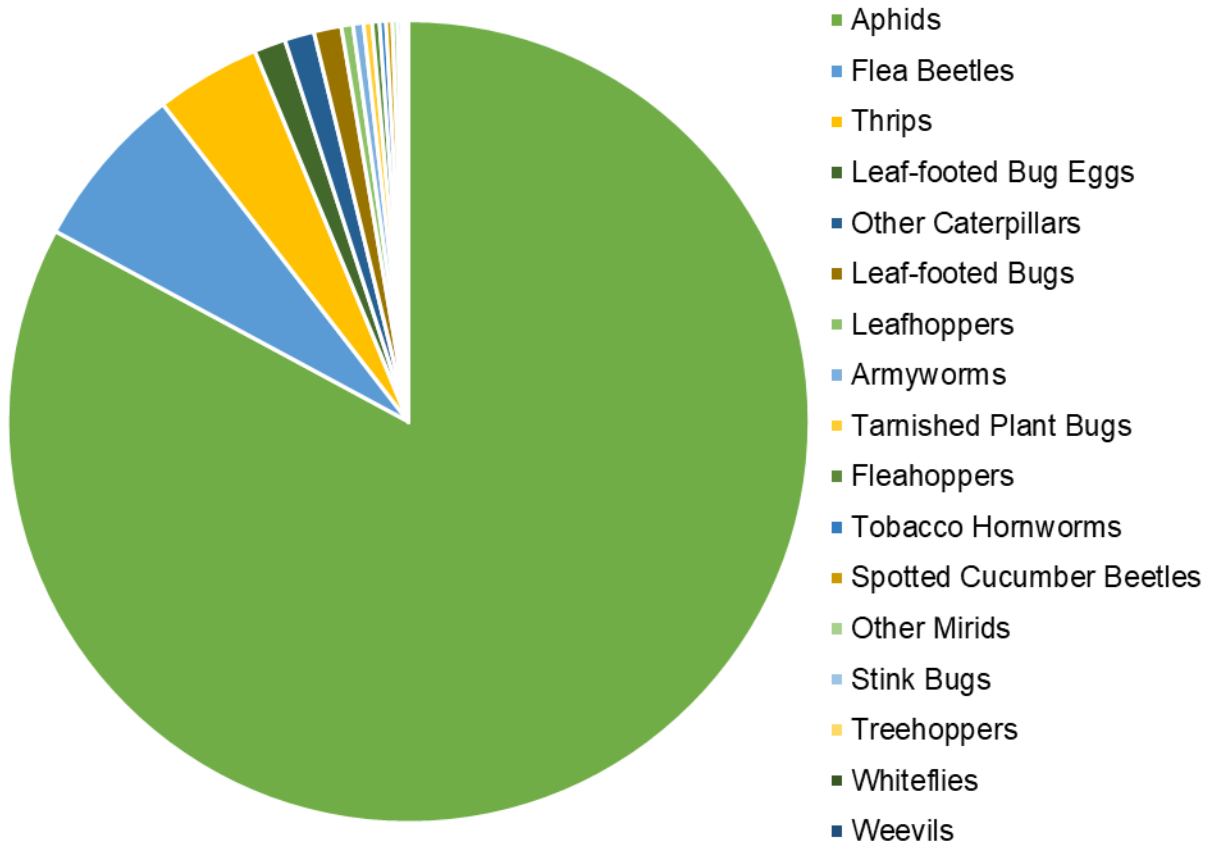
ARTHROPOD COMMUNITY COMPOSITIONS



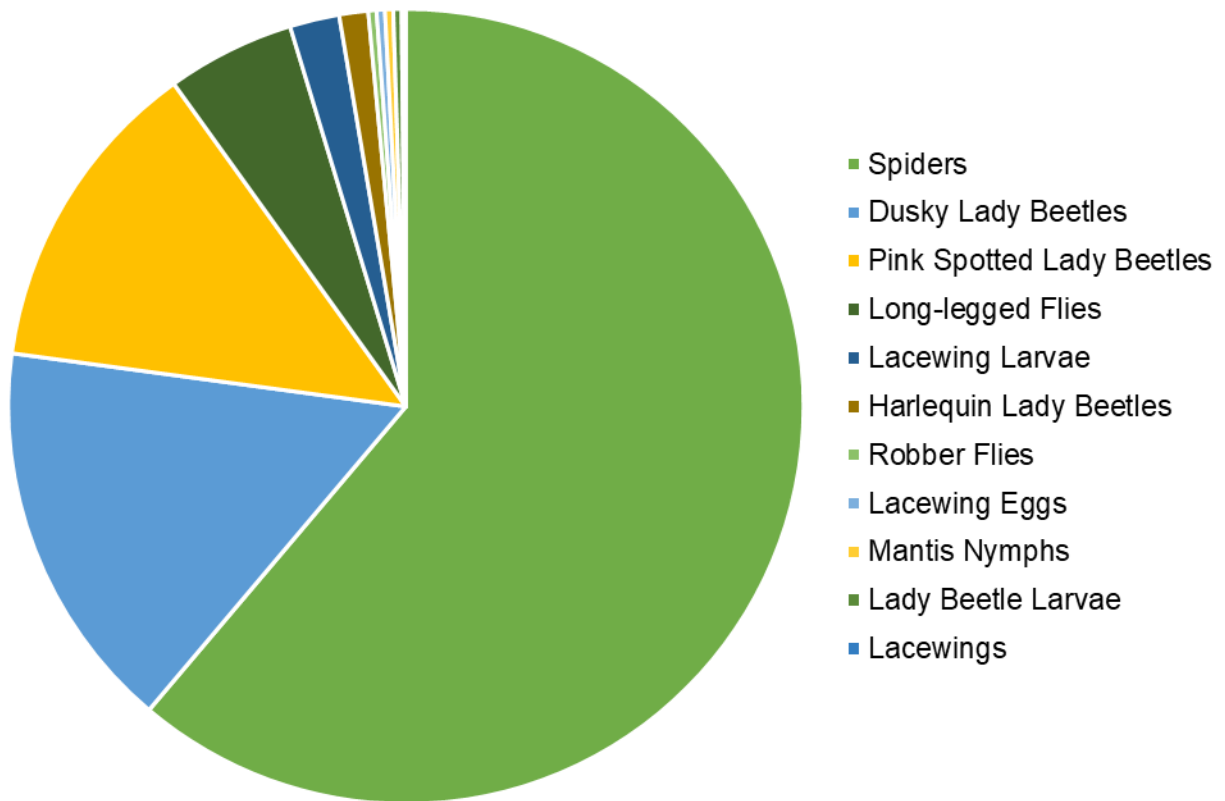
Supplementary Figure 5. Composition of generalist herbivores counted in visual surveys of zucchini plants.



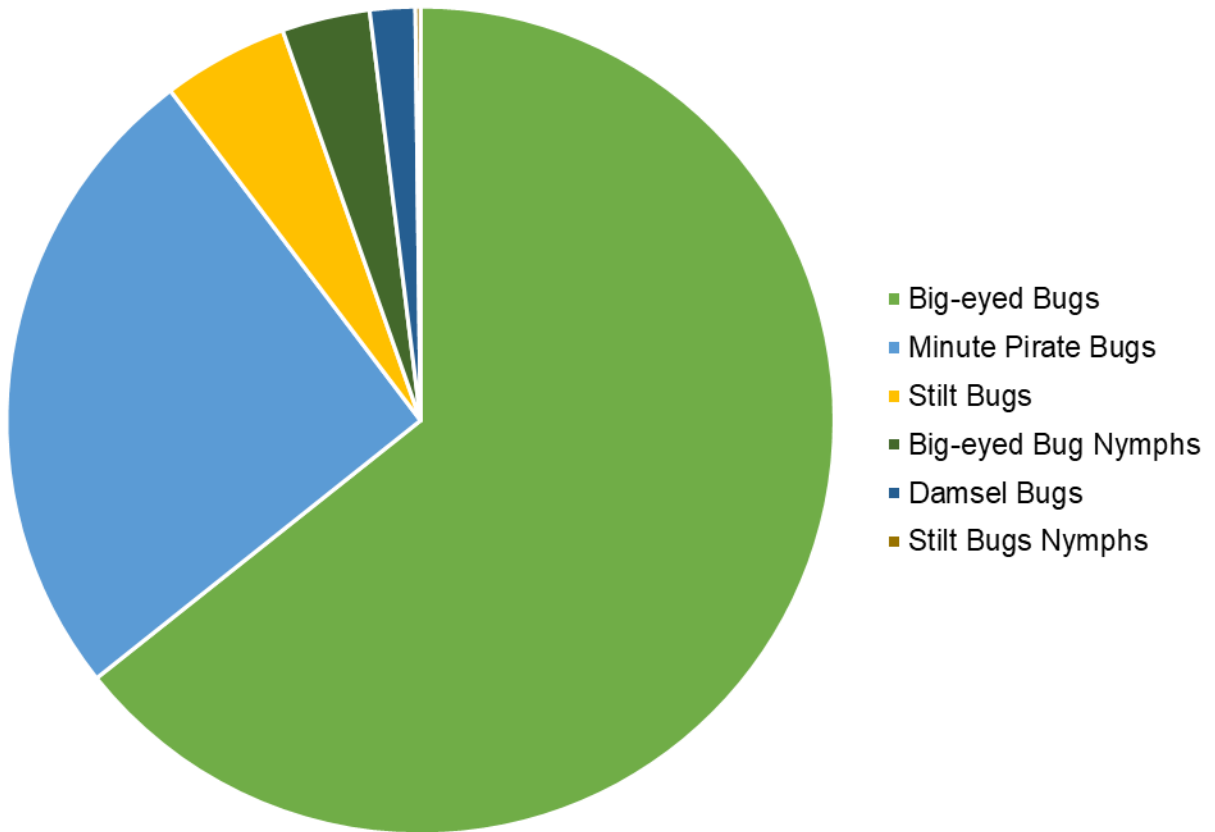
Supplementary Figure 6. *Composition of specialist herbivores counted in visual surveys of zucchini plants.*



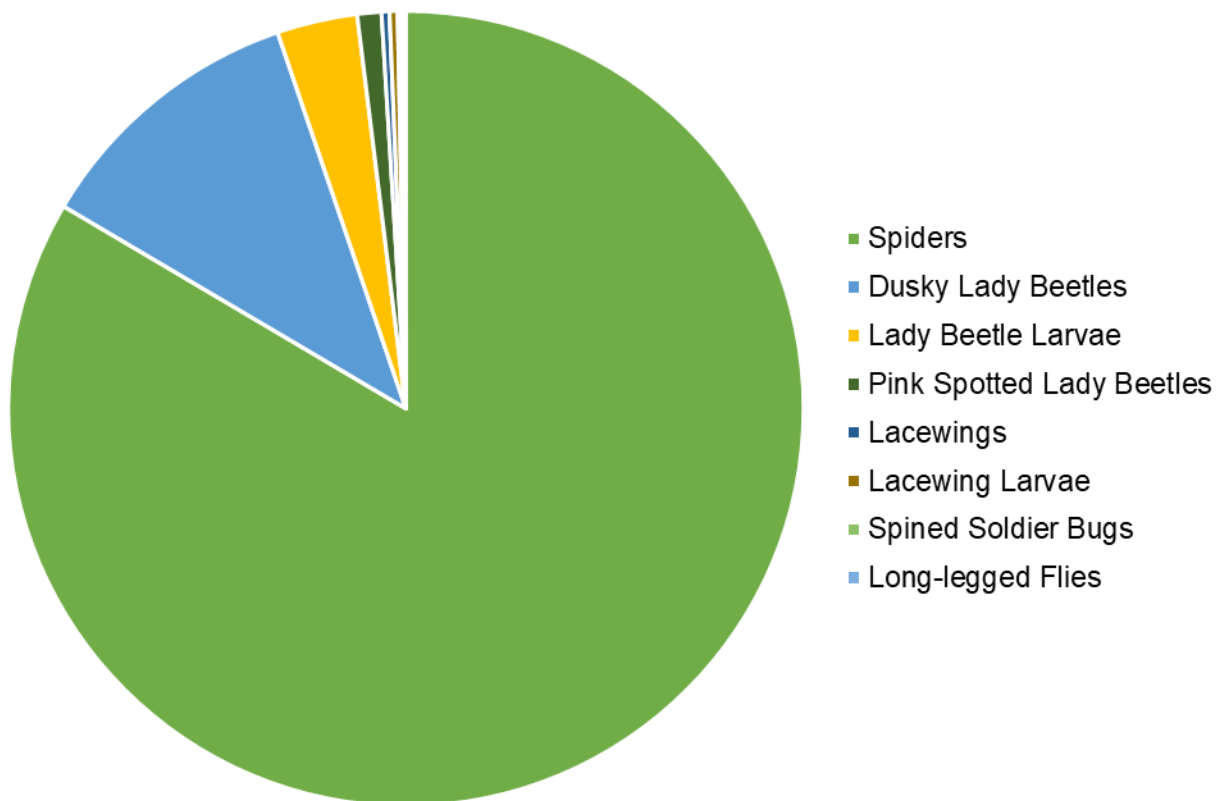
Supplementary Figure 7. Composition of herbivores counted in visual surveys of tomato plants.



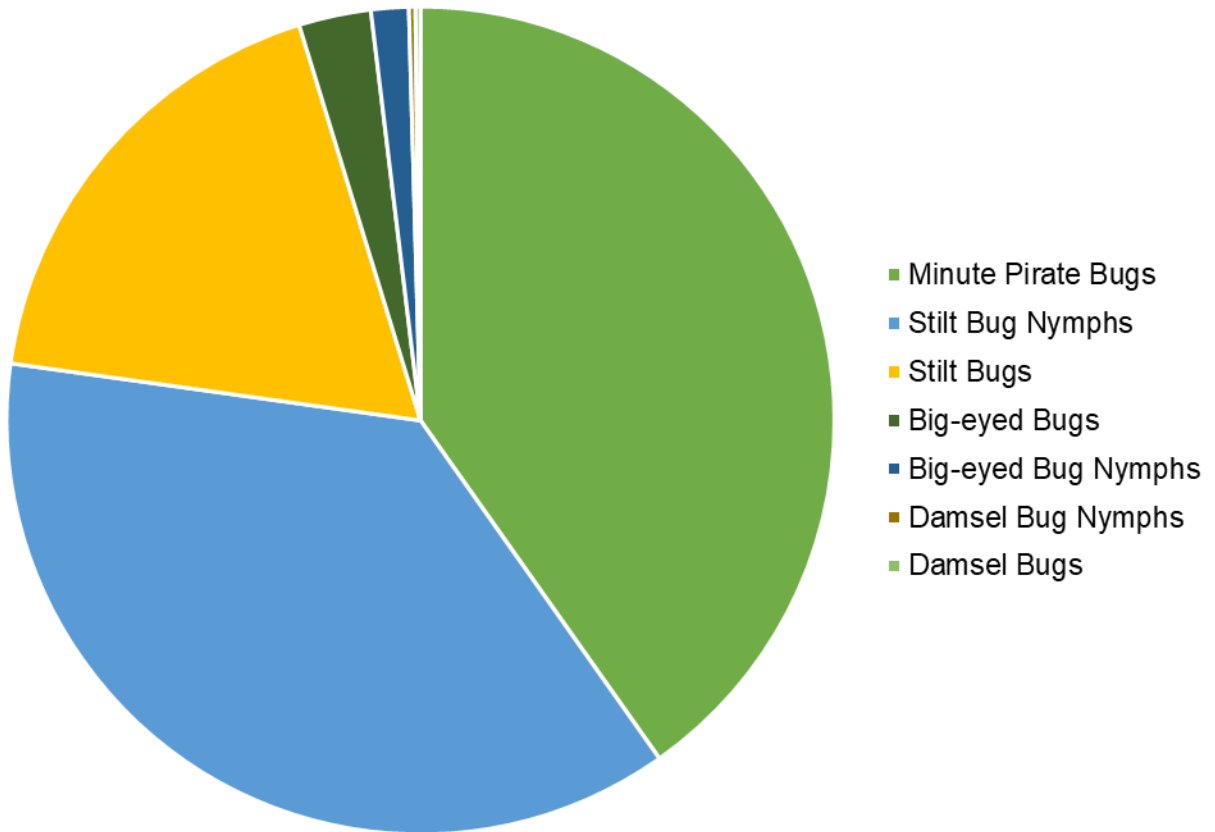
Supplementary Figure 8. Composition of generalist predators counted in vacuum samples from zucchini plants.



Supplementary Figure 9. Composition of omnivores counted in vacuum samples from zucchini plants.



Supplementary Figure 10. Composition of generalist predators counted in vacuum samples from tomato plants.

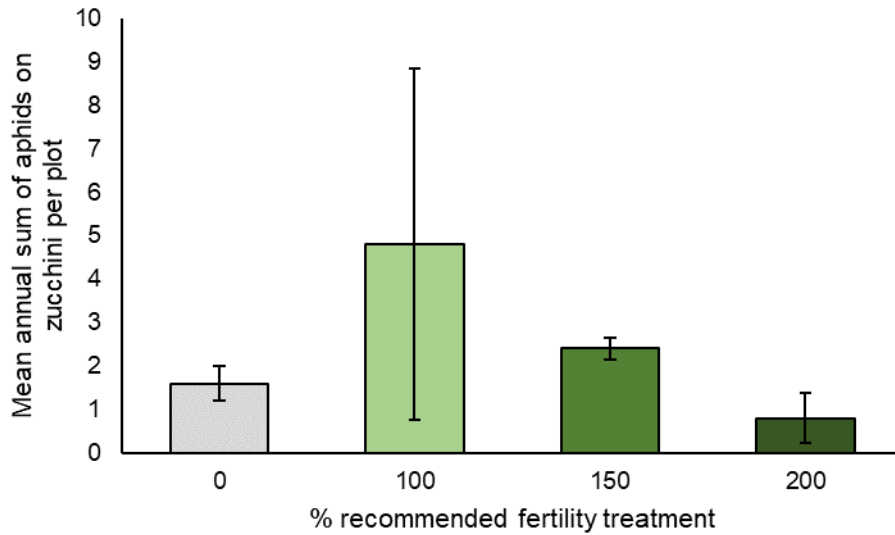


Supplementary Figure 11. Composition of omnivores counted in vacuum samples from tomato plants.

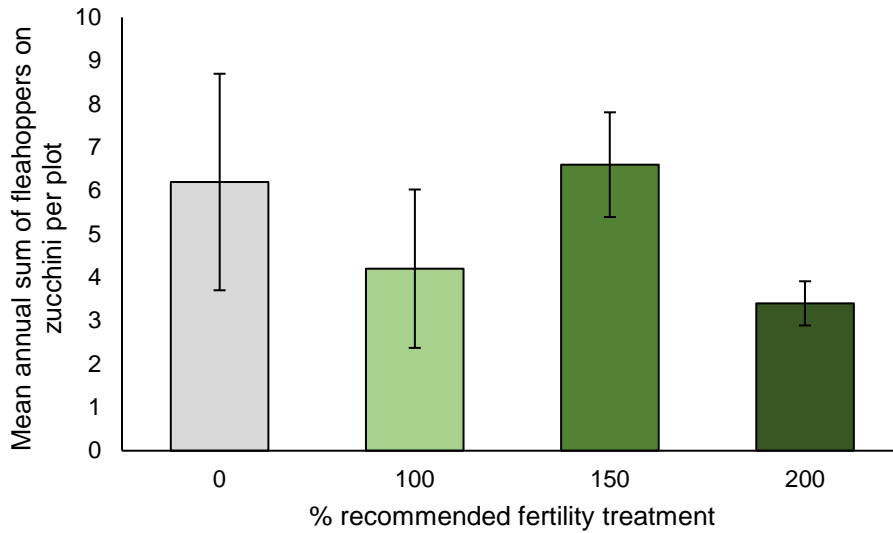
APPENDIX D

RESPONSES TO FERTILITY BY TAXA

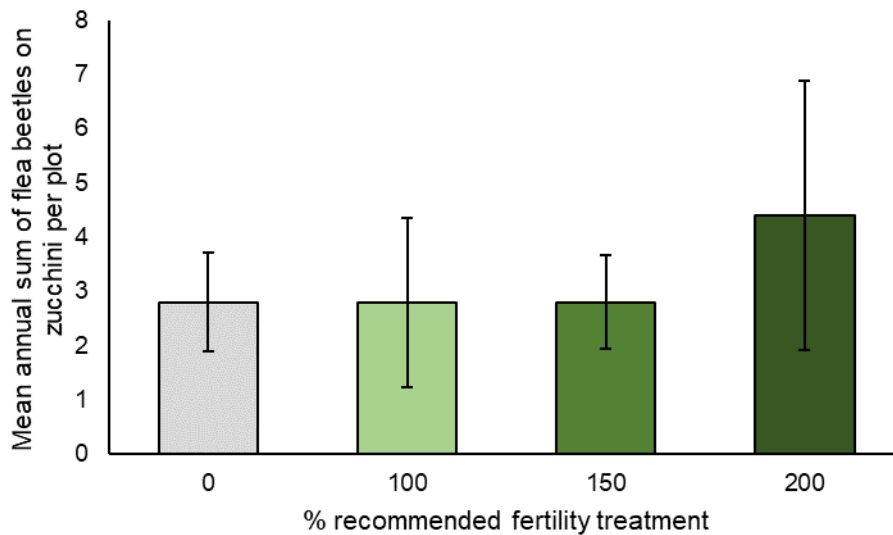
Generalist Herbivore Responses to Fertility on Zucchini



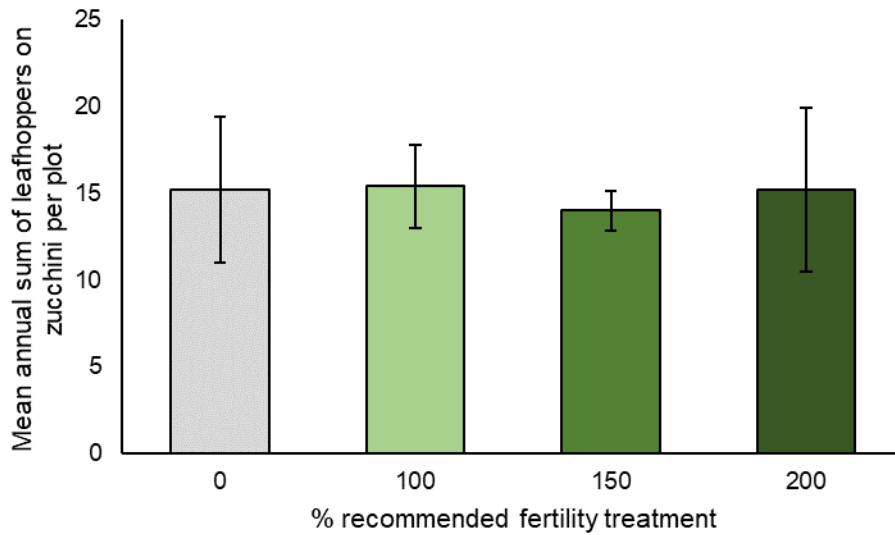
Supplementary Figure 12. Effects of fertility treatment on annual sums per plot of aphids counted via visual surveys on zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).



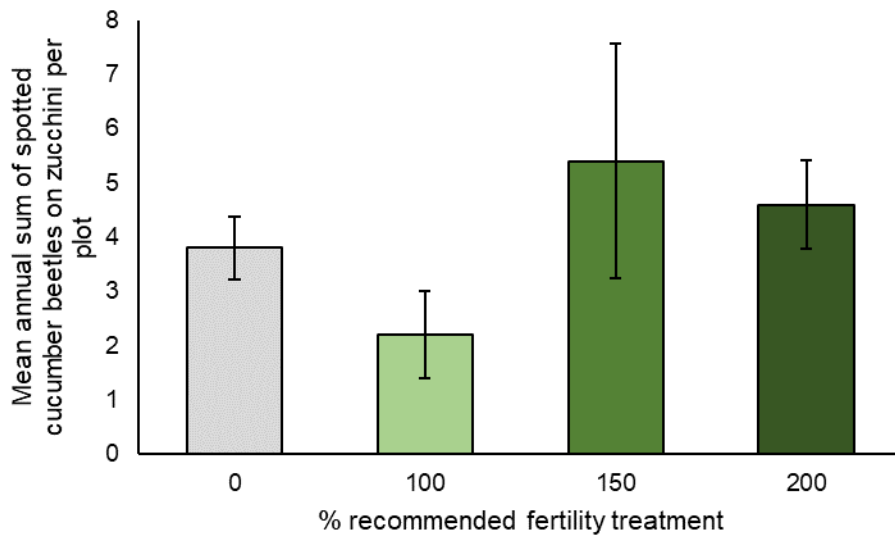
Supplementary Figure 13. Effects of fertility treatment on annual sums per plot of fleahoppers counted via visual surveys on zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).



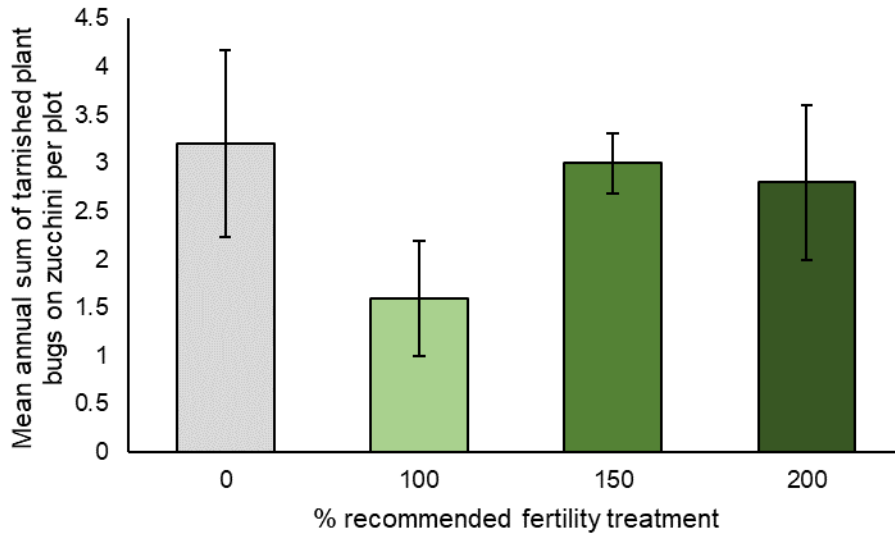
Supplementary Figure 14. Effects of fertility treatment on annual sums per plot of flea beetles counted via visual surveys on zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).



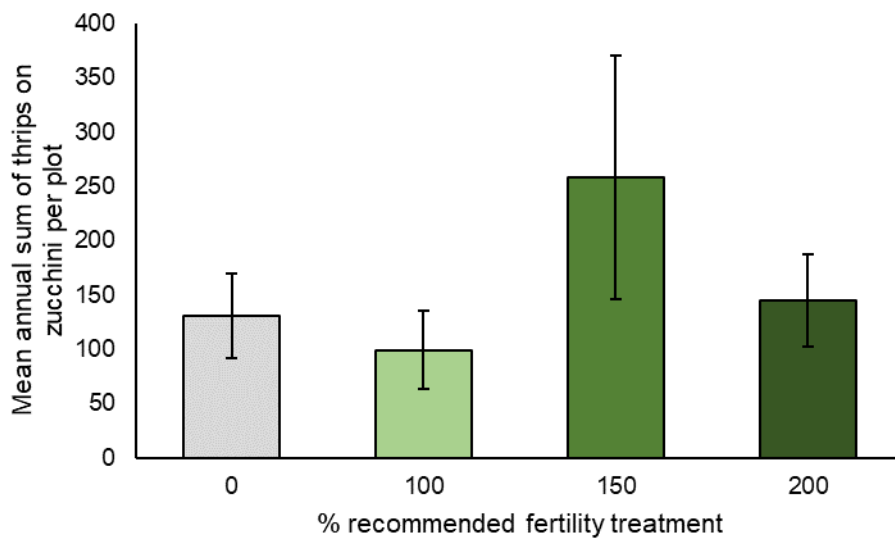
Supplementary Figure 15. Effects of fertility treatment on annual sums per plot of leafhoppers counted via visual surveys on zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).



Supplementary Figure 16. Effects of fertility treatment on annual sums per plot of spotted cucumber beetles counted via visual surveys on zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).

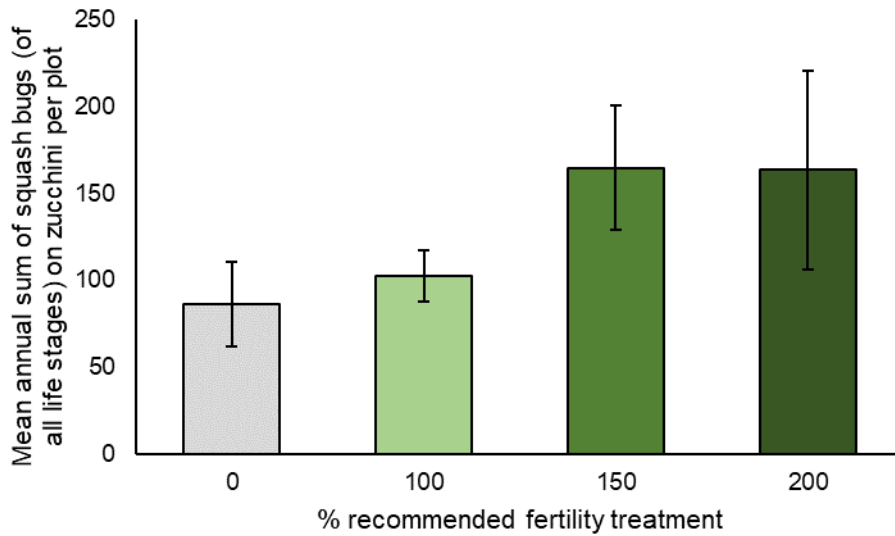


Supplementary Figure 17. Effects of fertility treatment on annual sums per plot of tarnished plant bugs counted via visual surveys on zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).

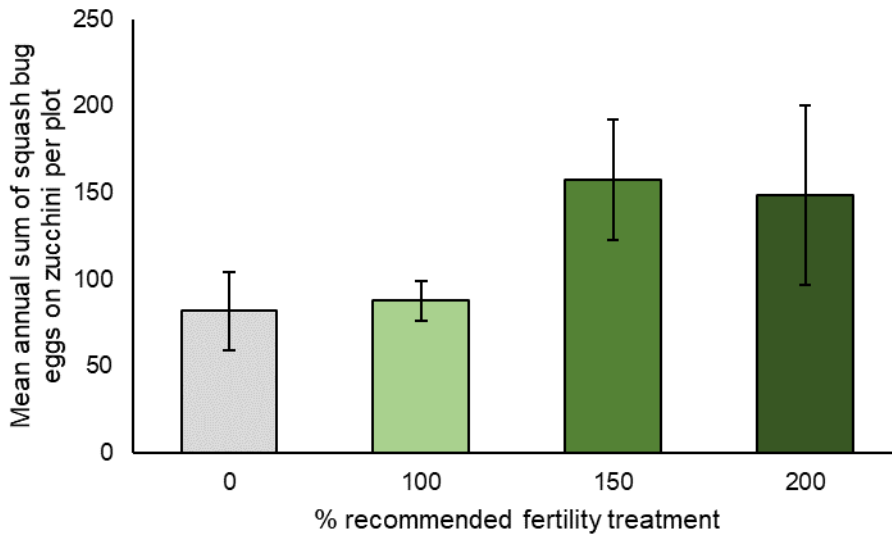


Supplementary Figure 18. Effects of fertility treatment on annual sums per plot of thrips counted via visual surveys on zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).

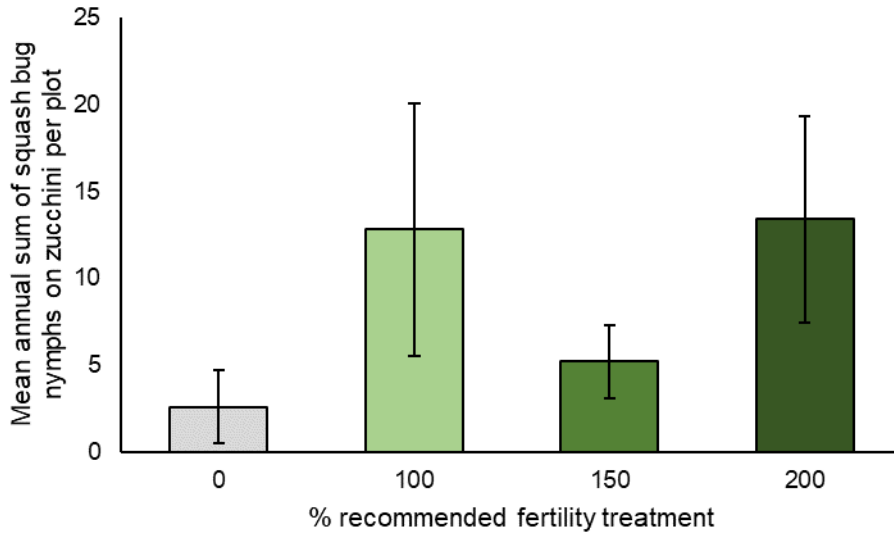
Specialist Herbivore Responses to Fertility on Zucchini



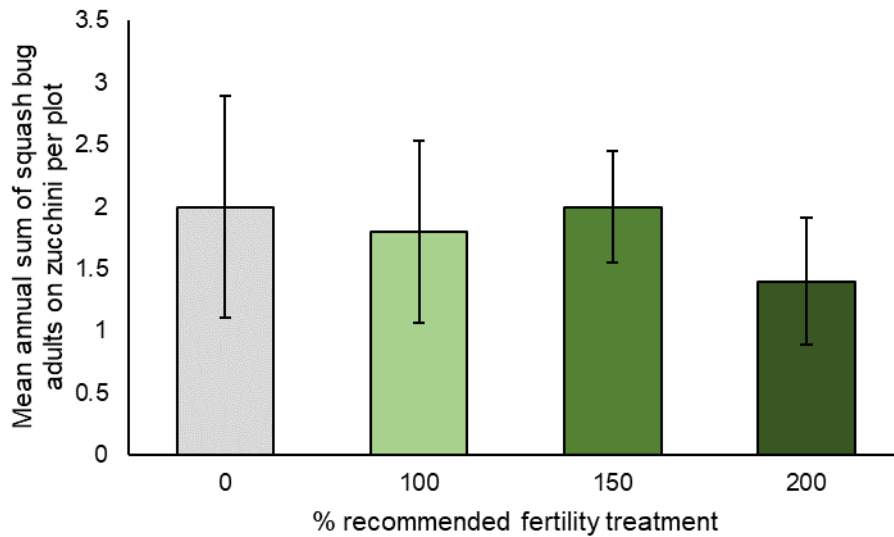
Supplementary Figure 19. Effects of fertility treatment on annual sums per plot of squash bugs (of all life stages) counted via visual surveys on zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).



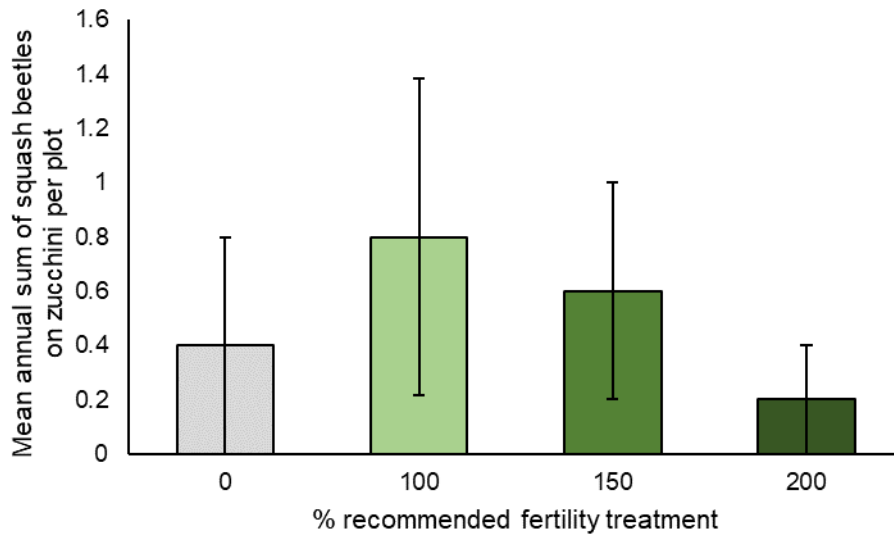
Supplementary Figure 19. Effects of fertility treatment on annual sums per plot of squash bugs eggs counted via visual surveys on zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).



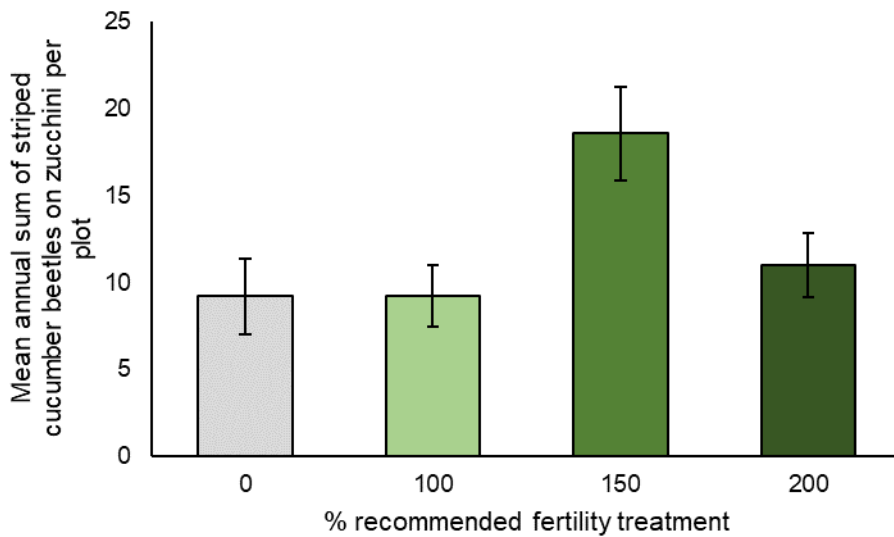
Supplementary Figure 20. Effects of fertility treatment on annual sums per plot of squash bugs nymphs counted via visual surveys on zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).



Supplementary Figure 21. Effects of fertility treatment on annual sums per plot of squash bugs adults counted via visual surveys on zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).

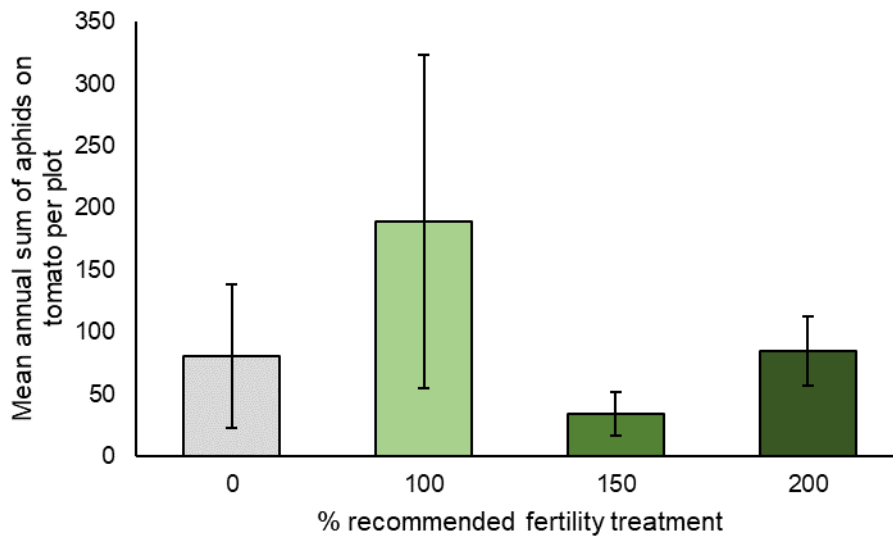


Supplementary Figure 22. Effects of fertility treatment on annual sums per plot of squash beetles (adults and larvae) counted via visual surveys on zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).

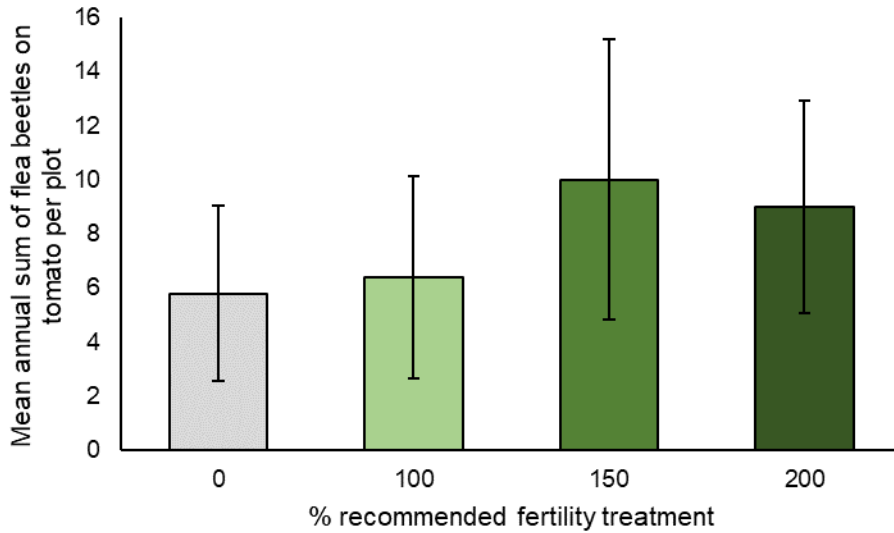


Supplementary Figure 23. Effects of fertility treatment on annual sums per plot of striped cucumber beetles counted via visual surveys on zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).

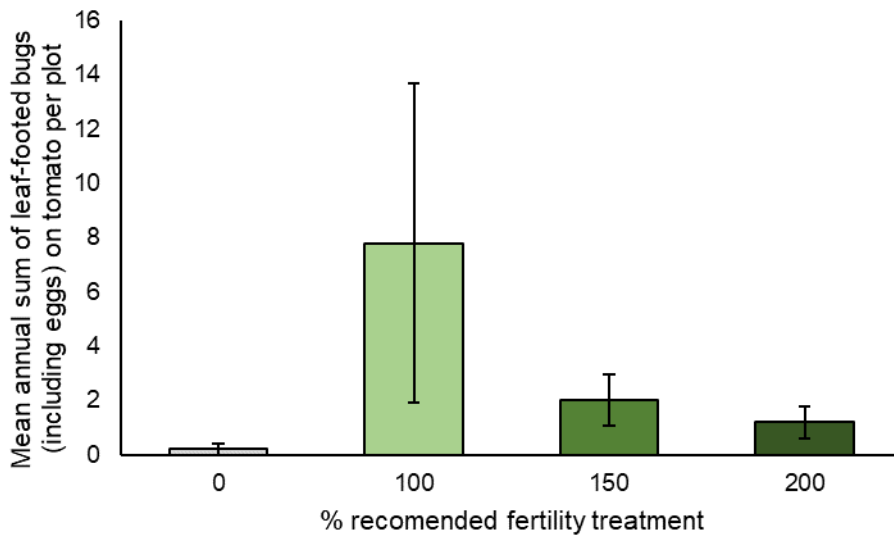
Herbivore Responses to Fertility on Tomato



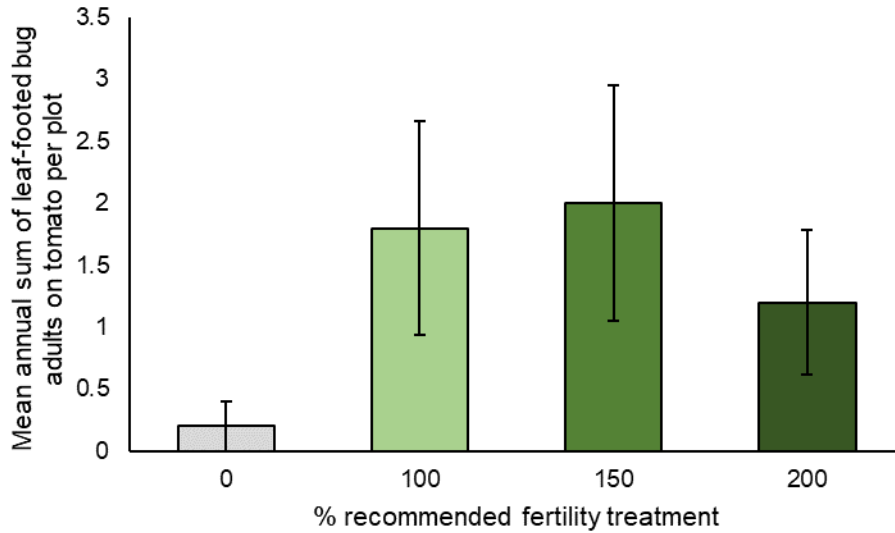
Supplementary Figure 24. Effects of fertility treatment on annual sums per plot of aphids counted via visual surveys on tomato. Error bars indicate standard error about the mean (N= five replicates per treatment).



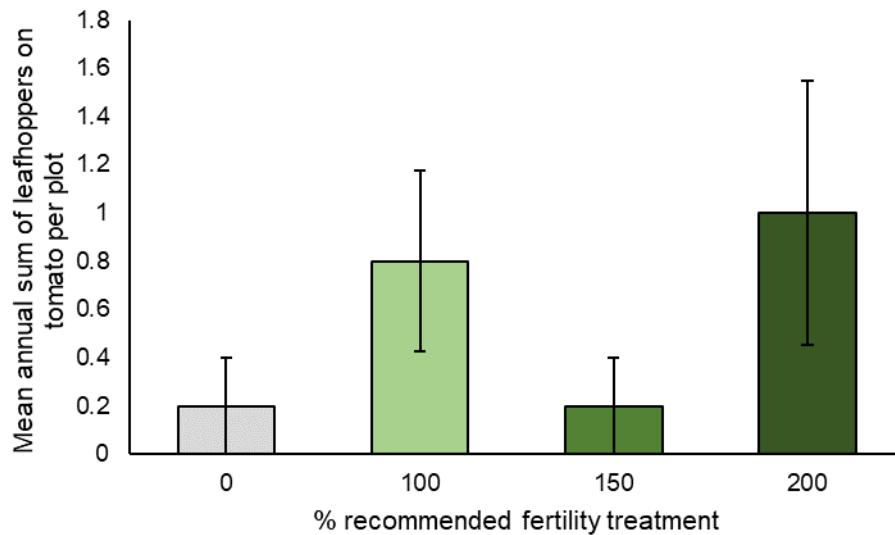
Supplementary Figure 25. Effects of fertility treatment on annual sums per plot of flea beetles counted via visual surveys on tomato. Error bars indicate standard error about the mean (N= five replicates per treatment).



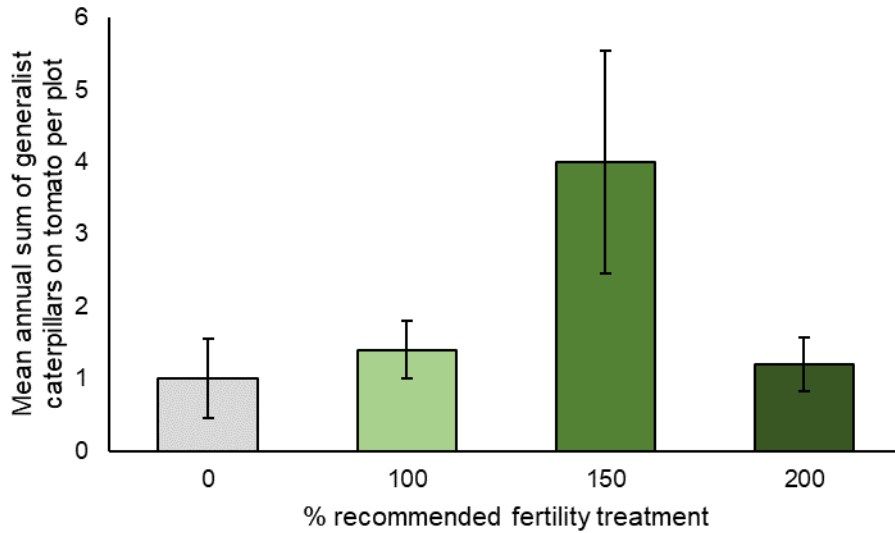
Supplementary Figure 26. Effects of fertility treatment on annual sums per plot of leaf-footed bugs (adults and eggs) counted via visual surveys on tomato. Error bars indicate standard error about the mean (N= five replicates per treatment).



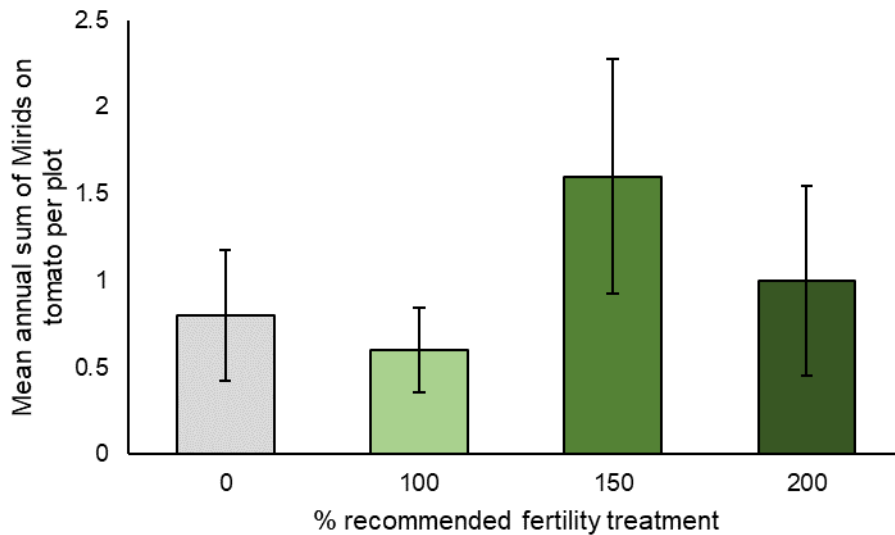
Supplementary Figure 27. Effects of fertility treatment on annual sums per plot of leaf-footed bug adults counted via visual surveys on tomato. Error bars indicate standard error about the mean (N= five replicates per treatment).



Supplementary Figure 28. Effects of fertility treatment on annual sums per plot of leafhoppers counted via visual surveys on tomato. Error bars indicate standard error about the mean (N= five replicates per treatment).

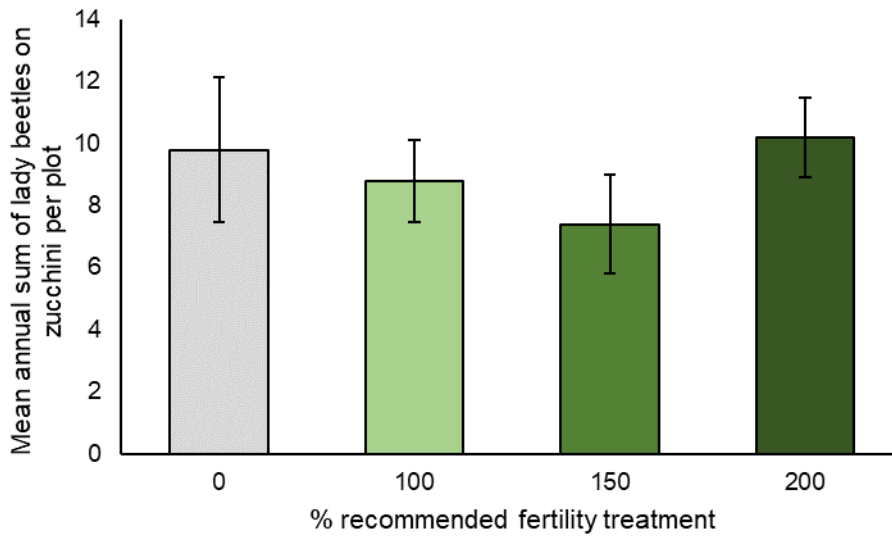


Supplementary Figure 29. Effects of fertility treatment on annual sums per plot of generalist caterpillars counted via visual surveys on tomato. Error bars indicate standard error about the mean (N= five replicates per treatment).

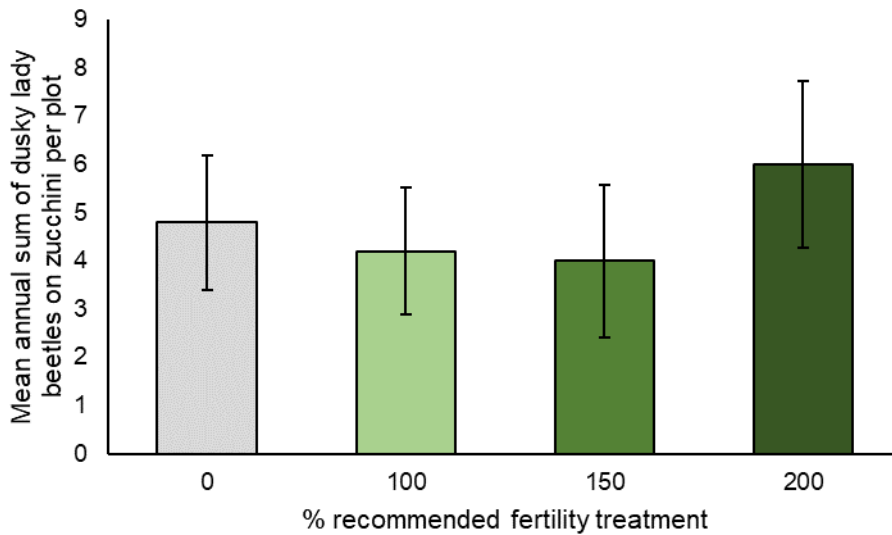


Supplementary Figure 30. Effects of fertility treatment on annual sums per plot of Mirids counted via visual surveys on tomato. Error bars indicate standard error about the mean (N= five replicates per treatment).

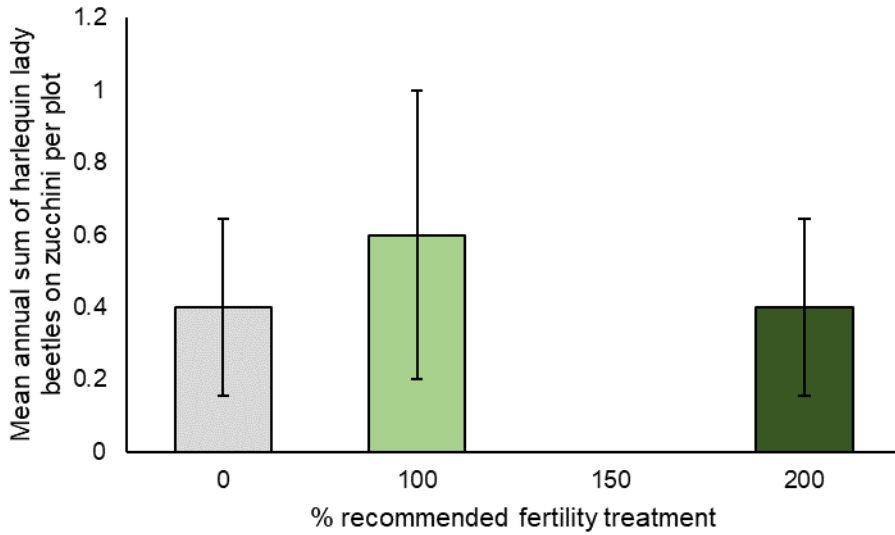
Generalist Predator Responses to Fertility on Zucchini



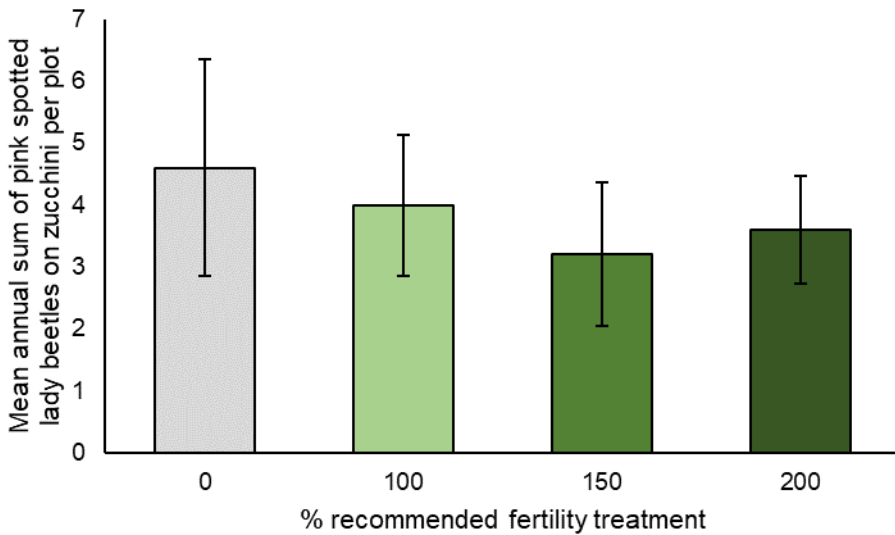
Supplementary Figure 31. Effects of fertility treatment on annual sums per plot of lady beetles (all taxa and life stages) counted in vacuum samples of zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).



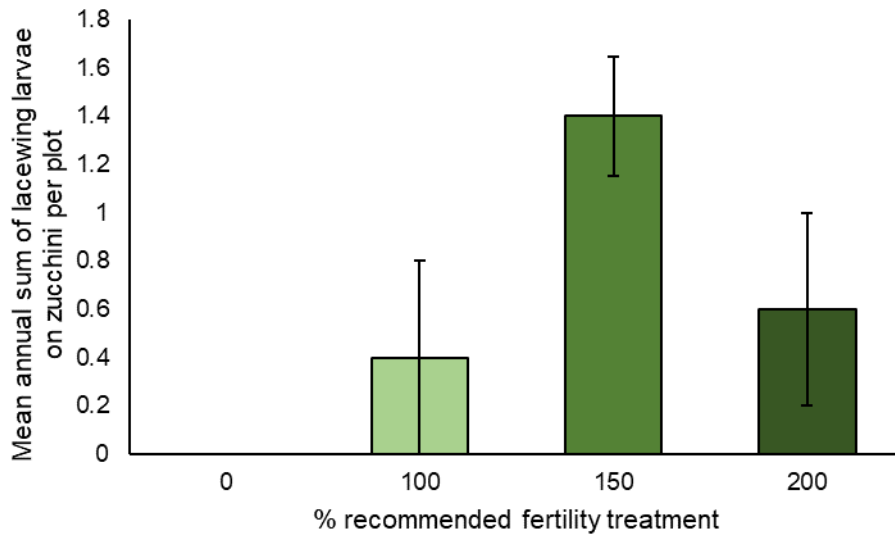
Supplementary Figure 32. Effects of fertility treatment on annual sums per plot of dusky lady beetle adults counted in vacuum samples of zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).



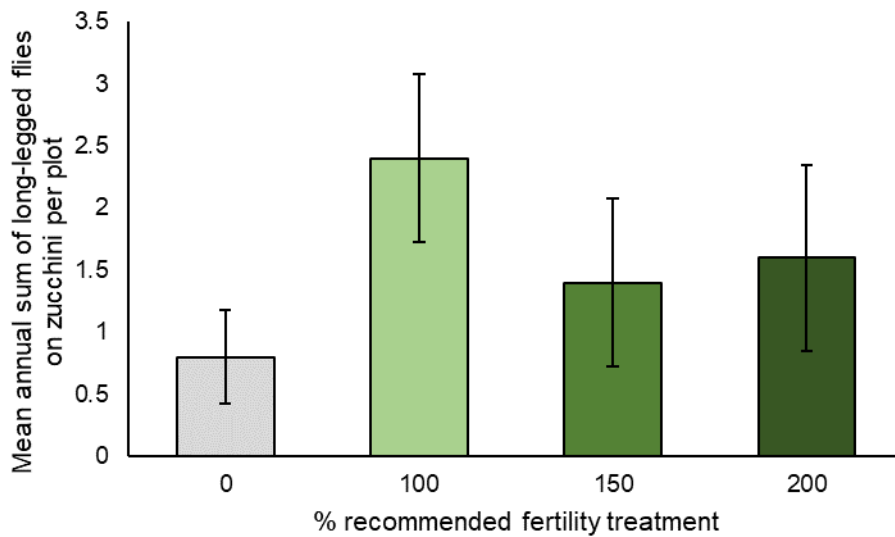
Supplementary Figure 33. Effects of fertility treatment on annual sums per plot of harlequin lady beetle adults counted in vacuum samples of zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).



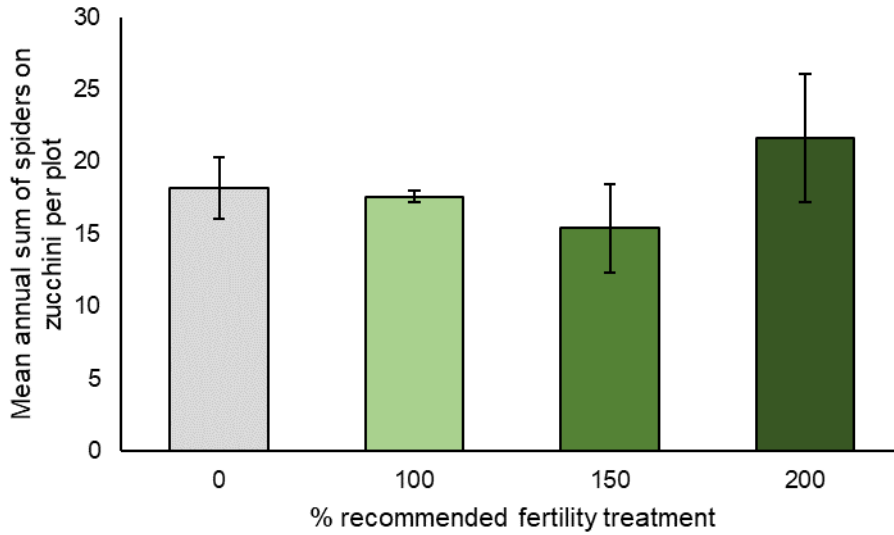
Supplementary Figure 34. Effects of fertility treatment on annual sums per plot of pink spotted lady beetle adults counted in vacuum samples of zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).



Supplementary Figure 35. Effects of fertility treatment on annual sums per plot of lacewing larvae counted in vacuum samples of zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).

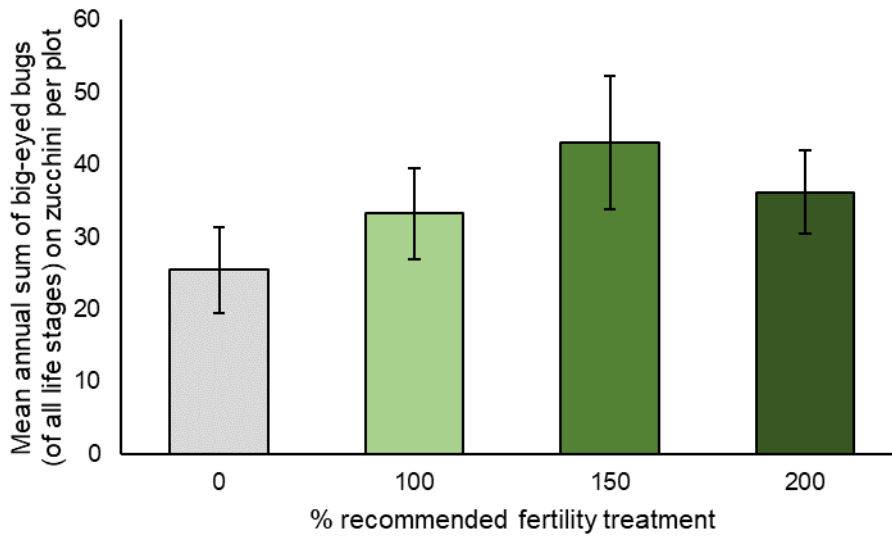


Supplementary Figure 36. Effects of fertility treatment on annual sums per plot of long-legged flies counted in vacuum samples of zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).

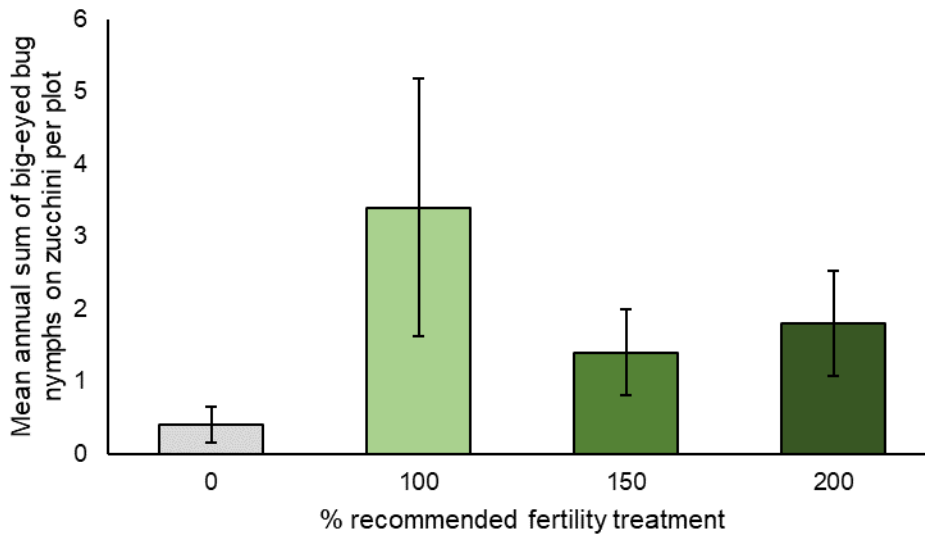


Supplementary Figure 37. Effects of fertility treatment on annual sums per plot of spiders counted in vacuum samples of zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).

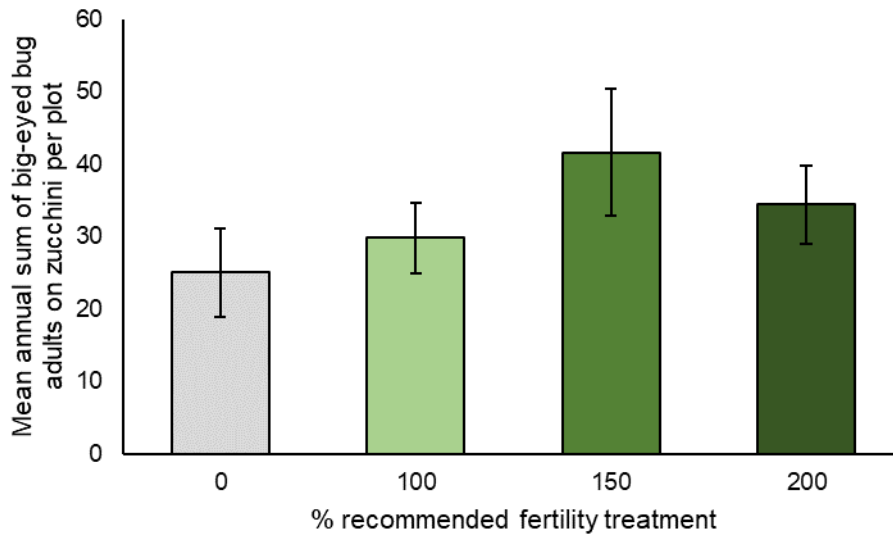
Omnivore Responses to Fertility on Zucchini



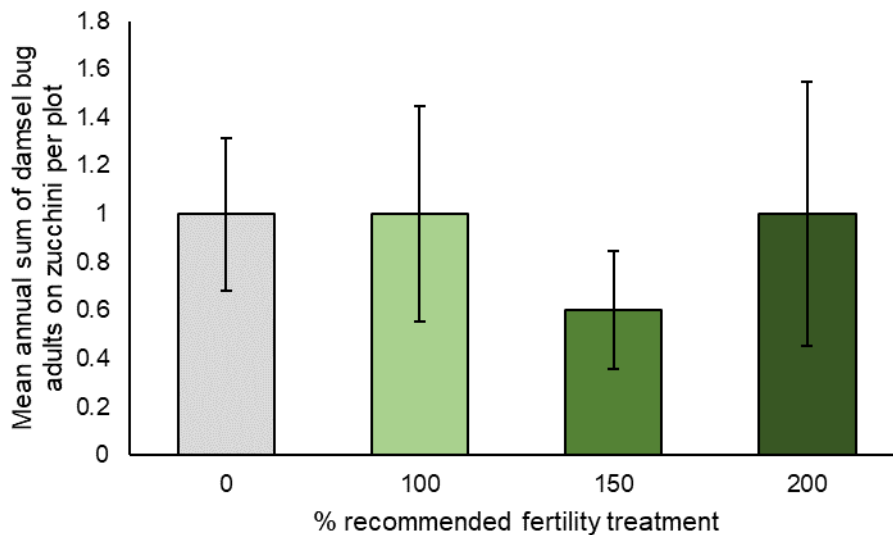
Supplementary Figure 38. Effects of fertility treatment on annual sums per plot of big-eyed bugs (nymphs and adults) in vacuum samples of zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).



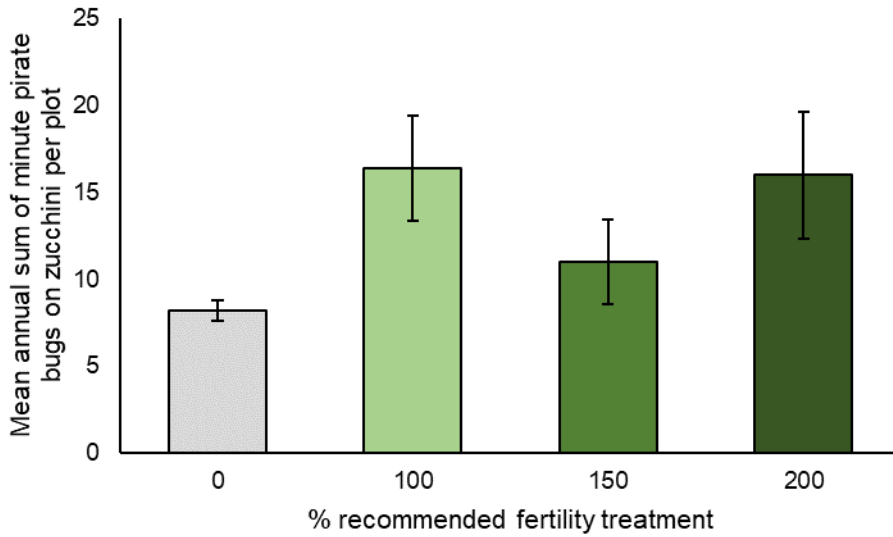
Supplementary Figure 39. Effects of fertility treatment on annual sums per plot of big-eyed bug nymphs in vacuum samples of zucchini. Error bars indicate standard error about the mean ($N=$ five replicates per treatment).



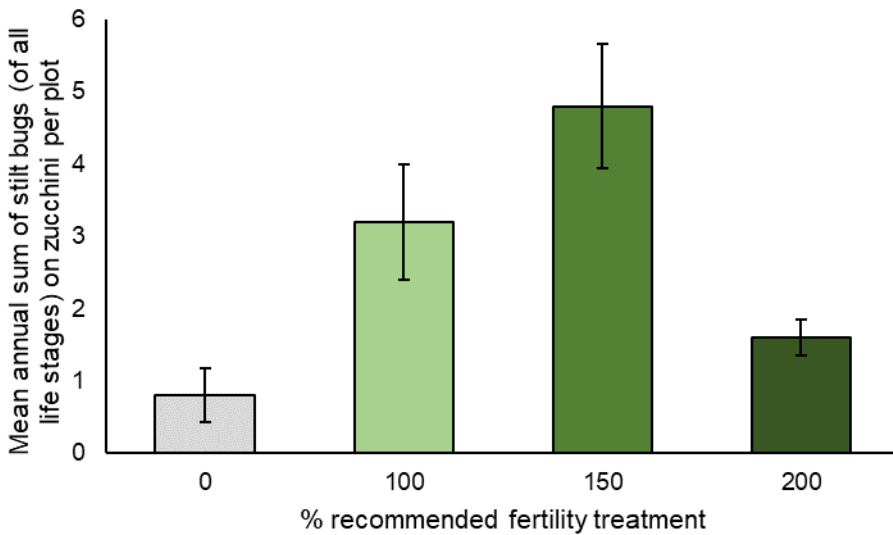
Supplementary Figure 40. Effects of fertility treatment on annual sums per plot of big-eyed bug adults in vacuum samples of zucchini. Error bars indicate standard error about the mean ($N=$ five replicates per treatment).



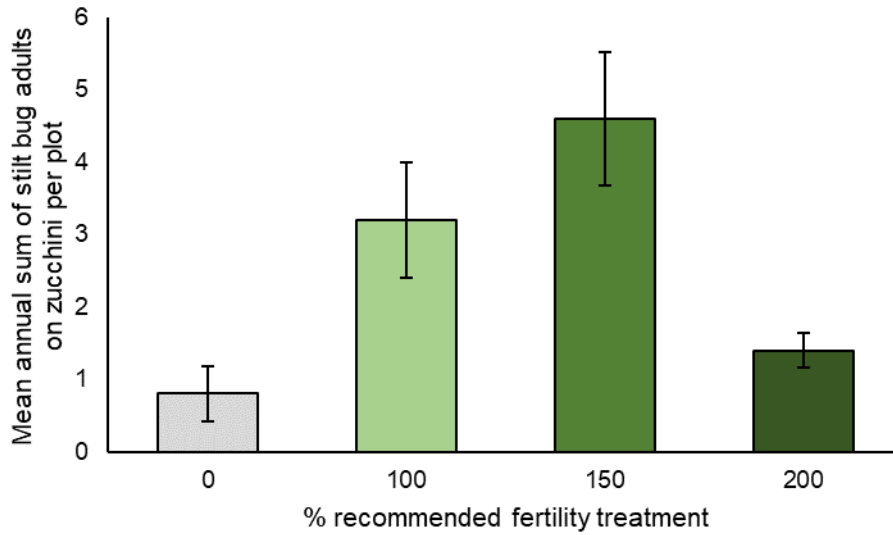
Supplementary Figure 41. Effects of fertility treatment on annual sums per plot of damsel bugs (nymphs and adults) in vacuum samples of zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).



Supplementary Figure 42. Effects of fertility treatment on annual sums per plot of minute pirate bugs in vacuum samples of zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).

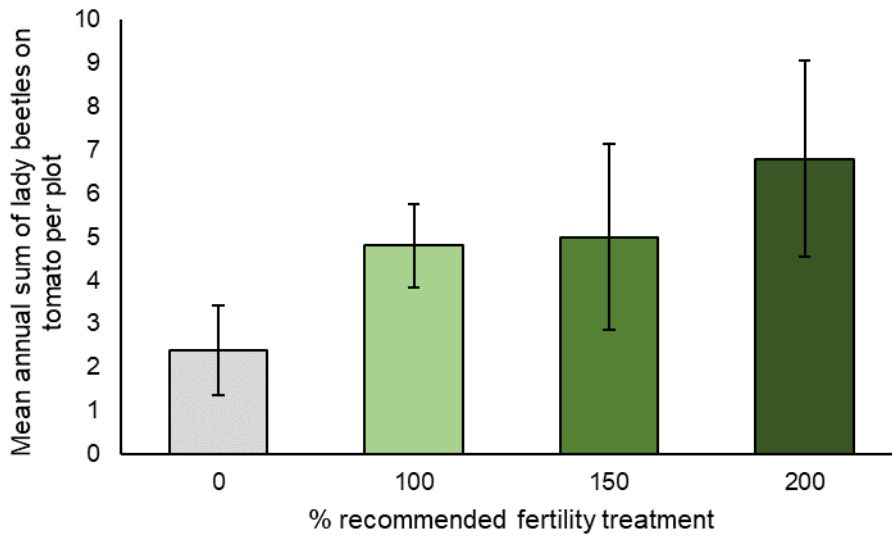


Supplementary Figure 43. Effects of fertility treatment on annual sums per plot of stilt bugs (nymphs and adults) in vacuum samples of zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).

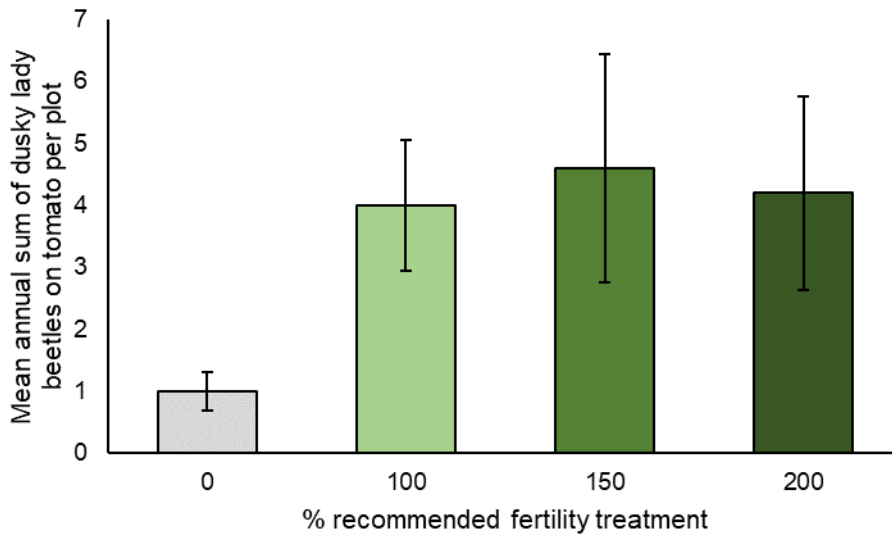


Supplementary Figure 44. Effects of fertility treatment on annual sums per plot of stilt bug adults in vacuum samples of zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).

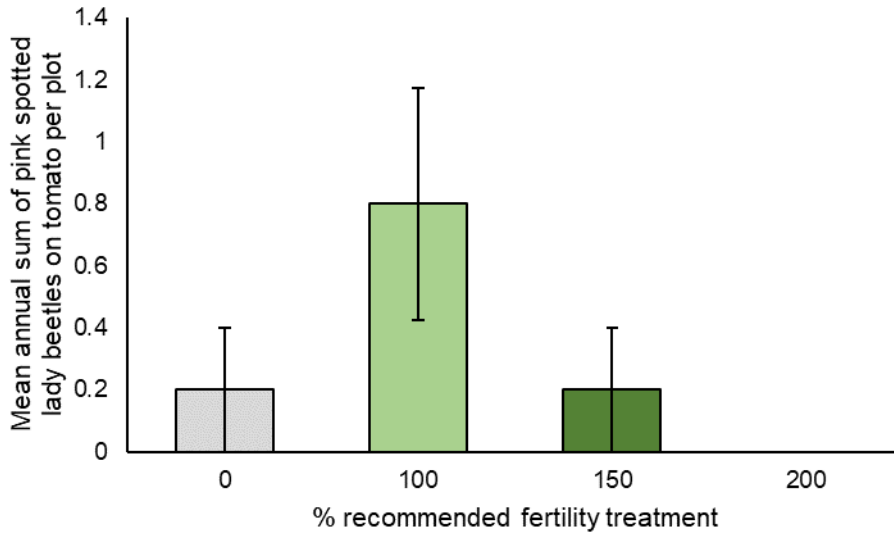
Generalist Predator Responses to Fertility on Tomato



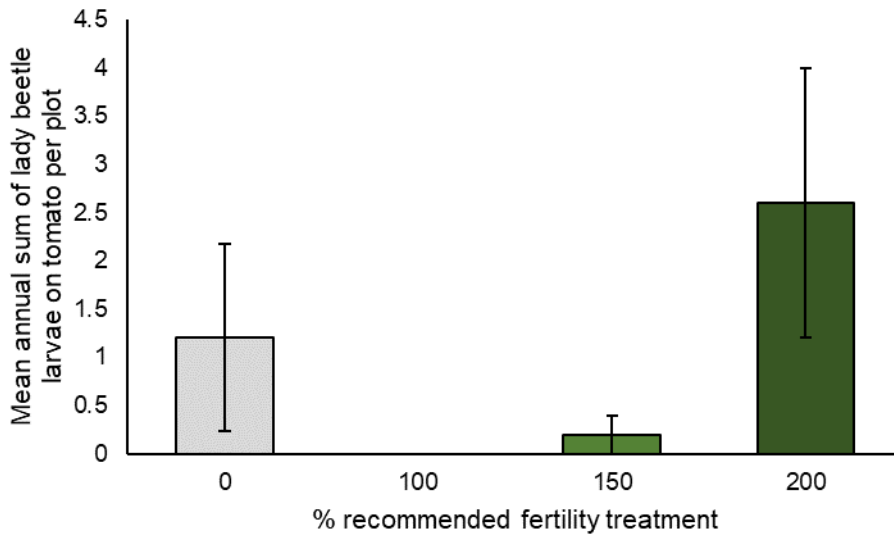
Supplementary Figure 45. Effects of fertility treatment on annual sums per plot of lady beetles (all taxa and life stages) in vacuum samples of zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).



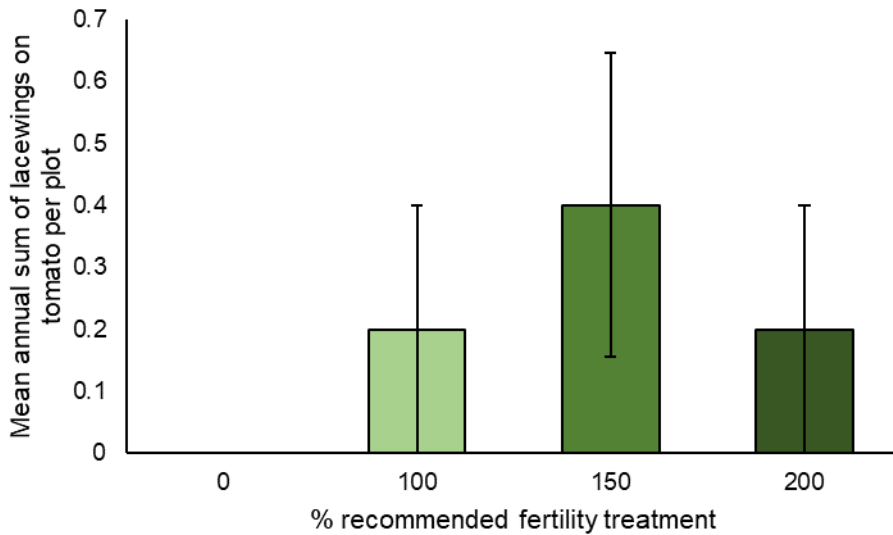
Supplementary Figure 46. Effects of fertility treatment on annual sums per plot of dusky lady beetle adults in vacuum samples of zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).



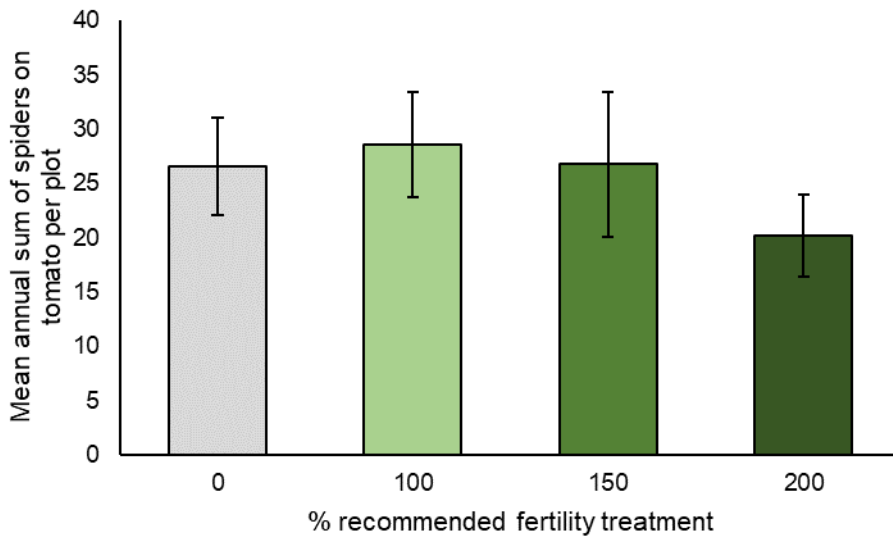
Supplementary Figure 47. Effects of fertility treatment on annual sums per plot of pink spotted lady beetle adults in vacuum samples of zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).



Supplementary Figure 48. Effects of fertility treatment on annual sums per plot of lady beetle larvae in vacuum samples of zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).

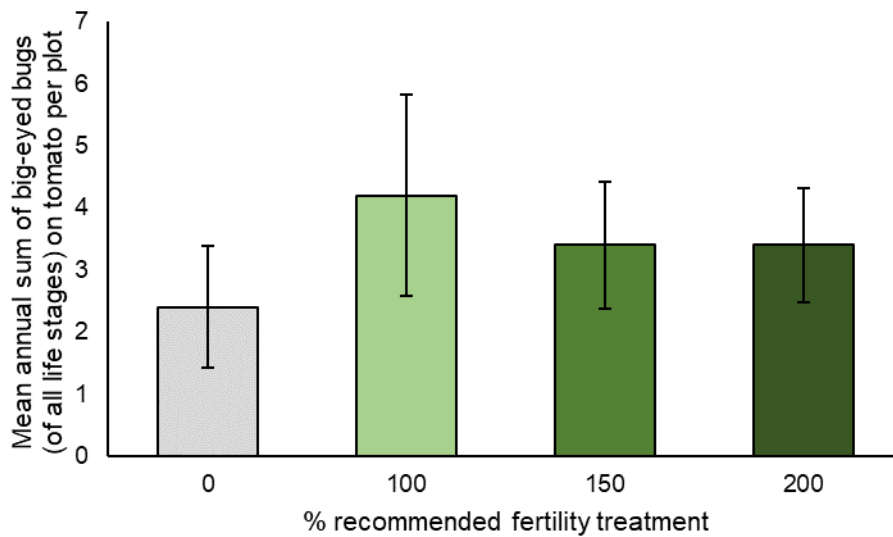


Supplementary Figure 49. Effects of fertility treatment on annual sums per plot of lacewings in vacuum samples of zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).

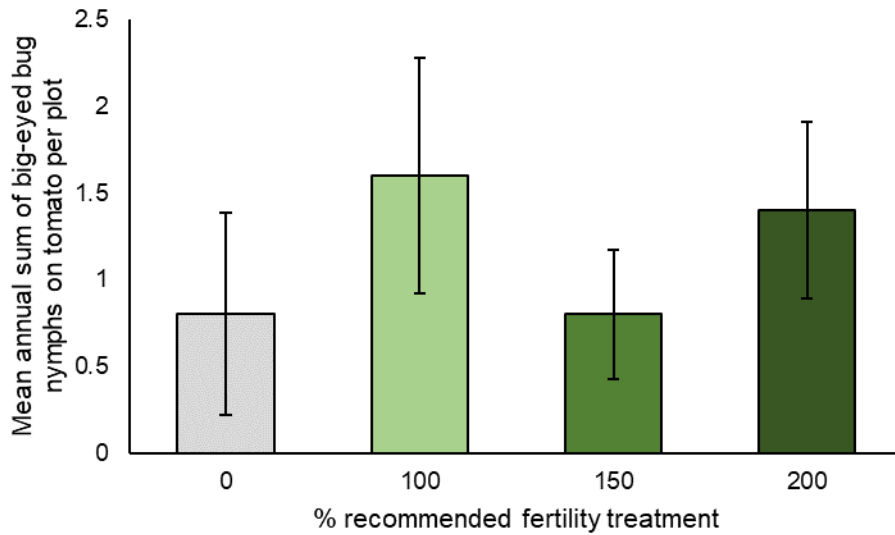


Supplementary Figure 50. Effects of fertility treatment on annual sums per plot of spiders in vacuum samples of zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).

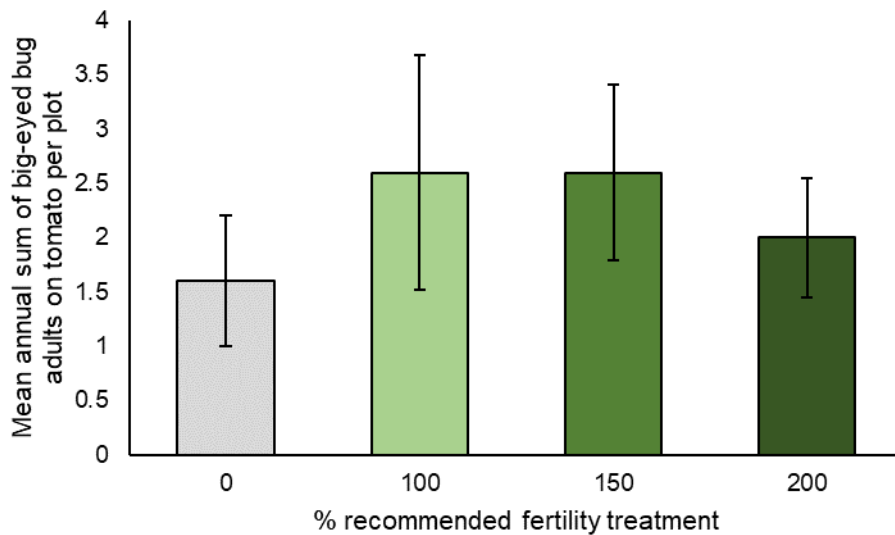
Omnivore Responses to Fertility on Tomato



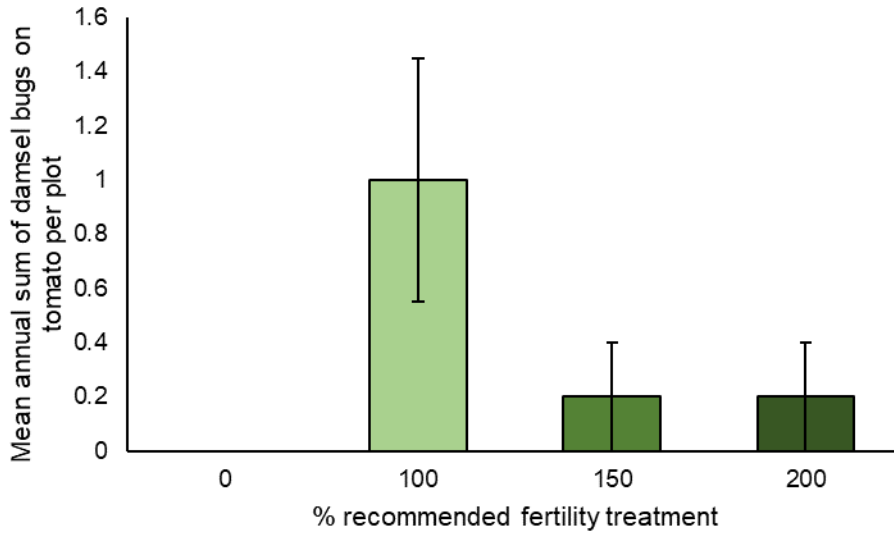
Supplementary Figure 51. Effects of fertility treatment on annual sums per plot of big-eyed bugs (nymphs and adults) in vacuum samples of zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).



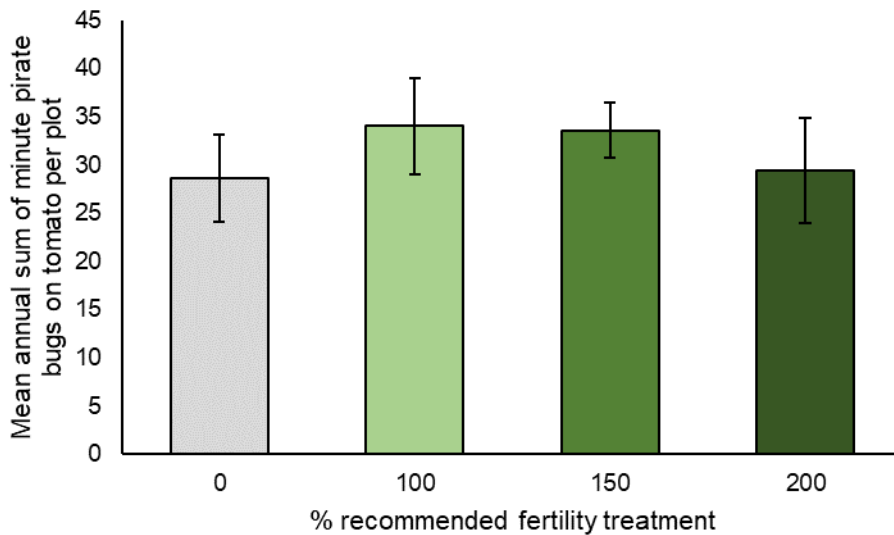
Supplementary Figure 52. Effects of fertility treatment on annual sums per plot of big-eyed bug nymphs in vacuum samples of zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).



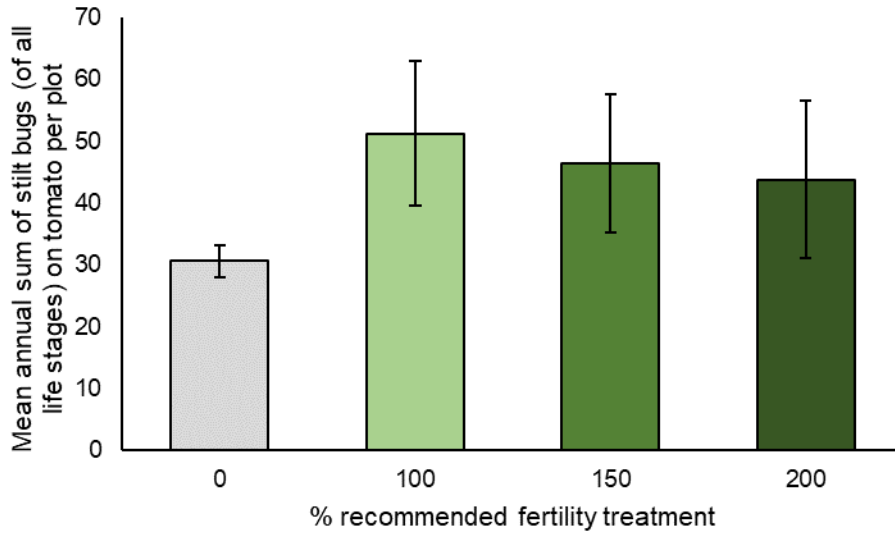
Supplementary Figure 53. Effects of fertility treatment on annual sums per plot of big-eyed bug adults in vacuum samples of zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).



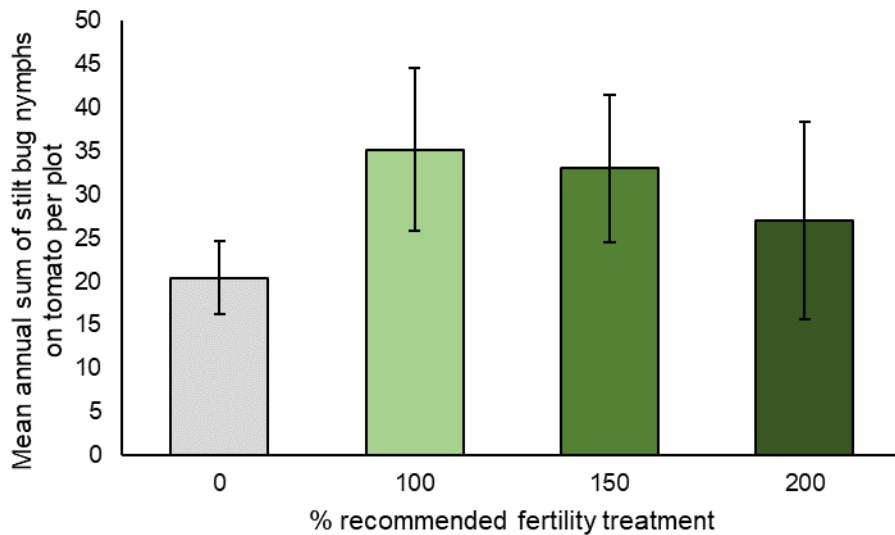
Supplementary Figure 54. Effects of fertility treatment on annual sums per plot of damsel bugs (nymphs and adults) in vacuum samples of zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).



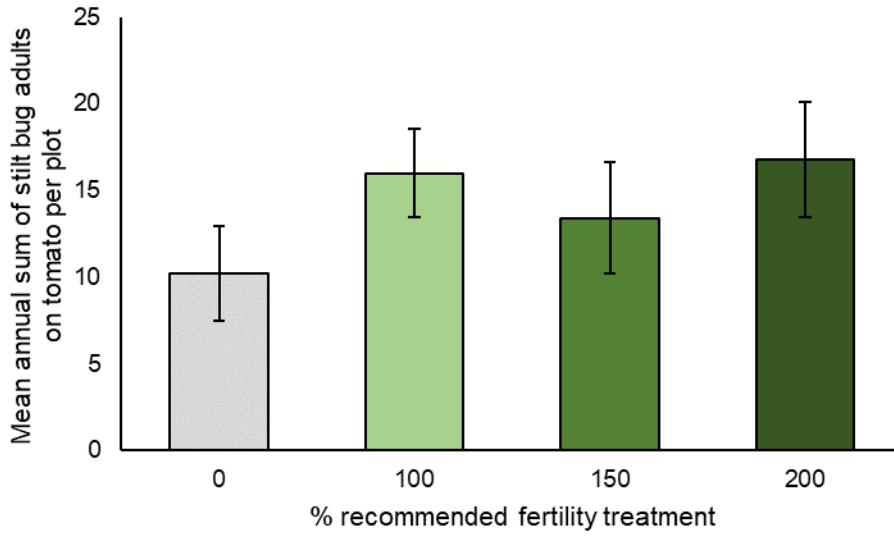
Supplementary Figure 55. Effects of fertility treatment on annual sums per plot of minute pirate bugs in vacuum samples of zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).



Supplementary Figure 56. Effects of fertility treatment on annual sums per plot of stilt bugs (nymphs and adults) in vacuum samples of zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).

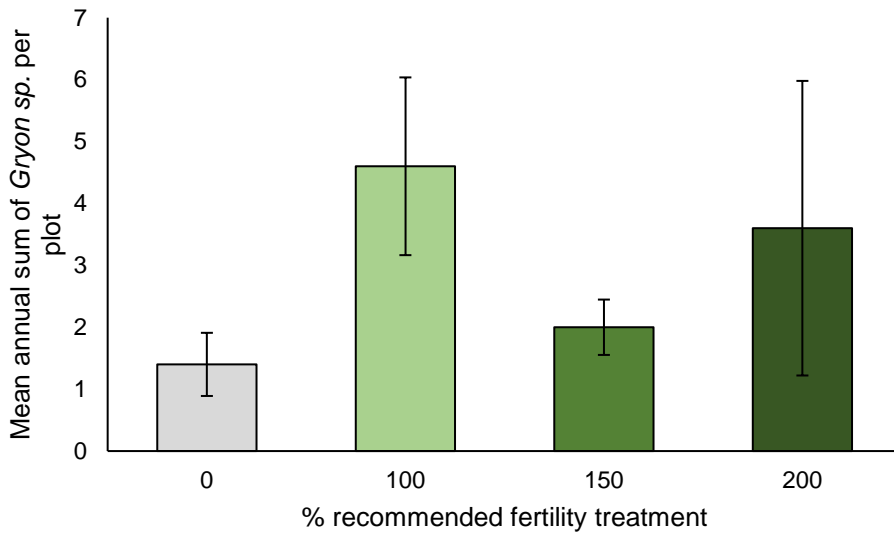


Supplementary Figure 57. Effects of fertility treatment on annual sums per plot of stilt bug nymphs in vacuum samples of zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).



Supplementary Figure 58. Effects of fertility treatment on annual sums per plot of stilt bug adults in vacuum samples of zucchini. Error bars indicate standard error about the mean (N= five replicates per treatment).

Specialist Parasitoid Response to Fertility



Supplementary Figure 59. Effects of fertility treatment on annual sums per plot of Gryon sp. in vacuum samples from both zucchini and tomato plants. Error bars indicate standard error about the mean (N= five replicates per treatment).