

Research Paper

Importance of plant diversity and structure for urban garden pest resistance



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HIGHLIGHTS

- Ornamental gardens provide ecosystem services that arthropod pests can limit.
- Dense plantings can decrease pest abundance.
- Species-rich and heterogeneous plantings can enhance richness and abundance of arthropod natural enemies.
- Findings suggest that pest resistance can be enhanced via garden design.

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ABSTRACT

Urbanization is occurring at a dramatic rate, driving numerous unfavorable environmental effects. Urban designed ecosystems have been used to mitigate these impacts through the provisioning of ecosystem services. These services may be enhanced by manipulating the plant community composition and structure of designed ecosystems. Here we test this possibility by determining the degree to which plant diversity and structure in ornamental gardens are related to the ecosystem service of pest resistance, as inferred by the taxonomic richness (at the family level) and abundance of arthropod pests that harm plants and arthropod natural enemies that feed on pests. To do so, we quantified plant diversity and structure and collected arthropod pests and natural enemies in the winter and summer from 13 ornamental gardens nested within four residential communities in north-central Florida, United States. Pest abundance decreased exponentially as vegetation clumping and volume increased, but only in winter when pests were most abundant. Natural enemy abundance and family richness increased with the number of plant species present and spatial variability in plant species composition, again in the winter, but not summer. These relationships were likely driven by the direct effects of vegetation on arthropod habitat and not its indirect effects on temperature. Our results demonstrate the potential to enhance pest resistance in ornamental gardens by manipulating vegetation and reveal the need to expand these investigations into other designer ecosystems to enhance the ecosystem services they provide in urban landscapes.

1. Introduction

Urbanization is occurring at an unprecedented rate, with over 50% of the global population now residing in urban areas (UNFPA, 2007). Urbanization drives a variety of unfavorable ecological changes, including habitat loss, biotic homogenization, biodiversity loss, and declines in ecosystem services (McKinney, 2002; Foley et al., 2005; Groffman et al., 2017). “Designed ecosystems” (sensu Palmer et al., 2004) defined as

ecosystems created to meet human and ecological goals within urban areas can be used to mitigate these impacts. While there is a growing body of literature on the utility of designed ecosystems (e.g., Ross et al., 2015; Awasthi et al., 2016; Bergey & Figueroa, 2016), we still have a poor understanding of the ecosystem services they provide. A better understanding of this contribution can inform the design of urban ecosystems that effectively and consistently promote ecosystem services for urban residents.

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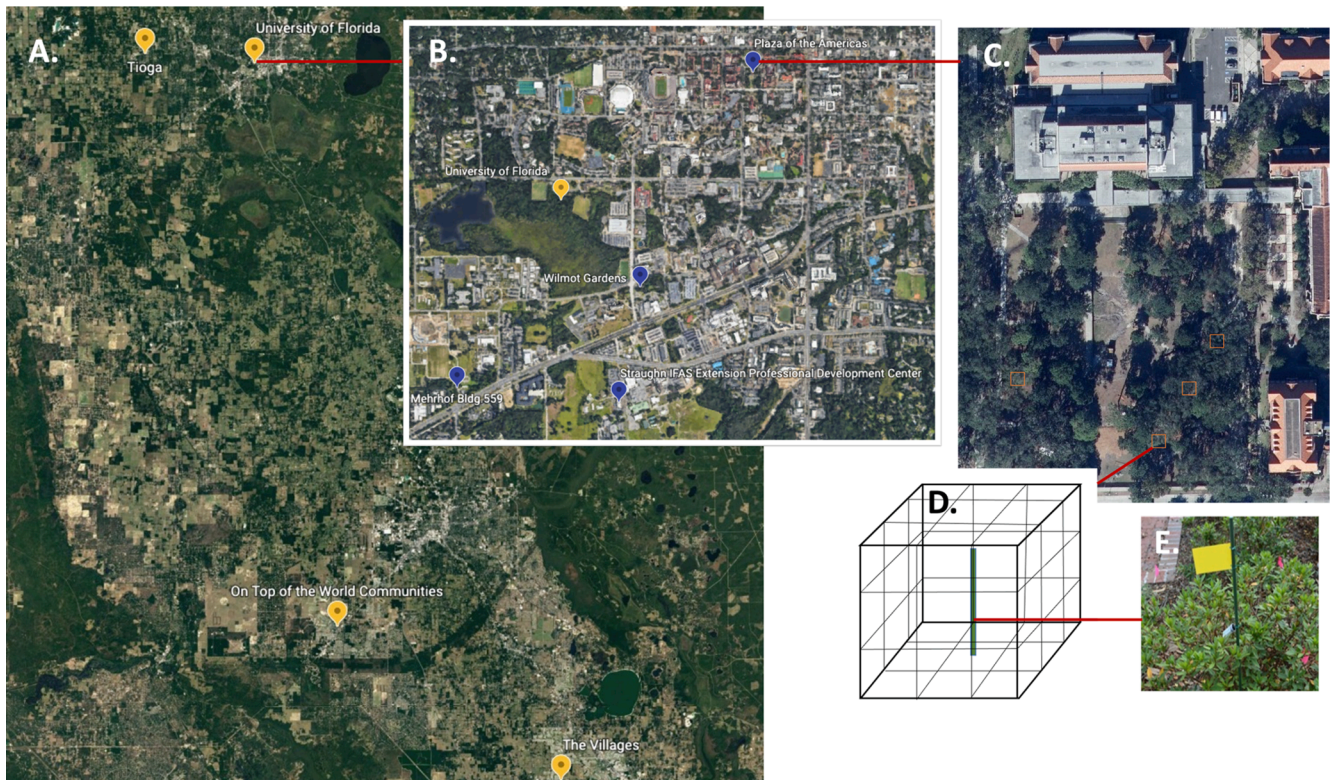


Fig. 1. Nested sampling design depicting (A) location of four communities containing sample gardens, (B) aerial view of all sampled gardens within one community (the University of Florida) (C) aerial image of one sample garden with four randomly located subplots, (D) illustration of 3 m³ subplot used to quantify vegetation structure, and (E) image of sticky card and temperature logger placed at each subplot's centroid.

Modifying plant community diversity and structure within designed ecosystems provides a potential avenue for optimizing ecosystem services. Plants are an integral component of designed ecosystems that underpin their services provided to humans (e.g., cooling, aesthetics, carbon storage, biodiversity) (Bolund & Hunhammar, 1999; Isbell et al., 2011; Nowak et al., 2013). Plants are also the taxonomic group most typically managed by humans in urban landscapes through practices such as mowing and/or landscape design (Kinzig, Warren, Martin, Hope, & Katti, 2005). Quantifying the degree to which various ecosystem services are related to plant diversity and structure would provide evidence of the ability to manipulate designed ecosystems to maximize the benefits they provide to urban landscapes. There is prior evidence of such associations. For example, designed ecosystems having a greater number of plant species (i.e., greater levels of alpha (α) diversity) can support more species from taxa such as birds and butterflies (Blair & Launer, 1997; Chong et al., 2014). Additionally, enhancing the vegetation structure in a designed ecosystem by incorporating a variety of trees and shrubs of different heights has been linked to the provision of various services, including cooling, improved habitat quality, seed dispersal, pest control, and enhanced primary productivity in forests, agroecosystems, and urban landscapes (McDonnell & Stiles, 1983; Bolund and Hunhammar, 1999; Shrewsbury & Raupp, 2000; Hardiman, Bohrer, Gough, Vogel, & Curtis, 2011; Jung, Kaiser, Böhm, Nieschulze, & Kalko, 2012; Dale & Frank, 2014a).

Considering the spatial variability in plant community species composition within a garden (i.e., beta (β) diversity) could also be a valuable tool for improving landscape functionality and ecosystem services. Most studies of β diversity concentrate on its relationship with overall biodiversity in ecological communities (Tscharrntke et al., 2007) rather than its effects on ecosystem services like pest resistance. Nevertheless, some have shown that β diversity can stabilize ecosystem properties across dispersal-linked communities (France & Duffy, 2006) and can enhance the ability of ecosystems to support multiple functions

(Pasari, Levi, Zavaleta, & Tilman, 2013). Given the overall ecological importance of β diversity, there is good reason to investigate if there is evidence of associations between β diversity and the ecosystem services provided by designer ecosystems (Lennon, Koleff, Greenwood, & Gaston, 2001; Baselga, 2010; Pasari et al., 2013).

Pest resistance is another important ecosystem service to consider because herbivory by arthropod pests limits the ecosystem services plants provide in urban ecosystems. Arthropod pests, defined here as arthropods that cause unwanted economic and/or environmental impact (Raupp, Koehler, & Davidson, 1992), can be more prevalent in urban than natural areas (e.g., Raupp, Shrewsbury, & Herms, 2010). Fortunately, the ecosystem service of pest resistance may be enhanced via proper design strategies, particularly by modifying plant diversity and structure. For instance, increased vegetation diversity and/or vegetation structure can reduce pest outbreaks by preventing pests from locating food sources (Andow, 1991), inhibiting pest movement (Avelino, Romero-Gurdián, Cruz-Cuellar, & Declerck, 2012), and increasing predators and parasitoids (hereafter referred to as "natural enemies") (Root, 1973; Dale, Perry, Cope, & Benda, 2019; Parsons, Sozanski, Wilson, & Frank, 2019). Increases in natural enemies can occur via multiple mechanisms, including increased prey abundance, refuge from other natural enemies, more favorable microclimates, access to alternative resources, and/or reduced competition (Landis, Wratten, & Gurr, 2000; Tooker & Hanks, 2000; Langellotto & Denno, 2004; Raupp et al., 2010; Tylianakis & Romo, 2010). Dispersed vegetation may also prompt pest outbreaks via effects on temperature, as less vegetation structure increases sun exposure and thus warming. This warming can increase insect pest fecundity and density (Dale & Frank, 2014a) and may disrupt pest regulation by creating phenological mismatches between natural enemies and pests (Meineke, Dunn, & Frank, 2014). Thus, modifying plant diversity and structural complexity may enhance pest resistance in designer ecosystems via multiple biotic and abiotic factors, thereby increasing the ecosystem services provided by urban vegetation.

Table 1

Mean (\bar{x}), median (Med), standard deviation (SD), minimum value (Min), and maximum value (Max) of all quantified variables across all gardens demonstrating the variability encountered in vegetation characteristics, pests, natural enemies, and diurnal temperature.

Variables		\bar{x}	Med	SD	Min	Max
Vegetation	α	2.3	2.3	0.4	1.8	3.3
	β	0.74	0.70	0.16	0.40	1.00
	λ	6	6	2	4	12
	Σ_{Str}	73	76	12	47	92
	$\bar{x}_{Scatter}$	1.86	1.87	0.04	1.74	1.92
Canopy (%)		69	70	31	19	100
Pests	Pest _{Ab}	168	31	360	4	1539
	Pest _{Rich}	5	4	2	1	8
Natural enemies	NE _{Ab}	123	95	93	22	449
	NE _{Rich}	12	12	3	7	16
Temperature	AvTemp (°C)	26.3	25.6	4.7	20.5	34.2

In this study, we investigate the degree to which plant α diversity, β diversity, and vegetation structure in urban ornamental gardens were related to arthropod pests and their natural enemies. We also investigated if vegetation structure affected pests and their natural enemies indirectly via effects on temperature. Ornamental gardens provide an ideal study system because these designed ecosystems are a common feature in residential and urban landscapes that provide a diversity of important ecosystem services to residents (e.g., biodiversity conservation, aesthetics, recreation) (Goddard, Dougill, & Benton, 2010; Aronson et al., 2017), and the plants within these gardens vary in diversity and structural complexity. Regarding the specific ecosystem service of pest regulation, ornamental gardens offer a well-suited model system because they are embedded within urban landscapes and are thus more susceptible to arthropod pests. These gardens may differ subtly in their management regimes; however, the objectives behind their management (e.g., aesthetics) remain similar. This study had two objectives:

1. Quantify the relationships between α diversity, β diversity and vegetation structure (i.e., volume/dispersion) and the richness and abundance of arthropod pests and their natural enemies in ornamental gardens.
2. Determine whether vegetation structure indirectly affects pests and natural enemies by affecting garden diurnal temperature.

Understanding these relationships will enable us to understand how to better enhance the ecosystem services provided by plants in urban landscapes, while also providing insight into the effects of plant β diversity on ecosystem services in urban areas. We can also deduce the associations between vegetation characteristics and the arthropod pest community as a whole, rather than associations with a single-pest species as often studied (e.g., Dale & Frank, 2014; Parsons, Sozanski, Wilson, & Frank, 2019).

2. Methodology

2.1. Study design and region

To meet our study objectives, we sampled vegetation, arthropods, and temperature from thirteen ornamental gardens ($N = 13$), ranging in area from approximately 0.10 ha to 1.51 ha, nested within four communities in north-central Florida, United States (US). The sampled communities were between 16 km and 112 km apart from one another (Fig. 1A) and were largely residential with a range of low- to high-density housing (~5–15 houses per hectare) intermingled with built and green infrastructure. We surveyed three gardens per community, except for the University of Florida, where we surveyed four gardens. Spacing among gardens within each community ranged from 30 m to 3.5 km. All gardens were in public areas and served similar functions of enhancing community aesthetics, but each were managed by separate entities, or

using separate management strategies, even within communities. Gardens also had walking trails and were dominated by smaller ornamental plants (e.g., shrubs and small trees) with varying degrees of tree canopy cover (Table 1). The study region is a sub-tropical climate, with average daily temperatures ranging from 14.4 °C in the winter to 27.8 °C in the summer (www.climatecenter.fsu.edu), thereby potentially creating conditions for pest outbreaks year-round. We collected vegetation, arthropod, and temperature data when plant biomass was expected to be at its annual low (February 8–20, 2018; winter) and high (August 30–September 11, 2018; summer). Data were collected from four 3 m³ cube-shaped subplots ($n = 52$) in randomly selected locations within each garden. Subplot locations consisted of flower beds and/or areas with ornamental trees and shrubs, having no turfgrass, and that were heavily treated for unwanted weeds. Locations were selected from a grid overlay in non-adjacent cells.

2.2. Vegetation survey

We observed a total of 48 unique plant species throughout all 13 gardens, 35% of which were native and 65% of which were non-native (Appendix A: Table A1). For each sampling period (hereafter referred to as “season”), we identified all plant species present in each subplot and calculated garden-level gamma (λ) diversity as the total number of species present across each garden’s subplots. We recorded an average λ diversity of 6 plant species at the garden level (Table 1). We then estimated garden-level alpha (α) diversity by averaging the number of plant species present across each garden’s subplots (Whittaker, 1960). Average α diversity across all gardens was somewhat low, with an average of 2.3 plant species per garden (Table 1). We estimated beta (β) diversity using the Simpson dissimilarity index,

$$\beta_{sim} = \frac{\min(b, c)}{a + \min(b, c)} \quad (2-1)$$

where b is the total number of plant species occurring in a neighboring subplot but not the focal subplot, c is the total number of species in the focal subplot but not the neighboring subplot, and a is the number of species common between subplots (Koleff, Gaston, & Lennon, 2003). We calculated this value for all possible subplot pairings and averaged these values to yield a garden-level estimate. Simpson’s dissimilarity ranges from 0 (complete similarity) to 1 (complete dissimilarity). Simpson dissimilarity index varies independently of α diversity, allowing for the simultaneous evaluation of both (Baselga, 2010). We excluded λ -diversity from analyses due to collinearity with α diversity; when included in our statistical models, λ -diversity had a variance inflation factor (VIFs) value of 22.6.

We calculated two separate metrics termed ‘summed structure’ (Σ_{Str}) and ‘scatter of structure’ ($\bar{x}_{Scatter}$) to estimate vegetation structural volume and dispersion, respectively. Summed structure estimates total vegetation cover in a given subplot, whereas scatter of structure estimates the degree to which a subplot’s vegetation is clumped (low scatter) or dispersed (high scatter). To estimate Σ_{Str} , we subdivided each 3 m³ subplot into 27 individual 1 m³ cells (Fig. 1D), counted the cells containing vegetation, divided this count by 27, and multiplied the resulting value by 100. This value therefore represented the percent of total subplot cells containing any vegetation. We then produced a garden-level estimate of Σ_{Str} by averaging Σ_{Str} values across garden subplots. To estimate $\bar{x}_{Scatter}$, we created a data matrix for each subplot by assigning X, Y, and Z coordinates to each subplot’s 1 m³ cells occupied by any vegetation. “NA” values were assigned to cells unoccupied by vegetation. We then created a dissimilarity matrix for each subplot of the Euclidean distances among all occupied cells, with distances ranging from 1 to 3.5 (i.e., the distance between the nearest and furthest points of the cube). We calculated the mean Euclidean distance for each subplot and averaged this value across all four subplots to obtain a garden-level estimate of $\bar{x}_{Scatter}$, with values ranging from 1.74 to 1.92

(Table 1). For this metric, higher values indicate more scattered vegetation (i.e., cells occupied by vegetation are further apart in the subplot), whereas lower values indicate more clumped vegetation (i.e., cells occupied by vegetation are closer together in the subplot). Finally, we estimated canopy cover for each subplot using a Model-A Convex Spherical Crown Densimeter (Forestry Suppliers, Jackson, MS, USA) and averaged estimates across subplots to render a garden-level estimate.

2.3. Arthropod pests and natural enemies

We sampled arthropods during both sampling periods using 7.6×12.7 cm sticky cards (Olson Products, Medina, Ohio, USA) and a modified leaf vacuum (Stihl SH 86 C-E, Virginia Beach, VA, USA). Sticky cards were used to capture flying taxa, typical of natural enemies (Raupp, Holmes, Sadop, Shrewsbury, & Davidson, 2001; Dale & Frank, 2014b), while the arthropod vacuum was used to collect a wider array of arthropods at low to medium vegetation heights, such as flying, motile, and sessile arthropods (Moir & Brennan, 2007; Doxon, Davis, & Fuhendorf, 2011). Sticky cards were placed at each subplot's center (Fig. 1D & E), approximately 1 m from the ground, for one-week intervals. Three 1 m^3 cells were selected randomly from each subplot, making sure to avoid adjacent cells when possible, and vegetation within those cells was vacuumed for 45 s. Although we were unable to sample ground-dwelling arthropods and/or endophagous or sedentary life stages of pests, our sampling techniques repeated over time allowed us to capture various arthropods from multiple trophic levels and seasons, including an array of flying insects and arthropods residing on the vegetation surface. Once collected, arthropods were taken to the lab, preserved at -18°C , and insect pest taxonomic groups known to commonly damage urban landscape plants in our region (based on Mizell et al., 2011; Frank, 2018) were identified to family, or superfamily if family members function similarly, e.g., members of Coccoidea. We also counted and identified all families of arthropods that according to Triplehorn, Johnson, & Borror (2005) and Frank (2018) are known to be composed of all, or nearly all, natural enemies to the pests. From these data, we then estimated the total types of pests (pest richness) and abundance, as both are of practical importance to pest management decisions. Despite declines in evenness being a potential indicator of pests, we did not quantify evenness. Evenness from our data would not serve such a purpose given that its values would have been derived from only the pests and natural enemies rather than the entire arthropod community.

2.4. Temperature

We quantified temperature measurements every 30 min from February 8–20, 2018 and from August 30–September 11, 2018 (the week-long period coinciding with arthropod collection) using a HOBO Pendant™ temperature logger (Onset Computer Corporation, Bourne, MA). Loggers were placed at the center of each subplot 0.5 m off the ground (Fig. 1D & E) and were placed in a shaded area to reduce exposure to direct sunlight. Diurnal average temperatures shown to impact arthropod populations (Meineke, Dunn, Sexton, Frank, & Bond-Lamberty, 2013) were calculated following Nasrin, Chakrabarty, Barman, Saha, & Rahman (2017). We did not consider nighttime temperatures as variability among gardens was low. The temperature distribution was right-skewed, likely due to the brief exposure of some probes to direct sunlight. We therefore removed the upper 5% of temperature values to control for this unwanted effect that can result in inaccurately high temperature values (Terando, Youngsteadt, Meineke, & Prado, 2017).

2.5. Statistical analyses

To determine if vegetation characteristics affected pest and natural

enemy abundance and/or richness (Objective 1), we modeled Pest_{Ab} , $\text{Pest}_{\text{Rich}}$, NE_{Ab} , and NE_{Rich} each in relation to α diversity (average plant diversity across subplots in a garden), β diversity (Simpson's dissimilarity), Σ_{Str} , and x_{Scatter}^- at the garden level. To identify temporal variability in effects, models included sampling season and two-way interactions between season and all other model terms. Season was not included in the Pest_{Ab} model due to difficulties in fitting dramatically different abundances and vegetation relationships between winter (mean pest abundance \pm SE of 311 ± 126 individuals garden $^{-1}$) versus summer (17 ± 3 individuals garden $^{-1}$) using a single statistical model. Instead, we constructed separate models for each season. We did not include canopy cover in our statistical models, given that we did not sample arthropods from that vegetation layer. In addition, preliminary statistical analyses revealed no relationship between canopy cover and any of our investigated response variables ($-0.24 \leq r \leq 0.21$, $p\text{-value} \geq 0.233$). In order to address the potential issue of β -diversity being confounded with garden size, we tested for correlation between garden size and β -diversity using a Pearson correlation test. We found no evidence of a relationship between these two variables ($p = 0.66$). $\text{Pest}_{\text{Rich}}$, NE_{Ab} , and NE_{Rich} were modeled using linear mixed-effects models with a Gaussian distribution (natural enemy abundance was log transformed), while Pest_{Ab} was modeled using generalized linear models (GLM) with Negative Binomial distributions and log link functions (Appendix B: Figs. B1 & B2). Dispersion for Pest_{Ab} models fell below 2 and was therefore sufficient for interpretation (Bolker et al., 2009).

All linear models described above also included categorical terms for each sampled garden as random intercept effects to account for potential non-independence of arthropods sampled from subplots within the same garden (e.g., differences in abundance, garden management). We also included garden as a random effect to account for the lack of statistical independence between data collected from the same garden during different seasons. Nevertheless, we investigated the utility of including community as a random effect in our statistical models (i.e., garden nested within community vs. only garden as a random effect). Despite the close proximity of some gardens within a given community, and therefore increased potential for dispersal of arthropods among these gardens, such proximity effects were not detected, as the model results did not change with the inclusion of community as a random effect. In fact, inspection of corrected AIC (AICc) values of preliminary statistical models (Burnham & Anderson, 2004) containing community as a random effect revealed no benefit of including this random effect based on increases in AICc values across all models ($\Delta\text{AICc} = +2.3$ to $+11.3$). Hence, it makes sense to exclude community as a random factor, given that management decisions also largely occurred at the garden and not community levels.

Statistically nonsignificant fixed effects were removed sequentially from statistical models using backward selection when doing so did not increase AICc values substantially (Burnham & Anderson, 2004). P-values were estimated using Type II Anovas and assuming a chi-squared distribution; type II Anovas provide greater statistical power in detecting interaction effects present in our models (Fox & Weisberg, 2019). We did not interpret statistically significant main effects for a given model term when that term was included in a statistically significant interactions (i.e., its effect varied over time). Restricted maximum likelihood (REML) was used to assess significance of model terms, while maximum likelihood (ML) was used compare and contrast AICc values among nested models (Zuur et al 2009). Removal of non-significant fixed terms either improved, or did not decrease, the quality of all statistical models ($\Delta\text{AICc} = -7.4$ to -0.3).

To determine whether vegetation structure affected pests and natural enemies indirectly via temperature (Objective 2), we first modeled pest abundance (Pest_{Ab}), pest richness ($\text{Pest}_{\text{Rich}}$), natural enemy abundance (NE_{Ab}), and natural enemy richness (NE_{Rich}) in relation to average diurnal temperature (AvTemp) using simple linear models. We analyzed winter and summer data separately, as average temperatures differed considerably between these seasons ($21.8 \pm 0.18^\circ\text{C}$ vs. $30.8 \pm 0.54^\circ\text{C}$,

Table 2

Slope estimates (\pm standard error) and coinciding levels of statistical significance of final reduced statistical models showing the degree to which pest and natural enemy abundance and richness are related to vegetation characteristics and how these relationships vary over time (Objective 1). Statistical models (excluding $Pest_{Ab}$) included garden (i.e., our sample unit) as a random effect to account for the lack of statistical independence across seasons and garden conditions. For $Pest_{Ab}$, we constructed separate GLMs and conducted analyses at each season; therefore, season, interactions and the random effect were not included in the models. $Pest_{Ab}$ models were built with Negative Binomial distributions and log-link functions. $Pest_{Ab}$ = pest abundance in winter (P1) and summer (P2); $Pest_{Rich}$ = pest richness; NE_{Ab} = natural enemy abundance; NE_{Rich} = natural enemy richness; average scatter of vegetation structure ($\bar{x}_{Scatter}$), alpha diversity (α), beta diversity (β), and sum of vegetation structure (Σ_{Str}). Df for main effects = 1,12; Df for interactions = 1,25.

Response variables		Season	$\bar{x}_{Scatter}$	α	β	Σ_{Str}	Season: α	Season: β	Season: Σ_{Str}	Season: $\bar{x}_{Scatter}$
Pests	$Pest_{Ab}$ (P1)		23.5 (± 8.4)^{**}	–	–	–	–	–	–	–
	$Pest_{Rich}$	–1.0 (± 0.3)^{**}	–	–	–	–	–	–	–	–
Natural enemies	NE_{Ab}	–	–	0.8 (± 0.2)^{**}	–	–	–	–	–	–
	NE_{Rich}	57.5 (± 28.5)	52.3 (± 29.3)	–	11.6 (± 6.8)	–	–	–6.6 (± 3.1)[*]	–	–28.3 (± 15.1)[*]

* $p \leq 0.10$.

** $p < 0.01$.

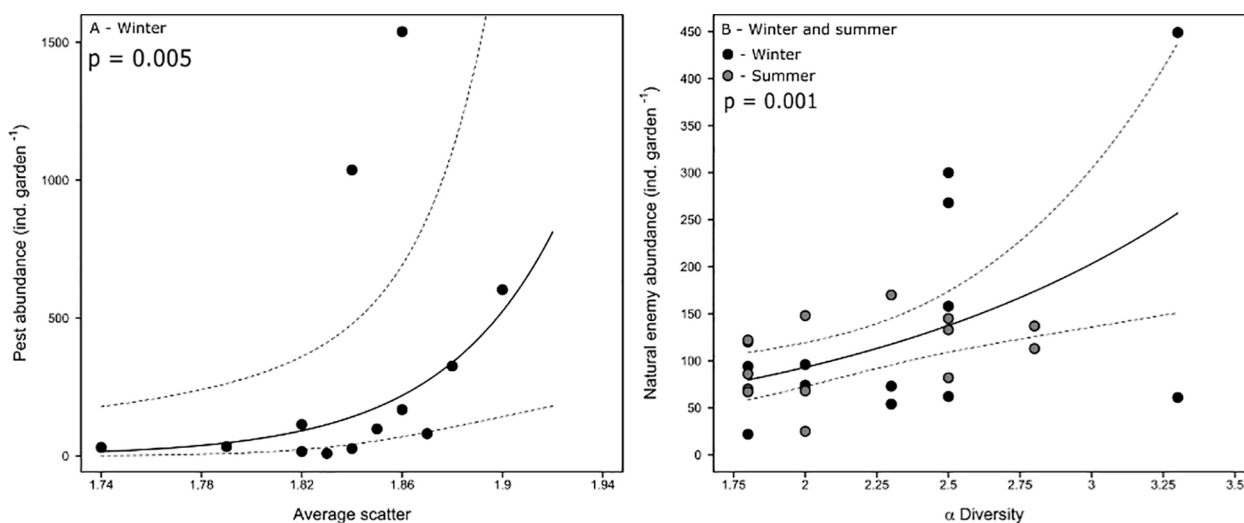


Fig. 2. Statistically significant associations between (A) vegetation scatter and pest abundance (individuals garden⁻¹) and (B) α diversity and natural enemy abundance. There was a positive association between average vegetation scatter ($\bar{x}_{Scatter}$) and pest abundance in winter and a positive effect of α diversity on natural enemy abundance (individuals garden⁻¹) across the entire study period. For pest abundance, we conducted separate winter and summer analyses due to inability to fit suitable statistical model across both seasons. Note the large differences in pest abundance across seasons. Solid lines represent the best-fit relationships and dotted lines represent confidence interval envelopes from the associated GLM and GLMM models. P-values given are derived from each significant main effect.

respectively), resulting in a bimodal distribution that prevented the inclusion of both seasons into a single statistical model. Using linear models, we then modeled AvTemp in relation to vegetation structure (Σ_{Str} and $\bar{x}_{Scatter}$) and canopy cover separately for winter and summer to determine which component(s) of vegetation structure affected arthropods indirectly via temperature. Models involving AvTemp did not include random effects as their inclusion did not improve models ($\Delta AICc = +13.9$ to $+17.4$).

In addition to our main objectives, we also modeled both $Pest_{Ab}$ and $Pest_{Rich}$ in relation to NE_{Ab} and NE_{Rich} to identify potential linkages between pests and natural enemies. These models also included season and all interactions between season and each natural enemy predictor as fixed effects, and garden as a random effect to account for the lack of statistical independence between repeated measures.

All analyses were conducted in “R” version 3.5.1 (R Development Core Team, 2018). Linear mixed-effects models were created using the lme4 package (Bates, Maechler, Bolker, & Walker, 2019). GLMs were built using the glmmADMB package (Fournier et al., 2012; Skaug, Fournier, Bolker, & Magnusson, 2016). Type II Anova assuming a chi-square distribution were conducted using the car package (Fox & Weisberg, 2019).

3. Results

3.1. Overall patterns in arthropod community

We recorded 12 total arthropod pest families and superfamilies across seasons. Six families occurred in over 50% of gardens, with the family Cecidomyiidae (gall midges) occurring in all gardens (Appendix B: Fig. B1). A mixture of adult and juvenile scale insects (superfamily Coccoidea) were the most common pests found among gardens, accounting for 77% (3372) of the 4385 pest individuals identified, 99% of which were encountered in winter. We found a greater diversity of natural enemies than pests. We recorded 34 natural enemy families, 19 of which occurred in most gardens (Appendix B: Fig. B2). Of those 19 taxa, Dolichopodidae (long-legged flies), Chalcididae (chalcid wasps), Platygasteridae (parasitoid wasps), and Formicidae (ants) were observed in all gardens in winter and summer (Appendix B: Fig. B2). Parasitoids dominated the natural enemy community, accounting for 60% of the 3197 natural enemy individuals collected. There were strong seasonal differences in pest abundance, but not natural enemy abundance. From winter to summer, average pest abundance across all gardens decreased considerably from 340 ± 912 (mean \pm SD) individuals garden⁻¹ in the winter down to 25 ± 8 individuals garden⁻¹ in the summer. This 93% decrease was largely driven by declines in Coccoidea, as many of those found in the winter were juvenile and may have dispersed or not

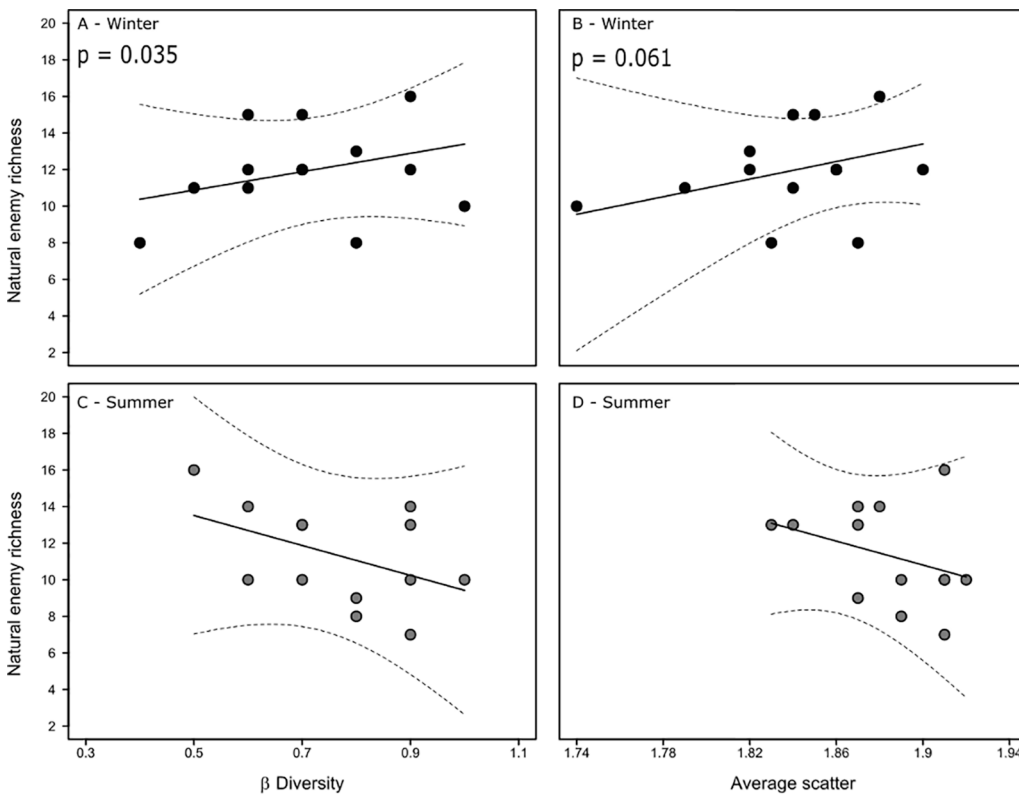


Fig. 3. Effects of vegetation on natural enemy richness. There were changes in relationships between natural enemy richness and β diversity across the winter (A) and summer (C) seasons; and changes in relationships between average scatter (\bar{x}_{Scatter}) and natural enemy richness across seasons. In (B) and (D), black points represent values for winter and grey points are for summer and solid lines represent the best-fit relationships and dotted lines represent confidence interval envelopes from the associated GLMM models. P-values given are derived from each significant interaction term.

Table 3

Slope estimates (\pm standard error) for relationships between diurnal average temperature at each season and structural complexity (\bar{x}_{Scatter} and Σ_{Str}) and overstorey canopy cover. Temperature was not incorporated into any further analyses with arthropods and vegetation characteristics, as there was insufficient evidence of an effect on both pests and natural enemies. AvTemp = average diurnal temperature in winter (P1) and summer (P2); average scatter of vegetation structure (\bar{x}_{Scatter}), sum of vegetation structure (Σ_{Str}), and Canopy = average tree canopy cover. Df for main effects = 1,12.

Response variables	\bar{x}_{Scatter}	Σ_{Str}	Canopy
AvTemp (P1)	–	0.04 (± 0.02)*	–
AvTemp (P2)	–	0.08 (± 0.03)*	–0.05 (± 0.01)**

* $p < 0.10$.

** $p < 0.01$.

survived to the summer (Appendix C: Table C1). Natural enemy abundance also changed between seasons, but to a lesser degree, declining by 26% from 54 ± 124 individuals garden⁻¹ in the winter to 40 ± 15 individuals garden⁻¹ in the summer (Appendix C: Table C1).

3.2. Pests Response to vegetation characteristics

Only vegetation scatter (\bar{x}_{Scatter}) was related to pest abundance (Table 2), a relationship that was largely driven by changes in Coccoidea abundance across seasons. In the winter, when pests, namely Coccoidea, were most abundant, pest abundance increased exponentially as garden vegetation became more scattered ($\chi^2_{1,12} = 2.81$; $p = 0.005$; Fig. 2A). For example, gardens with the highest values of scatter, such as those with just a few ornamental trees and shrubs, contained an average of 337 ± 59 pest individuals, whereas gardens with lower scatter values due to denser plantings of trees, shrubs, and flowering plants contained an average of 49 ± 10 pest individuals. There was no such effect of scatter on pest abundance in the summer ($p = 0.480$). No other

vegetation characteristics (Σ_{Str} , α and β diversity) were associated with pest abundance (Table 2) and removing these terms from statistical models improved model fit, as evidenced by reduced AICc values ($\Delta\text{AICc} = -7.4$ to -2.2). In contrast to pest abundance, pest richness was only associated with season ($\chi^2_{1,12} = 9.64$; $p = 0.002$) and was not related to any garden characteristics ($p \geq 0.129$; Table 2; ΔAICc for term removal = -6.6 to -0.3).

3.3. Natural enemies response to vegetation characteristics (Objective 1)

The abundance of natural enemies was positively related to α diversity in both winter and summer ($\chi^2_{1,12} = 7.06$; $p = 0.001$; Table 2; Fig. 2B), a relationship driven by Dolichopodidae, Chalcididae, and Platygasteridae. Natural enemy richness also increased from 8 to 16 taxa across the range of β diversity and vegetation scatter observed throughout our gardens but decreased as these variables increased in the summer ($\chi^2_{1,25} = 4.43$ and 3.51 ; $p = 0.035$ and 0.061 , respectively; Table 2; Fig. 3A–D). No other vegetation characteristics affected either natural enemy abundance or richness ($p \geq 0.118$; Table 2), and the removal of these other terms improved models, i.e., reduced AICc values ($\Delta\text{AICc} = -6.8$ to -2.3).

3.4. Indirect effects via temperature (Objective 2)

We detected a statistically significant positive relationship between temperature and pest richness in the summer ($t_{1,12} = 2.28$, $p = 0.043$; Appendix D: Fig. D1), but not in the winter ($p = 0.987$). We did not detect statistically significant associations between temperature and pest abundance ($p \geq 0.331$) nor between temperature and natural enemy abundance or richness in winter or summer ($p \geq 0.166$) despite summed vegetation structure and canopy cover being associated with average temperature (AvTemp) (Table 3). In the winter and summer, as summed structure increased, diurnal average temperature also increased (Appendix E: Fig. E1). In the summer, as canopy cover increased, diurnal average temperature decreased (Appendix E: Fig. E1).

Table 4

Slope estimates (\pm standard error) for relationships between natural enemies and pests. Temperature models were omitted due to the lack of significant effects on pests ($p \geq 0.15$). Slope estimates (\pm standard error) are given for each term. Df for main effects = 1,12; Df for interactions = 1,25.

Response variables	NE _{Ab}	NE _{Rich}	Season	Season: NE _{Ab}	Season: NE _{Rich}
Pest _{Ab}	2.1 (± 0.6)**	-	0.7 (± 0.6)	-0.5 (± 0.3)*	-
Pest _{Rich}	2.9 (± 0.9)**	-	-0.9 (± 0.3)**	-	-

* $p \leq 0.10$.

** $p < 0.01$.

Canopy cover was not significantly associated with temperature in the winter ($p \geq 0.505$), and we did not detect any associations between scatter and temperature in either the winter or summer ($p \geq 0.133$; Table 3).

3.5. Natural enemy response to pests

Pest and natural enemy abundance were positively associated in the winter, while no association between the two was detected in the summer ($\chi^2_{1,12} = 4.34$; $p < 0.001$; Table 4; Fig. 4A & C). Pest abundance increased by about 252% as the abundance of natural enemies increased from 22 to 158 individuals. Pest richness was also positively related to natural enemy abundance across seasons, with a 116% increase in richness across the same range of natural enemy abundance ($\chi^2_{1,12} = 2.87$; $p = 0.002$; Table 4; Fig. 4B & D). Neither pest abundance nor

richness were related to natural enemy richness ($p = 0.42$ and 0.77 respectively; Table 4); removal of these terms reduced AICc (Δ AICc = -4.1 to -2.8).

4. Discussion

Relationships between vegetation characteristics and pests and natural enemies indicated a potential to enhance pest resistance in ornamental gardens by modifying vegetation dispersion and diversity. Specifically, during seasonal peaks in pest abundance, gardens with more scattered vegetation harbored more pests than those that were more densely planted. During these same periods of elevated pest abundance, natural enemy abundance also increased in gardens with more plant species (i.e., greater α diversity) and natural enemy richness increased in gardens with greater spatial variation in plant species composition (i.e., β diversity) and greater vegetation scatter. These results suggest that, for our ornamental garden study system, pest abundance can be minimized, and natural enemy abundance maximized if gardens are planted with less spacing between vegetation, greater variety of plant species, and more variation in plant species used within nearby gardens.

Vegetation structure is among the most important factors affecting the abundance of damaging insect pests like lace bugs and scale insects via biotic and abiotic factors (Shrewsbury & Raupp, 2000; Dale & Frank, 2014b). Multiple mechanisms may be responsible for our observed effects of vegetation scatter on garden pests. First, the ability of herbivores to locate their hosts or establish and reproduce on them, commonly referred to as plant apparency (Feeny, 1976; Castagneyrol, Giffard, Péré, Jactel, & Sipes, 2013), can be limited in areas with more condensed

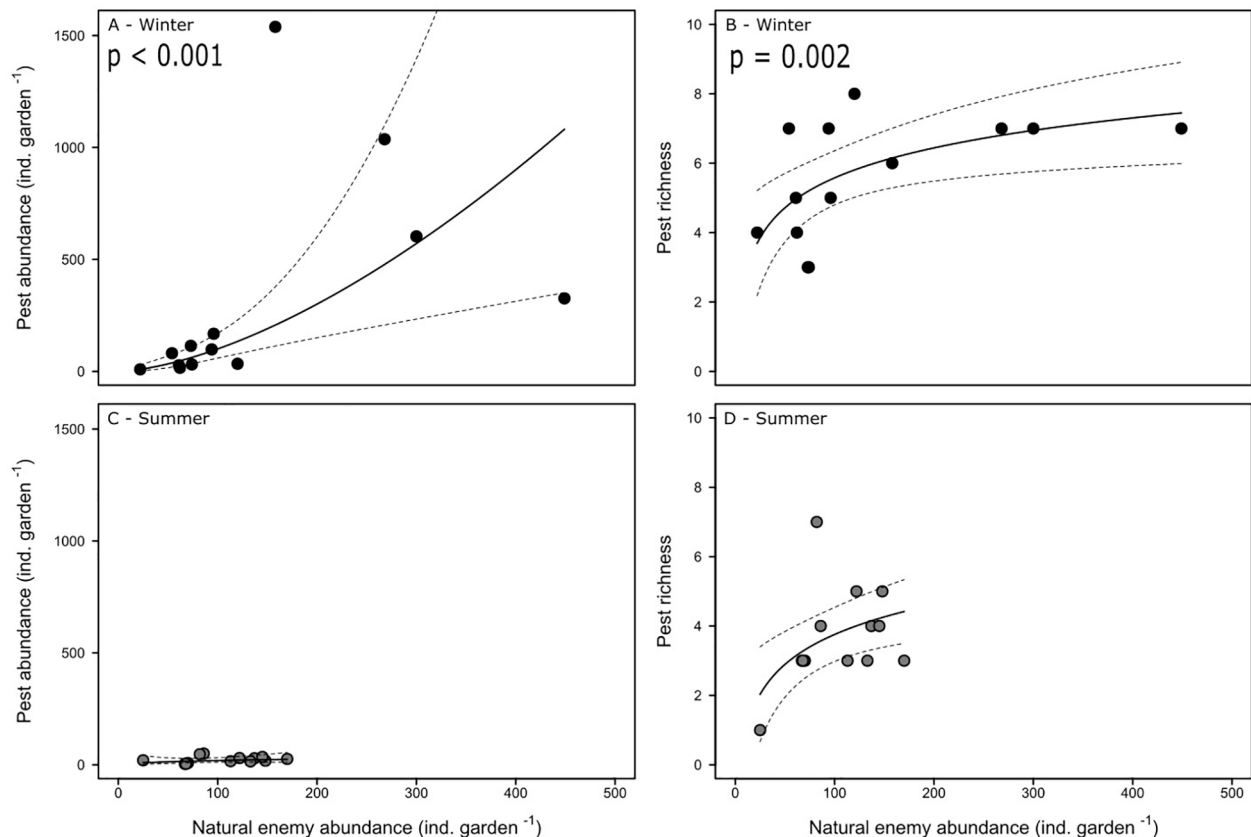


Fig. 4. Associations between winter (black points) and summer (grey points) natural enemy abundance (individuals garden⁻¹) and (A & C) pest abundance (individuals garden⁻¹) and (B & D) pest richness. There was a positive relationship between pest and natural enemy abundance in winter and no relationship in summer when pests were much less abundant. There were no seasonal differences in the associations between pest richness and natural enemy abundance, though pest richness tended to be higher in winter. Solid and dotted lines represent the best-fit relationships and the confidence interval envelopes, respectively, from the associated linear models. P-values given are derived from each significant interaction term.

Table A1

List of all plant species observed, their native status: native (N) vs. non-native (E), if they were woody (W) or herbaceous (H) species, and the percent of gardens (N = 13) and subplots (n = 52) containing each species.

Common Name	Scientific Name	Native status	Woody/ Herbaceous	% Garden Occ.	% Subplot Occ.
Coontie cycad	<i>Zamia pumila</i>	N	W	54	27
Liriope grass	<i>Liriope muscari</i>	E	H	46	23
Saw palmetto	<i>Serenoa repens</i>	N	W	38	15
Asiatic jasmine	<i>Trachelospermum asiaticum</i>	E	W	31	13
Yaupon holly	<i>Ilex vomitoria</i>	N	W	31	13
Dwarf fakahatchee grass	<i>Tripsacum floridanum</i>	N	H	23	10
Sabal palm	<i>Sabal palmetto</i>	N	W	23	8
Split leaf philodendron	<i>Philodendron selloum</i>	E	W	23	6
Muhly grass	<i>Muhlenbergia</i>	N	H	23	6
Parson's juniper	<i>Junip squamata "Parsonii"</i>	E	W	23	6
Sago palm	<i>Cycas revoluta</i>	E	W	23	6
Cast iron plant	<i>Aspidistra elatior</i>	E	H	23	6
Lily of the Nile	<i>Agapanthus africanus</i>	E	H	23	6
Needle palm	<i>Rhapidophyllum hystrix</i>	N	W	15	8
Camellia	<i>Camellia japonica</i>	E	W	15	8
Formosa azalea	<i>Rhododendron simsii</i>	E	W	15	6
Sword fern	<i>Nephrolepis exaltata</i>	N	H	15	6
Holly fern	<i>Cyrtomium falcatum</i>	E	H	15	6
Southern magnolia	<i>Magnolia grandiflora</i>	N	W	15	4
Little volcano	<i>Lespedeza tikuiensis</i>	E	W	15	4
Shore juniper	<i>Juniperus conferta</i>	E	W	15	4
Blue flax-lily	<i>Dianella tasmanica</i>	E	H	15	4
Tiplant	<i>Cordyline fruticosa</i>	E	W	15	4
Bulbine	<i>Bulbine frutescens "Hallmark"</i>	E	H	15	4
Oleander	<i>Nerium oleander</i>	E	W	8	6
St Augustine grass	<i>Stenotaphrum secundatum</i>	N	H	8	4
Crown grass	<i>Paspalum quadrifarium</i>	E	H	8	4
Lovegrass	<i>Eragrostis</i>	N	H	8	4
Bromeliad (<i>Aechmea</i> genus)	<i>Aechmea rubens</i>	E	H	8	4
Pansy	<i>Viola × wittrockiana Pansy</i>	N	H	8	2
Cleyera	<i>Ternstroemia gymnanthera</i>	E	W	8	2
Dusty miller	<i>Senecio cineraria</i>	E	H	8	2
Rose	<i>Rosa</i> spp.	E	W	8	2
Live oak	<i>Quercus virginiana</i>	N	W	8	2
Coleus	<i>Plectranthus scutellarioides</i>	E	H	8	2
Sylvestre palm	<i>Phoenix sylvestris</i>	E	W	8	2
Heavenly bamboo	<i>Nandina domestica</i>	E	W	8	2
Waxmyrtle	<i>Myrica cerifera</i>	N	W	8	2
Garden loosestrife	<i>Lysimachia vulgaris</i>	E	H	8	2
Blue flag iris	<i>Iris virginica</i>	N	H	8	2
Butterfly bush	<i>Buddleia davidii</i>	E	H	8	2
Clumping bamboo	<i>Bambusa textilis</i>	E	W	8	2
Saltbush	<i>Baccharis halimifolia</i>	N	W	8	2
Barbados aloe	<i>Aloe barbadensis</i>	E	H	8	2
Giant leather fern	<i>Acrostichum danaeifolium</i>	N	H	8	2
Glossy abelia	<i>Abelia × grandiflora</i>	E	W	8	2

vegetation. This mechanism may explain why more pests were observed in gardens with more dispersed/scattered vegetation. Additionally, dispersed vegetation can increase sun exposure, which has multiple potential effects on plants, pests, and natural enemies. Plants grown in high light conditions have been associated with outbreaks of multiple insect pests, including lace bugs, leaf miners, and scale insects, which has been attributed to increased leaf palatability and nutritional value (Collinge & Louda, 1988), increased pest fecundity (Dale & Frank, 2014b), and reduced natural enemy abundance and predation (Shrewsbury & Raupp, 2000). Our results, in combination with the above mechanisms by which vegetation scatter can affect pest abundance, suggest that modifying these garden characteristics could be a viable method for increasing the natural pest resistance of ornamental gardens.

The absence of effects of α and β diversity on pest abundance and richness contradicts findings from those detected in natural and agricultural ecosystems (e.g., Knops et al., 1999; Koricheva et al., 2000) potentially because arthropod abundance and richness may be driven by different mechanisms in urban landscapes (Dale & Frank, 2018). The effects of plant diversity on pests can depend upon which species are present (i.e., species identity; Garcia-Garcia, Sánchez-Medina, Alfonso-Corzo, & Gonzalez Garcia, 2016), the strength of the diversity

gradient (Shi et al., 2014), or the scale of study (Chong et al., 2014). For instance, the plant species 'coontie' (*Zamia pumila*) occurred in 54% of our sampled gardens and was heavily infested by scale insect pests, most of which were comprised of Florida red scale (Hemiptera: Diaspididae: *Chrysomphalus aonidum*) and mealybugs (Hemiptera: Pseudococcidae) (discussed further below). Whether a garden did or did not contain this heavily infested plant species may therefore have influenced pests more than the overall effects of plant α or β diversity. Furthermore, the range of α diversity values across subplots within gardens was generally low (1.8–3.3), thus our gradient of plant diversity may have been too narrow to detect its effects. Alternatively, urban ornamental gardens may exhibit different relationships between pests and plant diversity compared to other ecosystem types, as urban environments are characterized by ornamental vegetation, impervious surfaces, remnant habitat, and consequently, unique abiotic conditions (Dale & Frank, 2018). The contrasting effects of plant diversity in urban environments compared to other study systems may result from these distinct characteristics.

The response of natural enemies to most vegetation characteristics was potentially due to the effect of plant diversity on both food resources and habitat resources like shelter, suggesting greater opportunities to use changes to vegetation to affect pest resistance via augmenting

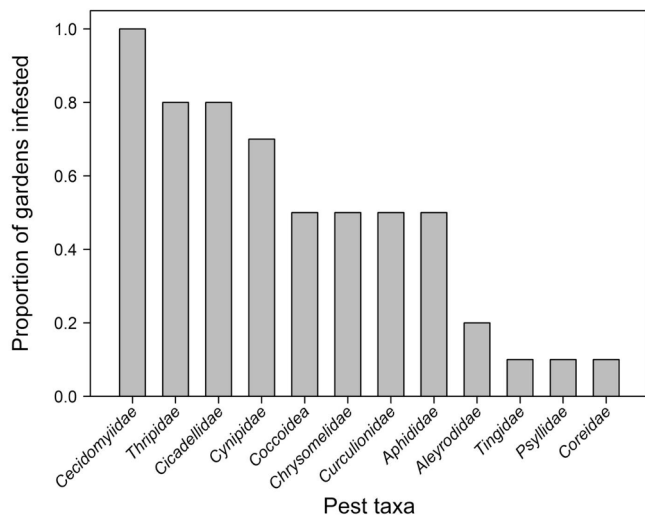


Fig. B1. Maximum proportion of occurrences from winter and spring for the 12 pest taxa identified across 13 sampled gardens. Note commonalities in occurrence (i.e., 6 taxa occurring in >50% of gardens).

natural enemies. Associations between natural enemies and plant α diversity can occur due to the effect of plant diversity on available food resources, such as non-pest arthropods (Knops et al., 1999), pollen and nectar sources (Langellotto & Denno, 2004; Dale, Perry, Cope, & Benda, 2019), as well as refuge from intraguild predation (Langellotto & Denno, 2004). Given our increased understanding of the relation of functional diversity (e.g., the number of plant resource types) to ecosystem services (Gross et al., 2017), functional diversity may be as relevant to promoting natural enemy abundance as plant species diversity, which represents a promising avenue for future research into how best to design urban plant communities to enhance pest resistance. However, it is unclear if greater natural enemy abundance is promoting pest resistance because natural enemy and pest abundances were positively related, and we did not quantify pest regulation through predation or parasitism. Thus, further work is required to determine the tri-trophic effects of vegetation on biological control.

Despite our original intention to focus on the pest arthropod

community as a whole, we deduced that the population dynamics of a highly abundant pest may explain the seasonal differences in how pest abundance related to vegetation scatter, and subsequently the relationship between scatter and natural enemy richness. Therefore, these results may be more similar to previous work that focused on the abundance of single urban pest groups (e.g., Tooker & Hanks, 2000; Shrewsbury & Raupp, 2000; Meineke et al., 2013; Dale & Frank, 2014b). In the winter, both pest abundance and natural enemy richness were positively associated with scatter, while scatter exhibited no relationship with summer pest abundance and a negative relationship with natural enemy richness. Notably, differences in pest abundance between seasons were driven by scale insects and mealybugs, a superfamily known to exhibit outbreaks in urban areas (Frank & Just, 2020), which were 18 times more abundant in the winter than in the summer. The nymphs of this superfamily were highly abundant in winter (Appendix C: Table C1) and their abundance dramatically declined in summer. This dramatic increase and decline align with scale insect reproduction and attrition, as the system is inundated with immature life stages but relatively few establish and reproduce. Although vacuum trapping captures sessile insects such as scales and mealybugs, it is primarily when they are in immature life stages (Moir & Brennan, 2007; Doxon, Davis, & Fuhlendorf, 2011). The observed decline in the summer was likely due to a combination of dispersal, mortality, and a reduced likelihood of detecting adults using our survey methods. Therefore, the seasonal effects of vegetation scatter on pest abundance were driven by the emergence and subsequent attrition of nymphs of this pest group. Similarly, the positive winter relationship between natural enemy richness and scatter, followed by a negative relationship in winter, may be driven by associated shifts in Coccoidea nymphs and adults because a majority of detected natural enemies (58%) were parasitoids, which are well-known natural enemies of scale insects (Ben-Dov & Hodgson, 1997; Miller, 2005). The relationships we detected between vegetation scatter, pest abundance, and natural enemy richness may thus be more reflective of the dominant arthropods in our sampled gardens rather than effects of scatter on the overall community. Therefore, evaluating pest-natural enemy associations at a finer taxonomic resolution (i.e., at the species level) or based on their functional groups may provide for a more accurate assessment of these associations and their mechanisms.

Unlike vegetation scatter, seasonal differences in the effects of plant β diversity on natural enemy richness were likely unrelated to the pest

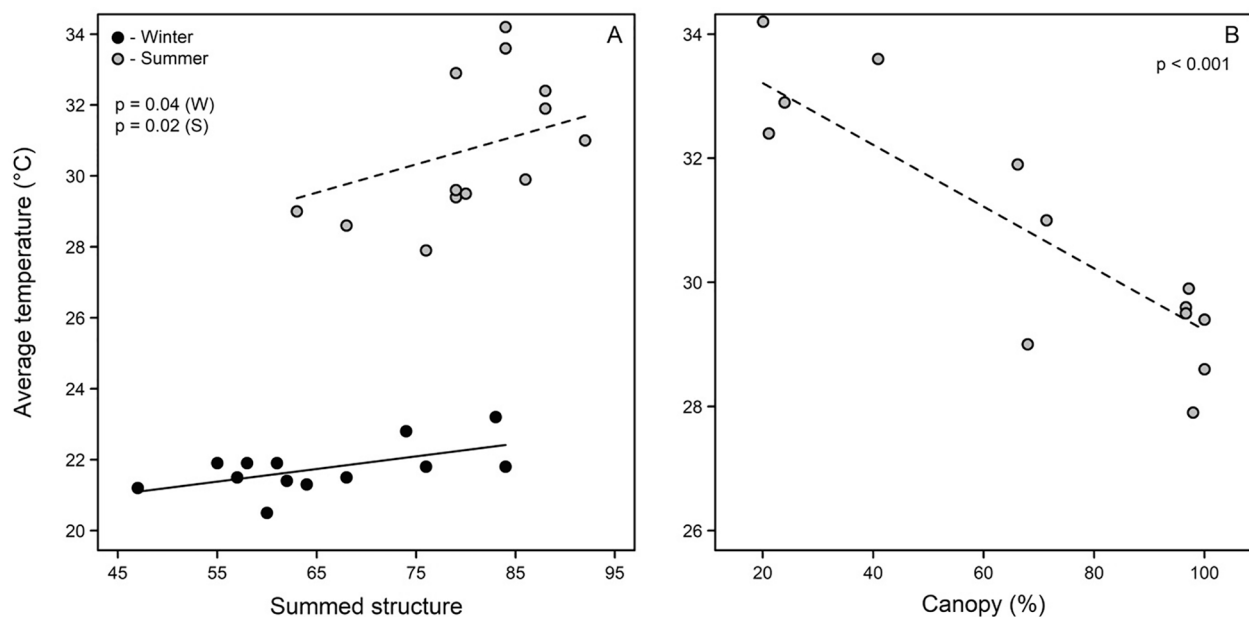


Fig. B2. Maximum proportion of occurrences from winter and spring for the 34 natural enemy taxa identified across 13 sampled gardens. Note commonalities in occurrence across gardens (e.g., 4 taxa occurring in 100% of gardens) and prevalence of parasitoids.

Table C1

Taxa-specific abundance of pests (P) and natural enemies (NE) in winter and summer. Abundance of individuals was summed across all gardens.

Taxa	P/NE	Winter (P1)	Summer (P3)
Coccoidea	P	3346	26
Cecidomyiidae	P	380	24
Thripidae	P	121	77
Aphididae	P	117	33
Cynipidae	P	45	81
Cicadellidae	P	34	51
Chrysomelidae	P	22	0
Curculionidae	P	11	5
Aleyrodidae	P	6	3
Coreidae	P	1	0
Tingidae	P	0	1
Psyllidae	P	0	1
Chalcididae	NE	644	275
Platygastridae	NE	296	115
Dolichopodidae	NE	218	395
Linyphiidae	NE	156	42
Formicidae	NE	152	139
Ceraphronidae	NE	127	174
Coccinellidae	NE	55	1
Braconidae	NE	46	19
Phytoseiidae	NE	36	2
Mymaridae	NE	26	19
Ichneumonidae	NE	17	35
Bethylidae	NE	10	6
Lycosidae	NE	8	1
Salticidae	NE	8	37
Oxyopidae	NE	7	5
Histeridae	NE	7	0
Thomisidae	NE	5	19
Lasiochilidae	NE	2	0
Coenagrionidae	NE	2	2
Syrphidae	NE	1	32
Rhinophoridae	NE	1	0
Empididae	NE	1	0
Tachinidae	NE	1	13
Megaspilidae	NE	1	0
Philodromidae	NE	1	0
Carabidae	NE	1	0
Hemerobiidae	NE	1	0
Chrysopidae	NE	1	2
Cheyletidae	NE	0	1
Clubionidae	NE	0	1
Tetragnathidae	NE	0	13
Anyphaenidae	NE	0	6
Araneidae	NE	0	9
Reduviidae	NE	0	3

community because we found no associated relationships between pests and β diversity. Given that increased natural enemy richness can increase top-down control of pests (Letourneau, Jedlicka, Bothwell, & Moreno, 2009), the positive relationship we detected between natural enemy richness and β diversity in the winter may be of greater practical importance than the negative summer relationship because winter was when pests were most abundant and thus likely in most need of control, but also most susceptible to control due to their life stage. β diversity has emerged as an understudied, yet essential component to urban biodiversity research (Mori, Isbell, & Seidl, 2018) with demonstrated effects on multiple ecosystem services (e.g., Pasari et al., 2013). The associations we found, along with those regarding other ecosystem services, justify the need for further investigation into the effects of β diversity on ecosystem services in urban ecosystems. In addition, because our study was observational, we have yet to determine the mechanisms behind these seasonal relationships, which may be better elucidated through manipulative experiments to isolate top-down and bottom-up drivers as well as simple surveys of predation and parasitism.

Contrary to the documented effects of temperature on urban tree pests (Meineke et al., 2013; Dale & Frank, 2014a; Meineke et al., 2014), we found no evidence of vegetation characteristics affecting arthropod pests or natural enemies via indirect effects on temperature. Although

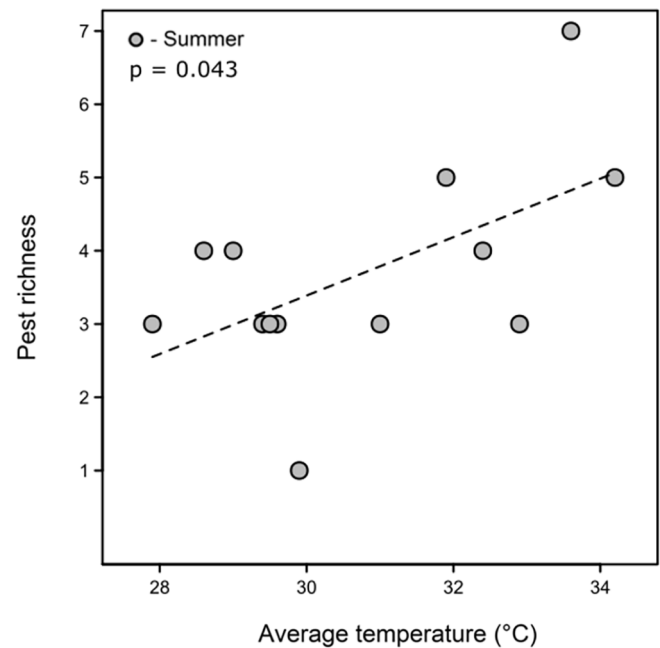


Fig. D1. Relationship between pest richness and average garden temperature (°C). Because we did not detect any evidence of an association between pest richness and the vegetation characteristics that were associated with temperature, we were unable to deduce that temperature affected pest richness by way of vegetation characteristics (Objective 2).

pest richness was associated with temperature, it was not associated with any vegetation characteristics; therefore, we do not have the evidence to support that vegetation characteristics are indirectly affecting pest richness via their effects on temperature. Urban pests and natural enemies can be strongly influenced by temperature effects related to heat from paved surfaces, but our sampled gardens were located in areas separated from major roads and with relatively low impervious surface area compared to these other investigations (Meineke et al., 2013; Dale & Frank, 2014a; Meineke et al., 2014). This low impervious surface cover may be why we did not detect any temperature effects. In addition, we only measured temperature data in a single location in our subplots. Sampling temperature at multiple locations may have been needed to detect temperature effects as doing so would account for variability within the microclimate of each garden, a largely understudied factor that affects arthropods (Woods & Wilson, 2013; Caillon, Suppo, Casas, Woods, & Pincebourde, 2014; Pincebourde, Murdock, Vickers, & Sears, 2016).

5. Conclusions

The associations found in this study suggest that plant communities in urban gardens can be designed to enhance pest resistance, providing an additional strategy for integrated pest management programs. For example, our study suggests that we can enhance pest resistance by planting gardens with less spacing between plants, greater species diversity, and greater spatial variability in plant species composition. Nevertheless, determining the applicability of these recommendations across cities in broader geographies, and identifying mechanisms driving the associations we found via manipulative experiments, can refine recommendations regarding pest-resistant garden design. Further studies should also determine whether scales and mealybugs drive pest abundance on a yearly basis in similar habitats. Given the potential effects of plant origin on pest pressure (e.g., Chun, Van Kleunen, & Dawson, 2010), we encourage studying the effects of plant origin on detected associations. Lastly, future work should consider how the community composition, diversity, and evenness of the entire arthropod

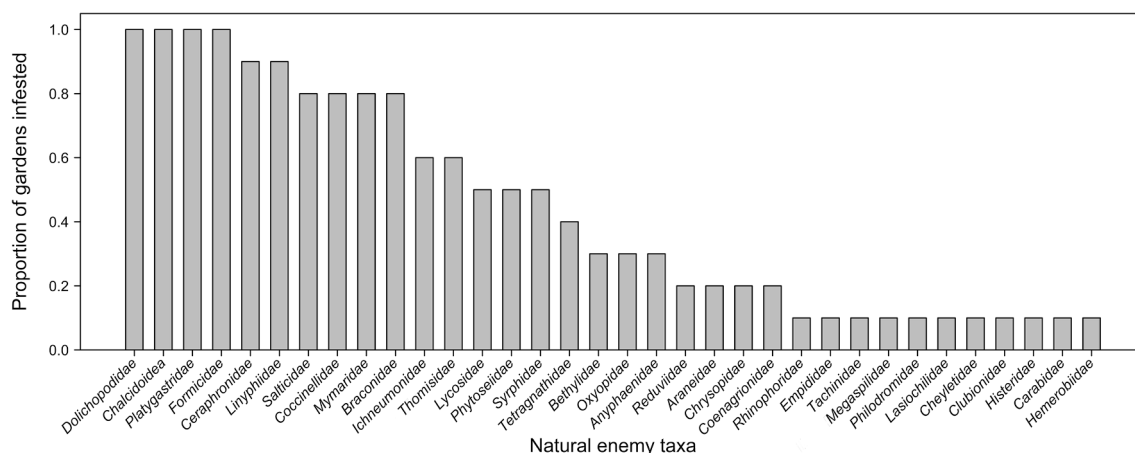


Fig. E1. Relationship between average garden temperature ($^{\circ}\text{C}$) and (A) summed structure (%) and (B) canopy cover (%). There was a positive effect of summed vegetation structure on diurnal average temperature in both winter and summer. There was a negative association between temperature and canopy cover in the summer, but no relationship in the winter.

community responds to variation in vegetation diversity and structure.

Enhancing urban ecosystem services via evidence-based ornamental garden design is reasonable given that plants are the most readily managed biotic component of urban landscapes (e.g., through landscape design and planning) (Kinzig et al., 2005). Nevertheless, strategies that modify vegetation dispersion, volume, or diversity to enhance urban ecosystem services must balance the delivery of these services with aesthetic expectations and social norms of the broader community (Li & Nassauer, 2020). While our study informs how to optimize pest resistance in urban gardens, further research is needed on how to enhance additional services in other designer ecosystems, as well as the underlying mechanisms that drive these services (e.g., Ross et al., 2015; Awasthi et al., 2016; Bergey & Figueroa, 2016), particularly pest resistance. Our findings, coupled with these future investigations, will help ensure that current and future urban and residential landscapes are designed to optimize ecosystem services and ecological functionality.

6. Data statement

Data used for this manuscript will be made publicly available from Institutional Repository at the University of Florida at <https://guides.uflib.ufl.edu/ufir>.

CRediT authorship contribution statement

Gisele P. Nighswander: Conceptualization, Methodology, Investigation, Formal analysis, Writing – original draft, Writing - review & editing. **James S. Sinclair:** Formal analysis, Writing – original draft, Writing - review & editing. **Adam G. Dale:** Conceptualization, Resources, Funding acquisition, Writing - review & editing. **Jiangxiao Qiu:** Conceptualization, Writing - review & editing. **Basil V. Iannone:** Conceptualization, Methodology, Formal analysis, Resources, Writing – original draft, Writing - review & editing, Supervision, Project administration, Funding acquisition.

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Appendix A. List of plant species, their native status, and occurrence in gardens and subplots.

Appendix B. Pest and natural enemy occurrence in gardens.

Appendix C. Taxa-specific seasonal abundance of pests and natural enemies.

Appendix D. Association between pest richness and temperature.

Appendix E. Associations between structural complexity, canopy cover, and temperature.

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