

Examining the effects of plant associations and individual traits on neighboring Arthropod community dynamics

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Abstract

Individual plant traits including plant defenses and host plant nutrition can have an effect on the magnitude of herbivory by insects on a given plant. Additionally, plant traits of surrounding individuals can also affect the magnitude of herbivory by insects on a given plant. This association between plant species (i.e., intermixing of plant traits) can result in reduced or increased herbivory on a target species. These phenomena in general are described as associational effects (hereafter AE). In this study, we were interested in quantifying AE within an empirical system. Our study provided results to help answer two focal questions. First, given that individual plant traits affect the magnitude of herbivory on a given plant species, how do neighborhood variables (e.g., con-specific plant density, hetero-specific plant density, and plant frequency) and individual plant traits affect the abundance of arthropods within a plant neighborhood? Secondly, how well do linear and non-linear models fit data on AE? The study species included two perennial old-field plants: *Solanum carolinense* and *Solidago altissima* (hereafter *Solanum* and *Solidago*). Our experiment used a two-species (*Solanum* and *Solidago*) fan design where plant frequency changes as one rotates around the fan, while the density of plants changes with distance from the center. We conducted a multiple regression analysis to examine how plant neighborhoods affect the abundance of arthropods. Each plant had two descriptors of arthropod abundance: the sum of all individual herbivores and the sum of all individual natural enemies. Our results show that there were no drastic effects between our comparisons. Both individual plant traits and neighborhood variables can significantly affect the arthropod community. Also, non-linear models can best fit data as well as linear models.

Introduction

The majority of plant species within ecosystems are subject to herbivory from insects. Individual plant traits including plant defenses (Feeney, 1976; Fritz & Simms, 1992) and host plant nutrition (Mattson, 1980; Kyto et al., 1996) can have an effect on the magnitude of herbivory by insects on a given plant. Additionally, plant traits of surrounding individuals can also affect the magnitude of herbivory by insects on a given plant (Bach, 1980; Letourneau,

1995). This association between plant species (i.e., intermixing of plant traits) can result in reduced or increased herbivory on a target species. The effects of plant associations that result in reduced herbivory on a target species are defined as associational resistance (Stiling et al., 2003). The effects of plant associations that result in increased herbivory on a target species are defined as associational susceptibility (Letourneau, 1995). These phenomena in general are described as associational effects (hereafter AE) (Tahvanainen and Root, 1972).

The mechanism through which AE between plants arise is not uniform for all communities. In fact, several mechanisms have been proposed to explain AE. The repellent plant hypothesis states that neighbors with low palatability can repel herbivores from plant patches (Tahvanainen & Root, 1972; McNaughton, 1978; Pfister & Hay, 1988). This hypothesis predicts associational susceptibility on a target species. In contrast, the attractant decoy hypothesis states that neighbors with high palatability can attract herbivores away from a target species (Atsatt & O'Dowd, 1976). This hypothesis predicts associational resistance on a target species. Also, certain plant species can emit volatile chemical substances which can prevent phytophagous insects from finding other plant species in association (Stanton, 1983; Hambäck et al., 2000). This hypothesis also predicts associational resistance on a target species. Finally, the natural enemies hypothesis explains how natural enemies are more abundant in communities with high plant diversity (Root, 1973). The majority of natural enemies are generalist predators (Stiling et al., 2003). Because communities with high plant diversity can support large herbivore populations, these generalist enemies can better survive off the richness of herbivores present. As a result, generalist natural enemies often suppress herbivore populations in diverse plant communities where there is sufficient plant association (Stiling et al., 2003).

In this study, we were interested in quantifying AE within an empirical system. Our overarching question was how does the neighborhood around a plant affect the arthropod community? The study species included two perennial old-field plants: *Solanum carolinense* and *Solidago altissima* (hereafter *Solanum* and *Solidago*). Previous studies examining the effects of insect herbivory on competition between *Solanum* and *Solidago* found that herbivores increased the likelihood that *Solidago* excludes *Solanum* (Kim et al. 2013). This study also found significant *non-linear* associational susceptibility for *Solanum* (Kim et al. 2013). These results provide evidence that AE exist in this system and that herbivores influence plant competition. Additionally, this non-linear associational susceptibility for *Solanum* is supported by theory (Hambäck et al. 2014) that suggest non-linear AE should be common for plant-insect systems compared to linear AE which are not what is most expected. Also, this non-linear associational susceptibility for *Solanum* was measured in terms of plant damage. We wanted to examine whether this effect on plant damage was due to an increase in insect abundance. It is plausible

that this increase in plant damage was due to higher rates of herbivory by insects. However, a high abundance of insect individuals may also increase damage on a given plant.

Our study provided results to help answer two focal questions. First, given that individual plant traits affect the magnitude of herbivory on a given plant species, how do neighborhood variables (e.g., con-specific plant density, hetero-specific plant density, and plant frequency) and individual plant traits affect the abundance of arthropods within a plant neighborhood? Secondly, how well do linear and non-linear models fit data on AE? We hypothesized that non-linear models will fit data better compared to linear models. Our rationale was that previous studies (Kim et al. 2013) and theory suggest non-linear AE should be common for plant-insect systems.

Methods

Experiments were conducted at the University of Florida / IFAS North Florida Research and Education Center near Quincy, FL. Plants were started from root cuttings in the Florida State University (FSU) greenhouses in 2-inch pots and transplanted to the field when they had 3-5 true leaves. Prior to experiments, the field was prepared by plowing and disking. After several weeks to allow weeds to germinate, the field was treated with herbicide. When the experiment was planted, all plots were seeded with grass (annual rye, *Lolium multiflorum*) to provide uniform background vegetation. Other species that invaded plots were weeded. We used irrigation only during plant establishment. We counted herbivores on each plant and identified them to the lowest taxonomic level possible. We also measured plant size which was defined as the sum of all stems and branches for a plant. Finally, we grew clonal replicates of *Solanum* and *Solidago* with different genotypes. Therefore, we knew the genotypes of each plant used in this experiment.

Nelder fan designs (Nelder 1962) are planting designs that vary the spacing of plants along 'spokes' which disperse from a central point. We created a similar design using a two-species (*Solanum* and *Solidago*) Nelder fan (e.g. Goelz 2001, Vanclay 2006) where plant frequency changes as one rotates around the fan, while the density of plants changes with distance from the center. Therefore, AE of *Solidago* on *Solanum* can be tested over a range of neighborhood sizes. One replicate of this experiment consisted of a fan with 18 spokes. Each spoke included 15 plants in a straight line. Plant density decreased from the center to the edges of the fan. Each replicate of the fan had 270 plants. Plant frequencies varied from the first to the last spoke in the fan. The first spoke had no *Solanum* and the last spoke had only *Solanum*.

Analysis

We conducted a multiple regression analysis to examine how plant neighborhoods affect the abundance of arthropods. The abundance of arthropods was defined as the number of arthropods observed per plant regardless of plant size. Each plant had two descriptors of arthropod abundance: the sum of all individual herbivores and the sum of all individual natural enemies.

We modeled arthropod abundance as a function of two types of predictor variables. Neighborhood variables included con-specific plant density, hetero-specific plant density, and plant frequency. Plant individual variables included plant genotype and plant size. We defined effects involving neighborhood variables into two groups: effects of con-specific plant density and associational effects (AE), which were defined as effects of hetero-specific plant frequency and/or density on arthropod abundance. In addition, we used model selection statistics (e.g., AIC) to examine how well our data on AE fit linear models compared to non-linear models. All analyses were conducted using the public computing program RStudio (RStudio Team, 2018).

Results

Plant neighborhood variables and individual plant traits both had effects on the arthropod community. We quantified significant effects of con-specific plant density and individual plant traits on *Solanum* arthropod abundance. Specifically, when examining *Solanum* as the host plant, areas of high *Solanum* density had less herbivores on *Solanum* (Estimate = -0.0025354, T = -3.184, p-value = 0.00156, Figure 1). Also, larger *Solanum* plants had an increase in herbivore abundance (Estimate = 0.0220565, T = 5.415, p-value = 1.03e-07, Figure 2). Individual plant traits also had effects on the abundance of natural enemies on *Solanum*. Larger *Solanum* plants had an increase in natural enemy abundance (Estimate = 7.259e-03, T = 11.250, p-value < 2e-16, Figure 3). *Solanum* genotype had no significant effects on arthropod abundance.

When examining *Solidago* as the host plant, plant neighborhood variables and individual plant traits both had effects on the arthropod community. However, *Solidago* genotype also had no significant effects on arthropod abundance. We quantified significant AE and effects of individual plant traits on *Solidago* arthropod abundance. *Solanum* frequency had significant AE on the abundance of herbivores on *Solidago*. Areas of high *Solanum* frequency had less herbivores on *Solidago* (Estimate = -1.575e+00, T = -2.037, p-value = 0.0423, Figure 4). Also,

Solidago plant size had significant effects on the abundance of herbivores on *Solidago*. Larger *Solidago* plants had an increase in herbivore abundance (Estimate = 3.848×10^{-3} , $T = 6.019$, $p\text{-value} = 3.72 \times 10^{-9}$, Figure 5). Individual plant traits also had effects on the abundance of natural enemies on *Solidago*. Larger *Solidago* plants had an increase in natural enemy abundance (Estimate = 0.0015066, $T = 2.615$, $p\text{-value} = 0.00924$, Figure 6).

Non-linear models fit data better compared to linear models when examining effects on the number of herbivores on *Solanum* and *Solidago*. When examining *Solanum* as the host plant, the non-linear model had the lower AIC value (Table 1). However, there were no significant non-linear effects involving neighborhood variables or individual plant traits on *Solanum* herbivore abundance. When examining *Solidago* as the host plant, the non-linear model had the lower AIC value (Table 2). *Solidago* plant size had a significant non-linear effect on *Solidago* herbivore abundance (Estimate = -6.899×10^{-6} , $T = -3.040$, $p\text{-value} = 0.00251$, Figure 7).

Discussion

Plant size had significant effects on the abundance of arthropods for both *Solanum* and *Solidago*. Large *Solanum* and *Solidago* plants had an increase in herbivore abundance compared to smaller plants (Figures 2 & 5). Large *Solanum* and *Solidago* plants also had an increase in natural enemy abundance (Figures 3 & 6). It is logical to infer that the increased herbivore abundance on large *Solanum* and *Solidago* plants may have attracted more of their natural enemies as well. Alternatively, it is plausible that larger *Solanum* and *Solidago* plants may result in increased natural enemy abundance independent from the effects on herbivore abundance. However, we did not examine the effects of plant size on natural enemy abundance in the absence of herbivores and vice versa. It would be interesting for future studies to examine whether the effects of plant size on natural enemy abundance is independent from the effects on herbivore abundance. However, efficiently controlling for these abundances in a natural system may be quite challenging.

It is also worth noting the lack of a genotype effect throughout our results. *Solanum* exhibit a variety of defense traits which have shown to influence the preference, performance, and survival of insect herbivores (Kariyat et al., 2013). These traits can vary among *Solanum* genotypes (Kariyat et al., 2013). Although we did not standardize the genotypes used to their corresponding traits, it is still surprising that genotype had no effect on the abundance of arthropods. Previous studies (McNutt and Underwood, 2016) also found that *Solanum* genotype had significant effects on resistance to herbivores and plant damage. It would be

interesting for future studies to standardize genotypes and their corresponding traits to better understand how genotype may or may not affect the arthropod community.

In addition to individual plant traits, neighborhood variables also had significant effects on the arthropod abundances of both *Solanum* and *Solidago*. We quantified significant effects of con-specific plant density on *Solanum* and significant AE on *Solidago*. Areas of high *Solanum* density had less herbivores on *Solanum* (Figure 1). Areas of high *Solanum* frequency had more herbivores on *Solidago* (Figure 4). In summary, dense patches of *Solanum* where there were also much more *Solanum* than *Solidago* had less herbivores on *Solanum* and more herbivores on *Solidago*. Our results predict that large *Solidago* plants surrounded by many *Solanum* plants those of which are densely distributed will have the most herbivores. This suggests associational susceptibility on *Solidago* exerted by *Solanum*.

Non-linear models fit data better compared to linear models when examining effects on the number of herbivores on *Solanum* and *Solidago* (Table 1 & 2). There were marginal non-linear effects of *Solidago* density (Estimate = -1.568×10^{-6} , $T = -0.448$, $p\text{-value} = 0.6543$) and *Solanum* plant size (Estimate = -1.305×10^{-5} , $T = -0.634$, $p\text{-value} = 0.5264$) on *Solanum* herbivore abundance which were not significant. There was also a significant non-linear effect of *Solidago* plant size (Estimate = -6.899×10^{-6} , $T = -3.040$, $p\text{-value} = 0.0025$) on *Solidago* herbivore abundance (Figure 7). It is logical to infer that these combined marginal non-linear effects on *Solanum* herbivore abundance, although not significant, were strong enough to best fit the data non-linearly rather than linearly. Similarly, the significant non-linear effect on *Solidago* herbivore abundance may have also been strong enough to result in non-linear models which fit the data the best.

Our results show that there were no drastic effects between our comparisons. Both individual plant traits and neighborhood variables can significantly affect the arthropod community. Also, non-linear models can best fit data as well as linear models. Further research should aim to continue to test different traits and neighborhood variables between *Solanum* and *Solidago* to better understand how plants can affect each other and their surrounding communities.

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Figures and Tables

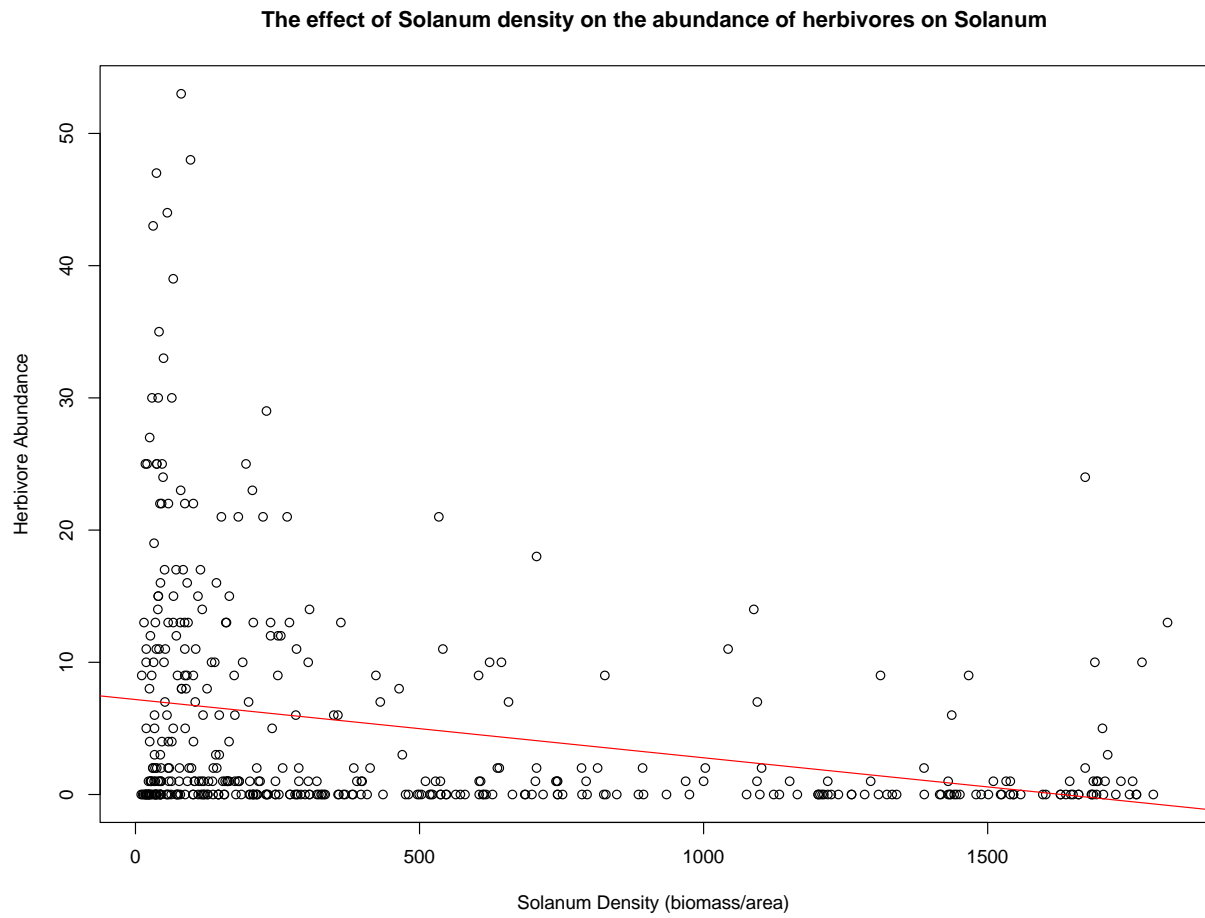


Figure 1: **The effect of *Solanum* density on *Solanum* herbivore abundance.** Estimate = - 0.0025354, T = -3.184, p = 0.00156. N = 434 plant individuals.

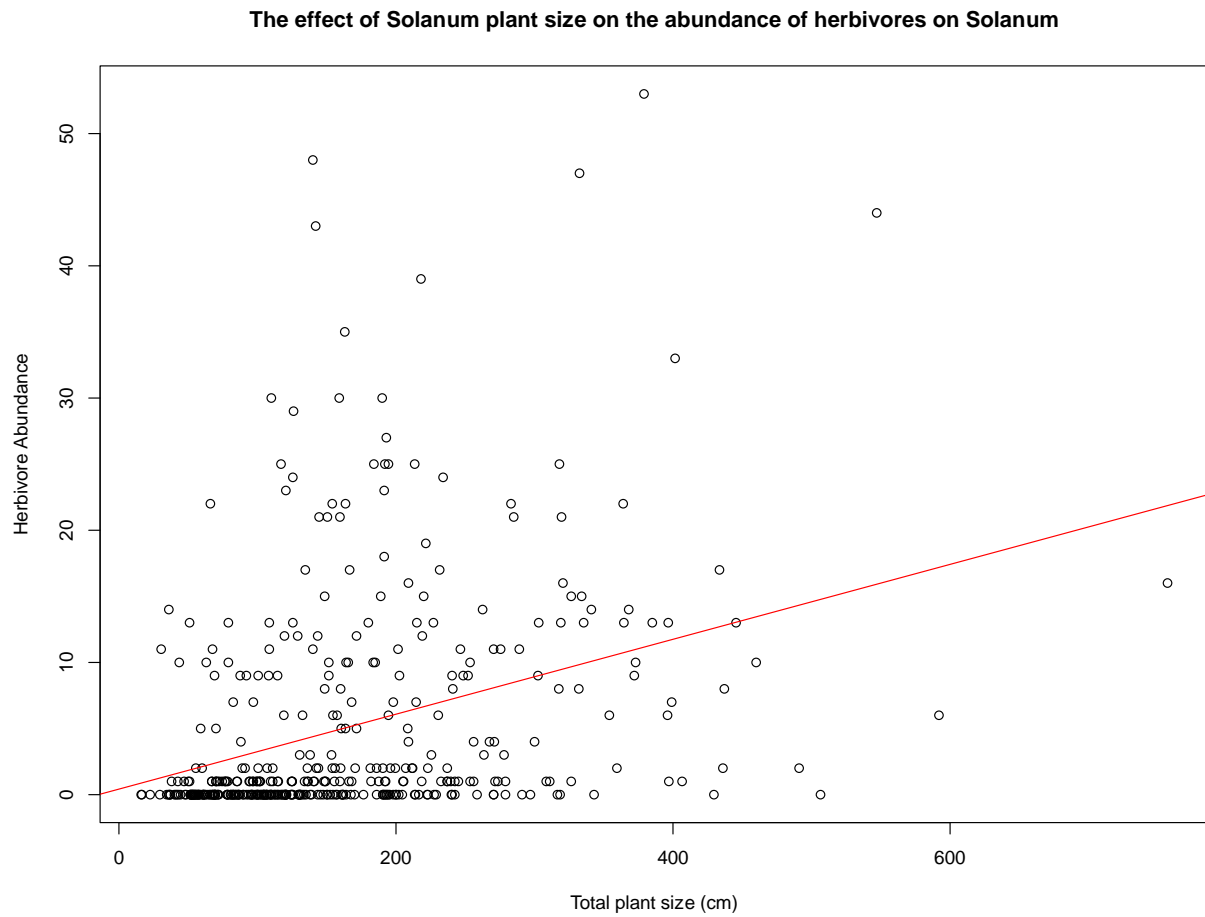


Figure 2: **The effect of *Solanum* plant size on the number of herbivores on *Solanum*.** Estimate = 0.0220565, $T = 5.415$, $p\text{-value} = 1.03\text{e-}07$. $N = 434$ plant individuals. Plant size was defined as the sum of all stems and branches for a plant.

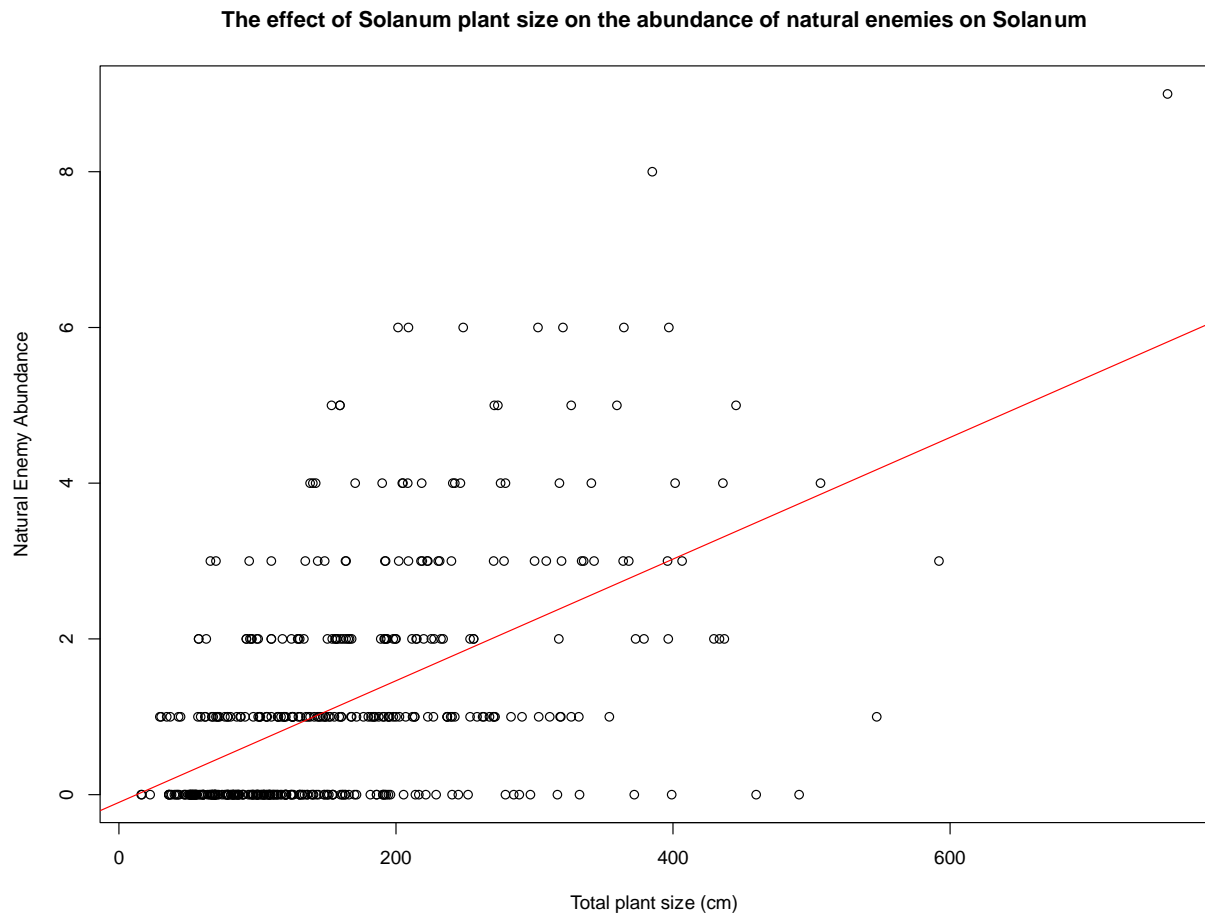


Figure 3: The effect of *Solanum* plant size on the number of natural enemies on *Solanum*. Estimate = 7.259×10^{-3} , $T = 11.250$, $p\text{-value} < 2 \times 10^{-16}$. $N = 434$ plant individuals. Plant size was defined as the sum of all stems and branches for a plant.

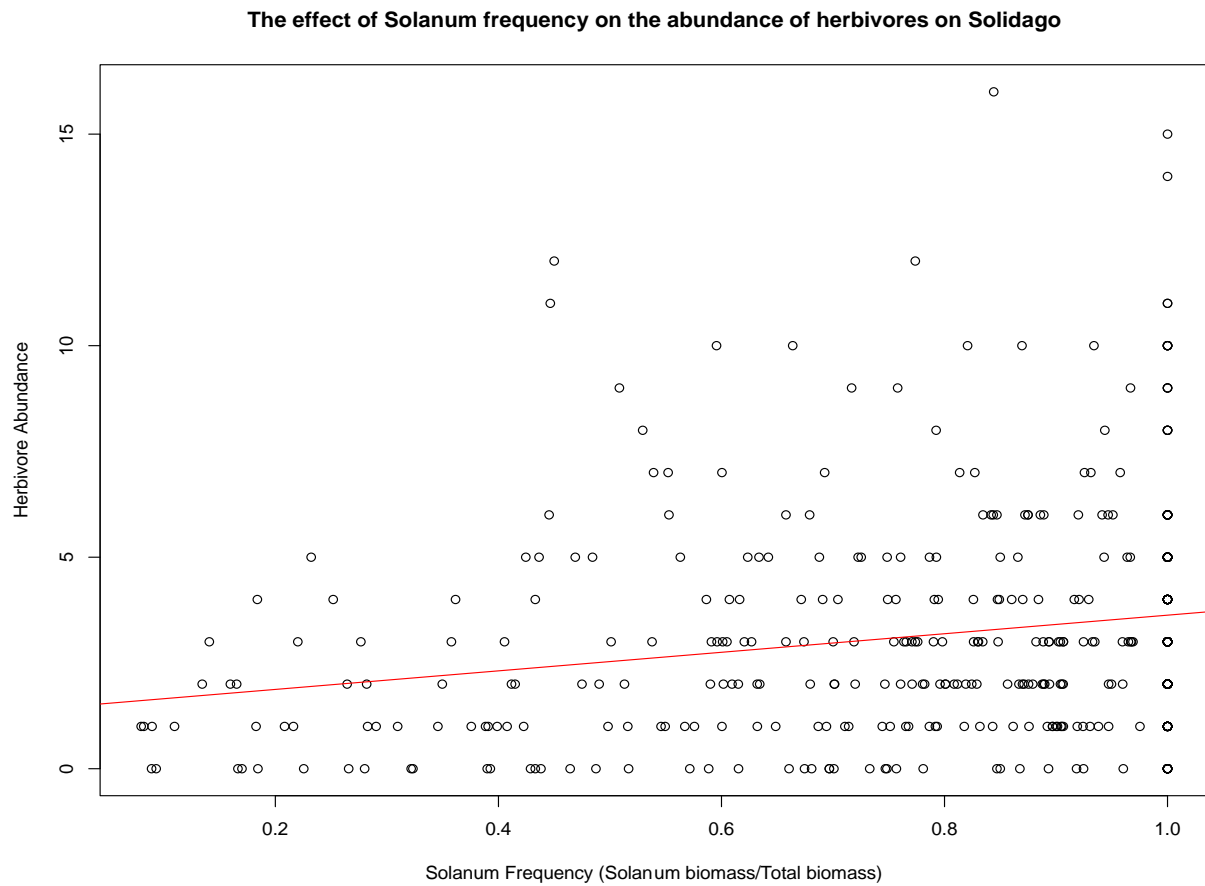


Figure 4: The effect of *Solanum* frequency on the abundance of herbivores on *Solidago*.
 Estimate = 1.575e+00, T = -2.037, p-value = 0.0423. N = 434 plant individuals.

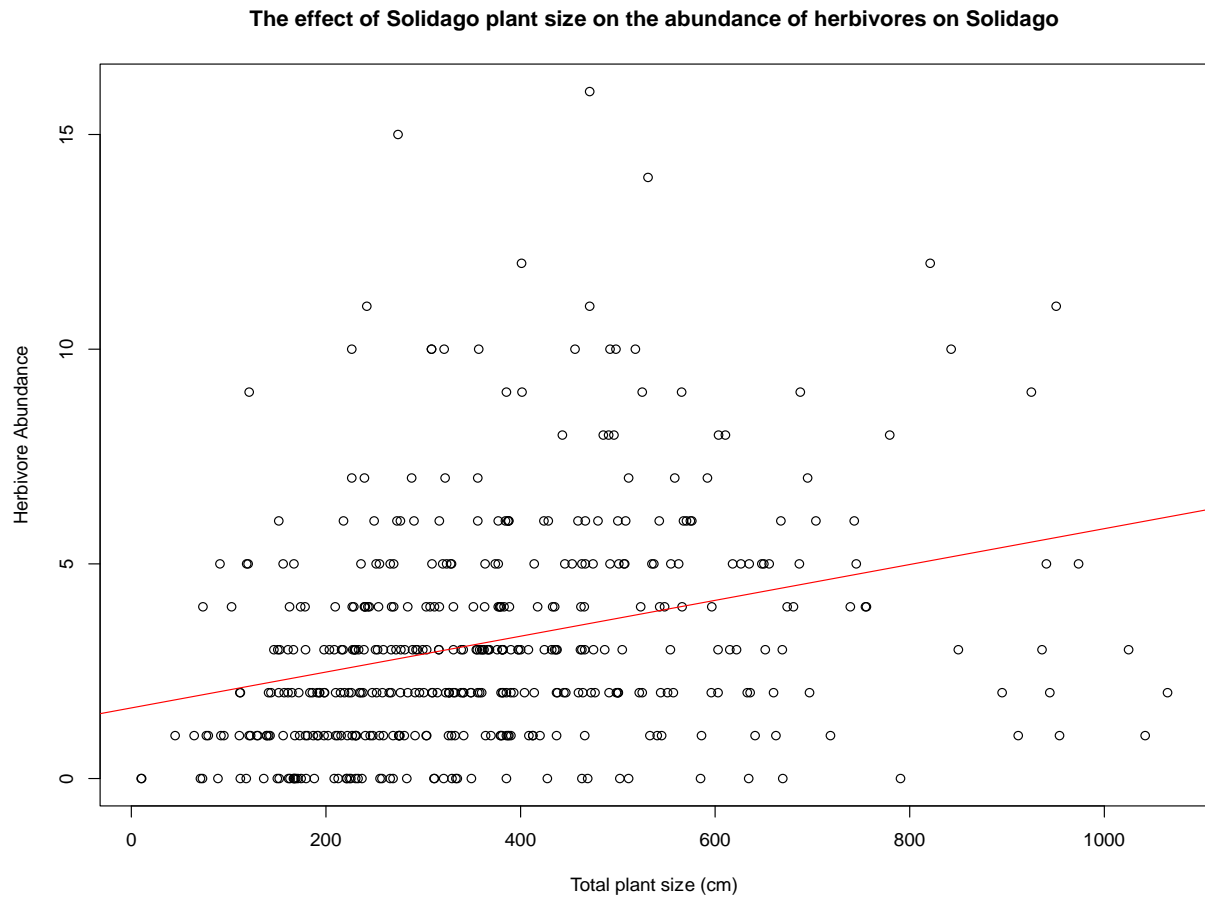


Figure 5: **The effect of *Solidago* plant size on the abundance of herbivores on *Solidago*.** Estimate = 3.848×10^{-3} , $T = 6.019$, $p\text{-value} = 3.72 \times 10^{-9}$. $N = 434$ plant individuals. Plant size was defined as the sum of all stems and branches for a plant.

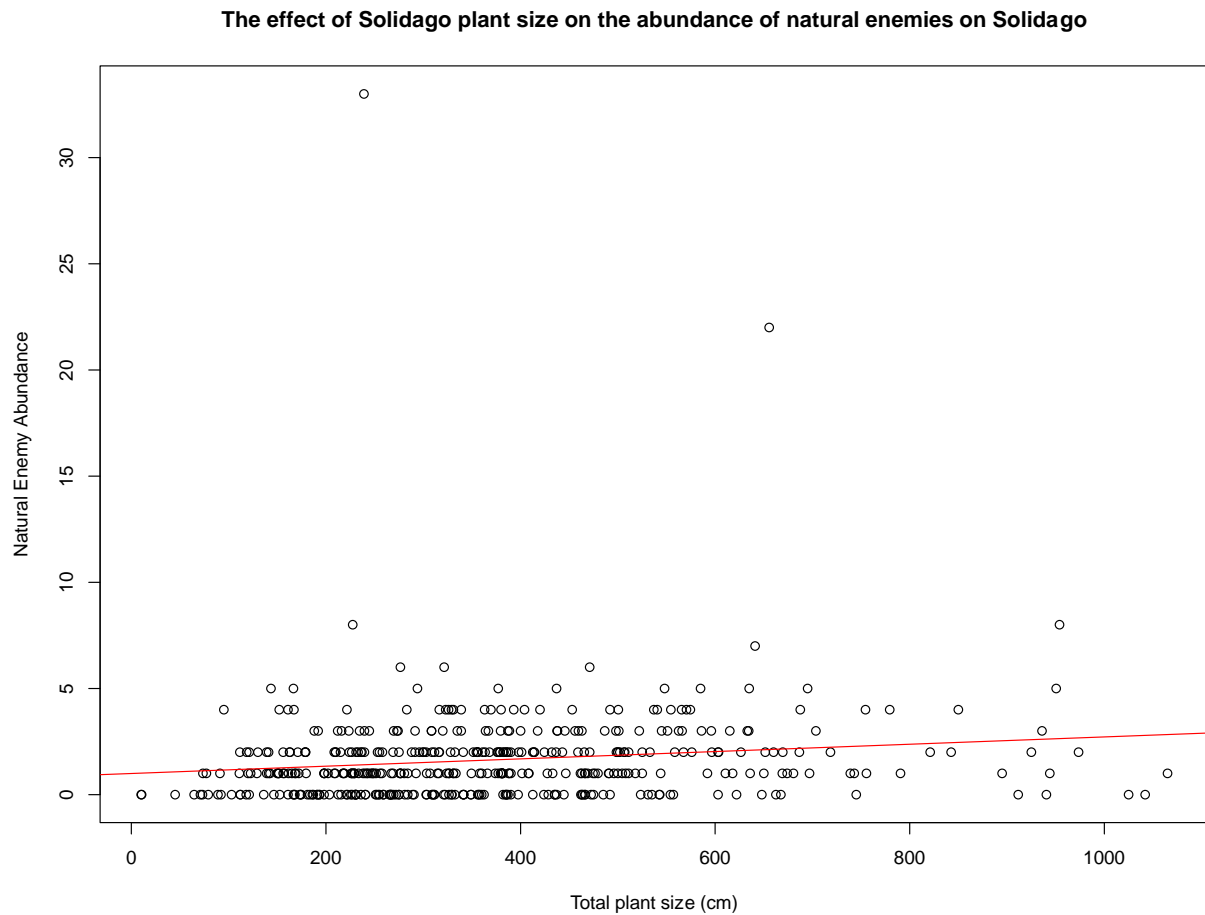


Figure 6: **The effect of *Solidago* plant size on the abundance of natural enemies on *Solidago*.** Estimate = 0.0015066, T = 2.615, p-value = 0.00924. N = 434 plant individuals. Plant size was defined as the sum of all stems and branches for a plant.

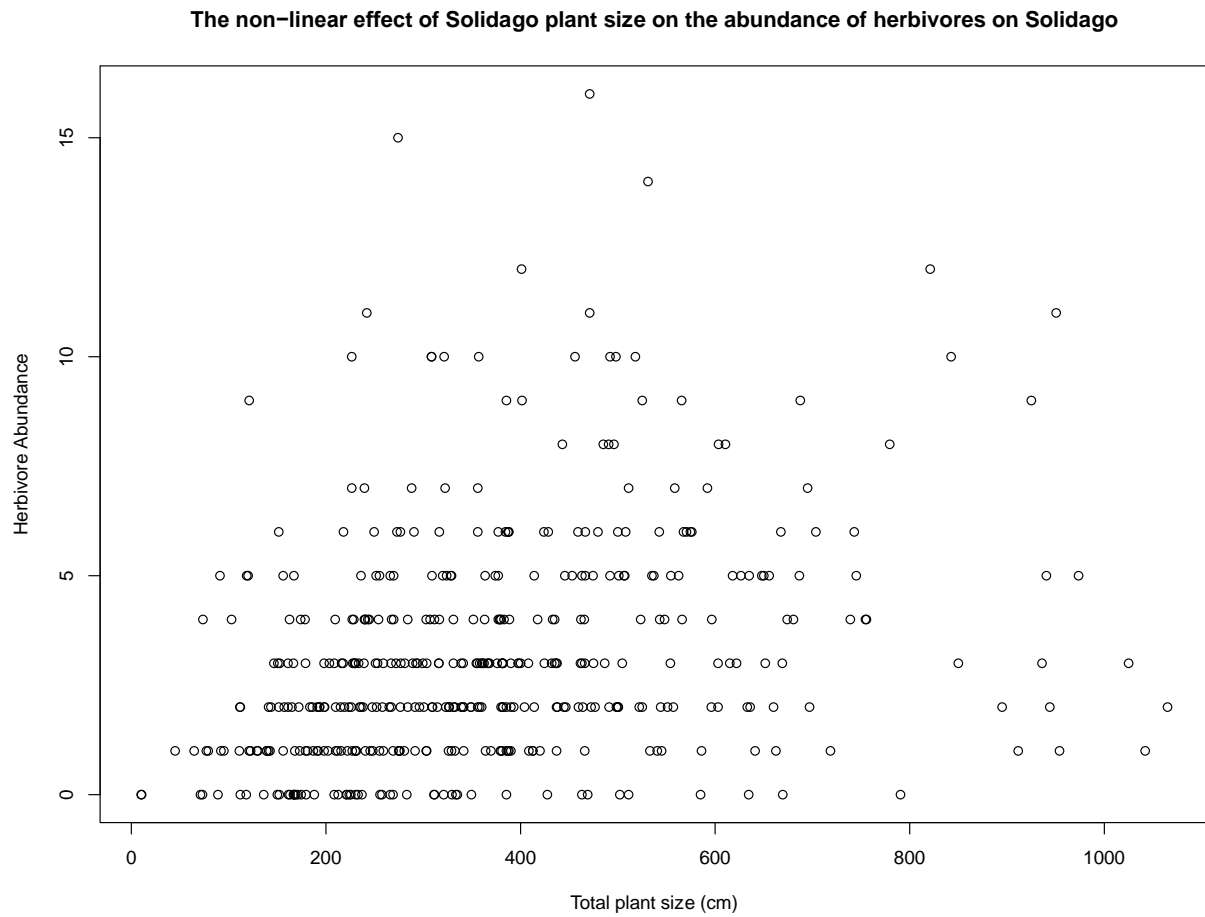


Figure 7: **The non-linear effect of *Solidago* plant size on the abundance of herbivores on *Solidago*.** Estimate = $-6.899\text{e-}06$, $T = -3.040$, $p\text{-value} = 0.00251$. $N = 434$ plant individuals. Plant size was defined as the sum of all stems and branches for a plant.

Model: Neighborhood and individual plant trait variables vs Herbivore abundance on *Solanum*

	df	AIC
Linear	6	2982.257
Non-linear	10	2977.111

Table 1: **AIC values for Linear vs Non-linear models.** This table illustrates the AIC values of linear and non-linear models. Each model tests the effect of *Solidago* frequency, *Solidago* density, *Solanum* density, and *Solanum* plant size on the abundance of herbivores on *Solanum*. Highlight indicates model with lowest AIC value.

Model: Neighborhood and individual plant trait variables vs Herbivore abundance on *Solidago*

	df	AIC
Linear	6	2080.342
Non-linear	10	2077.416

Table 2: **AIC values for Linear vs Non-linear models.** This table illustrates the AIC values of linear and non-linear models. Each model tests the effect of *Solanum* frequency, *Solanum* density, *Solidago* density, and *Solidago* plant size on the abundance of herbivores on *Solidago*. Highlight indicates model with lowest AIC value.