Intra-plant spatial interaction between *Delphastus catalinae* (Coleoptera: Coccinellidae) and *Bemisia tabaci* biotype B (Hemiptera: Aleyrodidae) and its effect on predation rates

Diego F. Rincon^{a,1*}, Luis A. Cañas^a, and Casey W. Hoy^{a,b}

^a Department of Entomology. The Ohio State University, Ohio Agricultural Research and Development Center (OARDC). 1680 Madison Ave Wooster, OH 44691, USA.

^b Agroecosystems Management Program, The Ohio State University, Ohio Agricultural Research and Development Center (OARDC). 1680 Madison Ave Wooster, OH 44691, USA.

¹ Permanent address: Grupo de Manejo Fitosanitario. Corporación Colombiana de Investigación Agropecuaria (Corpoica). Coordinación de Innovación Regional Tibaitatá. Centro de Investigación Tibaitatá, Km 14 vía Bogotá-Mosquera, Cundinamarca, Colombia.

* Corresponding author. Tel: +57 1 422-7300 ext. 1403 Office / ext. 1202 Fax / +57 315-824-3708 Mobile
E-mail addresses: drincon@corpoica.org.co (D.F. Rincon), canas.4@osu.edu (L.A. Canas), hoy.1@osu.edu (C.W. Hoy).

Abstract

Predictive models developed to provide recommendations about release rates and application methods for augmentative biological control often assume a constant probability of encounter between prey and predators within plants. We tested the assumed uniform probability of encounter between the coccinellid predator *Delphastus catalinae* and nymphs of the sweetpotato whitefly (SWF), *Bemisia tabaci* biotype B (Hemiptera: Aleyrodidae), on tomato plants. We hypothesized that *D. catalinae* non-random search patterns would result in a spatially non-uniform intra-plant probability of predator-prey interaction that ultimately affects predation rates. Tomato plants infested with a range of 14-50 SWF adult male-female pairs were placed individually in cages and *D. catalinae* individuals marked with different colors were released on them. The number of SWF nymphs before and after predator release and the predator visit frequency on each leaf and leaflet were recorded. We found that the distribution of predator visits and prey mortality is concentrated towards the mid and mid-lower region of the plant canopy and followed a different within-plant distribution than that of the SWF. The resulting non-uniform probability of prey encounter presumably affected the magnitude of predation rates and the shape of the functional response at the intra-plant scale. Results show that the assumption of uniform probability of encounter among leaves within a plant could be misleading at least for predictive models of the tomato-SWF-*D. catalinae* system, and that spatially explicit or individual-based modeling approaches could improve prediction accuracy.

Keywords: Biological control, Predator-prey models, Functional response, Non-random interactions, Search behavior, Spatial distribution.

1. Introduction

Despite the high consumption rates often measured for predators and parasitoids in laboratory settings, augmentative biological control has been less successful than conventional insecticide treatments (Collier and Van Steenwyk, 2004). One contributing factor seems to be the incorrect selection of release rates and methods, which leads to unsatisfactory pest reduction and decreases predictability of augmentation approach success (Orr and Fox, 2012). Ecological models have been developed to assist the implementation of biological control programs either by increasing understanding of the system or by providing useful predictions for management, including agent selection and/or potential outcomes. However, biological control models applied to specific systems rest upon assumptions that often restrict their application and sometimes compromise their performance (Barlow, 1999).

One common assumption of biological control models is that the probability of encounter between pest and natural enemy is uniform throughout the occupied area (i.e. populations are well-mixed within or among plants). Most models are written as a set of difference or differential equations that could represent insect life stages or entire populations, necessarily assuming random mixing among individuals within a given location (e.g. Hearne et al., 1994; Heinz et al., 1993; Throne et al., 2000; Urano et al., 2003; Yano, 1989). Some predator-prey models, however, account for some degree of spatial heterogeneity in their functional responses. Variation in number of prey in patches that are visited by an average predator typically is defined in terms of a probability distribution function that does not consider the location of predators and prey patches within the plant canopy explicitly (e.g. Hemerik and Yano, 2011; Nachman, 2006). However, non-uniform local predator-prey interactions that can affect population dynamics, ecosystem function, and system stability (e.g. Carter and Dixon, 1982; Costamagna and Landis, 2011; Straub and Snyder, 2008) may

require spatially explicit or individual-based modeling approaches (DeAngelis and Mooij, 2005; Fryxell et al., 2007; Judson, 1994).

Habitat structural complexity is a property of ecosystems that fundamentally influences population dynamics and predator-prey interactions (Denno et al., 2005; McCoy and Bell, 1991). Increased habitat structural complexity tends to result in spatially non-uniform predator-prey encounter probability distributions. First, structural complexity often leads to increased patchiness in the distribution of both prey and predators, which might result in profound differences in predation rates within a given patch and over all patches (Fryxell et al., 2007; Nachman, 2006). Second, habitat structural complexity can affect efficiency of predator foraging in various ways. Efficiency of active predators often decreases as habitat structural complexity increases, because more refuges are available for prey, predator movement may be reduced, and prey detection may become more difficult (Denno et al., 2005; Klecka and Boukal, 2014; Legrand and Barbosa, 2003).

There are at least four spatial scales that are relevant to structural complexity from an insect perspective: landscape (among different habitats), habitat (among plants, within a specific habitat), plant (among different plant parts, within single plants), and patch (within specific plant parts). The relative structural complexity is quantified by the number of different structural elements per unit volume (McCoy and Bell, 1991). How the structural complexity is measured in terms of the diversity of structural elements depends on the spatial scale at which the ecological interactions are being examined (Langellotto and Denno, 2004; Tokeshi and Arakaki, 2012). For instance, within monocultures, the structural complexity at the plant scale is often considered the highest because without diversity in plant species the primary source of variation is the difference in structural elements (plant parts) within plant canopies. The differences in physical and chemical properties among leaves within single

plants are the largest contributors to habitat structural complexity at the intra-plant scale (Langellotto and Denno, 2004; Raupp and Denno, 1983).

The sweetpotato whitefly (SWF), *Bemisia tabaci* (Gennadius) biotype B (= *Bemisia argentifolii*; = group “Middle East-Asia Minor 1”) (De Barro et al., 2011) (Hemiptera: Aleyrodidae), is a significant worldwide pest of a variety of production systems including field and greenhouse tomato (Stansly and Naranjo, 2010). Damage in plants is caused by reduction in plant vigor and production of honeydew, which serves as a substrate for sooty molds. The SWF also vectors many plant pathogenic viruses (Oliveira et al., 2001) and may induce growth and ripening disorders in vegetables (Schuster, 2001). Although adults are good flyers, all immature life stages (nymphs) are sessile except neonates (also known as crawlers), which move from a few millimeters to a few centimeters before settling during the first few minutes after hatching (Byrne and Bellows, 1991; Simmons, 2002). Most eggs are laid on the underside of leaves where nymphs then undergo four sessile instars. These two life stages together represent about 50% of the entire life span (Tsai and Wang, 1996). Not surprisingly, most predators and parasitoids used for SWF biological control specialize on egg and/or nymph consumption (Gerling et al., 2001).

Predacious Coccinellidae are widely used as biological control agents, partly because they often show high consumption rates in laboratory settings. However, their rate of success in controlling pests in the field is highly variable (Obrycki and Kring, 1998). Most Coccinellids are active predators of immature hemipterans, including whiteflies, aphids, mealybugs and scales, all of which exhibit low or no mobility (Hodek and Honek, 2009). The interaction between coccinellid predators and their herbivorous prey can be complicated, however, by differences in intra-plant spatial distributions. On the one hand, insect herbivores are often distributed in a nonrandom manner within the plant canopy, largely because their leaf preference patterns make certain plant regions consistently more likely to be infested

(Cates, 1980; McCornack et al., 2008; Raupp and Denno, 1983). On the other hand, coccinellid predators tend to restrict their intra-plant distribution to certain plant nodes to reduce interspecific competition, often leading to poor correlations between prey and predator distributions (Frazer and McGregor, 1994; Musser and Shelton, 2003). Not surprisingly, prey refuges within plants have been reported frequently for predator-prey systems involving coccinellid predators (e.g. Clark and Messina, 1998; Costamagna and Landis, 2011; Hodek et al., 2012; Reynolds and Cuddington, 2012).

The oligophagous predator *Delphastus catalinae* (Horn) (= *Delphastus pusillus*) (Gordon, 1994) is one of the more than 25 species of coccinellid predators that have been associated with the SWF (Gerling et al., 2001; Hodek et al., 2012). *Delphastus catalinae* is currently the only Coccinellid predator that is commercialized in the USA for SWF control and is considered to be one of the best commercially available predators of *Bemisia* spp. (Obrycki and Kring, 1998). Despite the relatively high predation rates that have been reported for *D. catalinae* in laboratory settings (Hoelmer et al., 1993; Liu and Stansly, 1999), releases in the field have shown variable results (Heinz et al., 1999; Heinz and Parrella, 1994a) and have been effective only when SWF densities are high (Heinz and Parrella, 1994b), a significant drawback considering the ability of SWF to vector plant pathogenic viruses. Understanding the interaction between the SWF and *D. catalinae* within plants will ultimately help fine-tune *D. catalinae* release rates and application methods and, if necessary, assess the development of complementary biological control strategies.

In previous research, we showed that the distribution of SWF immatures within tomato plants can be predicted using per-node infestation probabilities and aggregation patterns (Rincon et al., 2015). In this study, we hypothesized that *D. catalinae* would exhibit non-random search within the tomato plant canopy, resulting in a non-uniform intra-plant predator-prey spatial interaction. Thus, the objectives of this study were: 1) to test the null

hypothesis of uniform encounter rates between *D. catalinae* and SWF nymphs regardless of location within the canopy, and 2) to estimate the effect of a non-uniform interaction among prey and predator individuals, if present, on predation rates at the plant scale. To determine the nature of the spatial interaction between SWF and *D. catalinae* individuals, we examined the intra-plant search and predation pattern of adults of *D. catalinae* and compared them with the distribution of SWF nymphs within tomato plants. To examine the effect of non-uniform predator-prey interactions on predation rates, we compared the functional response of *D. catalinae* preying on SWF nymphs at two intra-plant spatial scales with contrasting levels of habitat structural complexity, namely within leaves and among leaves. We predicted that a type II (saturating) functional response would be observed at the intra-leaflet scale because this functional response is typically the result of uniform predator-prey encounter rates (Holling, 1961; Morozov, 2010; Nachman, 2006). However, we predicted that a non-uniform, heterogeneous spatial interaction at the intra-plant scale resulting from prey patchiness and localized higher predation rates would result in a type III (sigmoid) functional response (Morozov, 2010; Nachman, 2006).

2. Materials and Methods

The study was carried out at The Biological Sciences Greenhouse Facility of The Ohio State University, Columbus, OH (USA). Sweetpotato whitefly individuals were obtained from a colony maintained on potted tomato plants (*Solanum lycopersicum* L. var. Trust) and fertilized at each watering event using Miracle Gro® water soluble tomato plant food at a rate of 250 mg/l of nitrogen (18-18-21). Insects and plants were maintained in greenhouse conditions at 25±2°C and a photoperiod of 14:10 (light: dark). Adult *D. catalinae* individuals were purchased commercially (Rincon-Vitova Insectaries Inc., Ventura, CA, USA).

Forty seven tomato plants (*S. lycopersicum* var. Trust) with 6-12 leaves (7-10 weeks old) were grown in 15 × 14.5 cm (diameter × height) pots and PRO-MIX BX ® soilless media (Premier Tech Ltd., Rivière-du-Loup, Québec, Canada) and placed individually in 130 × 60 × 60 cm (height × width × depth) mesh cages. As typically recommended for greenhouse tomato production systems, plants were grown as single stems by removing all lateral buds as they appeared (Cockshull et al., 2001). To obtain an adequate range of whitefly nymph densities, according to the expected range of SWF adults per plant found at initial phases of infestation (Setiawati, 2009), 35 of the plants were infested with five different numbers of 3-day-old adult male-female pairs, which were assigned to the plants randomly as follows: 6 plants with 14 pairs, 4 with 20, 9 with 30, 11 with 40 and 5 with 50. The remaining 12 plants were left uninfested. The distribution of replications among levels of whitefly densities was chosen so that most observations would fall in the low region of the range, which should facilitate the distinction between predator functional response types (Juliano, 2001). The infested and uninfested cages with plants were kept in a greenhouse room at 25 ± 2°C and a photoperiod of 14:10 (light: dark).

After 48 h, the SWF adults were removed from the infested plants and the youngest fully formed, but not fully expanded, leaf of each plant was marked with a permanent marker to quickly identify the point in the plant below which leaves were infested with SWF. The plants were then kept in cages in the same greenhouse room for 12 days to let eggs develop into 2nd and 3rd instars. Leaves were numbered from the oldest to the youngest (bottom to top), and leaflets from the terminal to the most basal, as described by Rincon et al. (2015). The number of nymphs in each leaf and leaflet was counted using a 10X hand lens. The main stem of infested plants was cut right above the marked leaf to remove all the leaves that appeared after the initial infestation.

The next day, ten *D. catalinae* adult individuals that had been held without access to prey for approx. 30h were released in each plant cage onto the cage walls allowing the predators to arrive on the plant by their own means, usually by flight. Each predator was marked with a dot of ink of a different color extracted from TexPen ® markers (ITW Dykem, Olathe, KS, USA) previously diluted at 5:1 (paint : thinner) with turpentine substitute, following the procedure described in Bates and Sadler (2004). A small ink dot was applied to one of the elytra of each beetle using a No. 0 paint brush, without painting the elytral suture to make sure the beetle's ability to expand its wings and fly normally was not impaired. During the marking process beetles were not slowed down with CO₂ or by cooling. The ink used has been shown to produce durable marks (Wineriter and Walker, 1984) and to have no effect on longevity of adult beetles, at least when applied to elytra (Bates and Sadler, 2004). The sex ratio of predators varied randomly among cages, averaging 3.63:6.36 (SE = 0.13) (male : female), and did not attempt to distinguish between the sexes in predation rates or movement patterns. For the next 4 days, plants were observed at 2h intervals during photophase (9am to 6pm) to record the number and identification of individual predators that visited each leaf and leaflet. On the 4th day after predators were released, all the leaves and leaflets of each plant were cut to re-count the number of SWF nymphs on the underside of each leaflet using a dissecting stereomicroscope. We decided on this observation time period because it was sufficient for most of the predators to have either died or reached a plant and found prey, considering that less than 10% of *D. catalinae* adults survive without food after 4 days (Simmons et al., 2012). Also, a longer observation time would have complicated the distinction between SWF nymphs consumed by predators and those that completed their nymphal stage. The number of prey consumed by *D. catalinae* individuals was estimated as the difference between the number of SWF nymphs before and after the 4-day *D. catalinae*-SWF interaction period.

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195 **2.1. Data analysis**

196 The increase as a function of SWF nymph density in the proportions of leaves that
197 were infested with SWF nymphs and visited by *D. catalinae* were compared by fitting
198 modified monomolecular models (Madden et al., 2007), where the intercept is assumed to be
199 zero. Thus, the proportion of leaves either infested by SWF nymphs or visited by *D. catalinae*
200 is given by:

$$201 \quad y_{max} - \exp(r_m w)$$

202 (Eq. 1)

203 where r_m is an estimated rate parameter (1/SWF/plant), y_{max} represents the estimated
204 maximum proportion of leaves either infested by SWF nymphs or visited by *D. catalinae*
205 within tomato plants, and w is the observed SWF population density per plant. We chose this
206 model because it requires few parameters and allows comparison of maximum proportion of
207 leaves infested by SWF nymphs and visited by *D. catalinae* individuals as a function of SWF
208 nymph density. Equation 1 was also used to determine the maximum proportion of released
209 beetles that arrived on the plants as a function of SWF nymph density.

210 The recorded leaf nodal positions within each plant were standardized by dividing
211 them by the total number of nodes on the plant. The distribution of SWF nymphs along the
212 plant axis was compared with the distribution of proportions of both SWF nymphs consumed
213 and *D. catalinae* individuals that visited each plant. The comparison between distributions
214 was performed using the modified t test for the association between two spatial processes
215 (Clifford et al., 1989), with the standardized nodal positions as spatial coordinates. The intra-
216 plant distributions of SWF nymphs before predators were released, number of predators that
217 visited the plants, and proportion of SWF nymphs consumed were modeled across the
218 standardized nodal positions using polynomial logistic models. Parameter estimation was

performed with iteratively reweighted least squares using a logit link function (Venables et al., 2002). To determine if the number of SWF nymphs per leaf was a better predictor of the proportion of *D. catalinae* individuals per leaf than leaf nodal position, we compared the fit of logistic models using the Akaike Information Criterion (AIC), defined as:

$$AIC = -2L + 2k$$

(Eq. 2)

where L is the log-likelihood and k is the number of parameters of the model. Small AIC values represent better fit to data, such that adding a parameter with a negligible improvement in fit, penalizes the AIC by 2 log-likelihood units. By convention, models with AICs more than 10 apart ($= \Delta AIC$) are definitely different (Bolker, 2008).

To determine the potential effect of a non-uniform spatial interaction between *D. catalinae* and the SWF on predation rates, the functional response of *D. catalinae* preying on SWF nymphs was estimated at two spatial scales with contrasting degrees of structural complexity: within plants and within leaflets. To distinguish between type II and type III responses, the fit of both models to data was compared using the Likelihood Ratio Test (LRT) (Okuyama, 2013). The “random predation equation” (Rogers, 1972) was used to describe the functional responses, because it allows for prey depletion during the course of the experiment. Rogers’s type II response describing the number of prey eaten, N_e , by a given number of predators, D , is given by:

$$N_e = N(1 - \exp(a(T_h N_e - TD)))$$

(Eq. 3)

where T , the total time of the interaction between predators and prey, was set to one; N is prey density; a is a constant known as “attack rate” expressed in terms of area searched during time T ; and T_h is the handling time, or the time spent handling one prey by single predators,

expressed in terms of fraction of T . The main difference between type II and type III responses is that a is constant in the first but is a function of N in the second, which yields:

$$N_e = N(1 - \exp(-(bN + c)(T_h N_e - TD)))$$

(Eq. 4)

where b and c are the slope and the intercept, respectively, of a linear model describing attack rate (i.e. a) as a function of SWF density. Among the several mathematical forms that have been used to describe the relationship between attack rate and N (Juliano, 2001), we chose a linear function because it allowed us to compare type II and type III models as the first nested into the second, i.e., Eq. 4 becomes Eq. 3 if $b = 0$.

To express consumption on a per predator basis, we divided the number of SWF nymphs consumed at plant and leaflet scales by the number of individuals of *D. catalinae* that visited the respective plant or leaflet. Parameters of the monomolecular and functional response models were estimated by Maximum Likelihood. The Lambert W function was used to compute a closed-form solution of Rogers's equations for predation rates (Bolker, 2008). All analyses were conducted using R software version 3.1.1 (R Core Team, 2013). The R package "SpatialPack" was used for the spatial association analyses (Osorio and Vallejos, 2014) and "emdbook" for parameter estimation of functional response equations (Bolker, 2013).

3. Results

The proportion of leaves infested with SWF nymphs increased at a rate of 0.008 ± 0.002 (95% CI, $n = 35$) per SWF nymph, whereas the proportion of leaves visited by *D. catalinae* increased by 0.013 ± 0.005 (95% CI, $n = 47$) per SWF nymph. Although the two rates are not significantly different ($Z = 1.369$, $P = 0.170$), the maximum proportion of leaves infested with SWF nymphs was significantly higher than the maximum proportion of leaves

visited by *D. catalinae* ($Z = 5.831$, $P < 0.001$) (Figure 1a). On average, the maximum proportion of leaves infested by SWF nymphs was 0.900 ± 0.062 (95% CI, $n = 35$), whereas the maximum proportion of leaves visited by *D. catalinae* individuals was 0.601 ± 0.072 (95% CI, $n = 47$). The proportion of predators that arrived on the plant increased by 0.008 ± 0.002 (95% CI, $n = 35$) per SWF nymph and reached a maximum proportion of 0.851 ± 0.064 (95% CI, $n = 35$) (Figure 1b). Thus, the proportion of predators observed on plants increased as a function of SWF density, at a rate similar to the increase in the proportion of infested leaves. However, predators only visited a maximum of 60% of the leaves of a given plant, even though more than 80% of them reached the most infested plants, indicating that predators visited a relatively small portion of the plant.

We found that the intra-plant spatial distribution of SWF nymphs was significantly different from the distribution of mortality rates due to predation (modified t test: $F = 5.094$, $n = 322$, $P = 0.025$). We also found that the intra-plant distribution of SWF nymphs was significantly different from that of *D. catalinae* individuals (modified t test: $F = 38.150$, $n = 322$, $P < 0.001$). Interestingly, we observed that the intra-plant distribution of *D. catalinae* individuals and SWF mortality rates due to predation was also significantly different (modified t test: $F = 38.366$, $n = 322$, $P < 0.001$).

A closer look at the differences between SWF and *D. catalinae* distributions revealed that predators consistently concentrated their search in lower nodal positions regardless of the location of SWF nymphs. We found that the leaf nodal position is a better predictor (AIC = 1080.50, $k = 4$) than the number of SWF nymphs per leaf (AIC = 1140.15, $k = 2$) for the proportion of *D. catalinae* individuals per leaf, as revealed by the difference in fit between the polynomial logistic and the logistic model ($\Delta\text{AIC} = 59.7$). Sweetpotato whitefly nymphs were found more frequently in the middle to upper section of the tomato plant canopy (Figure 2a), whereas greater proportions of SWF mortality by *D. catalinae* predation and *D. catalinae*

individuals were observed towards the mid-low and middle section of the plant canopy, respectively (Figures 2b and 2c), with corresponding differences in the coefficients of the polynomial logistic models that used the standardized nodal positions as predictor (Table 1). The proportion of nymphs eaten and the number of nymphs and predators are all low in the lowest part of the tomato plant canopy, as can be interpreted from the low intercept estimates. The linear coefficient describes the rate of increase in each variable from the lowest to the highest part of the plant, being lowest for the distribution of SWF nymphs and highest for the distribution of predators. The quadratic coefficient, which was negative for all three distributions, describes how fast the curve descends or how “bumpy” the distribution peak is. The closer the estimate is to zero, the flatter the distribution peak. This coefficient is highest for the SWF distribution and lowest for the predator distribution. Our interpretation is that, although SWF nymphs are clustered towards the mid-high part of the plant canopy, they are more evenly distributed among nodal positions than the predators. The cubic coefficient, in this case, describes the rate at which the variable increases after the mid peak. The cubic coefficient is not significantly different from zero for the SWF distribution ($Z = 1.710$, $P = 0.087$), but it is significantly greater than zero for the distribution of both predators ($Z = -9.242$, $P < 0.001$) and proportions of SWF eaten ($Z = -13.300$, $P < 0.001$) (Table 1). This describes the difference in location of the distribution peak of SWF nymphs, of predators, and of proportions of SWF nymphs eaten.

We found that a type II functional response provided a better fit than the type III model for the number of SWF consumed per predator within leaflets (LRT: $X^2 = 4.618$, $P = 0.032$). However, the ‘handling time’ parameter found for predators foraging within leaflets was not significantly different from 0 (Table 2), which may indicate that the functional response at this spatial scale is in fact linear (type I). Type I functional responses are typically found in predators that consume a constant proportion of prey across prey densities (Figures

3a and b). As this type of functional response is unlikely to describe predation by active predators, such as *D. catalinae*, and mostly restricted to filter feeders, or passive (i.e. sit-and-wait) predators (Juliano, 2001), we suspect that the high variability in the observed number of prey killed and the relatively small range of SWF nymph numbers per leaflet to which predators were exposed prevented us from accurately estimating an asymptote for the type II model.

In contrast, the type III model provided a better description than the type II model for the number of SWF nymphs consumed per predator within plants (LRT: $X^2 = 18.236$, $P < 0.001$) (Table 2). In this case, the best fit model was the typical sigmoidal curve describing the number of prey consumed and the corresponding non-monotonic model describing the proportion eaten as a function of prey density (Juliano, 2001) (Figure 3c and d).

4. Discussion

To our knowledge, this is one of the first studies to examine the variation in functional responses of predators to prey based on spatial interactions that may vary because of the architectural structure of a plant canopy. Many predator-prey models assume a uniform spatial interaction among prey and predator individuals at this spatial scale. Here, we present evidence that contradicts this assumption. First, we found that the proportion of leaves visited by *D. catalinae* individuals increased as a function of SWF density per plant as fast as the proportion of leaves infested with SWF nymphs. However, *D. catalinae* adults only visited a maximum of 60% of the plant canopy on average, which is considerably lower than the maximum average proportion of leaves infested by SWF nymphs (over 90%). This relatively low proportion of the plant searched by *D. catalinae* is surprising, considering that predators visited plants more frequently as SWF density increased, suggesting an aggregative response of *D. catalinae* to SWF nymphs at the plant scale. Second, we found that the spatial

distributions of predators and SWF nymphs among leaf nodes were significantly different, and that the number of SWF nymphs is a poor predictor, when compared with the nodal position, of predator distribution within plants. Moreover, the lack of alignment between predator and prey distributions was reflected in a different distribution of SWF mortality among leaves than the distribution of either nymphs or predators. Third, we found that a non-uniform predator-prey encounter rate and the interaction between patchy prey distributions and predator search behavior might cause a significant reduction in predation rates within plants, and a shift in the type of functional response, compared with that expected for well-mixed populations.

The non-uniform intra-plant search pattern exhibited by *D. catalinae* adults implies that SWF patches in the top and bottom parts of plant canopies are less likely to be encountered by *D. catalinae* individuals, regardless of the availability of prey. However, this pattern does not fit in the ecological definition of refuge, since the lower predation risk in the top and bottom parts of tomato plants canopies is not the result of locations that are inaccessible to predators. Furthermore, because immature stages of SWF are all sessile, behavioral avoidance of predators or active seeking of intra-plant locations to reduce predation risk would only be possible for SWF adults. In this experiment, SWF adults were allowed to mate and oviposit freely for 48 h in absence of predators. The distribution of SWF adults is mostly driven by feeding and reproductive patterns, at least in absence of predators or parasitoids, and determines that of their immature offspring (Bentz et al., 1995; Rincon et al., 2015). In our experiments, the non-uniform predation pattern resulted from the search behavior of *D. catalinae* rather than from responses of SWF individuals to the presence of predators.

Although the examination of adaptive responses of SWF individuals to predation was not part of this study, SWF choice of intra-plant locations may have been selected over time

to reduce predation risk from predators such as *D. catalinae*. The intra-plant SWF distribution we found in this research is comparable to previous descriptions of SWF distribution within tomato plants in absence of natural enemies (Arno et al., 2006; Muniz et al., 2002; Rincon et al., 2015; Schuster, 1998). However, SWF adults tend to move upward within the canopy of cucumber plants when *D. catalinae* adults are present, apparently to reduce the predation risk of their progeny, since predators seem to remain in lower plant strata (Lee et al., 2014). Releases of *D. catalinae* are commonly performed as part of augmentative biological control programs, mostly in controlled environments when SWF infestations are high, or at least when the SWF is already present. Thus, it is unlikely that *D. catalinae* individuals released under augmentative regimes are exposed to intra-plant SWF distributions that were affected by predators. However, movement of SWF individuals into upper plant strata may result in significant population-level effects if SWF females are forced to lay their eggs in leaves that reduce survival, fecundity rates, or both. Zhang and Wan (2012) found that mortality of SWF nymphs is significantly greater and that females produce fewer eggs when they feed on tomato leaves that are less than two weeks old. The extent to which reductions in survival and fecundity of this kind are translated into SWF population-level effects is poorly understood, but it has been shown to be significant in other predator-prey systems involving Coccinellids (Costamagna et al., 2013). Understanding the relative contribution of consumptive and non-consumptive predation effects on SWF populations may lead to the development of better predator release protocols and complementary control strategies. Moreover, predator-prey models intended to simulate *D. catalinae*-SWF systems should incorporate spatial non-uniformity in consumption rates, survival, and fecundity at the intra-plant scale.

Structural complexity often interacts with arena size to negatively affect predation rates mainly because of the increase in number of prey refuges (Clark and Messina, 1998;

Costamagna and Landis, 2011; Reynolds and Cuddington, 2012). Although we observed a non-uniform predation pattern of *D. catalinae* on SWF nymphs within tomato plants, we do not have evidence of plant structures that allow prey to hide or become inaccessible to predators. An alternative mechanism is provided by Kaiser (1983) and Bergstrom and Englund (2002), who showed that predation rate might decrease with increased structural complexity by a dilution effect when predators and prey show preference for similar physical structures, such as leaves within plants. Predator-prey encounters are then more likely in simple arenas (such as single leaves or plants with few leaves) where preferred structures tend to be densely populated, than in more complex ones (such as plants with many leaves) that are richer in those structures. Structural complexity may also directly affect a predator's ability to capture and subdue prey. This effect can be particularly significant for active predators, such as *D. catalinae*, because structural complexity may obstruct predator movement, which favors prey escape, increase predator searching time, or both (Hauzy et al., 2010; Klecka and Boukal, 2014; Legrand and Barbosa, 2003). Although a dilution effect, obstruction of predator movement or both may affect *D. catalinae* predation rates within tomato plants, we showed that a reduction of SWF mortality in the top and bottom of the plant canopy may explain, at least partially, the disagreement between the rates found at the intra-leaflet scale, where predator and prey mixing is relatively uniform, and the intra-plant scale.

In this research we assumed that predation risk of SWF nymphs is uniform at the intra-leaflet scale. However, Keiser et al. (2013) showed that aphids located closer to the petiole, often the first place visited by Coccinellid predators once on the leaf, were at higher predation risk than their clone mates located along the leaf edges or veins. Apparently, aphids feeding on high-risk leaf regions help inform others about predator position and reduce the overall impact of predation. This pattern was not observed by Keiser et al. (2013) with flying parasitoids, which seemed to attack aphids regardless of their location within leaves. The type

II functional response of *D. catalinae* preying on SWF nymphs that we found at the intra-leaflet scale supports the assumption of uniform encounter probability between predators and prey at that spatial scale. Moreover, the petiole is not consistently the first leaflet region visited by *D. catalinae* individuals, because they often arrive on leaflets by flying or hopping (D. F. Rincon, *per. obs.*), similar to parasitoids and different from aphidophagous Coccinellids that search plants by walking (Hodek et al., 2012).

We found that the type of functional response of a predator is scale-dependent, likely as a result of changes in structural complexity, patchy prey distributions and non-random predator search patterns (Denno et al., 2005; Fryxell et al., 2007). This result supports our prediction that a non-uniform, heterogeneous spatial interaction between *D. catalinae* and the SWF at the intra-plant scale will result in a type III functional response (Figure 3c and d). Although we can only speculate on a causal relationship between increased structural complexity and a type III functional response, given our data, traditional explanations such as learning, refuges for prey, or prey switching, are unlikely under the conditions of our experiment. Moreover, we observed a type I response of *D. catalinae* within leaflets, although we suspect that a type II response should be observed if a wider range of prey densities per leaflet is evaluated or by controlling variability due to, for example, leaflet size or time predators spend within leaflets. Regardless of whether functional response at this spatial scale is type I or II, we found in our study that the variation in proportion of prey eaten by predators in homogenous, small-scale (local) environments is independent of prey density (i.e. density-independent).

Morozov (2010) observed that zooplankton feeding on algae exhibited a type III functional response in water columns when local functional responses were non-sigmoid (i.e., type I or II), due to the interplay between heterogeneous algae distribution and the active zooplankton foraging behavior. The exponential growth in predation rate, typical of type III

responses, resulted from a pronounced vertical algae gradient in the water column with algae density (due to self-shading), followed by a strong aggregative response of zooplankton to increasing algal prey gradients. This does not seem to be the case for the SWF-*D. catalinae* system. First, we cannot think of a mechanism that may increase intra-plant SWF nymph aggregation with SWF density, as algae do in water columns. In fact, Rincon et al. (2015) described and validated an algorithm to generate SWF distributions over a wide range of densities within tomato plants using a constant aggregation parameter. Moreover, our results showed a relatively weak aggregative response of *D. catalinae* to SWF nymph patchiness, because intra-plant predator distribution was better described by leaf nodal position than by SWF density within leaflets.

Scale-dependent shifts in functional response shapes have been explained by the presence of prey refuges at certain spatial scales. Messina and Hanks (1998) found that the host plant may alter the shape of the functional response of an aphidophagous coccinellid predator. They found that a type II response in small-scale lab experiments translated to a type III response when predators were released in single plants that apparently provide refuges for a given number of aphids. Although we found that SWF nymphs located at the top or bottom of tomato plants have lower predation risk than individuals located in the middle third of the plant canopy, nymphs in these parts of the canopy are still susceptible to being attacked. Moreover, refuges will only produce type III functional responses if they provide protection to a constant number of prey, rather than to a proportion of the prey population (Berryman et al., 2006). In the case of a non-uniform predation pattern, as we describe here for the SWF-*D. catalinae* system, the reduction in predation rate in certain plant regions is more likely to be proportional than numeric, at least for typical SWF densities.

We propose the following generic mechanism for emergence of a type III response within plant canopies with non-uniform predation patterns and patchy prey distributions.

468 When the SWF density is low, the patchy distribution along with the localized search pattern
469 of *D. catalinae* causes a very low predation rate. As SWF density increases, the probability of
470 encounter increases, which makes *D. catalinae* individuals stay longer within plants and visit
471 more leaflets on them. In fact, we found that search rate within plants is a linear function of
472 SWF density, as can be inferred analytically from the type III model (Eq. 4), and empirically
473 from the positive linear relationship between the SWF density and mean number of leaflets
474 visited per plant by *D. catalinae* individuals ($F_{1,45} = 80.88$, $R^2 = 0.642$, $P < 0.0001$). The
475 increase in search effort motivated by prey encounter resembles ‘area-concentrated search’,
476 defined as an increase in search effort after detecting a prey item because of the high
477 probability of encountering more prey nearby (Benhamou, 1992). Indeed, this adaptation is
478 the mechanism predicted by optimal foraging theory when prey are aggregated, but it is
479 maladaptive if resources are distributed randomly (Bell, 1991). ‘Area-concentrated search’
480 has been described for various species of coccinellid predators (e.g. Carter and Dixon, 1982;
481 Ferran et al., 1994; Munyaneza and Obrycki, 1998; Nakamuta, 1985), including *D. catalinae*
482 (Guershon and Gerling, 2006). However, this behavior is often described in terms of an
483 increase in turning angle (direct klinokinesis) along with a reduction in walking speed
484 (inverse orthokinesis) of predators in two-dimensional arenas, so that more time and energy
485 are invested in prey patches within which prey are randomly distributed. However, prey
486 distribution within leaves is often considered to be random (Hemerik and Yano, 2011;
487 Nachman, 2006; Rincon et al., 2015). Thus, an increase in search effort motivated by prey
488 encounter at the intra-leaflet scale would not provide, in theory, any benefit to the predator.
489 As such, even if *D. catalinae* search effort increases with SWF density at the intra-leaflet
490 scale (as described by Guershon and Gerling, 2006), the increase alone would not result in a
491 significant increase in encounter rate, and therefore a type II (saturating, with constant search
492 rate) emerges. In contrast, when encounter of infested leaflets results in an increase in the

number of leaflets visited, a higher chance of finding new infested leaflets in the same plant would result. In this case, the increase in search effort represents a benefit for the predator, which is reflected by an exponential increase in predation rates as a function of prey density. Thus, a functional increase in search effort may only result in an exponential increase in predation rate when prey are aggregated, and such a pattern is strengthened by a low probability of encountering prey patches when prey density is low. Interestingly, the mechanism described above provides a sound explanation for the change in functional response from type II to type III found analytically by Nachman (2006) when prey distribution was changed from random to aggregated.

The evidence for non-uniform predation patterns and their effects on predation rates presented in this paper is important at both fundamental and applied levels. On the one hand, we show that the common assumption of constant rates of encounter between predator and prey individuals within fields or greenhouses does not necessarily hold. Conventional models, written as a set of difference or differential equations, cannot mechanistically represent local population non-uniformity, because they do not take into account discrete individuals (DeAngelis and Mooij, 2005; Judson, 1994). Our results show that the interaction between non-random distributions of prey patches and predator patch-to-patch movement rules should be modeled using approaches such as spatially explicit individual-based simulation.

Our results also imply that the tomato-SWF-*D. catalinae* system could be stable. First, we show that the distribution of *D. catalinae* individuals among leaves is described more accurately by the leaf nodal position than by the number of SWF in the leaves. That is, predators are more likely to visit and predation rate is likely to be higher in leaflets or leaves located towards the middle and mid-lower region of the main stem, which are not necessarily the nodal positions with highest SWF nymph density. Predator aggregation can increase stability in predator-prey systems, especially if aggregation is independent of local (i.e. intra-

patch) prey density (Murdoch and Stewart-Oaten, 1989). Second, the emergence of a type III functional response at the intra-plant scale is important for mathematical modeling of SWF-*D. catalinae* dynamics to explore the stability properties of the system (Berryman, 1999; Berryman et al., 2006). Moreover, prey survival in regions where predation pressure is lower may increase stability by increasing predator survival during periods of prey scarcity. However, this stability may not be economically important for greenhouse tomato crops if prey populations exceed economic thresholds. In particular, the extent to which increases in *D. catalinae* release rates, or the use of complementary control strategies will help maintain SWF populations below economic injury levels would need to be examined. Ultimately, these questions can be addressed using ecological models that account for the variation in spatial interactions between predators and prey that were identified in this research.

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Figure captions

Figure 1. Response of *Delphastus catalinae* adults to sweetpotato whitefly nymph population density on tomato plants. a) Proportion of leaves visited by the predator ($\circ$, solid line) in comparison with the proportion of leaves infested with sweetpotato whitefly nymphs ($\times$, dashed line) as a function of sweetpotato whitefly population density. b) Proportion of predators observed in the tomato plant as a function of sweetpotato whitefly population density.

Figure 2. Intra-plant distribution of sweetpotato whitefly nymphs (a), the predator *Delphastus catalinae* (b) and sweetpotato whitefly mortality (c).

Figure 3. Functional response of *Delphastus catalinae* preying on sweetpotato whitefly nymphs at the intra-leaf (a - b) and the intra-plant (c - d) spatial scales. Relationships between number of prey consumed and prey density are depicted in a and c, whereas the corresponding relationships using proportions of prey eaten are depicted in b and d.

Table captions

Table 1. Regression coefficients of the polynomial logistic models fitted to describe the distribution of sweetpotato whitefly nymphs, *Delphastus catalinae*, and sweetpotato whitefly nymph mortality across leaf nodal positions of tomato plants.

Table 2. Parameter estimates of functional response models of the predator *Delphastus catalinae* at two spatial scales. Parameters were estimated by Maximum likelihood.

Tables

Table 1. Regression coefficients of the polynomial logistic models fitted to describe the distribution of: sweetpotato whitefly nymphs, the predator *Delphastus catalinae*, and sweetpotato whitefly nymph mortality across leaf nodal positions of tomato plants.

Coefficient	SWF† distribution	Predator distribution	SWF Mortality
Intercept	-5.352 (0.113)	-12.217 (1.322)*	-4.596 (0.345)
Linear	11.422 (0.671)	50.929 (6.790)	22.345 (1.954)
Quadratic	-9.405 (1.212)	-71.397 (10.979)	-40.456 (3.477)
Cubic	1.148 (0.671)*	31.266 (5.600)	20.622 (1.929)

† SWF = Sweetpotato whitefly nymph

* Estimate significantly different from the rest in the same row ($P < 0.001$)

Table 2. Parameter estimates of functional response models of the predator *Delphastus catalinae* at two spatial scales. Parameters were estimated by Maximum likelihood.

Spatial scale	Parameter	Estimate	SE	Z value	P
Intra-leaflet (type II)	<i>a</i>	0.2603	0.0126	20.643	< 0.0001
	<i>h</i>	0.0047	0.0061	0.770	0.441
Intra-plant (type III)	<i>b</i>	0.0001	< 0.0001	4.038	< 0.0001
	<i>c</i>	0.0173	0.005	3.449	0.0005
	<i>h</i>	0.0596	0.004	15.074	< 0.0001