

1 **Predators and alate immigration influence the season-long dynamics of**  
2 **soybean aphid (Hemiptera: Aphididae)**

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15 **Abstract**

16           The identification of key species within multi-predator assemblages suppressing  
17 agricultural pests is paramount to the incorporation of predators into pest management plans.  
18 Generalist predators have strong impacts on population growth of soybean aphids (*Aphis*  
19 *glycines*, Hemiptera: Aphidae) in North America, but their relative influence may vary  
20 seasonally, and potentially interact with immigration of alate aphids following initial field  
21 colonization. Here we present the results of a season-long study in Minnesota that used cage  
22 manipulations to estimate weekly impacts of predation on field populations of soybean aphids,  
23 while concurrently quantifying alate aphid and predator densities. We used generalized linear  
24 models based on field level aphid and predator counts, and aphid counts on caged and uncaged  
25 experimental plants, to show that *Harmonia axyridis* (Coleoptera: Coccinellidae) was negatively  
26 associated with *A. glycines* abundance, even under alate immigration levels associated with aphid  
27 outbreaks, suggesting potential regulation of aphid populations. In contrast, two other common  
28 predators, *Coccinella septempunctata* (Coleoptera: Coccinellidae) and *Orius insidiosus*  
29 (Hemiptera: Anthocoridae), did not show patterns of association with aphid dynamics. We also  
30 show that *A. glycines* populations only have significant positive associations with the number of  
31 immigrating alatae on uncaged experimental plants that had higher alate densities than the field  
32 average. The negative effect of *H. axyridis* on aphid populations was also observed on uncaged  
33 experimental plants, suggesting that even high levels of alate aphid immigration did not disrupt  
34 predator suppression. These results add to the growing body of evidence demonstrating that  
35 even low numbers of certain generalist predators can effectively suppress pest populations in  
36 agroecosystems. In particular, our findings suggest that the abundance of both *H. axyridis* and  
37 alate aphids are critical to soybean aphid seasonal dynamics.

38

39 **Keywords:** alatae; *Aphis glycines*, generalist predators; *Harmonia axyridis*; predator-prey  
40 dynamics

41

42 **Highlights:**

- 43 • *Harmonia axyridis* abundance was negatively associated with *Aphis glycines* abundance
- 44 • Aphids did not vary with abundance of *Coccinella septempunctata* or *Orius insidiosus*
- 45 • High levels of alate immigration did not disrupt aphid suppression by predators

- 46 • Generalist predators provided effective season-long aphid suppression in soybean

## 47 **1. Introduction**

48

49         Predators and parasitoids of arthropod pests are widely recognized for their role in  
50 causing mortality to pests in agricultural ecosystems and this pest control yields significant  
51 economic benefits (Landis et al., 2008; Losey and Vaughan, 2006; Schipanski et al., 2016; Zhao  
52 et al., 2016). There is considerable interest in determining the impacts of specific natural enemy  
53 guilds on pest suppression, particularly for newly introduced pests (Zhao et al., 2016). Though  
54 much of the focus in the past was on classical biological control, there has more recently been  
55 interest in quantifying the impact of naturally occurring natural enemies on pests, and in  
56 developing strategies to augment or otherwise improve these valuable ecosystem services (i.e.  
57 conservation biocontrol) (Landis et al., 2000; Symondson et al., 2002). This shift in focus has  
58 renewed interest in examining the characteristics of specific natural enemies that make them  
59 effective in suppressing pest populations. Traditionally, ‘ideal’ biocontrol agents were  
60 considered to be species with high prey specificity, since these ‘specialists’ have mechanisms to  
61 efficiently seek out particular prey/hosts and will not be diverted by the presence of alternative  
62 prey (Murdoch et al., 1985; Symondson et al., 2002). These assertions originate, at least  
63 partially, from early theoretical work that assumed the ideal outcome of biocontrol efforts was  
64 low, stable equilibrium populations of the biocontrol agent and pest (Murdoch, 1994; Murdoch et  
65 al., 1985). There is a growing body of both theoretical and experimental literature that  
66 demonstrates that generalist predators can act as effective biocontrol agents in agricultural  
67 ecosystems (Chang and Kareiva, 1999; Murdoch et al., 1985; Stiling and Cornelissen, 2005;  
68 Welch et al., 2012), and that low stable equilibrium populations are not a strict requirement for  
69 effective, long-term pest suppression (Murdoch et al., 1985; Symondson et al., 2002).

70         Generalist insect predators represent an important component of the natural enemy  
71 assemblage associated with insect pests (Bannerman et al., 2015; Symondson et al., 2002). Here  
72 we use the term generalist predators to include both polyphagous species with a wide prey range  
73 and stenophagous taxa that are opportunistic feeders on various resources (e.g. Coccinellidae)  
74 (Hodek and Evans, 2012; Welch et al., 2012). Common predators of insect pests in agricultural  
75 habitats includes beetles (Coleoptera: Coccinellidae & Carabidae), lacewings (Neuroptera:  
76 Chrysopidae), true bugs (Hemiptera: Anthocoridae, Nabidae, & Reduviidae), flies (Diptera:  
77 Syrphidae) and arachnids (Araneae) (Pedigo and Rice, 2009; van Emden, 2013). The way in

78 which these predators interact with, and respond to, pest populations in crop fields varies on a  
79 species-specific basis. Particular species of predators may remain closely associated with  
80 particular pest populations for extended periods of time (resident predators, e.g. coccinellid and  
81 lacewing larvae, anthocorid bugs), or rapidly move among pest populations, and among habitats  
82 (transient predators, e.g. coccinellid and lacewing adults) (Costamagna and Landis, 2007).  
83 Predator identity is an important element of any study that attempts to relate natural enemy  
84 activity to pest suppression since intraguild interactions within multi-predator assemblages can  
85 vary from positive to neutral to negative, with consequent effects on levels of pest suppression  
86 (Cardinale et al., 2003; Ferguson and Stiling, 1996; Henry et al., 2010; Losey and Denno, 1998;  
87 Sih et al., 1998; Straub and Snyder, 2006). Consequently, it is difficult to determine species or  
88 groups of species that are key to suppressing pests within multi-predator assemblages.

89 The soybean aphid, *Aphis glycines* Matsumura, (Hemiptera: Aphididae), is an introduced  
90 pest of soybean that was first detected in North America in 2000 (Ragsdale et al., 2004).  
91 Soybean aphid has subsequently become a serious economic pest of soybean and has rapidly  
92 spread across the soybean producing regions of North America (Ragsdale et al., 2011). In North  
93 America, the natural enemy guild associated with soybean aphid varies regionally but always  
94 contains a significant generalist predator component (Bannerman et al., 2015; Costamagna and  
95 Landis, 2007; Desneux et al., 2006; Gardiner et al., 2009b; Hallett et al., 2014; Mignault et al.,  
96 2006; Ragsdale et al., 2011). More than 50 species of aphidophagous predators and parasitoids  
97 feed on *A. glycines* (Maisonhaute et al., 2017; Ragsdale et al., 2011, and references within), and  
98 in many cases provide high levels of suppression (e.g. Fox et al. 2004, 2005, Rutledge et al.  
99 2004, Costamagna and Landis 2006, Costamagna et al. 2007). Although the relative abundance  
100 and importance of the generalist predators most commonly associated with soybean aphid  
101 suppression appears to vary regionally, most assemblages studied are numerically dominated by  
102 the coccinellids *Harmonia axyridis* (Pallas), *Coccinella septempunctata* L., and the anthocorid  
103 *Orius insidiosus* (Say) (Costamagna and Landis, 2007; Desneux et al., 2006; Gardiner et al.,  
104 2009b; Hallett et al., 2014; Koch and Costamagna, 2017; Mignault et al., 2006; Ragsdale et al.,  
105 2011). The impact of each predator species within the assemblage on soybean aphid remains  
106 unclear, as most previous studies used predator exclusion cages (Costamagna et al., 2007;  
107 Desneux et al., 2006; Gardiner et al., 2009a), rely solely on correlations (e.g. Maisonhaute et al.,

108 2017; Yoo and O’Neil, 2009), or used short term assessments of predation (Costamagna and  
109 Landis, 2007; Harwood et al., 2009; Petersen and Woltz, 2015; Woltz and Landis, 2013).

110 The soybean aphid is heteroecious (host alternating), overwintering on woody host plants  
111 that are located outside of crop habitats, and migrating into suitable crops in the spring or early  
112 summer via the production of alate (winged) morphs (Blackman, 1974; Hodgson et al., 2005b).  
113 These colonizing flights are assumed to be relatively local (Schmidt et al., 2012), and soybean  
114 aphids continue to produce alate migrants through the summer during all stages of soybean  
115 growth and reproduction (Hodgson et al., 2005a, 2005b). The production of alate virginoparae  
116 is induced by aphid crowding and declining plant quality (Ríos-Martínez, 2017) and results in  
117 both short range dispersal and long range migration. Winged aphids that join previously  
118 established colonies contribute directly to population growth rates (Zhang et al., 2009) and large  
119 influxes of alatae can disrupt top-down control by natural enemies, increasing aphid densities  
120 and thus, population growth rates (Costamagna et al., 2013). However, no studies have  
121 examined season-long interactions between alate immigration and predator impact on soybean  
122 aphid populations.

123 Previous studies that examined the impact of natural enemy assemblages on pest  
124 populations (see Symondson et al. 2002 for review), including soybean aphids (Costamagna and  
125 Landis, 2006; Costamagna et al., 2007; Fox et al., 2005, 2004; Gardiner et al., 2009a; Hallett et  
126 al., 2014; Labrie et al., 2016; Maisonhaute et al., 2017; Rutledge et al., 2004; Woltz et al., 2012),  
127 were frequently short in duration and often did not distinguish the relative contributions of  
128 individual predators within the assemblage. We conducted field population monitoring  
129 combined with a manipulative cage experiment for nine weeks (encompassing the period from  
130 early aphid colonization to population decline) that allowed us to: 1) identify the key generalist  
131 predators associated with soybean aphid throughout the growing season, 2) assess their impact  
132 on soybean aphid populations over the season, and 3) determine how summer alate aphid  
133 immigration affects season-long aphid population dynamics.

134

## 135 **2. Methods**

136

### 137 **2.1. Sampling locations**

138           The impact of predators and alate aphid immigration on soybean aphid populations was  
139 examined at four locations in Minnesota: Rosemount (three commercial soybean fields at the  
140 University of Minnesota Outreach Research and Education UMORE Park), LeSeur (three  
141 commercial soybean fields), Waseca (two experimental plots at the University of Minnesota  
142 Southern Research and Outreach Center and one commercial field), and Saint Paul (three  
143 experimental plots at the University of Minnesota St. Paul campus), during 2007. Commercial  
144 fields ranged from 14 to 28 ha, and experimental plots ranged from 0.5 to 0.9 ha and their aphid  
145 populations were not associated with field size (Linear Regression,  $F_{1,10} = 1.65$ ,  $P = 0.23$ ). This  
146 range of field sizes allows us robust inferences about aphid and predator dynamics and are well  
147 within the range of previous studies on this system, that ranged from 0.1 – 0.4 ha plots (Schmidt  
148 et al., 2008; Yoo and O’Neil, 2009) to 13.6 – 48.1 ha (Gardiner et al., 2009a). Outbreak  
149 populations of soybean aphids resulted in one insecticide application in a commercial field in  
150 Waseca (Waseca 3) during the first week of August. Sampling continued in a portion of the field  
151 (80 x 330 m) that was left untreated to continue our study. Since predator population trends  
152 remained the same in the untreated area and exploratory analysis yielded the same results with or  
153 without these data, the analyses presented here include the data from the untreated section of the  
154 sprayed field.

155

## 156 **2.2. Field observations**

157           Soybean aphid populations were assayed weekly using destructive, whole-plant counts  
158 from 12 June to 29 August, with apterous and alate aphids tallied separately. The methods used  
159 to count aphids changed over the course of the season in two ways. First, the number of plants  
160 per field was reduced (20 plants, 12 June to 13 July; 16, 12 or 8 plants from 16 July to 27  
161 August), a procedure that allowed us to maintain similar levels of precision as plant size and  
162 aphid populations increased (Hodgson et al., 2004; Ragsdale et al., 2007). Second, all aphids  
163 were counted per plant in June and July, but in August (the last three sampling dates) a node-  
164 based sampling method was used to estimate whole-plant aphid abundance (McCornack et al.,  
165 2008). Aphid population estimates from this method do not differ from whole-plant counts and  
166 consist of weighted estimates based on counts on three plant nodes (all plant material above the  
167 newest fully expanded leaf,  $N_1$ , the node two node positions below the new growth,  $N_3$ , and the  
168 middle node of all remaining nodes,  $N_{MR}$ ).

169 Predators were sampled weekly from 12 June until 27 August during a two-hour period  
170 between 8:30 and 16:30. Three methods were used to sample predators and parasitoid  
171 mummies: sweep-netting, destructive whole-plant counts, and 25 m walking transects  
172 (Bannerman et al., 2015). Each sweep-net sample consisted of 25, 180° sweeps through the  
173 soybean canopy along a linear transect, with 4 samples taken per field per week. Destructive  
174 whole-plant counts consisted of visual inspection, both before disturbance and after uprooting, of  
175 each plant on which aphid counts occurred. Each walking transect consisted of an observer  
176 walking a 25-m transect along linear soybean rows and recording all observed predators and  
177 parasitoid mummies that were visible on the upper leaves of each plant ( $736 \pm 11$  (mean  $\pm$  SD)  
178 soybean plants per 25m of row). The number of transect samples mirrored the number of whole-  
179 plant samples as the two were performed simultaneously. Transect counts were considered  
180 superior for sampling large predators like coccinellids, and destructive whole-plant counts  
181 superior for sampling small predators like *O. insidiosus* (Bannerman et al., 2015). Inclement  
182 weather prevented field level sampling on two occasions, from 9-13 July at Rosemount, and  
183 from 30 July to 3 August at St. Paul. The predator abundance data presented here was  
184 previously published in a study that compared sampling methods for soybean aphid predators  
185 (Bannerman et al., 2015). The presence of entomopathogenic fungi was not assessed, but no  
186 evidence of fungal epizootics was observed in any field.

187

### 188 **2.3. Exclusion study**

189 To determine the impact of predators on soybean aphid populations, exclusion cages  
190 were used to protect aphids from predation. Pairs of field plants were selected bearing numbers  
191 of aphids that approximated the mean aphid density in the field (based on the destructive plant  
192 counts). Each plant was then randomly assigned to one of two treatments: open plant or predator  
193 exclusion cage. Three sets of plants were established in each field every sampling week. In  
194 some cases, aphids were physically removed to better approximate the target aphid density.  
195 Open plants consisted of a marked soybean plant with the surrounding plants removed to  
196 eliminate plant-to-plant contact and provide more similar growing conditions as plants with  
197 exclusion cages. Previous studies using sham cages have demonstrated that removal of the  
198 surrounding plants around open plants, which may reduce between-plant movement of immature  
199 predators, has no meaningful effect on aphid densities (Costamagna et al., 2008). Exclusion



200 cages were constructed with cylindrical tomato wire cages (0.4 x 1.0 m), secured to the ground  
201 with four commercial plastic tent pegs passing through wire loops made at the base of the cage  
202 and covered with white no-see-um mesh (Kaplan Simon Co., Baintree, MA) (after Costamagna  
203 and Landis 2011). The cages were further secured by tying them to two sturdy stakes (1.52 m)  
204 located on opposite sides. Previous work indicated that this type of cage does not alter  
205 microclimatic conditions sufficient to change interactions among plants and aphids (Costamagna  
206 et al., 2013).

207         Apterous (wingless) and alate (winged) morphs were both counted one week after the  
208 imposition of treatments. Since new plants were assigned to treatments every week, the impact  
209 of predators could be partitioned weekly over the duration of the study. This procedure also  
210 reduced variance associated with aphid overcrowding and declining plant quality, which tends to  
211 occur when natural enemies are excluded from aphid colonies for long periods (Kucharik et al.,  
212 2016).

213         The start date of the exclusion study differed among locations, commencing during the  
214 week of 11-15 June in the three fields at St. Paul, and between 18-22 June in all other fields.  
215 Exclusion studies ended during the week of 23-27 July in St. Paul fields, and the week of 6-10  
216 August in all other fields, resulting in three fields with seven weeks of cage manipulations and  
217 nine fields with nine weeks. Because the duration of the cage experiments (7-9 weeks) was  
218 shorter than the duration of field-level assessments (11 weeks), any mention of 'week' in this  
219 paper refers to field-level assessment dates.

220         Since we initiated new cages each week for the duration of this experiment it was  
221 important that initial aphid density on caged plants was representative of the field mean. We  
222 were successful in achieving this objective with one caveat. In week three, the number of aphids  
223 on caged plants averaged 3.5 aphids (range = 3 to 5), higher than that of the field mean in the  
224 LeSeur and Waseca fields. This was necessary because aphid densities in these fields averaged <  
225 1 aphid per plant, and caging plants with only one or two aphids would provide no useful  
226 information. Overall, these slightly inflated initial values appear to have little impact on  
227 conclusions derived from our models (based on running models that include and exclude data  
228 from these early weeks) since they occurred when both aphid and predator populations were very  
229 low. For simplicity, we only show results including these fields.

230           There was a secondary influx of alate aphids into all fields in mid- to late-July which  
231 increased alate abundance. Furthermore, clearing immediately surrounding ‘open’ plants  
232 resulted in higher than normal attraction of alates, resulting in alatae densities on open plants  
233 well above the mean field density. This was probably a consequence of ‘edge’ or ‘bare ground’  
234 effects, which are often observed in other aphid species (Davis et al., 2015, 2009; Irwin et al.,  
235 2007). This immigration event interacted with our open plant treatment, providing us with an  
236 opportunity to compare predation under ‘normal’ immigration levels (i.e. aphid counts on  
237 unmanipulated plants, hereafter referred to as field counts) with predation under high  
238 immigration levels (i.e. aphid counts in open plant treatment, hereafter referred to as open plant  
239 counts).

240

#### 241 **2.4. Analysis**

242           Generalized linear models (GLMs) were constructed to assess the effects of predators and  
243 alate aphid immigration (dependent variables) on apterous aphid density (independent variables)  
244 through the growing season. We compared the fit of negative binomial and poisson  
245 distributions, both theoretically appropriate for count data, using the deviance/df ratio and  
246 diagnostic graphs. The negative binomial distribution fit best in all cases, so we used it for all  
247 models presented here. Several sets of predator predictor variables were tested: (1) A  
248 combination of destructive whole-plant counts for small predators and 25 m walking transect  
249 counts for large predators, (2) Sweep net counts for all predators, (3) Natural enemy units (a  
250 method that normalizes the impact of soybean aphid natural enemies into a single value), each  
251 based on recent soybean aphid natural enemy sampling literature (Table 1) (Bannerman et al.,  
252 2015; Hallett et al., 2014). Additional control predictor variables in all models included aphid  
253 density in the exclusion cage (to control for variable initial aphid numbers and environmental  
254 variables that may affect aphid population growth), field, and week. Initial exploratory models  
255 involved mixed models (GLMMs), and included 'field' nested within 'site', treated as a random  
256 variable. However, this did not improve model fit (using AIC as the index), so we did not  
257 include it in our analyses. Furthermore, including various combinations of random variables in  
258 models (i.e., 'field' as a random variable excluding 'site', and 'field' as a fixed variable), did not  
259 change any conclusions, so we decided to present the simplest models based on AIC. All

260 analyses were performed using the Mass package in R version 3.2.1 (R Core Team, 2015;  
261 Venables and Ripley, 2002).

262         Although we constructed exploratory models to test for the impact of most predatory taxa  
263 observed, the models presented here focus on only three species: *H. axyridis*, *C. septempunctata*,  
264 and *O. insidiosus*. These three species represented 65% of the total predators observed using  
265 either sweep-netting or a combination of destructive whole-plant counts and 25 m walking  
266 transects. These three predators have been reported as important natural enemies of soybean  
267 aphid across North America (Costamagna and Landis, 2007; Desneux et al., 2006; Gardiner et  
268 al., 2009b; Hallett et al., 2014; Koch and Costamagna, 2017; Mignault et al., 2006; Ragsdale et  
269 al., 2011). In addition, we observed too few individuals of many species to reasonably include  
270 them as an independent variable. We also constructed exploratory models that included larval *H.*  
271 *axyridis* and *C. septempunctata* counts as independent variables and as combined variables (as  
272 done with *O. insidiosus*). Larval coccinellid counts were not significant predictors of apterous  
273 aphid abundance and since the inclusion of these predictors did not change the significance or  
274 direction of response of any other predictor variable, the models are not shown or discussed  
275 further.

276         Since alate aphid immigration influenced aphid density in the open plant treatments, we  
277 constructed two sets of models: the first set used field-based aphid counts for apterous and alate  
278 aphid densities (field models, normal immigration levels) and the second set used open plant-  
279 based aphid counts (open models, high immigration levels). We then used the parameter  
280 estimates from two models to predict aphid abundance in response to a range of *H. axyridis*  
281 abundances to illustrate the strength of the predator-prey interaction in this system. This  
282 required a two-step process. First, to model *H. axyridis* abundance, we constructed a set of  
283 representative numerical responses (zero, low, medium and high), approximating the range of  
284 responses observed across our 12 focal fields. We then predicted the effect of *H. axyridis*  
285 abundance on apterous aphid abundance while setting all other predictor variables to their mean  
286 weekly values (i.e. we varied the intensity of the *H. axyridis* numerical response while keeping  
287 the values of all other predictor variables constant to isolate and illustrate the impact of *H.*  
288 *axyridis* on apterous aphid abundance). Since 'field' was also a significant predictor of apterous  
289 aphid abundance, we show the results for three fields representative of low, intermediate and  
290 high peak aphid densities, respectively.

## 291 **3. Results**

292

### 293 **3.1. Soybean aphids**

294 Although all 12 fields had been colonized by soybean aphids by 15 June (week 1), peak  
295 aphid abundance and its timing varied (Figure 1). Peak abundance ranged from  $144.8 \pm 95.8$  to  
296  $1726.2 \pm 897.1$  aphids per plant (mean  $\pm$  SEM), providing us a broad range of aphid population  
297 levels to investigate relationships with predator assemblages. For all fields and sample dates,  
298 alate aphids represented less than 5% (mean = 0.77%, SD = 0.11%) of the aphid population at  
299 field level, but up to 23% (mean = 2.3%, SD = 3.1%) on the open plants. Peak aphid abundance  
300 occurred between 23 July and 15 August (weeks 7, 8, 9 & 10) while soybean plants were in the  
301 R3, R4 or R5 reproductive stage, and was followed by swift declines in all fields by the end of  
302 August. Peak aphid abundance occurred during the cage experiment for 11 of 12 study fields  
303 (Figure 1).

304

### 305 **3.2. Predator responses**

306 The most abundant predators collected throughout the season were the coccinellids *H.*  
307 *axyridis* and *C. septempunctata* and the anthocorid bug *O. insidiosus*, collectively representing  
308 65% of the aphidophagous predators captured using sweep-nets or observed with a combination  
309 of 25 m walking transects and destructive whole-plant counts across all fields and sampling dates  
310 (Bannerman et al., 2015). The abundances of these predators changed throughout the season and  
311 varied among fields (Figure 2, and Appendix A Figures A.1 and A.2), but reflected the range of  
312 abundances previously reported from soybean in the Midwest USA (see references in  
313 Bannerman et al. 2015). Peak *H. axyridis* densities varied among fields, ranging from 0.25 to  
314 more than 30 adult beetles per transect. We observed a distinct numerical response by *H.*  
315 *axyridis* in 11 of 12 fields with peak abundance occurring between 0 and 3 weeks after peak  
316 aphid abundance. Synchronized numerical responses of *C. septempunctata* and *O. insidiosus* to  
317 increasing aphid abundance were observed in some fields but were inconsistent (Figures A.1 and  
318 A.2). Though plots of predators abundances based on sweep-netting are not provided, the  
319 patterns described are similar to those reported based on walking transects. There were no  
320 parasitoid mummies observed in any field in Minnesota in 2007.

321

### 322 3.3. Exclusion study

323 All models indicated a non-linear increase in aphid populations followed by a decrease  
324 with significant 'week' and 'week<sup>2</sup>' terms, and various levels of aphids with significant field terms  
325 (Table 2 and Appendix A Tables A.1 and A.2). In models that measured predators using a  
326 combination of transect counts and whole-plant counts, apterous aphid abundance was negatively  
327 associated with adult *H. axyridis* abundance in both unmanipulated field plants (Estimate = -  
328 0.065, SE = 0.024,  $p = 0.006$ ), and open plants (Estimate = -0.076, SE = 0.021,  $p = 0.0002$ ; Table  
329 2). No relationships were observed between apterous aphid abundance and adult *C.*  
330 *septempunctata* or adult + juvenile *O. insidiosus* abundance. Numbers of aphids in exclusion  
331 cages and numbers of alate aphids in fields did not predict apterous aphid abundance  
332 significantly in our field-based model, but did in our open model (aphid counts in exclusion  
333 cages: Estimate = 0.0008, SE = 0.0002,  $p < 0.0001$ ; alate aphid counts on open plants: Estimate  
334 = 0.042, SE = 0.011,  $p < 0.0001$ ). This demonstrated the impact of higher than normal alate  
335 aphid abundance on our 'open cage' plants. In both models, adult *H. axyridis* abundance was the  
336 only predictor to be negatively associated with soybean aphid abundance.

337 Additional models were constructed to determine whether the above results were robust  
338 or dependent on the specific predator/sampling method variables used. Field and open models  
339 using sweep-count data for all three predatory species produced similar models to those using  
340 transect and plant count data, with one difference. In the field + sweep-net model, apterous  
341 aphid abundance was positively associated with *O. insidiosus* abundance, supporting other  
342 models in our study that suggest this predator does not negatively affect aphid population  
343 growth, although it does exhibit a functional response to aphid density (Appendix A: Table A.1). The  
344 natural enemy units predictor variable did not significantly affect apterous aphid populations in  
345 either the field or open models (Appendix A: Table A.2). In summary, all models constructed  
346 and variables tested suggest that the only predator with consistent negative associations with  
347 aphid abundance was adult *H. axyridis*.

348 Modeling aphid population responses to *H. axyridis* revealed the strength of the impact of  
349 this predator in the system. The abundance of *H. axyridis* observed across the 12 sample fields  
350 suggested that numerical responses peaking at 1, 5, and 25 adults / transect would be realistic  
351 representations of the range of responses in our area of study (Figures 2 and 3). We used a null  
352 response (i.e., zero *H. axyridis*) and these three numerical responses to predict aphid populations

353 using mean weekly values and model parameters for three fields representing a range of aphid  
354 populations. Both field and open models predicted that a high numerical response of *H. axyridis*  
355 will result in a strong aphid population reduction in all three cases (Figure 4). Intermediate and  
356 low numerical responses by *H. axyridis* resulted in either slowed aphid population growth or  
357 reduced aphid populations when compared with models without *H. axyridis*, although to a lesser  
358 extent than observed with a high numerical response. Under normal alate immigration levels  
359 (field models), seven modelled populations with *H. axyridis* reached the economic threshold  
360 (ET) of 250 aphids per plant, but only three exceeded the economic injury level (EIL) of 674  
361 aphids per plant (Ragsdale et al., 2007) (Figures 4a-c). Similarly, eight modelled populations  
362 exceeded the ET and five populations exceeded the EIL in models under high alate immigration  
363 (open models, Figures 4d-f). High alate aphid immigration levels resulted in an accelerated  
364 growth and decline of aphid populations (Figures 4d-f).

365

#### 366 **4. Discussion**

367

368 Our study demonstrated that generalist predators can exert season-long suppression of  
369 aphids, even under high rates of alate immigration. We found that within an assemblage  
370 dominated by three generalist predators, *H. axyridis* was the critical species, exhibiting  
371 consistent, season-long negative associations with soybean aphid populations in Minnesota.  
372 Throughout the season, generalist predators from 12 insect and 2 arachnid families were  
373 recorded in Minnesota soybean fields with the coccinellids *H. axyridis* and *C. septempunctata*  
374 and the anthocorid bug *O. insidiosus* being most abundant. These three species have been  
375 identified in previous studies as potentially important soybean aphid predators in several regions  
376 in North America (Costamagna and Landis, 2007, 2006; Fox et al., 2005, 2004; Koch and  
377 Costamagna, 2017; Labrie et al., 2016; Maisonhaute et al., 2017; Rutledge and O'Neil, 2005;  
378 Rutledge et al., 2004). Though these three species were all abundant, our results confirm  
379 previous studies suggesting that coccinellids were the key predators suppressing *A. glycines*  
380 (Costamagna and Landis, 2007; Costamagna et al., 2008, 2007), although the present results  
381 suggest a key role of *H. axyridis*, but not *C. septempunctata*, in contrast with previous  
382 observations in this system (Costamagna and Landis, 2007). This discrepancy may result from  
383 the use of smaller spatial or temporal scales in previous studies of aphid suppression by *C.*

384 *septempunctata*, such as individual or groups of fireweed stems (Ives et al., 1993) or 1-m<sup>2</sup>  
385 soybean patches (Costamagna and Landis, 2007), and typically for observation periods of a few  
386 hours or days. Our results suggest that at the whole-field level over season-long scales, *C.*  
387 *septempunctata* does not show an association with *A. glycines* suppression.

388 Similarly, previous studies suggesting that *O. insidiosus* can suppress soybean aphid  
389 populations focused on their impact on early-season aphid populations, rather than on season-  
390 long dynamics (Brosius et al., 2007; Yoo and O'Neil, 2009). Although we did not consistently  
391 detect statistically significant patterns of association between *O. insidiosus* and aphid abundance,  
392 their abundance did increase in response to increasing aphid populations in most fields,  
393 suggesting that larger aphid populations will attract larger numbers of this predator. The results  
394 demonstrate that *H. axyridis* can contribute to both prevention and suppression of *A. glycines*  
395 outbreaks throughout the growing season (Koch and Costamagna, 2017), and underscore the  
396 importance of studies that can identify and quantify the impact of particular species within a  
397 natural enemy assemblage (Symondson et al., 2002) since presence alone, even in high  
398 abundance, does not necessarily imply pest population reduction.

399 In order for generalist predators to significantly reduce pest populations, theory suggests  
400 that either early arrival (while pest populations are still small) or a strong numerical response is  
401 key (Bianchi et al., 2006; Chang and Kareiva, 1999; Rutledge et al., 2004). For *H. axyridis*  
402 feeding on soybean aphid, a strong numerical response occurred in most fields near the end of  
403 July or early August, between 0 and 2 weeks after peak aphid abundance. Peak *H. axyridis*  
404 abundance was higher in fields with higher peak aphid populations, further demonstrating that  
405 adult *H. axyridis* are attracted to higher aphid densities. The densities of *H. axyridis* observed in  
406 our study were also well within the range observed in previous studies (e.g. Costamagna and  
407 Landis 2006, Desneux et al. 2006). Given variation in the strength of the *H. axyridis* numerical  
408 response, we modelled four response levels, all within the observed range of responses, to  
409 demonstrate the potential impact of *H. axyridis* on aphid populations. The results of this exercise  
410 demonstrated that *H. axyridis* can control aphids at low/intermediate aphid infestation levels, but  
411 that high aphid populations can still escape control if *H. axyridis* fails to respond in sufficiently  
412 high numbers. For perspective, an increase of one *H. axyridis* adult per transect count is  
413 approximately equivalent to one 'visible' beetle (i.e. visual samples on transects only reflect adult  
414 beetles on the upper side of upper leaves, see Bannerman et al. 2015 for more details) per 736 ±

415 11 soybean plants (mean number of soybean plants per 25 m of one row of soybean), so although  
416 the *H. axyridis* parameter estimates are small in our models, the per capita effect size of *H.*  
417 *axyridis* on aphid populations is large, even at densities well below 1 visible adult per 30 plants.

418         Secondary influxes of alate aphids have been associated with outbreak populations in  
419 soybean aphid (Hodgson et al., 2005b; Labrie et al., 2016; Rhainds et al., 2010). Surprisingly,  
420 only when artificially elevated rates of alate immigration occurred (on open treatment plants) did  
421 this immigration increase apterous aphid populations, and even then, it did not counter the  
422 impact of *H. axyridis* on aphid numbers. Thus, our results suggest that aphid populations can  
423 still be suppressed by predators despite continued alate immigration.

424         Our study supports the view that naturally occurring generalist predators can significantly  
425 reduce agricultural pest populations (Murdoch, 1994; Symondson et al., 2002) and has several  
426 implications for agricultural pest management. First, even though all twelve fields sampled  
427 experienced a period of rapid aphid population growth, this did not guarantee that aphid  
428 populations would exceed the economic injury level (Ragsdale et al., 2007), which is at least  
429 partially attributable to the activity of generalist predators. Second, as efforts advance to  
430 integrate measures of natural enemy abundance into economic decision making (e.g. Elliott et al.  
431 2004, Giles and Walker 2009, Hallett et al. 2014), it will become increasingly important to  
432 predict how natural enemy abundance affects pest populations in time and space. We did not  
433 detect a relationship between natural enemy units (as per Hallett et al. 2014) and apterous aphid  
434 abundance. This was likely caused by combining the impact (abundance x voracity) of one  
435 species with a strong numerical response to aphids with that of two species that did not, thereby  
436 weakening our ability to relate natural enemy abundance to aphid abundance. In addition, during  
437 our 2007 studies we observed no parasitoids and these comprised a larger component of the  
438 natural enemy assemblage in Ontario where the natural enemy unit concept was developed and  
439 validated (Hallett et al., 2014), and parasitoids of soybean aphids are now increasing in other  
440 regions in North America (Kaser, 2016). Therefore, regional differences in the assemblage of  
441 soybean aphid natural enemies may affect the applicability of methodology developed to assess  
442 their impact in one particular region. Similarly, temporal changes in natural enemy assemblages,  
443 particularly an increase in parasitism by the adventive parasitoid *Aphelinus certus*  
444 (Hymenoptera: Aphelinidae), should be addressed in future studies (Kaser, 2016).



445           Our study demonstrated the important role of *H. axyridis*, a transient generalist predator,  
446 in reducing soybean aphid populations, adding to evidence that naturally occurring generalist  
447 predators can regulate aphid populations, even under levels of high alate immigration. We also  
448 showed that the numerical response of *H. axyridis* is strong when aphid abundance is high. At  
449 the same time, we found that some generalist predators, even though abundant, may have little  
450 impact on increasing aphid populations. These findings should ultimately be useful to improve  
451 decision-making in pest management programs as we seek to enhance natural pest control  
452 services through the development and implementation of dynamic action thresholds (e.g. Hallett  
453 et al. 2014) and conservation biocontrol (Landis et al., 2000).

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455

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463

464 **Author contributions**

465

466 ACC, BPM and DWR designed the experiments; ACC and BPM performed the experiments; JB,  
467 ACC, and NK performed the data analysis, JB wrote the first version of the manuscript; all  
468 authors contributed to the final version of the manuscript.

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- 666

667 **Table Captions**

668 Table 1. Predator predictor variable sets used for GLM models to examine the impacts of  
669 predators on season-long apterous aphid populations in 12 Minnesota soybean fields from 25  
670 June 2007 – 10 August 2007.

671 Table 2. Relationship between predator and aphid populations using transect + plant count  
672 predator predictor variables for 12 Minnesota soybean fields from 25 June 2007 – 10 August  
673 2007.



674 **Tables**

675 Table 1.

Variable description	Justification
Mean # of adult <i>H. axyridis</i> per transect	Combination of the two methods determined to be efficient and effective for sampling both large and small predators of soybean aphid (Bannerman et al. 2015)
Mean # of adult <i>C. septempunctata</i> per transect	
Mean # of juvenile + adult <i>O. insidiosus</i> per plant	
Mean # of adult <i>H. axyridis</i> per 25 sweeps	Sweep netting represents a good method for sampling both large and small natural enemies of soybean aphid when efficiency is not paramount (Bannerman et al. 2015)
Mean # of adult <i>C. septempunctata</i> per 25 sweeps	
Mean # of juvenile + adult <i>O. insidiosus</i> per 25 sweeps	
Mean natural enemy units per plant	Method developed by Hallett et al. (2014) to normalize the impact of soybean aphid natural enemies into a single value. 1 NEU represents 100 aphids consumed or parasitized per day and is calculated using the equation:
	$NEU_{total} = \sum_{i=1}^N n_i V_i$
	Where $n_i$ is the total number of individuals of species $i$ and $V_i$ is the mean voracity of species $i$ divided by 100. Our NEU calculations used the mean abundance of juvenile and adults stages of <i>H. axyridis</i> , <i>C. septempunctata</i> and <i>O. insidiosus</i> per destructive plant count.

676

677

Apterous aphid = Aphid density exclusion + Alate density + <i>H. axyridis</i> adult + <i>C. septempunctata</i> adult + <i>O. insidiosus</i> all stages + Week + Week <sup>2</sup> + Field <sup>a</sup>				
Transect + plant count				
Field counts <sup>b</sup>	Estimate	Standard error	Z-value	p-value
Intercept	-3.448	0.730	-4.72	2.33 x 10 <sup>-6</sup>
Aphid exclusion cage	0.0003	0.0002	1.77	7.69 x 10 <sup>-2</sup>
Alate field	0.0777	0.0913	0.85	0.39
<i>H. axyridis</i> adult transect	-0.0650	0.024	-2.74	6.06 x 10 <sup>-3</sup>
<i>C. septempunctata</i> adult transect	-0.0953	0.129	-0.74	0.46
<i>O. insidiosus</i> all stages plant count	-0.340	0.211	-1.61	0.11
Week	2.102	0.253	8.31	< 2.0 x 10 <sup>-16</sup>
Week <sup>2</sup>	-0.104	0.021	-5.07	4.06 x 10 <sup>-7</sup>
Open plant counts <sup>c</sup>				
Intercept	-0.599	0.558	-1.07	0.28
Aphid exclusion cage	0.0008	0.0002	-0.57	1.52 x 10 <sup>-6</sup>
Alate open plant	0.0419	0.0107	3.92	9.04 x 10 <sup>-5</sup>
<i>H. axyridis</i> adult transect	-0.0762	0.0206	-3.71	2.09 x 10 <sup>-4</sup>
<i>C. septempunctata</i> adult transect	-0.169	0.114	-1.49	0.14
<i>O. insidiosus</i> all stages plant count	-0.101	0.178	-0.57	0.57
Week	1.334	0.201	6.65	2.88 x 10 <sup>-11</sup>
Week <sup>2</sup>	-0.0718	0.0167	-4.30	1.74 x 10 <sup>-5</sup>

<sup>a</sup> For simplicity, estimates for the effect of each field on aphid abundance not shown. Field is a significant predictor of Apterous aphid abundance (Analysis of deviance: Field counts model, df = 11,  $p < 0.0001$ ; Open plant counts model, df = 11,  $p < 0.0001$ )

<sup>b</sup> Apterous aphid response variable and Alate aphid predictor variable based on field counts

<sup>c</sup> Apterous aphid response variable and Alate aphid predictor variable based on open plant counts

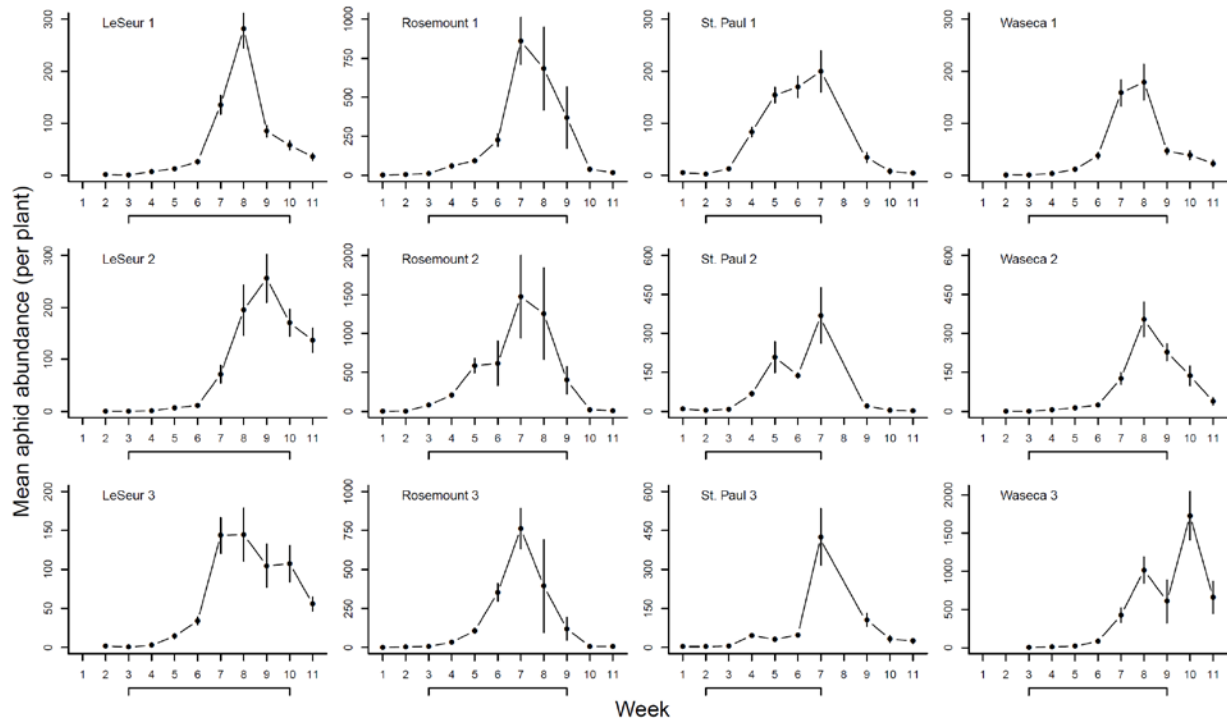
## 680 **Figure Captions**

681 Figure 1. Mean ( $\pm$  SEM) weekly soybean aphid abundance per plant observed in 12 Minnesota  
682 soybean fields from 25 June 2007 – 10 August 2007. Line below x-axis indicates duration of  
683 cage experiment in the respective field.

684 Figure 2. Mean ( $\pm$  SEM) weekly adult *Harmonia axyridis* abundance per 25 m walking transect  
685 observed in 12 Minnesota soybean fields from 25 June 2007 – 10 August 2007.

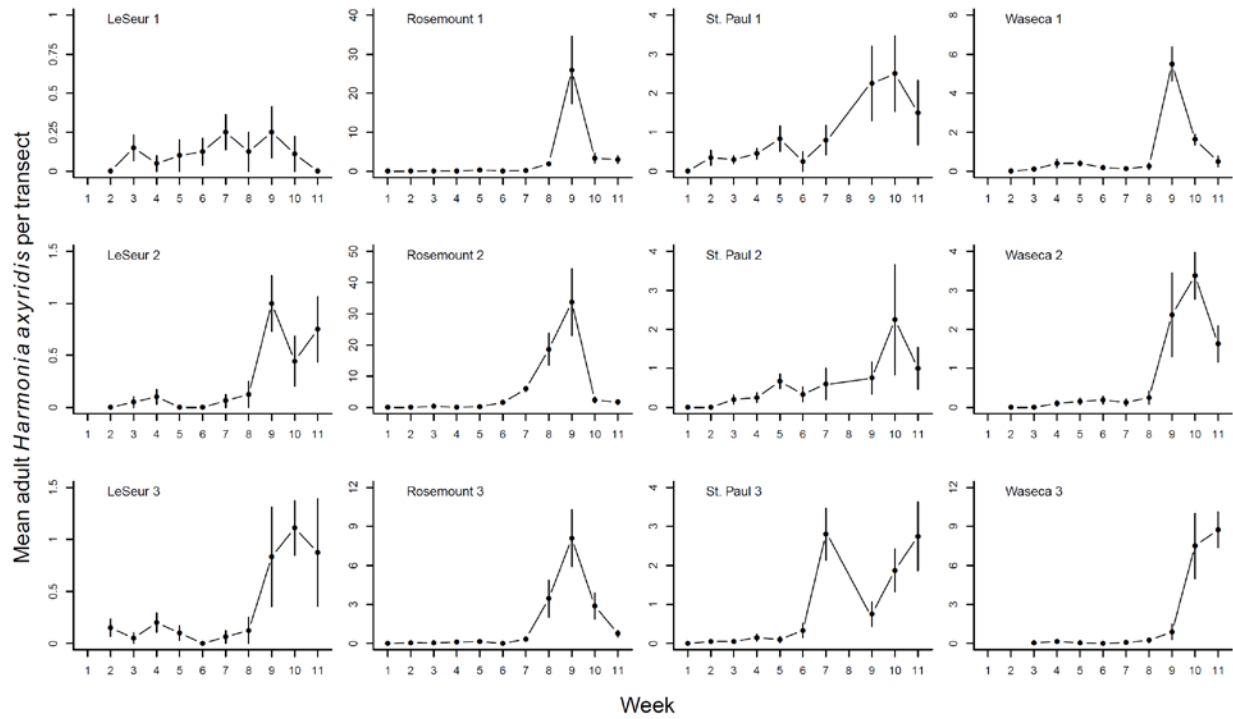
686 Figure 3. Modeled numerical response intensities for *Harmonia axyridis*. Value ranges were set  
687 to represent the range of responses observed in Minnesota soybean fields in 2007 and used for  
688 predictive purposes to visualize the effect of *H. axyridis* on soybean aphids (Figure 4) based on  
689 our GLM models. Each transect represents 25 linear-m of soybean.

690 Figure 4. Predicted effect of *Harmonia axyridis* on apterous aphid abundance for three  
691 representative soybean fields using Field (subplots A,B,C) and Open models (subplots D,E,F)  
692 (Table 2). The low aphid population field was Waseca 2 (peak density close to the ET); the  
693 intermediate aphid population field was Rosemount 3 (peak aphid density  $>$  ET,  $<$  EIL); and the  
694 high aphid population field was Rosemount 1 (peak density  $\gg$  EIL). Dotted line = No numerical  
695 response by *H. axyridis*; Dot-dash line = low intensity numerical response; dashed line =  
696 intermediate intensity numerical response; solid line = high intensity numerical response (see  
697 Figure 3 for *H. axyridis* numerical responses.



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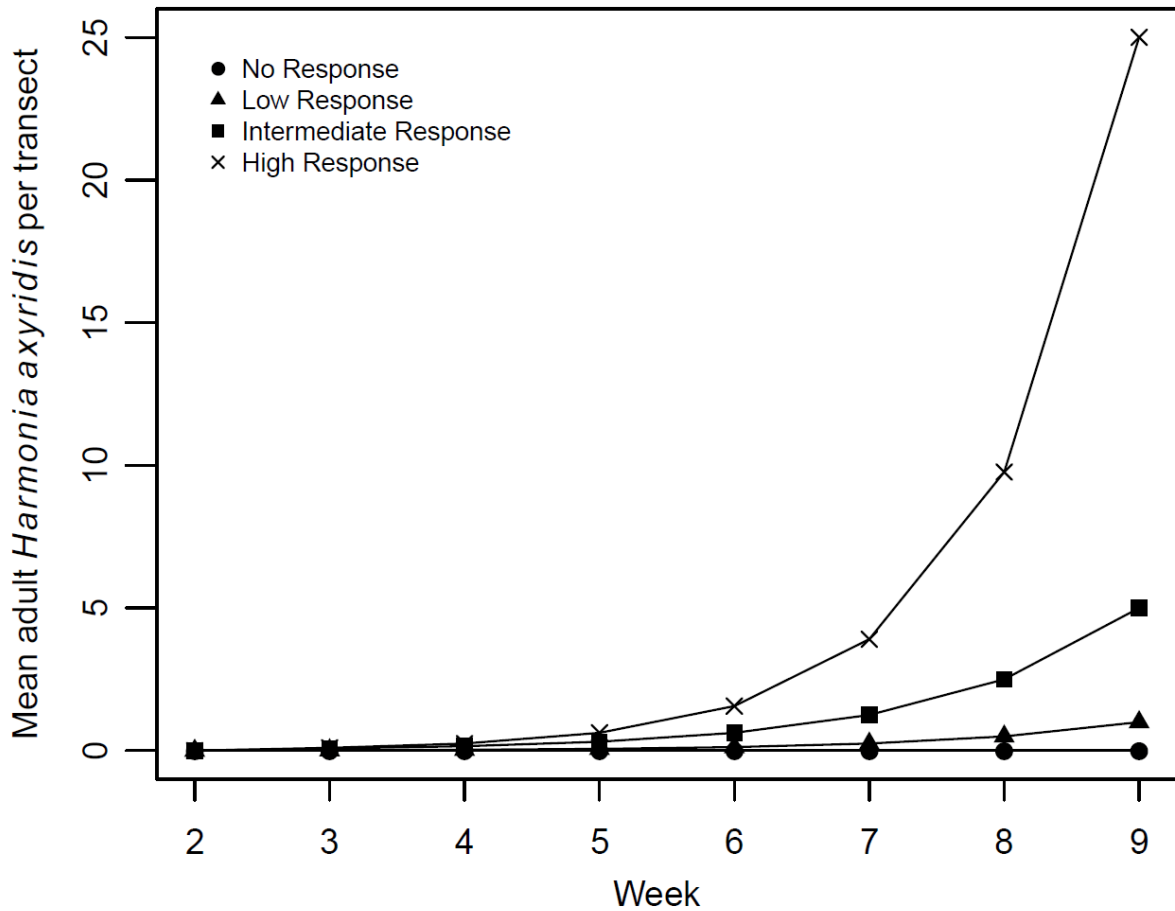
699 Figure 1. Mean ( $\pm$  SEM) weekly soybean aphid abundance per plant observed in 12 Minnesota  
 700 soybean fields from 25 June 2007 – 10 August 2007. Line below x-axis indicates duration of  
 701 cage experiment in the respective field.



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703 Figure 2. Mean ( $\pm$  SEM) weekly adult *Harmonia axyridis* abundance per 25 m walking transect  
 704 observed in 12 Minnesota soybean fields from 25 June 2007 – 10 August 2007.

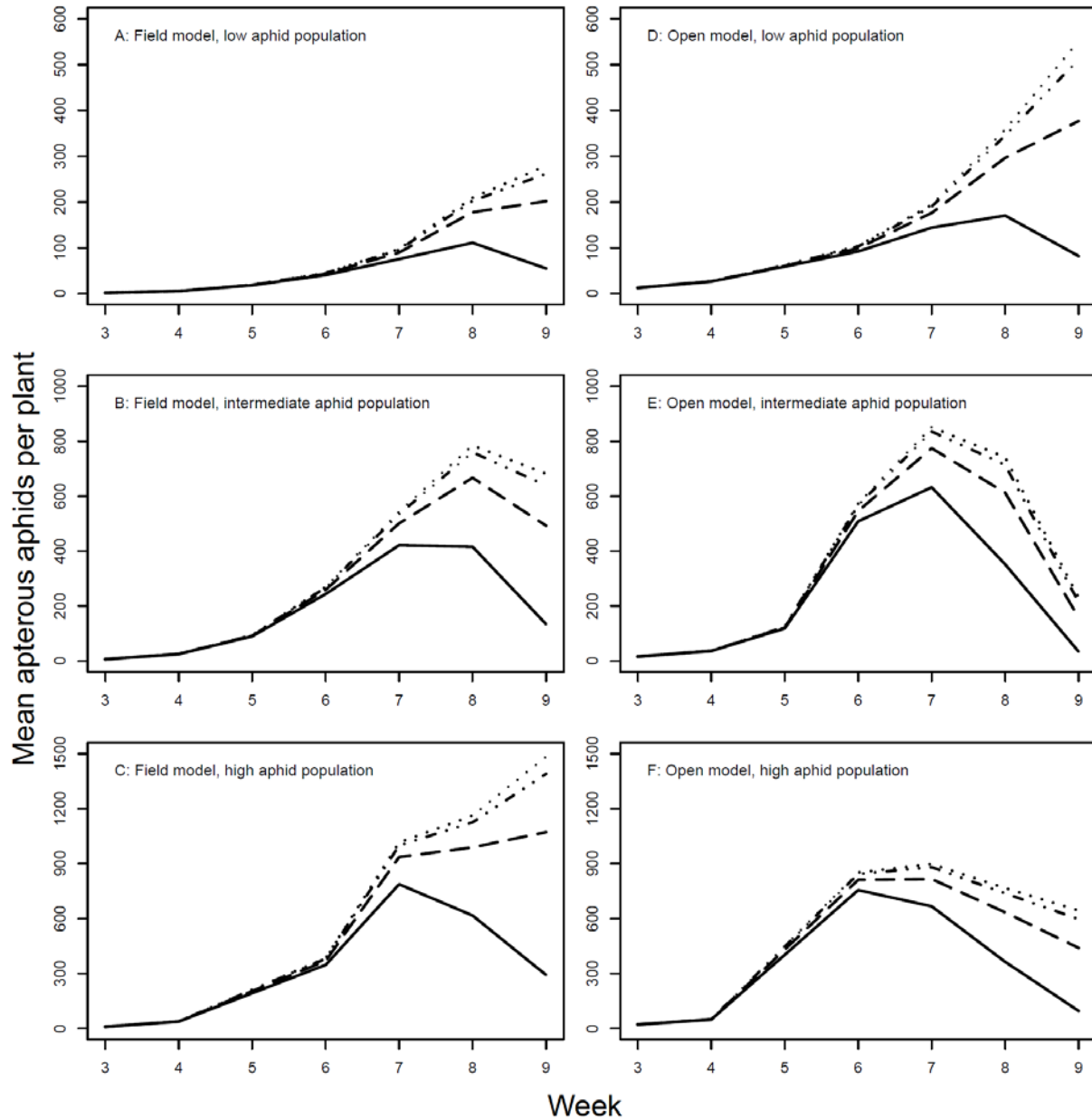
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707 Figure 3. Modeled numerical response intensities for *Harmonia axyridis*. Value ranges were set  
 708 to represent the range of responses observed in Minnesota soybean fields in 2007 and used for  
 709 predictive purposes to visualize the effect of *H. axyridis* on soybean aphids (Figure 4) based on  
 710 our GLM models. Each transect represents 25 linear-m of soybean.

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713 Figure 4. Predicted effect of *Harmonia axyridis* on apterous aphid abundance for three  
 714 representative soybean fields using Field (subplots A,B,C) and Open models (subplots D,E,F)  
 715 (Table 2). The low aphid population field was Waseca 2 (peak density close to the ET); the  
 716 intermediate aphid population field was Rosemount 3 (peak aphid density > ET, < EIL); and the  
 717 high aphid population field was Rosemount 1 (peak density >> EIL). Dotted line = No numerical  
 718 response by *H. axyridis*; Dot-dash line = low intensity numerical response; dashed line =  
 719 intermediate intensity numerical response; solid line = high intensity numerical response (see  
 720 Figure 3 for *H. axyridis* numerical responses.

721

722 **Appendix A**

723 Table A.1. Relationship between natural enemy and aphid populations using sweep-net count natural enemy predictor variables for 12  
 724 Minnesota soybean fields from 25 June 2007 – 10 August 2007.

Apterous aphid = Aphid density exclusion + Alate density + <i>H. axyridis</i> adult + <i>C. septempunctata</i> adult + <i>O. insidiosus</i> all stages + Week + Week <sup>2</sup> + Field <sup>a</sup>				
Sweep-net				
Field counts <sup>b</sup>	Estimate	Standard error	Z-value	p-value
Intercept	-2.2541	0.754	-2.99	2.78 x 10 <sup>-3</sup>
Aphid exclusion cage	-0.0001	0.0002	-0.41	0.68
Alate field	-0.0242	0.0761	-0.32	0.75
<i>H. axyridis</i> adult sweep-net	-0.1864	0.0372	-5.01	5.55 x 10 <sup>-7</sup>
<i>C. septempunctata</i> adult sweep-net	0.1706	0.197	0.86	0.39
<i>O. insidiosus</i> all stages sweep-net	0.1820	0.0448	4.07	4.81 x 10 <sup>-5</sup>
Week	1.6700	0.251	6.66	2.69 x 10 <sup>-11</sup>
Week <sup>2</sup>	-0.0661	0.0211	-3.13	1.76 x 10 <sup>-3</sup>
Open plant counts <sup>c</sup>				
Intercept	0.1733	0.641	0.27	0.79
Aphid exclusion cage	0.0006	0.0002	3.32	9.08 x 10 <sup>-4</sup>
Alate open plant	0.0441	0.0109	4.04	5.25 x 10 <sup>-5</sup>
<i>H. axyridis</i> adult sweep-net	-0.1280	0.0373	-3.43	6.03 x 10 <sup>-4</sup>
<i>C. septempunctata</i> adult sweep-net	-0.0087	0.186	-0.05	0.96
<i>O. insidiosus</i> all stages sweep-net	0.0978	0.0450	2.17	0.03
Week	1.0503	0.216	4.88	1.09 x 10 <sup>-6</sup>
Week <sup>2</sup>	-0.0479	0.0190	-2.52	0.01

<sup>a</sup> For simplicity, estimates for the effect of each field on aphid abundance not shown. Field is a significant predictor of Apterous aphid abundance (Analysis of deviance: Field counts model, df = 11,  $p < 0.0001$ ; Open plant counts model, df = 11,  $p < 0.0001$ )

<sup>b</sup> Apterous aphid response variable and Alate aphid predictor variable based on field counts

<sup>c</sup> Apterous aphid response variable and Alate aphid predictor variable based on open plant counts



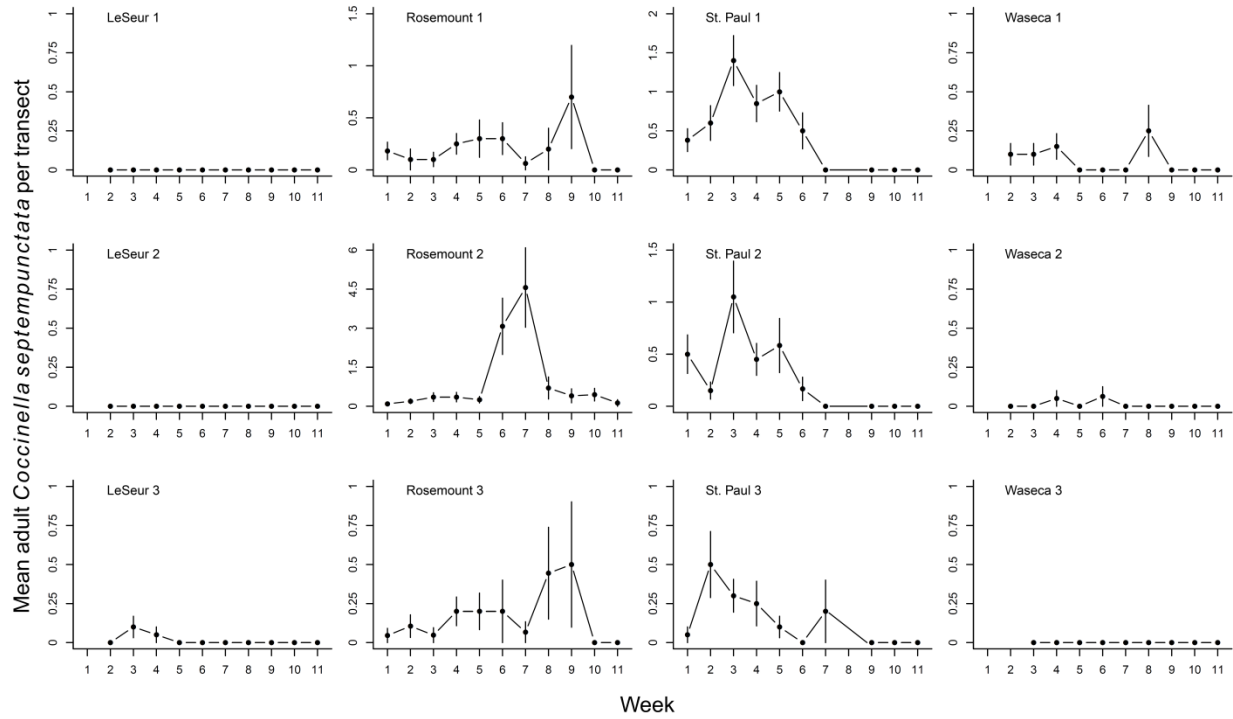
725 Table A.2. Relationship between natural enemy and aphid populations using NEU plant count natural enemy predictor variables for 12  
 726 Minnesota soybean fields from 25 June 2007 – 10 August 2007.

Apterous aphid = Aphid density exclusion + Alate density + NEU + Week + Week <sup>2</sup> + Field <sup>a</sup>				
Natural enemy units (per plant)				
Field counts <sup>b</sup>	Estimate	Standard error	Z-value	p-value
Intercept	-3.063	0.737	-4.16	3.20 x 10 <sup>-5</sup>
Aphid exclusion cage	0.0004	0.0002	1.92	5.49 x 10 <sup>-2</sup>
Alate field	0.140	0.0853	1.64	0.10
NEU	-0.125	0.536	-0.23	0.82
Week	1.987	0.255	7.78	7.14 x 10 <sup>-15</sup>
Week <sup>2</sup>	-0.106	0.0210	-5.07	4.06 x 10 <sup>-7</sup>
Open plant counts <sup>c</sup>	Estimate	Standard error	Z-value	p-value
Intercept	-0.538	0.569	-0.94	0.35
Aphid exclusion cage	0.0009	0.0002	4.86	1.18 x 10 <sup>-6</sup>
Alate open plant	0.0543	0.0111	4.91	9.10 x 10 <sup>-7</sup>
NEU	0.254	0.488	0.52	0.60
Week	1.289	0.204	6.34	2.38 x 10 <sup>-10</sup>
Week <sup>2</sup>	-0.0773	0.0171	-4.53	5.84 x 10 <sup>-6</sup>

<sup>a</sup> For simplicity, estimates for the effect of each field on aphid abundance not shown. Field is a significant predictor of Apterous aphid abundance (Analysis of deviance: Field counts model, df = 11,  $p < 0.0001$ ; Open plant counts model, df = 11,  $p < 0.0001$ )

<sup>b</sup> Apterous aphid response variable and Alate aphid predictor variable based on field counts

<sup>c</sup> Apterous aphid response variable and Alate aphid predictor variable based on open plant counts

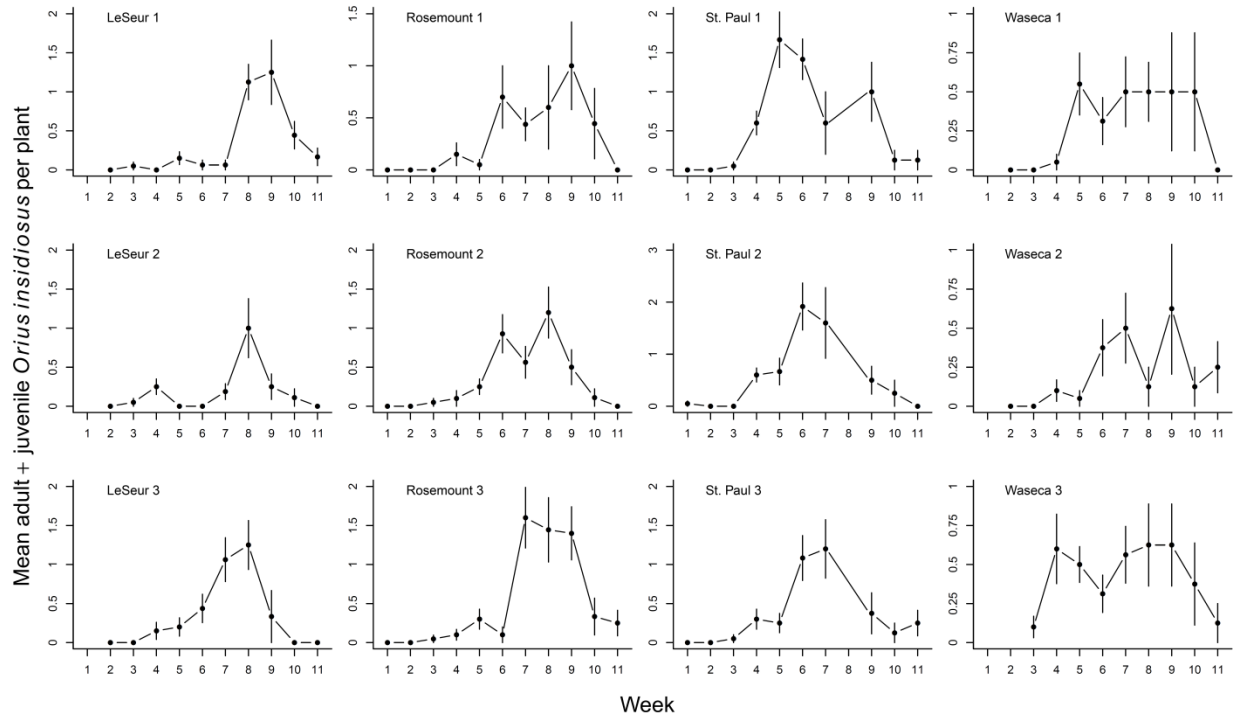


727

728 Figure A.1. Mean ( $\pm$  SEM) weekly adult *Coccinella septempunctata* abundance per transect

729 observed in 12 Minnesota soybean fields from 25 June 2007 – 10 August 2007.

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731

732 Figure A.2. Mean ( $\pm$  SEM) weekly adult + juvenile *Orius insidiosus* abundance per plant

733 observed in 12 Minnesota soybean fields from 25 June 2007 – 10 August 2007.

734