

1 **Brassica aphid (Hemiptera: Aphididae) populations are conditioned by**  
2 **climatic variables and parasitism level: a study case of Triângulo**  
3 **Mineiro, Brazil.**

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6 **Marcus V. Sampaio<sup>1</sup>, Ana P. Korndörfer<sup>1</sup>, Juli Pujade-Villar<sup>2</sup>, Jorge E. A.**  
7 **Hubaide<sup>1</sup>, Samira E. Ferreira<sup>1</sup>, Suelen O. Arantes<sup>1</sup>, Dener M. Bortoletto<sup>1</sup>, Cássia**  
8 **M. Guimarães<sup>1</sup>, Josep A. Sánchez-Espigares<sup>3</sup>, Berta Caballero-López<sup>4,5\*</sup>**

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10 <sup>1</sup> Federal University of Uberlândia, Agronomic Institute, Uberlândia – Minas Gerais, Brazil.

11 <sup>2</sup> Dept. of Animal Biology, Faculty of Biology, University of Barcelona, Spain.

12 <sup>3</sup> Dept. of Statistics and Operations Research, Technical University of Catalonia, Barcelona, Spain.

13 <sup>4</sup> MCNB. Natural Sciences Museum of Barcelona, Laboratory of Nature, Arthropods Dept., Barcelona, Spain

14 <sup>5</sup> Agroecosystems research group Dept. of Plant Biology, Faculty of Biology, University of Barcelona, Barcelona,  
15 Spain

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18 **Keywords:** *Brevicoryne brassicae*; *Lipaphis pseudobrassicae*; *Myzus persicae*;  
19 parasitism; climatic variables; hurdle models.

20  
21 **Key message:**

- 22 • Aphids are one of the most important pests of Brassicaceae crops.
- 23 • A correct assessment of the biotic and the abiotic factors that regulate insect
- 24 populations is an essential component of Integrated Pest Management.
- 25 • *Brevicoryne brassicae* were found in similar numbers on all leaves of plants.
- 26 • *Myzus persicae* and *Lipaphis pseudobrassicae* were found in greater numbers on
- 27 middle and lower leaves.
- 28 • The interaction of temperature and precipitation negatively affected aphid
- 29 populations.
- 30 • Parasitoids have the same distribution on plants as their hosts.
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\* Corresponding author's address: Arthropods Dept, Lab. of Nature, Museu de Ciències Naturals de Barcelona, Picasso Av., E-08003 Barcelona (Catalonia/Spain). E-mail address: [bcaballerolo@bcn.cat](mailto:bcaballerolo@bcn.cat), Phone: (+34) 93 256 22 11.

## 32 **Abstract**

33 Cosmopolitan pests such as *Brevicoryne brassicae*, *Lipaphis pseudobrassicae*, and  
34 *Myzus persicae* (Aphididae) cause significant damage to Brassicaceae crops.  
35 Assessment of the important biotic and abiotic factors that regulate these pests is an  
36 essential step in the development of effective Integrated Pest Management programs for  
37 these aphids. This study evaluated the influence of leaf position, precipitation,  
38 temperature, and parasitism on populations of *L. pseudobrassicae*, *M. persicae*, and *B.*  
39 *brassicae* in collard greens fields in the Triângulo Mineiro region (Minas Gerais state),  
40 Brazil. Similar numbers of *B. brassicae* were found on all parts of the collard green  
41 plants, whereas *M. persicae* and *L. pseudobrassicae* were found in greatest numbers on  
42 the middle and lower parts of the plant. While temperature and precipitation were  
43 positively related to aphid population size, their effects were not accumulative, as  
44 indicated by a negative interaction term. Although *Diaeretiella rapae* was the main  
45 parasitoid of these aphids, hyperparasitism was dominant; the main hyperparasitoid  
46 species recovered from plant samples was *Alloxysta fuscicornis*. Parasitoids seem to  
47 have similar distributions on plants as their hosts. These results may help predict aphid  
48 outbreaks and gives clues for specific intra-plant locations when searching for and  
49 monitoring aphid populations.

50

## 51 **Introduction**

52 The aphid species *Brevicoryne brassicae* (L.), *Lipaphis pseudobrassicae* (Davis),  
53 and *Myzus persicae* (Sulzer) are cosmopolitan pests that cause substantial damages to  
54 plants in the Brassicaceae family (Blackman and Eastop 2000; Micic, 2005, Collier and  
55 Finch, 2007, Gu et al. 2007).

56 Aphid-parasitoid interactions on Brassica crops constitute a complex system that

57 has been much studied because of its importance to biological control (Waterhouse and  
58 Sands 2001, Cividanes 2002; Akhtar et al. 2010). For instance, the endoparasitoid  
59 *Diaeretiella rapae* (McIntosh) (Braconidae, Aphidiinae) may significantly affect the  
60 biotic regulation of aphid populations (Mackauer and Völkl 1993; Sullivan and Völkl  
61 1999) including those of *Brevicoryne brassicae*, *L. pseudobrassicae*, and *M. persicae*,  
62 all known hosts of *D. rapae* (Starý et al. 2007). Nonetheless, it is well known that both  
63 abiotic and biotic factors regulate insect populations (Price et al. 2011) and so assessing  
64 the relative effects of these factors on natural pest populations is as difficult as it is  
65 essential for improving future controls of these aphid species (Dent 1995). For example,  
66 studies aimed to establish whether or not hyperparasitoids interfere with the impact  
67 of primary parasitoids on aphid populations (Höller et al., 1993), works dealing with  
68 the effect of environmental conditions on the parasitism rate (Zamani et al., 2006), and  
69 research into the feasibility of the Integrated Pest Management of certain parasitoids  
70 that naturally occur under fluctuating conditions (Desneux & Ramirez-Romero, 2006)  
71 have all been widely conducted in the Northern Hemisphere. However, a broader  
72 perspective of the maintenance of natural aphid-natural enemy interactions in tropical  
73 regions is lacking. Thus, the study of Brassica aphids appears to be a suitable model for  
74 further exploring the effect of abiotic conditions on aphid-parasitoid interactions. This  
75 approach is particularly interesting, as few studies have ever been carried out under field  
76 conditions in the Tropical region.

77         The research reported here aimed to examine the influence of abiotic and biotic  
78 variables on Brassica aphids under field conditions. We first investigated the influence  
79 of leaf position, precipitation (estimated as seven-day accumulated values), and average  
80 temperature on populations of *L. pseudobrassicae*, *M. persicae*, and *B. brassicae*. We  
81 hypothesized that the response of aphid species to temperature would follow the same

82 gradient in the field as it had under laboratory conditions. In addition, we expected that  
83 leaf position would also have an effect on aphid distribution and that species colonizing  
84 the lower leaves of the plant would be less affected by precipitation than those  
85 colonizing upper leaves. Secondly, we investigated the influence of abiotic and biotic  
86 variables on the communities of *L. pseudobrassicae*, *M. persicae*, and *B. brassicae*  
87 parasitoids in collard fields.

## 88 **Materials and methods**

### 89 *Experiment setup*

90 Our study was conducted in the fields of the Glória Experimental Farm of the  
91 Federal University of Uberlândia in southeastern Brazil (18°57'07"S, 48°12'27"W).  
92 This farm is in the Triângulo Mineiro region and lies in the Brazilian Savannah  
93 ecosystem, locally known as the Cerrado. This ecosystem occupies about 20% (206  
94 million ha) of Brazil's land surface, although in the past 30 years 50% of the natural  
95 vegetation has been replaced by agricultural crops and cultivated pastures (Assunção  
96 and Chiavari 2015). The agriculture of the Cerrado provides 60% of Brazilian grain  
97 (mainly soybean and corn), 75% of its cotton, and 19% of its sugar cane, and also  
98 harbours 50% of its cattle, which demand large areas of pastureland (CONAB 2015).  
99 The Cerrado includes a great diversity of habitats, from open fields to dense forest  
100 formations, and has two well-defined seasons (dry winter and rainy summer). Although  
101 its soils' morphological and physical characteristics vary widely, the predominant soils  
102 (about 54%) are latosols that are generally nutrient-poor (especially phosphorus) and  
103 highly weathered, and have a low cation exchange capacity and high acid and  
104 aluminium toxicity (Malavolta and Kliemann 1985).

105 The farm's fields are surrounded by cropland (corn and soybean) and pastures.  
106 The crops are rotated and the position of each crop is changed every year. The rotation

107 schedule include collard greens, cabbages, cauliflowers, lettuces, beet, and carrots.  
108 Taking into account the crop rotation system adopted in the fields, the study was  
109 conducted in a similar matrix structure in two enclosed areas (100 m apart) inside the  
110 fields. Collard greens *Brassica oleracea* var. *acephala* L. was chosen as the aphids' host  
111 plant due to its importance as a food crop in Brazil and the peculiarities of the  
112 disposition of its leaves. This species constantly produces new leaves from the top of  
113 the plant, which allows the plant's aphid distribution to be observed for longer than on  
114 other Brassica crop species. By contrast, other Brassicae crops such as cabbage,  
115 cauliflower, and broccoli stop producing new leaves in order to form flowering heads  
116 (Filgueira 2003).

117         Seedlings were taken from the lateral shoots of the mother plants of the Talo  
118 Roxo cultivar and kept in 2-litre plastic bags with organic substrate in a greenhouse for  
119 one month. Afterwards, seedlings were transplanted into the field. The plants in the  
120 experiment in Area 1 were planted in July 2005 and sampling was carried out in August  
121 2005–March 2006. This experimental field consisted of two rows, each of 35 plants,  
122 and one row of 19 plants, giving a total of 89 collard green plants. The second study site  
123 (Area 2) was planted in September 2006 and sampling was carried out in October 2006–  
124 January 2008. In this case, the experimental field had three rows, each of 25 plants,  
125 giving a total of 75 collard green plants. In both areas, the spacing between plants was  
126 constant: one meter between rows and 0.5 meters between plants.

127         In both experimental areas, only organic fertilizer was applied (at 10 kg cattle  
128 manure per meter) and no insecticides were used. Sprinkler irrigation was performed  
129 daily and lateral shoots were manually removed each week.

130         In southeastern Brazil, where this study was conducted, the highest  
131 temperatures and rainfall occur in September–March (IBGE, 2010). We counted aphid

132 populations in 101 samples taken in the hot rainy season, since the chief aim of the  
133 study was to assess the effects of high temperatures and precipitation on aphid  
134 populations. Climatic data were obtained from a meteorological station located about  
135 500 m from the experimental areas.

136

137 *Sampling of insects and species identification*

138 To quantify aphid population dynamics, samples were taken on a weekly basis  
139 (32 samples over the course of the experiment for Area 1 and 69 for Area 2). Each  
140 sample consisted of three randomly selected plants, one from each row in each plot. A  
141 total of three leaves per plant were removed and examined, one from each of the three  
142 positions (upper, middle, and lower). Upper leaves were considered to be upright and  
143 still expanding; middle leaves were fully expanded but not yet senescent; and lower  
144 leaves had already reached senescence. All samples were taken from plants that had  
145 been in the field for at least one month, enough time to permit aphid colonization. In  
146 order to guarantee the independence of the samples taken from a plant, the sampling  
147 design include a restriction that the same plant would not be sampled again for another  
148 four weeks.

149 In the lab, the parasitized and non-parasitized individuals of each of the three  
150 aphid species were counted and studied under a stereoscopic microscope. After  
151 identifying the parasitized aphid species, including mummified individuals and empty  
152 mummies (bearing the parasitoid's exit hole), mummies were removed from leaves and  
153 placed in separate Eppendorf tubes. These tubes were kept for up to a year to allow  
154 primary and secondary parasitoids to hatch. However, practically all parasitoids and  
155 hyperparasitoids emerged within two weeks and were identified to family, genera, or  
156 species level whenever possible following (Pike et al. 1997; Powell, 1982).

157 *Data analyses*

158           Since aphids tend to congregate, when monitoring aphid population dynamics  
159 in crops it is not unusual to find no aphids on successive samples but then find a very  
160 large concentration once a colony is encountered (Maunder and Punt 2004). One  
161 solution to this clumping is to adopt what are generally known as ‘hurdle models’ since  
162 sampling rates of zero can complicate calculations and, in addition, if not properly  
163 modeled the presence of many zero rates can invalidate an analysis’ assumptions and  
164 jeopardize the integrity of the inferences (Potts and Elith 2006). The use of hurdle  
165 models is particularly suited to datasets with many zeros (Maunder and Punt 2004;  
166 Mayer et al. 2005).

167           Hurdle modeling combines two components that are simply two particular  
168 examples of generalized linear models (McCullagh and Nelder 1989). For the binary  
169 component of the conditional model, we used a logistic model assuming a binomial  
170 distribution given the binary nature (presence/absence) of the zero catch rates (Mayer et  
171 al. 2005; O’Neill and Faddy 2003; Potts and Elith 2006). By contrast, for the second  
172 component of the conditional model we used a log-normal distribution (conditional  
173 upon their presence), the most commonly selected distribution model (Maunder and  
174 Punt 2004; Potts and Elith 2006), after checking the normal distribution of the residuals  
175 of the obtained data set.

176           In order to meet the assumption of the dependence of simultaneously taken  
177 observations, the analyses of the biotic and abiotic factors affecting aphids’ density and  
178 parasitism rates were tested using generalized linear mixed models (Bates et al., 2008).

179           Analyses were conducted for the three main aphid species, *B. brassicae*, *L.*  
180 *pseudobrassicae*, and *M. persicae*. In all analyses, leaf position (upper, middle, and  
181 lower), average weekly temperature, seven-day accumulated precipitation, and the

182 interaction between average temperature and accumulated precipitation were included  
183 as fixed factors. The sampling period was included as a random effect term to account  
184 for the fact that samples taken at the same time were not independent.

185 In the analyses, aphid density was taken as the number of parasitized aphids +  
186 the number of non-parasitized aphids, while the parasitism rate was the number of  
187 mummified aphids/aphid density. All mummified aphids are used in the analyses,  
188 including both empty mummies and mummies from which parasitoids did not emerge.

189 *Ad hoc* contrasts from ANOVA variance were evaluated for the three species  
190 of aphid to compare their relative abundance after adjusting for leaf position.

191 All analyses were performed on R 3.0.2 (R Development Core Team 2013);  
192 library lme4 (Bates et al. 2008) was used for model fitting and library lmerTest  
193 (Kuznetsova et al, 2013) was used for inference methods with mixed models.

194

## 195 **Results**

### 196 *Aphid, parasitoid and hyperparasitoid abundance*

197 A total of 469,795 Brassicae aphids were counted during the 101 sampling  
198 sessions. With a total of 303,200 individuals, *Brevicoryne brassicae* was the most  
199 abundant aphid species found, followed by *L. pseudobrassicae* (153,364) and *M.*  
200 *persicae* (13,231). In terms of the average population density of the three aphid species,  
201 *B. brassicae* was more abundant than both *L. pseudobrassicae* ( $t = -3.58$ ,  $P < 0.001$ ) and  
202 *M. persicae* ( $t = -6.93$ ,  $P < 0.001$ ); the population of *L. pseudobrassicae* was greater than  
203 that of *M. persicae* ( $t = 3.35$ ,  $P < 0.002$ ). The population dynamics of each aphid species  
204 was distinct: while *L. pseudobrassicae* was abundant throughout the sampling period, *B.*  
205 *brassicae* was all but absent in October 2005–August 2007 and *M. persicae* in  
206 December 2006–August 2007. Aphid species have their own endogenous intra-annual

207 rhythm: *B. brassicae* is mostly unimodal, while *M. persicae* and *L. pseudobrassicae* are  
208 both bimodal (Figure 1).

209 The relative abundance of the hyperparasitoids that emerged from the mummies  
210 of the three aphid species was greater than that of the primary parasitoids (Table 1). The  
211 most abundant primary parasitoid was *D. rapae*, while *Alloxysta fuscicornis* (Hartig)  
212 was the most abundant hyperparasitoid. However, a large number of *Syrphophagus*  
213 hyperparasitoids also emerged from *L. pseudobrassicae* and *M. persicae* mummies.  
214 Hyperparasitoids belonging to the genus *Pachyneuron* were infrequent and parasitoids  
215 of the genus *Aphelinus* and hyperparasitoids of the genera *Dendrocerus* and  
216 *Tetrastichus* only occurred sporadically (Table 1).

217 Aphid parasitism of *B. brassicae* averaged  $16.2 \pm 2.28$  %, with a maximum of  
218 87.5 % from a single sampling sessions. For *L. pseudobrassicae*, parasitism averaged  
219  $0.8 \pm 0.19$  %, with a maximum parasitism of 11.1%, while for *M. persicae* parasitism  
220 averaged  $8.5 \pm 1.44$  %, with a maximum of 72.2 %.

221

#### 222 *Influence of climatic factors on aphids and parasitism*

223 During the sampling period, climatic conditions followed the typical pattern for  
224 southeastern Brazil in the rainy season (September–March). The highest temperatures  
225 were registered during this period (Figure 1). A common feature of the three aphids'  
226 populations was the occurrence of a population peak between September and November  
227 (spring) at the beginning of the rainy season. Aphid population patterns are also  
228 correlated with peaks in the populations of primary and secondary parasitoids, which  
229 was especially obvious in the case of *B. brassicae* (Figure 1).

230 Responses to temperature and precipitation in these Brassica aphids varied  
231 according to species. Higher temperatures benefited the presence of *B. brassicae* and *M.*

232 *persicae*, and favoured their abundances whenever they were present (Tables 2 and 3).  
233 Similarly, precipitation positively affected the presence of *B. brassicae* and *M. persicae*,  
234 although only the abundance of *B. brassicae* seems to be determined by precipitation  
235 patterns. By contrast, the presence and range of abundance of these two species was  
236 negatively related to the interaction between temperature and precipitation (Tables 2  
237 and 3). Variation in *L. pseudobrassicae* colonies was not significantly related to any of  
238 those climatic variables.

239 In turn, parasitism rates of the three species varied in relation to climatic variables.  
240 Although both precipitation and temperature increased the parasitism rates in these  
241 species, the interaction between these two climatic variables had a negative effect on the  
242 parasitized aphids' presence (Tables 5, 6, 7).

243

#### 244 *Intra-plant distribution effects on aphids and parasitism*

245 Both *L. pseudobrassicae* and *M. persicae* populations were significantly related  
246 to leaf position. The logistic model showed that there was a greater probability of  
247 finding colonies of both species on the middle and lower leaves than on the upper  
248 leaves. Nevertheless, the lognormal model indicates that when colonies of these species  
249 are present the number of individuals is also positively related with those positions, with  
250 greater populations on middle and lower leaves than on upper leaves (Tables 3 and 4).  
251 The presence of parasitized aphids of these two species followed the same pattern as for  
252 the aphid species themselves: more on middle and lower leaves than on upper leaves  
253 (Tables 6 and 7).

254 By contrast, neither the presence nor density of *B. brassicae* was significantly  
255 affected by intra-plant location, a phenomena that might be explained by the greater  
256 abundance of *B. brassicae*, a species that forms larger colonies with more individuals

257 than the other two species. Nonetheless, intra-plant locations do explain the greater  
258 range of *B. brassicae* parasitism on the bottom leaves than on the upper ones, as the  
259 significant effect indicates (Table 5). However, the probability of finding parasitized  
260 individuals showed no significant relation to leaf position.

261

## 262 **Discussion**

263 Our results add to a growing body of work that indicates that both abiotic and  
264 biotic factors play an important role in Brassica aphid regulation (Waterhouse and  
265 Sands 2001; Cividanis 2002; Micic 2005; Akhtar et al. 2010). However, the particular  
266 effects of these factors differed between species.

267 During each of the 101 weekly sampling periods 303 plants and 909 leaves were  
268 inspected and in total 469,795 Brassicae aphids were counted. Of the three aphid  
269 species monitored, *B. brassicae* and *L. pseudobrassicae* were the most abundant.  
270 Although *B. brassicae* reaches higher population levels than the other two aphid  
271 species, its populations may decline in number and even disappear for several months.  
272 According to Micic (2005), *B. brassicae* tends to colonize heavily single plants or small  
273 groups of plants and create 'hot spots' within crops. High aphid populations may reduce  
274 plant quality and, according to Dixon (1977) and Karley et al. (2004), such a reduction  
275 may negatively influence aphid population size.

276

### 277 *Effects of intra-plant distribution on aphids*

278 *Brevicoryne brassicae* was the only species that was evenly distributed across all  
279 three plant strata. Both *L. pseudobrassicae* and *M. persicae* were more abundant in the  
280 middle and lower regions of the collard plants. A greater concentration of defensive  
281 compounds is expected to exist in young upper-region collard leaves due their

282 importance in areas with greater photosynthetic activity (Brown et al. 2003; Reifenth  
283 and Müller 2007). Thus, their ability to avoid Brassicaceae defense compounds, i.e.  
284 glucosinolates (MacGibbon and Beuzenberg 1978; Weber et al. 1986; Bridges 2002),  
285 may explain differences in the intra-plant distributions of the aphid species that colonize  
286 Brassica species. Both *B. brassicae* and *L. pseudobrassicae* can synthesize the enzyme  
287 myrosinase and thus hydrolyze glucosinolates as a defence against their toxic effects  
288 (MacGibbon and Beuzenberg 1978; Weber et al. 1986; Bridges 2002); conversely, *M.*  
289 *persicae* cannot (Weber et al. 1986). According to MacGibbon and Beuzenberg (1978),  
290 *B. brassicae* has higher levels of myrosinase activity than *L. pseudobrassicae*, which  
291 may allow it to colonize young leaves with greater glucosinolate levels. Other feasible  
292 explanations for the presence *B. brassicae* on higher leaves is that its greyish-white  
293 powdery wax covering offers greater waterproofing, or that the colour of its wax makes  
294 it less obvious to would-be predators (Pope, 1983).

295         These varying intra-plant distributions of the aphid species that colonize  
296 *Brassica* indicate that the upper leaves of these plants are the best for searching for and  
297 monitoring *B. brassicae* populations; on the other hand, the middle leaves are the most  
298 useful for searching for populations of all three aphid species.

299

### 300 *Abiotic factors effects on aphids*

301         A rise in temperature provoked a population increase in *B. brassicae* and *M.*  
302 *persicae* without seeming to affect *L. pseudobrassicae*. Constant-temperature laboratory  
303 studies of the biology of aphids that attack *Brassica* suggest that *L. pseudobrassicae* has  
304 a greater tolerance (Liu and Meng 2000; Godoy and Cividanes 2002) to higher  
305 temperatures than either *M. persicae* (Liu and Meng 1999; Kanegae and Lomônaco  
306 2003) or *B. brassicae* (Cividanes 2003; Satar et al. 2005). However, at a constant

307 temperature of 30°C, *M. persicae* did not develop and all individuals died (Kanegae and  
308 Lomônaco 2003). At the same temperature, *B. brassicae* merely showed a reduction in  
309 its development speed that did not affect its relative mortality rate (Cividanes 2003). By  
310 contrast, at 30°C the development rate of *L. pseudobrassicae* continued with no negative  
311 effects (Godoy and Cividanes 2002), thereby suggesting that *L. pseudobrassicae* has the  
312 greatest tolerance of these three aphid species to high temperatures. That there was no  
313 negative effect of high temperature on these three aphid species indicates that the  
314 average temperature during the sampling period was optimal for the development of  
315 Brassica aphids.

316 As in the case of temperature, a rise in precipitation increased the populations of  
317 both *B. brassicae* and *M. persicae* but did not influence those of *L. pseudobrassicae*.  
318 The mechanical effect of precipitation – for example, during intense rainstorms – may  
319 cause aphid populations to fall or even disappear from a crop (Pinto et al. 2000; Karley  
320 et al. 2004), and is likely to affect most of all the species that use the plant's apical  
321 leaves (Pinto et al. 2000) since the upright position of these leaves offers little  
322 protection. Although other studies have observed a reduction in *B. brassicae*  
323 populations coinciding with an increase in precipitation (Dixon 1977; Cividanes 2002),  
324 we observed no such reduction in *B. brassicae* in our study. Thus, the effect of rain and  
325 its relationship with upper leaf colonization needs to be more fully investigated for this  
326 aphid species.

327 The significant negative interaction between temperature and precipitation  
328 indicating that the combination of high temperatures and precipitation has a negative  
329 impact on aphid populations could be interpreted in biological terms (as we discuss  
330 below) or from a more technical standpoint.

331 In spring and summer, heavy rains and high temperatures are common in the

332 study region. The positive effect of precipitation and temperature on aphid populations  
333 suggests that increases could be represented by a straight line. However, this pattern is  
334 only true for a certain range of values and will not increase indefinitely, since extreme  
335 temperatures will not have a positive effect on any aphid population. Thus, when these  
336 continually increasing variables begin to approach an asymptote, their interaction  
337 should be understood as a small negative correction or adjustment of their sum.

338

### 339 *Population dynamics of aphids and parasitoids*

340 *Brevicoryne brassicae* peaked once a year between the second week of  
341 September and the second week of October. Conversely, *L. pseudobrassicae* and *M.*  
342 *persicae* peaked twice a year, with one peak in September–November and another in  
343 January–March.

344 It is impossible to determine when aphid species reach the fields in Uberlandia  
345 because they are almost always there and so it is rare to fail to find aphids in, for  
346 example, a two-week sampling period. Unlike in temperate regions, where aphids  
347 disappear for some months, this pattern is common in the Tropics. Of the total of  
348 samples taken, in 67% *L. pseudobrassicae* was present, in 48 % *B. brassicae* was  
349 present, and in 33 % *M. persicae* was present. Similarly, Auad *et al.* (1997) found  
350 aphids on peach leaves throughout the year in Brazil, while Jenkins *et al.* (2011) report  
351 that aphids could be a problem in canola in Australia in autumn, winter and spring, that  
352 is, almost the whole year.

353 A whipsaw effect in parasitoid populations can generally be explained by  
354 fluctuations in host populations (Haddad *et al.* 2001; Caballero-López *et al.* 2012); thus,  
355 the response of *D. rapae* to temperature and precipitation was quite similar to patterns  
356 in their hosts. Likewise, the spatial distribution of parasitism across plants followed the

357 same trend as that of the host aphid, with an increase in the percentage of parasitism  
358 wherever aphid density was greatest. These findings can be linked to observations that  
359 the parasitoid *D. rapae* prefers to search and increase patch time on plant parts with  
360 hosts or where they find cues such as honeydew indicating the presence of hosts (Ayal  
361 1987; Sheehan and Shelton 1989). Additionally, as Shaltiel and Ayal (1998) have  
362 reported, the number of aphids attacked by *D. rapae* is greater in large host populations.  
363 Nonetheless, the emergence rates of primary parasitoids for *L. pseudobrassicae* is very  
364 low, 11% parasitism being much lower than the 60% previously reported (Jeon et al.  
365 2005; Akhtar et al. 2010). Conversely, emergence rates of secondary parasitoids are  
366 astonishingly high. Thus, our findings support previous studies that suggest that primary  
367 parasitoids may be constrained by the presence of secondary parasitoids (Mackauer and  
368 Völkl 1993; Sullivan and Völkl 1999), which may also significantly affect the biotic  
369 regulation of aphid populations. According to our results, the impact of *D. rapae* on  
370 aphid regulation is limited due to the abundance of secondary parasitoids such as *A.*  
371 *fuscicornis*. The low parasitism rate of *L. pseudobrassicae* could be explained by a  
372 resistance effect in the aphid population to *D. rapae*. Laboratory studies have detected  
373 high mortality rates in immature *D. rapae*, which seems to indicate the presence of  
374 aphid clones of *L. pseudobrassicae* that are resistant to this parasitoid (Oliveira et al.  
375 2013). Aphid resistance to certain parasitoid species has been attributed to the presence  
376 of a secondary symbiont (Leclair et al. 2016, Rothacher et al. 2016) but in some cases  
377 the cause of this resistance remains unknown because it occurs in the absence of any  
378 secondary symbiont (Martinez et al. 2014). Nonetheless, we were unable to identify  
379 which was the most relevant factor for explaining the pattern of secondary parasitoid  
380 dominance or the low rate of parasitism on *L. pseudobrassicae*.

381

## 382 **Conclusions**

383 Our results show that an increase in either precipitation or temperature favours  
384 an increase in aphid populations. Nevertheless, high levels of precipitation combined  
385 with high temperatures did seem to act as a brake on Brassica aphid populations. The  
386 close match between the distribution of parasitoids and that of their hosts also suggests  
387 that there is an important biotic element in aphid population control. Thus, an efficient  
388 monitoring system taking both abiotic and biotic factors into account has the potential to  
389 improve Integrated Pest Management strategies and reduce the risk of Brassica aphid  
390 outbreaks.

391

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404

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406 **References**

- 407 **Akhtar, M.S., Dey, D., Usmani, M.K. & Choudhury, R.A.** (2010) Seasonal  
408 abundance of *Diaeretiella rapae* (M'Intosh) (Braconidae: Aphidiinae)  
409 parasitizing *Lipaphis erysimi* (Kaltenbach) (Hemiptera: Aphididae) in *Brassica*  
410 *juncea* variety Pusa bold. *Munis Entomology and Zoology* **5**, 692-696.
- 411 **Assunção, J. & Chiavari, J.** (2015) Towards efficient land use in Brazil. The New  
412 Climate Economy. URL [http://2015.newclimateeconomy.report/wp-](http://2015.newclimateeconomy.report/wp-content/uploads/2015/09/Towards-Efficient-Land-Use-Brazil.pdf)  
413 [content/uploads/2015/09/Towards-Efficient-Land-Use-Brazil.pdf](http://2015.newclimateeconomy.report/wp-content/uploads/2015/09/Towards-Efficient-Land-Use-Brazil.pdf). Accessed on  
414 [20/10/2015](http://2015.newclimateeconomy.report/wp-content/uploads/2015/09/Towards-Efficient-Land-Use-Brazil.pdf).
- 415 **Auad, A.M., Bueno, V.H.P, Kato, C.M. & Gamarra, D.C.** (1997). Ocorrência e  
416 Flutuação Populacional de Predadores e Parasitóides de *Brachycaudus* (*Appelia*)  
417 *schwartzi* (Börner) (Homoptera:Aphididae), em Pessegueiro, em Jacuí-MG.  
418 *Anais da Sociedade Entomológica do Brasil* **26**(2) 257-263
- 419 **Ayal, Y.** (1987) The foraging strategy of *Diaeretiella rapae*. *Journal of Animal Ecology*  
420 **56**, 1057-1068.
- 421 **Bates, D., Maechler, M. & Dai B.** (2008) Lme4: linear mixed-effects models using S4  
422 classes. R package version 0.999375-28 (CD.ROM)
- 423 **Blackman, R.L. & Eastop, V.P.** (2000) Aphids on the world's crops: an identification  
424 and information guide (2nd ed.) New York, J. Wiley & Sons.
- 425 **Brown, P.D., Tokuhsa, J.G., Reichelt, M. & Gershenzon, J.** (2003) Variation of  
426 glucosinolate accumulation among different organs and developmental stages of  
427 *Arabidopsis thaliana*. *Phytochemistry* **62**, 471-481.
- 428 **Bridges, M., Jones, A.M.E., Bones, A.M., Hodgson, C., Cole, R., Bartlet, E.,**  
429 **Wallsgrave, R., Karapapa, V.K., Watts, N. & Rossiter, J.** (2002) Spatial  
430 organization of the glucosinolate-myrosinase system in brassicae specialist

- 431 aphids is similar to that of the host plant. Proceedings of the Royal Society of  
432 London B **269**,187-191
- 433 **Caballero-López, B., Blanco-Moreno, J.M., Pérez, N., Michelena, J.M., Pujade-**  
434 **Villar, J., Guerreri, E., Sánchez-Espigares, J.A. & Sans, F.X.** (2012) Weeds  
435 and aphid-parasitoid communities benefit differently from organic and  
436 conventional cropping of spring cereals. Journal of Pest Science **85** (1): 81-88
- 437 **Cividanes, F.J.** (2002) Impacto de inimigos naturais e de fatores meteorológicos sobre  
438 uma população de *Brevicoryne brassicae* (L.) (Hemiptera: Aphididae) em couve.  
439 Neotropical Entomology **31**, 249-255.
- 440 **Cividanes, F.J.** (2003) Exigências térmicas de *Brevicoryne brassicae* e previsão de pios  
441 populacionais. Pesquisa Agropecuaria Brasileira **38**, 561-566.
- 442 **Cividanes, F.J. & Souza, V.P.** (2004) Distribuição vertical de pulgões (Hemiptera:  
443 Aphididae) em couve. Arquivos do Instituto Biológico **71**, 254-256.
- 444 **CONAB** (2015) (Companhia Nacional de Abastecimento). Séries Históricas. Open  
445 source. URL <http://www.conab.gov.br/conteudos.php?a=1252&>. Accessed on  
446 20/10/2015.
- 447 **Collier, R.H., Finch, S.** (2007) IPM Case Studies: Brassicas. In: van Emden, H,  
448 Harrington, R (eds.) Aphids as Crop Pests, pp. 549-559. Wallingford, United  
449 Kingdom, CABI.
- 450 **Dent, D.** (1995) Insect Pest Management. London, Chapman & Hall.
- 451 **Desneux, N. & Ramirez-Romero, R.** (2009) Plant characteristics mediated by growing  
452 conditions can impact parasitoid's ability to attack host aphids in winter canola.  
453 Journal of Pest Science **82**, 335-342.
- 454 **Dixon, A.F.G.** (1977) Aphid ecology: life cycles, polymorphism, and population  
455 regulation. Annual Review of Ecology, Evolution and Systematics **8**, 329-353

- 456 **Filgueira, F.A.R.** (2003) Novo manual de olericultura: agrotecnologia moderna na  
457 produção e comercialização de hortaliças (2nd ed) Viçosa, UFV.
- 458 **Godoy, K.B. & Cividanes, F.J.** (2002) Tabelas de esperança de vida e fertilidade para  
459 *Lipaphis erysimi* (Kalt.) (Hemiptera:Aphididae) em condições de laboratório e  
460 campo. Neotropical Entomology **31**, 41-48.
- 461 **Gu, H., Fitt, G.P., & Baker, G.H.** (2007) Invertebrate pests of canola and their  
462 management in Australia: a review. Australian Journal of Entomology **46**, 231-  
463 243.
- 464 **Haddad, N.M., Tilman, D., Haarstad, J., Ritchie, M. & Knopa, M.H.** (2001)  
465 Contrasting effects of plant richness and composition on insect communities: a  
466 field experiment. The American Naturalist **158**, 17-35.
- 467 **Höller, C, Borgemeister, C, Haardt, H. & Powell, W.** (1993) The relationship between  
468 primary parasitoids and hyperparasitoids of cereal aphids: an analysis of field  
469 data. Journal of Animal Ecology **62**, 12-21.
- 470 **Hughes, R.D.** (1962) A method for estimating the effects of mortality on aphid  
471 populations. Journal of Animal Ecology **31**, 389-396.
- 472 **IBGE** (Instituto Brasileiro de Geografia e Estatística) (2010) Open source. URL  
473 <http://www.ibge.gov.br>. Accessed on 17/12/2011.
- 474 **Jenkins, L., Brill, R. & McCaffery, D.** (2011) Managing aphids in flowering canola in  
475 central west NSW p.82 in Proceedings of seventeenth Australian Research  
476 Assembly on Brassicas (ARAB) organized by the Australian Oilseeds  
477 Federation, 15-17 August 2011 Wagga Wagga New South Wales, Australia.
- 478 **Jeon, H.Y., Kim, H.H., Lee, Y.H., Chang, Y.D. & Yiem, M.S.** (2005) Biological  
479 control of the turnip aphid (*Lipaphis erysimi* K.) using the braconid wasp

- 480           (*Diaeretiella rapae* M.). Korean Journal of Horticultural Science and  
481           Technology **23**, 337-341.
- 482   **Kanegae, A.P. & Lomônaco, C.** (2003) Plasticidade morfológica, reprodutiva e  
483           assimetria flutuante de *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) sob  
484           diferentes temperaturas. Neotropical Entomology **32**, 37-43.
- 485   **Karley, A.J., Parker, W.E. & Pitchford, J.W.** (2004) The mid-season crash in aphid  
486           populations: why and how does it occur? Ecological Entomology **29**, 383-388.
- 487   **Kuznetsova, A., Brockhoff, P.B. & Christensen, R.H.B.** (2013). lmerTest: Tests for  
488           random and fixed effects for linear mixed effect models (lmer objects of lme4  
489           package).R-Version:1.1-0.  
490           <http://cran.rproject.org/web/packages/lmerTest/index.html>
- 491   **Leclair, M., Pons,I., Mahéo, F., Morlière, S., Simon, J.C & Outreman, Y.** (2016)  
492           Diversity in symbiont consortia in the pea aphid complex is associated with  
493           large phenotypic variation in the insect host. Evolutionary Ecology **30**, 925-941
- 494   **Liu, S.S. & Meng, X.D.** (1999) Modeling development time of *Myzus persicae*  
495           (Hemiptera: Aphididae) at constant and natural temperatures. Bulletin of  
496           Entomological Research **89**, 53-63.
- 497   **Liu, S.S. & Meng, X.D.** (2000) Modeling development time of *Lipaphis erysimi*  
498           (Hemiptera: Aphididae) at constant and variable temperatures. Bulletin of  
499           Entomological Research **90**, 337-347.
- 500   **MacGibbon, D.B. & Beuzenberg, E.J.** (1978) Location of glucosinolase in  
501           *Brevicoryne brassicae* and *Lipaphis erysimi* (Aphididae). New Zealand Journal  
502           of Science **21**, 389–392.
- 503   **Mackauer, M. & Völkl, W.** (1993) Regulation of aphid populations by aphidian  
504           wasps: does parasitoid foraging behaviour or hyperparasitism limit impact?

- 505           Oecologia **94**, 339-350.
- 506   **Malavolta, E. & Kliemann, H.J.** (1985) Desordens nutricionais nos cerrados. 136p.,  
507           Piracicaba, POTAFOS.
- 508   **Martinez, A.J., Ritter, S.G., Doremus, M.R., Russell, J.A. & Oliver, K.M. (2014)**  
509           Aphid-encoded variability in susceptibility to a parasitoid. BMC Evolutionary  
510           Biology **14**, 127
- 511   **Maunder, M.N. & Punt, A.E.** (2004) Standardizing catch and effort data: a review of  
512           recent approaches. Fisheries Research **70**,141-159.
- 513   **Mayer, D., Roy, D., Robins, J., Halliday, I. & Sellinet, M.** (2005) Modelling zero-  
514           inflated fish counts in estuaries: a comparison of alternative statistical  
515           distributions. In: Zenger A, Argent RM (eds.) International Congress on  
516           Modelling and Simulation, pp. 2581-2587. Anaheim, Nano Science and  
517           Technology Institute.
- 518   **McCullagh, P. & Nelder, J.A.** (1989) Generalized Linear Models. Chapman & Hall,  
519           London.
- 520   **Micic, S.** (2005) Identification and cultural control of insect and applied pests of canola.  
521           Bulletin 4650. Department of Agriculture, South Perth, Western Australia,  
522           Australia
- 523   **Oliveira, R.S., Sampaio, M.V., Ferreira, S.E., Ribeiro, L.C.M. & Tannús-Neto, J.**  
524           (2013) Low parasitism by *Diaeretiella rapae* (Hym.: Braconidae) of *Lipaphis*  
525           *pseudobrassicae* (Hemip.: Aphididae): pre- or post-ovipositional host  
526           resistance? Biocontrol Science and Technology **23**, 79-91.
- 527   **O'Neill, M.F. & Faddy, M.J.** (2003) Use of binary and truncated negative binomial  
528           modeling in the analysis of recreational catch data. Fisheries Research **60**, 471-  
529           477

- 530 **Pope, R.D.** (1983) Some aphid waxes, their form and function (Homoptera: Aphididae).  
531 *Journal of Natural History*, **17**, 489-506
- 532 **Pike, K. S., Starý, P., Miller, T., Allison, D., Boydston, L., Graf, G., & Gillespie, R.**  
533 (1997). Small-grain aphid parasitoids (Hymenoptera: Aphelinidae and  
534 Aphidiidae) of Washington: distribution, relative abundance, seasonal  
535 occurrence, and key to known North American species. *Environmental*  
536 *Entomology*, **16**, 1299-1311.
- 537 **Pike, K.S., Starý, P., Miller, T., Allison, D., Graf, G., Boydston, L., Miller, R. &**  
538 **Gillespie, R.** (1999) Host range and habitats of the aphid parasitoid *Diaeretiella*  
539 *rapae* (Hymenoptera: Aphidiidae) in Washington state. *Environmental*  
540 *Entomology* **28**, 61-71.
- 541 **Pinto, R.M., Bueno, V.H.P. & Santa-Cecília, L.V.C.** (2000) Flutuação populacional  
542 de afídeos (Hemiptera: Aphididae) associados à cultura da batata *Solanum*  
543 *tuberosum* L., no plantio de inverno em Alfenas, Sul de Minas Gerais. *Anais da*  
544 *Sociedade Entomologica do Brasil* **29**, 649-657.
- 545 **Potts, J.M. & Elith, J.** (2006) Comparing species abundance models. *Ecological*  
546 *Modelling*, **199**, 153-163.
- 547 **Powell, W.** (1982). The identification of hymenopterous parasitoids attacking cereal  
548 aphids in Britain. *Systematic Entomology* **7**, 465-473.
- 549 **Price, P.W., Denno, R.F., Eubanks, M.D., Finke, D.L. & Kaplan, I.** (2011) *Insect*  
550 *ecology: behavior, population and communities*. Cambridge, UK, Cambridge  
551 University Press.
- 552 **R Development Core Team, R.** (2013) *A Language and Environment for Statistical*  
553 *Computing*. R Foundation for Statistical Computing. In: *R Development Core*  
554 *Team*. Vienna, Austria. Open source. URL <http://www.R-project.org>

- 555 **Reifenrath, K. & Müller, C.** (2007) Species-specific and leaf-age dependent effects of  
556 ultraviolet radiation on two Brassicaceae. *Phytochemistry*, **68**, 875-885.
- 557 **Rothacher, L., Ferrer-Suay, M. & Vorburger, C.** (2016) Bacterial endosymbionts  
558 protect aphids in the field and alter parasitoid community composition. *Ecology*,  
559 **97**, 1712–1723.
- 560 **Satar, S., Kersting, U. & Ulusoy, M.** (2005) Temperature dependent life history traits  
561 of *Brevicoryne brassicae* (L.) (Hom., Aphididae) on white cabbage. *Turkish*  
562 *Journal of Agriculture and Forestry* **29**, 341-346.
- 563 **Shaltiel, L. & Ayal, Y.** (1998) The use of kairomones for foraging decisions by an  
564 aphid parasitoid in small host aggregations. *Ecological Entomology* **23**, 319-329.
- 565 **Sheehan, W. & Shelton, A.M.** (1989) Parasitoid response to concentration of herbivore  
566 food plants: finding and leaving plants. *Ecology* **70**, 993-998.
- 567 **Starý, P., Sampaio, M.V., Bueno, V.H.P.** (2007) Aphid parasitoids (Hymenoptera,  
568 Braconidae, Aphidiinae) and their associations related to biological control in  
569 Brazil. *Revista Brasileira de Entomologia* **51**, 107-118.
- 570 **Sullivan, D.J. & Völkl, W.** (1999) Hyperparasitism: multitrophic ecology and  
571 behavior. *Annual Review of Entomology* **44**, 291-315.
- 572 **Waterhouse, D.F. & Sands, D.P.A.** (2001) Classical biological control of arthropods  
573 in Australia. *Csiro Entomology, Australian Centre for International Agricultural*  
574 *Research, Canberra, Australia*
- 575 **Weber, G., Oswald, S. & Zollner, U.** (1986) Suitability of rape cultivars with different  
576 glucosinolate content for *Brevicoryne brassicae* (L.) and *Myzus persicae*  
577 (Sulzer) (Hemiptera: Aphididae). *Journal of Plant Diseases and Protection* **93**,  
578 113-124.

579 **Zamani, A.A., Talebi, A.A., Fathipour, Y. & Baniameri, V.** (2006) Temperature-  
580 dependent functional response of two aphid parasitoids, *Aphidius colemani* and  
581 *Aphidius matricariae* (Hymenoptera: Aphidiidae), on the cotton aphid. Journal  
582 of Pest Science **79**, 183-188.

583 **Author contribution**

584 M.V.S. conceived and designed the research. M.V.S., J.E.A.H., S.E.F., S.O.A.,  
585 D.M.B., and C.M.G. conducted the experiments. M.V.S. and J.P.V. identified the  
586 insects. B.C.L. and J.A.S.E. analyzed the data. M.V.S., A.P.K., and B.C.L. wrote the  
587 manuscript. All authors have read and approved the manuscript.

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