



Host plant and competitor identity matter in genotypex genotypexenvironment interactions between vetch and pea aphids

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1 **Article to the *Ecological Entomology***

2

3 **Host plant and identity matter in Genotype by Genotype by Environment**
4 **interactions between vetch and pea aphids**

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14 **Running Head: Host plant and identity matter**

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21 **Abstract**

22 1. Selection does not only operate in a Genotype (G) x Environment (E) context, but
23 can also be modulated by the activities of the plant-associated players in interaction
24 with their embedding environment in a GxGxE fashion.

25 2. We investigated the influence of aphid identity and intraspecific genetic variation of
26 *Vicia faba* on the performance of five genotypes of pea aphid (*Acyrtosiphon pisum*)
27 — with and without interaction with a heterospecific clone of vetch aphid (*Megoura*
28 *viciae*).

29 3. Contrasting pea-aphid conspecific performance between the GxE and the GxGxE
30 settings revealed strong context-dependent, genotype-specific shifts in performance,
31 which was influenced by plant cultivar, the presence of the competitor and their
32 interaction.

33 4. We also compared the competitive performance of *M. viciae* against each of its pea-
34 aphid counterparts. Here, competitor's genotype and abundance underlay a
35 remarkably varied response by *M. viciae* across interaction scenarios.

36 5. We show that aphid genotype can exhibit a varying degree of risk spreading,
37 contingent on competitor identity and the patterns of aggregation across three plant
38 cultivars. Owing to feedback loops between species activities and selective forces
39 acting on them, we suggest context-dependent responses by competitors that are
40 shaped via the interplay of the co-occurring species and their biotic environment.

41 6. Our work highlights the importance of investigating reciprocity between
42 competition and intraspecific genetic variation, towards a better understanding of the
43 interaction between ecology and evolution in agroecosystems.

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46 **Keywords**

47 Genetic variability, interspecific competition, aphids, ecoevolutionary dynamics

48 **Introduction**

49 *Selective forces vs. species activities, order and feedback loops*

50 Genotype by Environment (GxE) interactions foster variation in the expressed
51 genotype of plant-associated arthropods (Johnson & Agrawal, 2005; Tétard-Jones *et*
52 *al.*, 2007; Tétard-Jones *et al.*, 2011; Kanvil *et al.*, 2014; Zytynska *et al.*, 2014).
53 Phloem-feeders, like aphids, are highly dependent on the diet they pump out of their
54 embedding environment (host plants) and they display sensitivity and rapid response
55 to phenotypic changes in their hosts (Hunter & Price, 1992; Dungey *et al.*, 2000;
56 Whitham *et al.*, 2003; Johnson *et al.*, 2006; Zytynska & Preziosi, 2011). While
57 striving to multiply, aphids get involved in a plethora of interactions on various levels
58 relevant to the circumstances of the environments where they reside (Wiens, 1991;
59 Wade 2003; Zehnder *et al.*, 2007; Zytynska *et al.*, 2014). Host plants will display a
60 large panel of responses relative to the varied virulence of their Homopteran enemies
61 (Kanvil *et al.*, 2014) and varying plant resistance *per se* (Dogimont *et al.*, 2010). The
62 variation in the resistance and quality of the host plant (Powell *et al.*, 2006; Dogimont
63 *et al.*, 2010), partly attributed to intraspecific genetic variation (Underwood &
64 Rausher, 2000; Underwood, 2009), will incur constant yet varied on going responses
65 by aphids (Bergmüller & Taborsky, 2010; Schuett *et al.*, 2011; Kanvil *et al.*, 2014). It
66 is possible that an “ecological crunch” (Wiens, 1977, 1991) may take place as a result
67 of inconsistencies in plant vigour under attack of more than one enemy.

68 Evidence has accrued on the influence of plant genetic variation on associated
69 faunal communities (*e.g.* Dungey *et al.*, 2000; Whitham *et al.*, 2003; Johnson *et al.*,
70 2006; Moya-Laraño *et al.*, 2014). However, rather fewer studies have examined the

71 reciprocal interaction between within-species genetic variation and competition [*e.g.*
72 Mcguire & Johnson, 2006; Smith *et al.*, 2008; Fridley & Grime, 2010. Ongoingly, in a
73 GxGxE context, interacting parties reciprocally and diffusely (Fox, 1988; Strauss *et*
74 *al.*, 2004) modify, through their constant activities, the context embedding their
75 actions and interactions (Odling-Smee *et al.*, 2003; Laland, 2004). Such feedback
76 loops bespoke ceaseless change in the fitness of the inter-players in the short and long
77 runs (Dungey *et al.*, 2000; Underwood & Rausher, 2000; McIntyre & Whitham, 2003;
78 Pfennig & McGee, 2010).

79 *Species do not exist in a vacuum*

80 Indeed, the shareable space between plant cohabiting phloem feeding insects
81 is not void. For two species to co-exist the magnitude of within-clone competition
82 must be greater than the one of inter-clonal (in this case also inter-specific)
83 competition (Smith *et al.*, 2008). However, generalist aphids show sophistication in
84 plant perception hence consequent preference and decision making for micro-feeding
85 sites on available resources (Powell *et al.*, 2006). Therefore, social niche
86 specialisation in the light of the decisions made to aggregate separately or jointly with
87 heterospecifics will be influenced by the presence of other interacting species (Strauss
88 *et al.*, 2004). This may also be shaped by the exchange of feedback between
89 organisms' activities and selective stressors (Odling-Smee *et al.*, 2003; Juarrero,
90 2010).

91 *Rapidly responsive, highly plastic and context-dependent*

92 Aphids possess highly versatile genomes fueling extensive phenotypic
93 plasticity (Brisson & Stern, 2006; Whitman & Agrawal, 2009). The remarkable
94 plasticity in aphid response to environmental stimuli can be manifested via
95 morphological, ontogenic and behavioural means which can mediate their GxGxE

96 interactions on the interface between nature and nurture (Fordyce, 2006; Pfennig &
97 McGee; 2010, Bateson & Gluckman, 2011). Experience or preconditioning of
98 offspring can transfer across generations to produce a range of plastic, and thus
99 adaptable to change, individuals (Dixon, 1998; Dombrovsky *et al.*, 2009; Schuett *et*
100 *al.*, 2011). However, any plausible induced shifts in niche and resource utilisation
101 should be considered interdependent and contingent on the adaptive plastic behaviour
102 of aphids and their differential capacity to respond to environmental cues (Stearns,
103 1989; Langerhans & DeWitt; 2004; Bergmüller & Taborsky, 2010; Muratori, 2010).
104 The activities and the genetics of the biotic environment of an aphid species,
105 including its host plants and other cohabiting species, will shape aphid fitness,
106 dynamics and survival (Odling-Smee *et al.*, 2003; Strauss *et al.*, 2004; Rowntree *et al.*,
107 2011; Moya-Laraño *et al.*, 2014). Little is known about the role of aphid and host
108 plant intraspecific genetic variation in such process. Thus, there is a heightened need
109 to highlight the eco-evolutionary aspects (Pelletier *et al.*, 2009) of the niche-centred
110 context-dependency of GxG norms (Bergmüller & Tabrosky, 2010) and trait-mediated
111 species interactions (Inbar *et al.*, 1995; Werner & Peacor, 2003), where congeneric
112 choices to aggregate or segregate on their hosts may rise or fall together with a fitness
113 gain or loss (Whitham, 1986; Yong & Miikkulainen, 2009; Rajagopalan *et al.*, 2011).
114 This also portrays aphids as a showpiece in the investigation of co-evolutionary arms-
115 race (Dawkins & Krebs, 1979) in multi-trophic systems, where there is still a
116 considerable thirst for linking up reproductive success and behaviour in the light of
117 the genetic variation of host plants and the GxG interactions of parthenogenetic
118 aphids of different species.

119 In the present piece, we studied the importance of context in shaping the
120 response of five pea aphid conspecifics when interacting with vetch aphid *Megoura*

121 *viciae*. Not only we observed such response in terms of reproductive success, but we
122 also recorded on-plant distribution of aphids. Indeed pea and vetch aphids are
123 attracted to *Vicia faba* and in general they show propensity to infest meristematic
124 tissues on top and bottom parts of the plant, where the new growth may be less
125 defended against aphid infestation. These two species may co-occur on the host plant,
126 but our knowledge is limited about their potential to co-exist on shared hosts.
127 However, there is a suggestion by van Veen *et al.* (2005) that there is an indirect
128 benefit for pea aphid in sharing a host plant with vetch aphid as the latter can be
129 poisonous to natural enemies of pea aphid.

130 Where context is defined by three different faba bean cultivars in the absence
131 or presence of competition with a heterospecific clone, we endeavour to raise the
132 following questions:

133 1- Do pea aphid genotypes respond differently to the presence of a competitor, and is
134 this response dependent of host plant cultivar (E)?

135 2- Does the outcome of the interaction between pea aphid genotype and plant cultivar
136 shift between the state of performing solo (GxE) and the state of performing against a
137 heterospecific (GxGxE)?

138 3- Across cultivars, does interspecific competition stimulate a varied performance and
139 behaviour of the focal heterospecific competitor *versus* distinct identities of pea aphid?

140 **Methods**

141 *Host Plant*

142 Three faba bean lines (Long Pod Green Masterpiece, Optica, and Sutton; LP, O,
143 and Sut; hereafter) were obtained from a British horticultural company (Unwins©)
144 due to their popularity as award-winning heirlooms ("AGM — RHS", 2017). LP is

145 hardier than Sut (dark green dwarf) and O (prolific modern variety) and all represent a
146 portion of the genetic diversity of the var major of *Vicia faba*. These stable synthetic
147 cultivars do not exist in the wild as they are obtained through genetic diversity from
148 extensive artificial selective breeding, thereof branded as accessions (Duc et al., 2010).
149 However, within-cultivar differences have not yet been clearly identified (Underwood,
150 2009), and therefore little is known about the influence of these economically
151 important cultivars on the GxGxE interactions involving their sap-feeders.

152 We grew the plants in 6cm diameter x 10cm deep plastic pots supplied with
153 sterilised compost (John Innes no.3). All seeds were first sown in a cubicle at the
154 University of Manchester botanical grounds before being transferred to growth
155 chambers (16 hour daylight, 22°C) for the duration of the experiment. We ensured all
156 plants were of the same age (*ca.* 1 month) and the same height (~10 cm) before
157 initiating interactions with aphids. Prior to infestation, individual plants were kept
158 upright by tethering to a wooden stick in individual plastic meshed enclosures, and
159 watered as needed.

160 *Aphid genotypes*

161 We selected 5 different conspecific clones of pea aphid *Acyrtosiphon pisum*
162 (Harris) of different biotypes and life histories (Kanvil et al., 2014). This included two
163 pink genotypes P127 (N127) and P2 (lab-maintained lineage for *ca.* 1 year by the time
164 we commenced the experiment), and three green genotypes: GORG (JF01/29), G116
165 (N116), and GBOT (The foundress of this clone was trapped on a broad bean plant in
166 Manchester, UK). Apart from GBOT, all pea aphids were descendants of initial
167 supplies from the Imperial College (London), UK. We also used a single
168 heterospecific clone of vetch aphid, *Megoura viciae* (Buckton), Meg, henceforth. Meg
169 population descended from one mother captured on *V. faba* in Manchester, UK.

170 Every aphid identity in this work was initiated from a single gravid mother and
171 thus due to parthenogenesis each line is a clone of genetically identical individuals.
172 We thereby ensured that the observed fitness of each aphid clone is as close as
173 possible to the fitness of its underlying genotype (Weisser & Stadler, 1994). To
174 control for maternal effects we used 2nd instars, and to minimise any preconditioning
175 effect, we raised all clones beforehand, for a few months, on a different variety of *V.*
176 *faba* var. major.

177 *Experimental design and analyses*

178 The work was designed into two complementary parts:

179 ***1- Pea-aphid perspective: Pea aphid conspecific clones; with and without*** 180 ***interactions with vetch aphid***

181 Taking into account aphid high dependency on their host plant, we consider the
182 latter with its microcosm as aphid's biotic environment (E). We focus in this part of
183 the study on pea aphid Genotype x Environment (GxE) interaction in the
184 absence/presence of a heterospecific clone (Meg). As such, we investigate pea aphid
185 reproductive success and behaviour between the state of performing solo (without
186 Meg) and the state of performing against a heterospecific clone (Meg).

187 Four 2nd instars of each pea-aphid genotype (G) were reared solo on each of the
188 three faba bean cultivars (E), while two 2nd instars of each pea aphid genotype (G)
189 were paired with two 2nd instars of Meg (G) on each of the three cultivars (E). Aphid
190 instars were placed off-plant near the edge of each pot using a fine damp brush at the
191 beginning of the experiment. The experiment lasted for 14 days after aphid
192 introduction.

193 Measured pea aphid traits

194 *Performance shift*

195 Relevant to faba bean cultivar, the aim was to survey any shifts in performance
196 (reproductive success measured via population growth rate) of each of the five pea-
197 aphid contestants under Meg influence. Since the initial aphid starter population
198 makes a difference (4 individuals in the GxE and 2:2 in the GxGxE), we calculated
199 the exponential population growth rate for each pea aphid genotype following
200 Agrawal *et al.* (2004):

201

$$202 \quad GR = \frac{\ln(N_2) - \ln(N_1)}{t} \quad (\text{Eqn 1})$$

203 where **GR** is Population growth rate, N_1 is the Initial number of aphids, and N_2 is the
204 final aphid number at day 14.

205 A GLM model, ‘multcomp’ package (Hothorn *et al.*, 2008), was applied with
206 a gaussian family to compare the growth rates of the focal pea-aphid genotypes in the
207 GxE context, where Meg was absent, with their readings in the GxGxE setting, where
208 Meg was present (see Appendix 1, Table A1, for the full model including
209 interactions). We allocated 10 replicates per treatment (5 pea aphid genotypes x 2
210 [with Meg, without Meg] x 3 cultivars) for a total of 300 enclosures, but the final total
211 number of enclosures was 247 because we discarded any dead or dying plants. Our
212 explanatory variables were: I) Cultivar effect (faba bean genetic variability comprised
213 by three cultivars). II) Pea aphid genotype (five levels). III) The absence or presence
214 of Meg (No, Yes). IV) We also integrated the Levin’s niche breadth index (B , Eqn2,
215 Colwell & Futuyama, 1971) as a covariate in the model. Each plant was sectioned
216 upon data collection at the day 14 of the experiment using a ruler and a marker into

217 three strata (Top third, middle third and bottom third of plant height). The index was
218 calculated for each plant across the three strata. The integration of this measure in the
219 analysis of performance provided the added benefit of tying a contestant's use of
220 space (spread along resource) to the contrast of its concomitant reproductive success,
221 towards more precision of the quantification of the effects under focus.

222

$$223 \quad B_j = \frac{1}{\sum_i P_{ij}^2} \quad (\text{Eqn 2})$$

224 where i represents the 'i-th' resource state (plant stratum), while j represent the 'j-th'
225 species/clone respectively. The letter P represents fraction of total individual number
226 of a given conspecific on a given plant stratum.

227 For a better highlight of any shift in reproductive success, we also visually
228 colligated pea-aphid population growth rates, with and without Meg presence, to
229 descriptively quantify the magnitude of any possible by-context change in
230 performance (Appendix 1). The main focus in this part of the study was on pea aphid
231 genotypes. However, by analogy, we provide supportive further insights on Meg
232 performance in the absence/presence of pea aphid as supplementary materials via
233 Appendix 2.

234 *Behavioural shift*

235 We defined pea-aphid contestant behaviour as on-plant distribution (aphid raw
236 numbers signifying a choice of aggregation on top, middle or bottom thirds, *i.e.* host
237 plant strata). We used a neural multinomial model, 'nnet' package (Venables &
238 Ripley, 2002) and 'car' package (Fox & Weisberg, 2011). The aim was to examine

239 any possible shifts in on-plant distribution of pea aphids, with and without interaction
240 with the heterospecific clone (Meg) as function of the explanatory variables (I-III,
241 described above) and there interactions.

242 *2- Vetch-aphid perspective: Meg competitive performance under the influence of*
243 *pea aphid genotype (identity)*

244 Exploring the GxGxE interactions from the perspective of Meg, our aim was
245 to examine the competitive performance of this clone, where severally paired up with
246 different pea aphid identities across three faba bean cultivars (E), relative to niche
247 differentiation on their shared biotic environment (E). We advocate that this part of
248 our study provides a relative frame of reference for the context-dependency of pea
249 aphids spotlighted in the first part. The focus here is on vetch-pea aphid competitive
250 dynamics and thus logically helps illustrate the matters of identity, context and niche
251 differentiation from a different heterospecific angle.

252 Measured Meg traits under interspecific competition

253 *Comparative competitive performance*

254 The response variable was Meg competitive performance (reproductive success;
255 measured as total aphid numbers per plant) in response to competition with each of a
256 group of pea aphid genotypes. Here, we allocated 10 replicates per interaction
257 scenario (6 levels for Meg [Meg alone, Meg vs. 5 pea aphid genotypes] x 3 cultivars)
258 for a total of 180 enclosures, but the final total number of enclosures was 168 because
259 we discarded any dead or dying plants.

260 We applied a GLM with a Gamma family and log link (highly positively skewed
261 distribution), ‘car’ package (Fox & Weisberg, 2011). The control treatment of Meg
262 performing alone (absence of competition) were used as a reference in the model (see

263 Appendix 1, Table A4, for the full model including interactions). The explanatory
 264 variables were: I) Cultivar effect (faba bean genetic variability composed of three
 265 cultivars). II) Interspecific competitor identity (five levels of identities matching the
 266 five pea aphid genotypes). III) Interspecific competitive pressure (total number of pea
 267 aphid competitors) was integrated as a covariate. IV) We also calculated and
 268 integrated Pianka's niche overlap index (O , equation 3, Pianka, 1974) as a covariate in
 269 the model. This measure allowed for a comprehensive characterisation of Meg's use
 270 of shareable space (plant strata) relative to the identity and co-occurrence of each of
 271 the competitive pea-aphid plant cohabittees.

$$272 \quad O_{jk} = \frac{\sum_i^n P_{ij} P_{ik}}{\sqrt{\sum_i^n P_{ij}^2 \sum_i^n P_{ik}^2}} \quad (\text{Eqn 3})$$

273 where i represents the 'i-th' resource state (plant stratum), while j and k represent the
 274 'j-th' or 'k-th' heterospecifics respectively. Hence the letter P represents fraction of
 275 total individuals of a given heterospecific on a given plant stratum.

276 For better visibility of Meg performance under the GxGxE scenarios, we
 277 quantified and illustrated Meg's performance, as a measure of consistency, throughout
 278 the interaction matrix, and made the populations of Meg and competitors proportional
 279 relative to average Meg competitive permanence (AM , hereafter). We also annotated
 280 the illustration with lower-case alphabetical letters following a post-hoc Tukey's HSD,
 281 package 'agricolae' (Mendiburu, 2016). Furthermore, we provide, in Appendix 2,
 282 supplementary insights on Meg performance in the absence/presence of competition
 283 with pea aphid.

284 *Differential competitive behaviour*

285 We aimed at investigating any differential choice of on-plant aggregation by Meg
286 pertaining to the influence of the different identities of the deployed pea aphids. We
287 executed a neural multinomial model, ‘nnet’ and ‘car’ package, to examine Meg
288 choice to aggregate on plant strata *versus* any pea aphid co-occurrences. We used the
289 explanatory variables (I-II, described above) and their interactions.

290 We note that for the GLMs, in order to quantify the relative importance of factor
291 contribution and the magnitude of the focal effects, we estimated the contribution to
292 the explained deviance as percentage for each explanatory variable. In the same
293 fashion as variance partitioning, we obtained a “deviance partition” *i.e.* the
294 contribution of each factor on the total explained deviance by dividing, for each factor,
295 the factor’s deviance by the total of explained deviance (null deviance minus final
296 residual deviance). We performed the statistical analyses in R (R Core Team, 2013)
297 and revised the infographics in Inkscape ver. 0.91 under GLP licence. The dataset is
298 available from the figshare repository:

299 < <https://figshare.com/s/9960e72a0b58d2a99791> >

300 **Results**

301 ***1. Five pea aphid clones with and without interaction with a heterospecific on three*** 302 ***host plant cultivars***

303 Pea aphid performance

304 The presence of the interspecific competitor Meg strongly affected the
305 performance of the five pea aphid conspecifics ($F_{1,240}= 45.60$, $P<0.0001$, 22.29% of
306 explained deviance), and pea aphid genotypes responded differently ($FF_{4,241}=10.90$,
307 $P<0.0001$, 21.30% of explained deviance). Faba bean cultivar also affected pea aphid
308 performance ($F_{2,238}=9.73$, $P<0001$, 9.51% of explained deviance). Moreover, the

309 interaction between pea aphid genotypes and Meg presence had a highly significant
310 effect on the former's performance ($F_{4,234}=13.73$, $P<0.0001$), with a considerable
311 contribution of 26.84% to the explained deviance. The interaction (pea aphid
312 genotype x cultivar x Meg presence) was marginally significant ($F_{8,216}= 2.04$, $P=0.043$)
313 and contributed 7.97% to the explained variance. This highlighted the relevancy of
314 context and signalled a modulated pea-aphid reproductive success under the influence
315 of interspecific interaction. Moreover, niche breadth contributed 8.95% to the
316 explained deviance and had a strong effect on pea aphid conspecific performance
317 ($F_{1,245}=18.31$, $P<0.0001$). See Appendix 1, Table A1 for further details.

318 Looking at the population growth rates, Figure 1, it appears that the presence
319 of the heterospecific clone (Meg) elicited a notably deferential increase in
320 reproductive success across pea aphid genotypes. For example, the presence of Meg
321 boosted G116's performance on all cultivars, and in particular G116's rank rose
322 dramatically on O to make 317% of its solo performance (the highest performance
323 shift in this context), See Appendix 1, Tables A2 and A3 for further information on
324 performance shift/rank and pea aphid densities. Another example is P127, on Sut,
325 which rocketed from being fifth (Meg absent) to occupy the top of the chart in Meg
326 presence. Conversely, GORG's performance rank dropped significantly on LP from
327 first (solo performance) to fourth (Meg present). GBOT showed similar pattern on Sut.
328 Interestingly, the conspecific ranks of the genotypes P2 and GBOT on LP remained
329 unchanged in the absence/presence of Meg, although their performance, where Meg
330 was present, outweighed their solo performance in that context.

331 As such, the presence of a foreign clone had a contrasted effect on pea aphid
332 performance: It specifically led to a decrease in the performance of certain pea aphid

333 genotypes doing better alone, but induced better performance by others which
334 performed poorly solo, (Figure 1; see also Appendix 1, Table A2).

335 Pea aphid behaviour

336 The presence of Meg had a highly significant effect on the on-plant
337 distribution of pea aphids ($LR\chi^2=83.93$, $DF=2$, $P<0.0001$), with a genotype-specific
338 response ($LR\chi^2=356.54$, $DF=8$, $P<0.0001$). Faba bean cultivar also strongly
339 influenced pea aphid behaviour ($LR\chi^2=222.43$, $DF=4$, $P<0.0001$) so did the interaction
340 between Meg presence and faba bean cultivar ($LR\chi^2=45.01$, $DF=4$, $P<0.0001$), and
341 pea aphid genotype by cultivar interaction ($LR\chi^2=605.77$, $DF=16$, $P<0.0001$). The
342 interaction between pea aphid genotype and Meg presence was also highly significant
343 ($LR\chi^2=562.64$, $DF=8$, $P<0.0001$). Furthermore, the three-way interaction amongst
344 Meg presence, pea aphid genotype and faba bean cultivar was also highly significant
345 ($LR\chi^2=405.68$, $DF=16$, $P<0.0001$), Figure 2.

346 The general picture is a decreased propensity to occupy the plant upper
347 stratum within the GxGxE context *i.e.* where the heterospecific clone (Meg) was
348 present, if compared with the readings of pea aphids within the GxE context (absence
349 of Meg). For instance, under Meg influence, lower proportions of P127 were recorded
350 on the top stratum for cultivars O and Sut (but not on LP). However, on O and Sut, P2
351 aggregated more on the lower part of the plant under Meg presence. G116 generally
352 showed less affinity for the upper stratum with Meg than it did where Meg was absent.
353 Still, G116 behaviour shifted on cultivar O from a higher density on the upper stratum
354 of the plant (under poor solo performance) to even on-plant distribution where Meg
355 was present. A similar pattern was shown, under competition, by GORG on Sut, but
356 with poorer performance rank than G116. In contrast, GORG's behaviour shifted from

357 showing balanced on-strata densities on O in the absence of Meg to increased
358 aggregation on the mid and bottom strata against Meg. Whereas, GBOT's affinity to
359 the plant bottom third in the presence of Meg was consistent and GBOT's behaviour
360 remained largely unchanged by Meg presence on LP, and likewise its performance
361 rank, Figure 2 and Appendix 1 (Table A2).

362 *II. Vetch aphid differential performance in response to different interspecific* 363 *competitive identities across host plant cultivars*

364 Meg comparative competitive performance

365 Meg competitive reproductive success was highly influenced by which pea aphid
366 genotype it performed against ($LR\chi^2=105.02$, $DF=5$, $P<0.0001$) and this had the lion's
367 share of the estimated variance components (58.45%). Meg was significantly
368 influenced by the co-varying numerical pressures of the co-occurring pea aphid
369 identities ($LR\chi^2=7.97$, $DF=1$, $P=0.005$) that contributed to 4.44% of the explained
370 variance. Also, Meg performance was significantly affected by faba bean cultivar
371 ($LR\chi^2=7.48$, $DF=2$, $P=0.024$), 4.16% of the explained variance). Moreover, the
372 interaction between the effects of competitor identity and the corresponding
373 competitive pressure was also significant ($LR\chi^2=12.49$, $DF=4$, $P=0.014$) and
374 contributed 6.95% to the explained variance. The three-way interaction (competitive
375 pressure x competitive identity x cultivar) was also significant ($LR\chi^2=33.09$, $DF=10$,
376 $P=0.0003$), contributing 18.42% to the explained variance). The effect of niche
377 overlap on plant strata made 7.59% of the explained variance and was highly
378 significant ($LR\chi^2=13.64$, $DF=1$, $P=0.0002$), Figure 3. See Appendix 1, Table A4 for
379 further details.

380 As illustrated in Figure 3, Meg's reproductive success considerably varied up and
381 down across the different scenarios of interaction with pea aphids, but pairing Meg up

382 with P127 led to a notable increase in Meg competitive performance on all cultivars.
383 In a particular case (Meg vs. P127 on Sut), both heterospecific genotypes thrived
384 together in a stunning fashion, and their GxG population showed the highest readings
385 across all GxGxE scenarios. By contrast, the populations of Meg and GORG both
386 shrank in size under their interaction on O. Moreover, Meg was outnumbered by
387 G116 on two cultivars, under intensified competitive pressure at the expense of Meg.

388 The largest total number for Meg was against P127 on O, making 77% of the GxG
389 population worth 1.5 of Meg average competitive performance (*AM*). Whereas, the
390 highest Meg proportion (82%) was before diminishing P2 on Sut, where Meg
391 displayed the second highest competitive performance on this cultivar, but the GxG
392 population therein was almost half Meg average competitive performance (*AM*).
393 Interestingly, on the contrary, *versus* GORG on LP, Meg was superior (59% of a poor
394 GxG population worth 0.3 *AM*), but Meg had therein the lowest numbers across all
395 contexts. However, having almost the same proportion, but of a larger GxG
396 populations on LP, Meg total numbers sprang to their highest *versus* P127 and to the
397 second highest against GBOT for that context. See also Appendix 2 (Tables A1 and
398 A2), for a supplementary investigation of Meg performance shift +/- interaction with
399 pea aphid.

400 Meg behaviour

401 Competitor identity and faba bean cultivar significantly affected Meg's
402 distribution on plant ($LR_{\chi^2}=17.826$, $DF=8$, $P=0.022$ and $LR_{\chi^2}=48.798$, $DF=4$,
403 $P<0.0001$, respectively). Meg's behaviour was significantly affected by the interaction
404 between faba bean cultivar and pea aphid identity ($LR_{\chi^2}=45.019$, $DF=16$, $P=0.0001$).
405 Meg proportional occupation of the space of interaction remarkably varied across
406 strata and by context in response to pea aphid identities. For example, as displayed in

407 Figure 4, Meg was superior against P127, with larger proportions present on almost
408 all strata on O. Meg was also more present than GBOT on the top and bottom strata of
409 LP. Conversely, the dominance over Meg by GORG on Sut, by GBOT on O (mid and
410 bottom strata), by P127 on Sut, and by G116 on O and Sut, is easy to identify.
411 Moreover, P2, mostly outnumbered by Meg, was on par with Meg on O bottom third,
412 so was Meg *versus* G116 on LP top and mid thirds, and GBOT on Sut lower strata.

413 **Discussion**

414 We spotlight a strong context-dependent influence of aphid genotype and faba
415 bean cultivar on the performance and behaviour of a group of contestants performing
416 alone or in pairs under different competitive pressures. We advocate that such clone-
417 specific response would be shaped by a plausible interplay between ecology
418 (interspecific competition) and evolution (host plant and aphid within-species genetic
419 variation), (Mcguire & Johnson, 2006; Rowntree *et al.*, 2011; Schoener, 2011).

420 *The presence of a heterospecific differentially alters performance for clonal*
421 *conspecifics*

422 The presence of the heterospecific clone (Meg) triggered diverse responses by
423 *A. pisum* clones. The relatively poor performances of clones such as G116 and P127
424 in certain contexts were dramatically ameliorated in the presence of Meg. On the
425 contrary, clones (GBOT and GORG), with high relative population growth rates in the
426 absence of Meg, showed context-dependent lower rates when Meg was present. By
427 and large, the presence of vetch aphid boosted a positive shift in the reproductive
428 successes of pea aphid (compared to solo performance). Furthermore, the shift
429 observed in behaviour (on-plant distribution), +/- Meg, was also varied as well as
430 pronounced. These relatively positive or negative effects of interspecific competition

431 on pea aphid fitness can be attributed to a group of diffusely acting factors including: i)
432 A differential response of aphid genotype to the differences in dietary quality of their
433 hosts (Sandström, 1994), ii) variation in plant resistance (Fritz & Simms, 1992;
434 Kaloshian & Walling 2005; Dogimont *et al.*, 2010; Verdugo *et al.*, 2012) and aphid
435 countermeasures (Walling, 2008) iii) inter-player identity within the GxGxE context
436 (Strauss *et al.*, 2004; Tétard-Jones *et al.*, 2007).

437 Simultaneously, the vetch aphid clone (Meg) expressed remarkably successful
438 competitive performance and varied behaviours against the co-occurring pea aphid
439 identities. For example, surprisingly, there was no competitive exclusion, rather, G116
440 bested Meg on two faba cultivars and they were roughly equivalent on LP. In contrast,
441 Meg outperformed P2 (inferior competitor) on LP and Meg dominated most strata.
442 However, on the same cultivar and with higher densities than expressed before P2,
443 Meg showed a similar pattern of dominance against a P127 (potent competitor).

444 All in all, our findings distinctly show that the presence of a heterospecific clone
445 can be a game changer, whereby interspecific competition affected both inter-players
446 in our example. However, the outcome of the competition and the size of the complete
447 aphid population (both Meg and pea-aphid competitors) relatively differed depending
448 on the individual Meg-pea-aphid pairing. On different cultivars with varying
449 resistance to pest infestation (Dogimont *et al.*, 2010; Verdugo *et al.*, 2012), coexisting
450 aphid species are expected to vary their reproductive and behavioural means to cope
451 with constantly changing environment (Dixon, 1998; Whitman & Agrawal, 2009,
452 Bergmüller & Tabrosky, 2010; Sadek *et al.*, 2013). The space utilised by a given
453 genotype and positioning on micro-feeding sites may affect its reproductive success,
454 where fitness prerequisites reciprocate behaviour (Bergmüller & Tabrosky, 2010).
455 Fridley & Grime (2010), who focused on the dynamics of genotype competition

456 relationship, suggested a dependency effect to likely ‘dilute’ the interaction strengths
457 among species and thus influence community structure and diversity.

458 An increase in niche partitioning is expected to reduce the competition effect
459 and promote coexistence (Pianka, 1974; Armstrong & McGehee, 1980). However, for
460 each aphid pairing, despite being in competition for resources from the same plant,
461 competitive exclusion did not occur and the competitors in our study appeared to
462 reduce competition’s negative impacts through spatial niche partitioning. However,
463 niche partitioning alone cannot explain the absence of competitive exclusion (DeLong
464 & Vasseur, 2012). Akin to the density-dependent ‘gregarious’ and ‘non-gregarious’
465 phases expressed by locusts, the inclusion of the concept of behavioural phenotype
466 determination in aphids as a ‘density-dependent phase polyphenism’ (Simpson *et al.*,
467 2011, see also Simon *et al.*, 2011) can help further explain the dynamics that lead to
468 reduced competitive exclusion. Coexistence may arise from either ‘safe play’ (*i.e.*
469 niche segregation and reduced abundance leading to moderated competition and
470 hence co-occurrence), or ‘risk taking’ (*e.g.* reduced niche partitioning and interference
471 competition resulting in a ‘win-lose’ game of dominance on shared resources). This
472 takes part into a cyclical, rather than linear, relationship occurring between each
473 organism’s activities (*e.g.* niche construction) and the selective forces in operation
474 (Odling-Smee *et al.*, 2003; Laland, 2004), resulting in eco-evolutionary dynamics
475 (Pelletier *et al.*, 2009, see also Schoener, 2011). The genotype-specific
476 interdependence between aphid performance and behaviour can be seen as a form of
477 bet hedging (Hopper, 1999).

478 *Aphid mothers hedge the bets of the clone*

479 The patterns of reproductive success and behaviour we observed in the presence
480 and absence of interspecific competition can be understood as a variant of an eco-

481 evolutionary game of risk-spreading (Philippi and Seger, 1989, Hopper, 1999). “Bet
482 hedging occurs when a single genotype shows a variety of phenotypes in the same
483 environment, and each phenotype is successful only when the particular
484 circumstances to which it is adapted occur”, Hopper *et al.* (2003). As such, risk
485 spreading is expected to be a constantly varying evolutionary-game (Hopper, 1999;
486 Olofsson *et al.*, 2009) by aphid clones in response to the effects of competition,
487 genetic variability (cultivar effect) and their interaction. Here, the ‘within-generation’
488 fine-tuning of offspring phenotype is under varying and unequal selective pressures
489 (Hopper *et al.*, 2003), and occurs within the context of colonising hosts that are shared
490 with competitors (*e.g.* Mooney *et al.*, 2008; Smith *et al.*, 2008) and the plasticity
491 arising through maternal effects (Marshall & Uller, 2007; Tariq *et al.*, 2010). The
492 extent of resource utilisation and reproductive success are expected to shape aphid
493 survival in this way (Hopper *et al.*, 2003; see also Plaistow *et al.*, 2006, 2007; and
494 Underwood, 2009). The trajectories of any trans-generational effects, nevertheless,
495 will be contingent on host plant quality (Zehnder, 2006), aphid intra- and inter-clonal
496 interactions (*e.g.* Smith *et al.*, 2008), and the past responses to selection and current
497 selection (Plaistow *et al.*, 2006, 2007; Zehnder *et al.*, 2007). Moreover, responses to
498 selection may be transmitted to offspring through non-hereditary epigenetic
499 mechanisms (Plaistow *et al.*, 2006) and induced responses may occur in response to
500 past and contemporary inter- and intra-generational interactions (Plaistow *et al.*, 2006,
501 2007). These contemporary interactions may be a response to interactions between
502 phenotypes via Indirect Genetic Effects (Wolf *et al.*, 1999), which allow for highly
503 plastic responses (Whitman & Agrawal, 2009), likely mediated by the phenotypic
504 plasticity of the congeners involved (Fordyce, 2006, Pfennig & McGee, 2010,
505 Bergmüller & Tabrosky, 2010). The differences in aphid responses could also be

506 partially attributed to a symbiont effect (Simon *et al.*, 2011). These factors combined
507 produce vast behavioural flexibility (Sih *et al.*, 2004), much of which can be
508 attributed to an emergent aphid ‘personality’ (Schuett *et al.*, 2011), and thus may
509 underpin the ecological success of aphids (Forsman, 2015).

510 *The emergence of extended phenotype*

511 Driven by the necessity to multiply, thrive, and offset plant countermeasures
512 (Dawkins, 1989, Walling, 2008; Verdugo, *et al.*, 2012), the aphid genotypes in our
513 study responded differentially to competition by modifying their reproductive rates
514 and aggregation behaviour to counteract the adversity of competition (Dawkins, 1982).
515 This can be, in the light of our findings, conceived as analogous to the concept of
516 ‘safe fail’ or ‘fail safe’ as conveyed by Juarrero (2010), whereby plant-cohabiting
517 competitors of extreme phenotypic plasticity (Simon *et al.*, 2011), may act so as to
518 meliorate their inclusive fitness by reducing interference through behavioural and
519 reproductive means. Notably, vetch aphid is poisonous to a variety of aphidophagous
520 organisms and since pea aphid responses are envisaged to be cost-sensitive (*e.g.*
521 McAllister *et al.*, 1990), co-occurring with vetch aphid would be beneficial for pea
522 aphid as means to evade natural enemies (van Veen *et al.* 2005). In such system,
523 optimal reproduction and distribution on a shared host will not only be density-
524 dependent and context-dependent, but also trait-mediated (Inbar *et al.*, 1995; Werner
525 & Peacor, 2003). Also, the genomes of the plant-dependent aphids may function
526 beyond the species level as a form of extended phenotype, where the genome of the
527 shared host plant defines the environment in which the genomes of the inter-players
528 interact (Dawkins, 1982, 1989; Whitham *et al.*, 2003; Gardner, 2016). Under the
529 notion of GxGxE (Tétard-Jones *et al.*, 2007; Johnson & Stinchcombe, 2007), an
530 extended phenotype (Dawkins, 1982) favouring conflict avoidance (Huntingford &

531 Turner, 1987; Rajagopalan *et al.*, 2010), however, would arise from a possible
532 modulation amongst ecology (*e.g.* competition), evolution (differential reproductive
533 success) and host plant genetic variation (Odling-Smee *et al.*, 2003; Rowntree *et al.*,
534 2011). As such, the selection and colonisation of host plants, and portions of host
535 plants, in the presence of aphid-aphid-plant interactions, might necessitate (Dawkins
536 1989) a continuum spanning antagonism to facilitation. This may arguably entail a
537 fitness reward up to a density-dependent threshold (Yong & Miikkulainen, 2009;
538 Rajagopalan *et al.*, 2010; Rajagopalan *et al.*, 2011).

539 **Concluding remarks**

540 In his masterpiece ‘Through the looking glass’, Lewis Carroll captured a vivid
541 image of natural selection: “It takes all the running you can do to keep at the same
542 place” says the red queen”, Van Valen (1973). In their feverish race to replicate their
543 genetic constitution, species can develop a flexible set of tactics and strategies,
544 interact with each other, and cause changes in their environment. When the
545 environment is biotic (*e.g.* a host plant) it will respond in turn and so forth creating an
546 eco-evolutionary treadmill (Odling-Smee *et al.*, 2003; Juarrero, 2010) of a diffuse co-
547 evolutionary arms race (Dawkins & Krebs, 1979; Strauss *et al.*, 2004). There is an
548 increased need for an amalgamative approach that integrates the variation in host and
549 aphid genetics, as well as the GxGxE interactions, as contributory factors to the
550 ecology and evolution of phloem-feeding organisms (Hersch-Green *et al.*, 2011;
551 Moya-Laraño *et al.*, 2014). In this work we highlight that it is crucial to canvass GxE
552 and GxGxE interactions from different angles in a relative framework, whilst
553 investigating the eco-evolutionary dynamics of species interactions in model
554 agroecosystems.

555

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567 **Contribution of authors**

568 **MSK** designed, performed and developed the experimental work. MSK also collected,
569 entered data and produced earlier versions of this work, envisaged and co-shaped the
570 analysis and visualisation with C.S.E G and hence wrote up the manuscript.

571 **C.S.E G** co-developed and carried out the analysis and visualisation with MSK. C.S.E
572 G also contributed to the manuscript writing up, and helped in augmenting the work.

573 **RFP** supervised and hosted the experimental work, supported the development of the
574 experimental design, and both the conceptual and analytical approaches. RFP also
575 contributed to the writing up and optimisation of the manuscript.

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868 **Figure Legends**

869 **Figure 1. Comparative pea aphid conspecific performance across faba bean**
870 **cultivars, with and without interaction with a heterospecific clone (Meg),**
871 **averages \pm SE.** Relevant to the context of interaction with faba bean cultivar, pea
872 aphid genotype showed differential shifts in performance (population growth rates)
873 between the state of performing alone and the state of performing in the presence of
874 vetch aphid.

875 **Figure 2. Contrast of conspecific pea-aphid behaviour on strata with and without**
876 **interaction with a heterospecific clone (Meg), on three faba bean cultivars.**
877 Through contrasting pea aphid on-plant aggregation $-/+$ Meg presence, the illustration
878 highlights a genotype-specific response to competition and a differential paradigm
879 shift between the GxG and GxGxE contexts.

880 **Figure 3. Contrast of Meg relative performance under varied competitive**
881 **pressures, averages \pm SE.** Proportional doughnuts are used to compare Meg
882 reproductive success whilst competing against different pea-aphid genotypes on three
883 faba bean cultivars. Average Meg competitive performance across contexts (the
884 legend's complete blue doughnut) is used as a yardstick (*AM*) relevant to which all
885 Meg x Pea aphid populations were normalised, as a measure of relative comparative
886 performance. As such, the doughnut size reflects the relative size of the entire
887 population of Meg (blue) and the co-occurring competitor (green or pink) *i.e.* GxG
888 population. Whereas, the doughnut parts explicate the average proportion of Meg *vs.*
889 competitor per context. We also annotated each doughnut with average total numbers
890 (densities) of every inter-payer and provided corresponding lower-case alphabetical
891 letters following a post-hoc Tukey's HSD to denote any mean dissimilarities. Meg
892 control (performance alone) readings are provided as a frame of reference.

893 **Figure 4. Behaviour (on-plant distribution) of focal clone Meg under varying**
894 **interspecific competitive pressures per cultivar.** Meg (blue) showed high
895 compatibility of space use vs. varied pea aphid identities (green and pink). Occupation
896 of shareable space is in due proportion (vertically [proportionate plant strata) and
897 horizontally [stratum proportions relative to each identity of each competitive
898 pairing]).

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