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**

Abstract

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

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

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

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

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

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

Keywords

Genetic variability, interspecific competition, aphids, ecoevolutionary dynamics

Introduction

Selective forces vs. species activities, order and feedback loops

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

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

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

Species do not exist in a vacuum

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

Rapidly responsive, highly plastic and context-dependent

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

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

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

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

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

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

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

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

Methods

Host Plant

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

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

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

Aphid genotypes

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

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

Experimental design and analyses

The work was designed into two complementary parts:

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

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

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

Measured pea aphid traits

Performance shift

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

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

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

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

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

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

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

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

Behavioural shift

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

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

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

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

Measured Meg traits under interspecific competition

Comparative competitive performance

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

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

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

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

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

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

Differential competitive behaviour

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

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

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

Results

I. Five pea aphid clones with and without interaction with a heterospecific on three host plant cultivars

Pea aphid performance

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

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

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

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

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

Pea aphid behaviour

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

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

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

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

Meg comparative competitive performance

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

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

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

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

Meg behaviour

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

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

Discussion

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

The presence of a heterospecific differentially alters performance for clonal conspecifics

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

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

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

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

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

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

Aphid mothers hedge the bets of the clone

The patterns of reproductive success and behaviour we observed in the presence 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

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

The emergence of extended phenotype

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

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

Concluding remarks

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

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Contribution of authors

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

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

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

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Figure Legends

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

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

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

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