

Potential for insecticide-mediated shift in ecological dominance between two competing aphid species

Abd Allah A. H. Mohammed, Nicolas Desneux, Lucie S Monticelli, Yinjun

Fan, Xueyan Shi, Raul N. C. Guedes, Xiwu Gao

▶ To cite this version:

Abd Allah A. H. Mohammed, Nicolas Desneux, Lucie S Monticelli, Yinjun Fan, Xueyan Shi, et al.. Potential for insecticide-mediated shift in ecological dominance between two competing aphid species. Chemosphere, 2019, 226, pp.651-658. 10.1016/j.chemosphere.2019.03.114 . hal-02629113

HAL Id: hal-02629113 https://hal.inrae.fr/hal-02629113

Submitted on 22 Oct 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

Version of Record: https://www.sciencedirect.com/science/article/pii/S0045653519305569 Manuscript_c46ff9cff7b583cc2299f3d981629807

1 Potential for insecticide-mediated shift in ecological dominance between two competing

- 2 aphid species
- 3
- 4 Abd Allah A. H. Mohammed¹, Nicolas Desneux^{2*}, Lucie S. Monticelli², Fan Yinjun¹, Xueyan
- 5 Shi¹, Raul N.C. Guedes³, Xiwu Gao^{1*}
- 6
- ⁷ ¹Department of Entomology, College of Plant Protection, China Agricultural University,
- 8 Beijing 100193, China.
- 9 ² INRA (French National Institute for Agricultural Research), Université Côte d'Azur, CNRS,
- 10 UMR 1355-7254 Institute Sophia Agrobiotech, Sophia Antipolis 06903, France.
- ¹¹ ³ Departamento de Entomologia, Universidade Federal de Viçosa, Viçosa, Minas Gerais
- 12 36570-900, Brazil
- 13
- 14 *nicolas.desneux@sophia.inra.fr (ND), gaoxiwu@263.net.cn (XWG).
- 15

16 Abstract

17 Competition is a key structuring component of biological communities, which is affected by both biotic and abiotic environmental stressors. Among the latter, anthropic stressors and 18 19 particularly pesticides are noteworthy due to their intrinsic toxicity and large use in agroecosystems. However this issue has been scarcely documented so far. In this context, we 20 21 carried out experiments under laboratory conditions to evaluate stress imposed by the 22 neonicotinoid insecticide imidacloprid on intra and interspecific competition among two major wheat pest aphids. The bird cherry-oat aphid Rhopalosiphum padi L. and the English 23 grain aphid Sitobion avenae F. were subjected to competition on wheat seedlings under 24 25 varying density combinations of both species and subjected or not to imidacloprid exposure. Intraspecific competition does take place without insecticide exposure, but so does 26 interspecific competition between both aphid species with R. padi prevailing over S. avenae. 27 28 Imidacloprid interfered with both intra and interspecific competition suppressing the former and even the latter for up to 14 days, but not afterwards when a shift in dominance takes place 29 30 favoring S. avenae over R. padi, in contrast with the interspecific competition without 31 imidacloprid exposure. These findings hinted that insecticides are indeed able to mediate species interaction and competition influencing community structure and raising management 32 33 concerns for favoring potential secondary pest outbreaks. Keywords: Intraspecific competition, interspecific competition, *Rhopalosiphum padi*, 34

- 35 *Sitobion avenae*, imidacloprid, dominance shift.
- 36

37 Introduction

38 Resource-sharing organisms are the subject of competition when the shared resource is limited forcing their interaction, what may take place among individuals of the same species 39 resulting in intraspecific competition, or among individuals of different species leading to 40 interspecific competition (Reitz and Trumble, 2002; van Veen et al., 2006; Villemereuil and 41 Lopez-Sepulcre, 2011; Barabás et al., 2016; Naselli et al. 2016; Zhao et al., 2017). 42 43 Competition is an important community structuring phenomenon in nature (Iwabuchi and Urabe, 2012; Soares, 2013) but impact of pesticides on competition processes has been 44 scarcely studied in agroecosystems. The few studies available suggest that such anthropic 45 46 compounds could be important in shaping arthropod communities associated with various crops or crop-related systems (Oliveira et al., 2007; Cordeiro et al. 2014). For example 47 community structure may be compromised as population recovery may be delayed after 48 49 pesticide application(s), and species dominance may shift favoring secondary pest outbreaks (Liess and Foit, 2010; Guedes et al., 2016; 2017) 50

51 The outcome of competition varies with the competing species ranging from 52 potentially negative impact on both species (Oliveira et al., 2007; Moon et al., 2010; Jaworski et al., 2015), or on the weaker competitors (Paini et al., 2008; Bompard et al. 2013; Jaworski 53 et al. 2013; Tuelher et al. 2017), to not affecting either or even favoring at least one of them 54 (Vilca Mallqui et al. 2013). Regardless, intraspecific competition is usually considered more 55 important and stronger than interspecific competition (Moon et al., 2010; Villemereuil and 56 Lopez-Sepulcre, 2011; Del Arco et al., 2015), but both need to be considered in any given 57 scenario to assess their relative impacts. Furthermore, initial evidence is suggestive that 58 variation in intraspecific competition can change the outcome of interspecific competition 59 among aphids (Hazell et al., 2006). 60

61

Several environmental factors, both biotic and abiotic, may affect arthropod

competitive interactions (Gergs et al., 2013; Duan et al., 2016; Jordan and Tomberlin, 2017). 62 Temperature, light, relative humidity and rainfall among others, are regarded as important 63 abiotic factors for competition (Marchioro and Foerster, 2011; Savopoulou-Soultani et al., 64 2012; Marchioro and Foerster, 2016). Nonetheless anthropogenic abiotic stressors are also 65 potentially important for species competition, but they are frequently neglected in such 66 framework (Guedes et al., 2016, 2017; Zhao et al., 2017). Pesticides, and particularly 67 68 insecticides, are representatives of such stressors, whose distribution in agroecosystems is ubiquitous and deserves attention (Desneux et al., 2005; 2007; Sánchez-Bayo, 2011; Passos et 69 al. 2018), as they may promote species outbreaks through changing the arthropod community 70 71 structure associated with such environments (Biondi et al. 2012; Lu et al. 2012; Gao et al., 2014; Guedes et al., 2016, 2017; Zhao et al., 2017). 72

73 The relevance of pesticides on competition goes beyond lethal effects, as sublethal 74 stresses are likely as important or even more important drivers of competition than actual mortality (Cordeiro et al., 2014; Gao et al., 2014; Guedes et al., 2017; Zhao et al., 2017). 75 76 Frequent and widespread use of pesticides in crops lead to an almost chronic exposure to 77 sublethal concentrations of pesticides in organisms inhabiting such habitats (Boone and Semlitsch, 2002, Pisa et al., 2017). However, this issue only received only limited attention 78 (Knillmann et al., 2012; Cordeiro et al., 2014), even less in the case of systemic pesticides 79 80 despite their prevalent use in agriculture nowadays (which actually is increasing due to their versatile use, Miao et al., 2014; Wang et al. 2017; Zhang et al., 2015). The systemic 81 insecticides and specially neonicotinoids have been the target of concerns because of their 82 83 harmful effects on non-target species and their broad agriculture use (Damalas and Eleftherohorinos, 2011; Wu et al., 2011; Zhu et al., 2017). However, we still lack a thorough 84 85 understanding of complex interactions taking place in agroecosystems in which neonicotinoids are frequently applied, despite that it appears essential for potentially 86

improving pest management programs and minimizing environmental impact of crop 87 88 protection methods (Chailleux et al., 2014; Bebber, 2015; Mohammed et al., 2018). Systemic pesticides, notably imidacloprid, have been largely used to target the wheat 89 90 pest species, particularly the bird cherry-oat aphid *Rhopalosiphum padi* L. and the English 91 grain aphid Sitobion avenae F. (Tang et al., 2013; Chagnon et al., 2015; Simon-Delso et al., 2015; Mohammed et al., 2018) which are two key pests on wheat worldwide (Duan et al. 92 2017; Luo et al. 2018; Ali et al. 2018; Ortiz-Martinez et al. 2018). However, the relative 93 impact of this compound in both these aphid species and their interaction remains unknown. 94 Therefore, the present study aimed to assess the impact of the systemic (neonicotinoid) 95 96 insecticide imidacloprid on intra and interspecific competition between R. padi and S. avenae. 97 The laboratory experiments were carried out by using varying combinations of both aphid species. The goal was to test whether imidacloprid would mediate and thus affect the intra and 98 99 interspecific competitive interaction between both aphid pest species.

100

101 Materials and Methods

102 **Biological materials**

Wheat seeds used in competition experiments were provided by the Zhuozhou Experimental 103 Station of the China Agricultural University (Hebei, China). Seeds were planted in plastic 104 pots (10 cm in diameter and 9 cm high), and all of the pots were filled with fertile soil 105 (granularly (mm): 4.0-8.0; pH: 5.5-6.5; N mg/kg: 300-600; P2O5 mg/Kg: 150-300; K₂O 106 mg/kg: 300-550; humidity: % 45-60; organic matter $\% \ge 30$). The soil was purchased from 107 the Fangjie Huahui Yingyang Tu Company (Beijing, China). Five days after germination, the 108 seedlings were thinned to 10 healthy wheat seedlings per pot. The colonies of cherry-oat (R. 109 110 padi) and grain aphids (S. avenae) were obtained from laboratory insect cultures and maintained at the Toxicology Lab of the Department of Entomology, College of Plant 111

Protection, China Agricultural University (Beijing, China). Aphid populations of both species were reared from single parthenogenetic adults and held in the laboratory for several years without insecticide exposure (Lu and Gao, 2009; Lu et al., 2009; Lu et al., 2013). The aphid populations used as stock cultures for the laboratory experiments were reared on insecticidefree wheat seedling in rearing cages (30 cm in width, 30 cm in length and 30 cm in height) within growth chamber (23 - 25 C°, 60- 70% RH, and 16:8 L:D). The competition experiments were carried out under the same environmental conditions.

119 Insecticide

The neonicotinoid insecticide imidacloprid was used in the competition experiments as the 120 abiotic agent of stress. The commercial formulation of imidacloprid (Bi Chong Lin, 10 %) 121 used was purchased from the Jiang Su Kesheng Company (Jiangsu, China). This formulation 122 is one of the main formulations registered and used in China at the manufacture's label rate 123 for aphid control in the wheat field (40-70 g a.i. ha⁻¹). Concentration-mortality bioassays with 124 this insecticide and formulation were carried out to assess its toxicity to both aphid species 125 allowing to recognize the sublethal range based on the LC₅. The commercial formulation of 126 127 imidacloprid was diluted in distilled water for use in the experiments described below.

128 Insecticide bioassay

129 Imidacloprid toxicity was assessed with apterous adult aphids by using the leaf dip method

130 (Guo et al. 2013; Liu et al. 2017). Six serial dilutions (mg/L) of imidacloprid were prepared

131 for treating the wheat seedlings (5 days old), which were dipped into the desired

132 concentrations for 10 seconds; the seedlings were subsequently removed from the solution,

133 whose excess was adsorbed off with clean, dry filter paper pieces. The treated seedlings were

then transferred to plastic Petri dishes lined with moistened filter paper (to keep humidity on

seedling roots) and placed under room temperature. Twenty apterous adults of either aphid

136 species were used for each insecticide concentration using three replicates per concentration

and species. The aphids in the control group fed on seedlings dipped in distilled water. The 137 insects were then maintained under laboratory conditions at 23-25 °C temperature, 60-70% 138 relative humidity, and 16:8 h [L:D] photoperiod. Insect mortality was recorded after 24 h 139 exposure and the aphids were recognized as dead when failing to exhibit movement after a 140 gentle touch with a camel's hair brush. The results obtained were subjected to probit analysis 141 and the respective LC_5 was thus estimated. The estimated LC_5 of each aphid species was 142 143 further checked against the control insects in an additional 24 h exposure bioassay where mortality was again recorded as detailed above, but using 12 replicates. These estimated LC₅ 144 were subsequently used to in the competition experiments. 145

146 Imidacloprid and intraspecific competition

The intraspecific (single species) competition experiments were carried out under the same 147 experimental conditions detailed above. Three densities of either aphid species (5, 15, 30 148 149 apterous adults) were inoculated on each pot containing wheat seedlings treated or not with imidacloprid at 6.86 mg/l a.i. (= LC_5), following a three-way factorial arrangement (2 species 150 151 x 3 densities x 2 insecticidal treatment conditions) in a completely randomized design. The 152 insecticide was sprayed to the seedlings at the desired concentration always using distilled water for the dilutions; only distillated water was used to spray the seedlings of the control 153 pots and insects. The aphid species were released in each experimental unit 24 hours after 154 spraying. The pots were subsequently covered with cylindrical transparent plastic bag (9 cm 155 in diameter, and 21 cm high, with 0.5 mm mesh from top) to prevent the aphids from 156 escaping. The number of live aphids in each experimental unit was recorded after 7 days. 157 Each treatment was replicated 12 times. 158

159 Imidacloprid and interspecific competition

160 Two experiments of interspecific competition between the cherry-oat and the grain aphids

161 were performed. The first followed a treatment series placing the two competing species in

three even densities (5:5, 15:15, and 30:30). The second set followed a uneven treatment series using the following density combinations 30:0, 25:5, 20:10, 15:15, 10: 20, 5:25 and 0:30. Both experiments were performed as described for the intraspecific experiments established in a three-way factorial arrangement in a completely randomized design with 12 replications. The number of aphids of each species was recorded in each replicate and treatment 7 days after the start of the experiments.

168 Statistical analyses

The mortality results from the concentration-mortality bioassays were subjected to probit 169 analyses using the software PoloPlus 2.0 (LeOra software, 2006) to allow the assessment of 170 171 the imidacloprid toxicity to each aphid species, which also allowed the estimates of the LC5 and LC_{50} 's. The toxicity curves were considered as significantly different when the 172 confidence limits (95%) at their LC₅ and LC₅₀ values did not overlap (Prabhaker et al., 2011). 173 174 The instantaneous rate of population growth (ri), a strong surrogate estimator of the intrinsic rate of population growth (rm) (Stark and Banks 2003), was calculated using the formula r_i = 175 176 [Ln(Nj /Ni)]/Dt, where Nj and Ni are the final and initial number of live insects (in each cage), respectively, and Dt is the duration of the experiment (i.e., 7 days). The following 177 statistical analyses were performed using R version 3.3.3. After checking the assumptions of 178 normality and homoscedasciticy, three-way analyses of variance using generalized linear 179 model were carried out to test the impact of the initial aphid density (intra and interspecific 180 competition) and the presence of insecticide on the final insect population and on the 181 instantaneous rate of population growth (r_i) . The results of interspecific competition were 182 183 subjected to regression analyses with initial insect density of both aphid species as independent variables and their final density and rate of population growth as dependent 184 variables. The regressions models were obtained using the curve-fitting procedure of the 185 software TableCurve 3D (Systat, San Jose, CA, USA). The significant regression models were 186

187 selected based on the criteria of parsimony, high F-value, and sudden increase in R^2 with

188 model complexity. The residual distributions were checked to validate parametric

assumptions.

190

191 **Results**

192 Concentration-mortality response

193 The results of the leaf dip bioassays of imidacloprid toxicity to adult aphids enabled

- 194 estimating the toxicity of the neonicotinoid to both aphid species; it proved to be about 3-fold
- less toxic to the grain aphid *S. avenae* than to the cherry-oat aphid *R. padi* (Table 1). LC₅
- values for *S. avenae* and *R. padi* were 10.22 and 3.49 ppm, respectively (Table 1), with an

197 average LC₅ for both species of 6.86 ppm (this average value was used when both species

198 were exposed to the insecticide simultaneously i.e. during the inter-specific competition

199 experiments). Control mortality was < 5% in all replicates.

200 Imidacloprid and intra-specific competition

201 The presence of insecticide had a negative impact on the final population density and r_i of 202 both aphid species 7 days after treatment ($F_{1,132} = 1030.10$, $P \le 0.001$ and $F_{1,132} = 547.14$, $P \le 0.001$ 0.001 respectively), as were the effects of insect species and density combinations ($F_{1,132}$ > 203 35.35, P < 0.001). The cherry-oat aphid *R. padi* exhibited steady increase in final density with 204 increase in initial density, as did the wheat aphid S. avenae although always at lower densities 205 (Fig. 1A). Such trend was however inverted when the insects were exposed to imidacloprid 206 and the density of R. padi became slightly lower than S. avenae for the whole range of initial 207 208 densities considered (Fig. 1B). The same trends were observed when the rate of population growth was considered, with the cherry-oat aphid maintaining higher growth without 209 insecticide exposure (Fig. 2A), but the reverse taking place when imidacloprid was used (Fig. 210 2B). At the highest density of each species, there was a convergence in population growth of 211

both species exhibiting similar values (Fig. 2B).

213 Imidacloprid and inter-specific competition

The regression analyses assessing the final aphid populations based on their competing initial 214 215 densities subjected or not to imidacloprid exposure indicated a contrasting pattern between R. padi and S. avenae. Without imidacloprid R. padi was significantly affected by its own initial 216 217 density and that of S. avenae, although at a smaller degree (Fig. 3). The final population 218 densities of R. padi reached levels above 500 insects per experimental unit at initial 219 conspecific densities as low as 20 insects/unit and such high densities took place even with up densities of the competing S. avenae as high as 30 insects/unit. In contrast, the final density of 220 221 S, avenae was much lower reaching 300 insects/unit just at its highest initial densities and just with little or non-existent heterospecific competition by R. padi (Fig. 3). Both outcomes 222 indicate interference between competing species, but with a stronger effect of *R. padi*, which 223 224 is the dominant competitor when facing S. avenae.

Imidacloprid exposure allowed for a very different scenario imposing a drastic stress 225 on the competition between R. padi and S. avenae. The high final populations of R. padi 226 227 observed without imidacloprid did not occur with contamination by this insecticide reaching final peak of populations barely extending to 200 insects/unit and only at its highest initial 228 229 density (i.e., 30 insects/unit) (Fig. 3). In contrast, the performance of S. avenae suffered little change with imidacloprid contamination, although its final population levels were slightly 230 reduced (Fig. 3). Again, the effect of heterospecific competition was significant for both 231 species, as indicated by the respective regression models where the initial density of both 232 species was necessary to reliably estimate the final population densities of both *R. padi* and *S.* 233 avenae, although the influence of conspecifics was always stronger (Fig. 3). 234

The effect of intraspecific competition on the population growth of both competingaphid species was even more revealing than that of the final populations although the general

237	trends were similar. Again <i>R. padi</i> was a much stronger competitor without imidacloprid
238	contamination maintaining high rates of population growth at initial conspecific densities
239	lower than 5 insects/unit with only limited effect of S. avenae. The opposite is true for S.
240	avenae, which was more drastically affected by R. padi and reached only intermediary rates
241	of population growth (\leq 35 insects/ day) even at highest <i>S. avenae</i> density (Fig. 3).
242	Imidacloprid nullified the species interference in the intraspecific competition (i.e.,
243	heterospecific initial density was not necessary for the regression models) and favored higher
244	population growth of S. avenae rather than the previously dominant R. padi shift their
245	respective status as competitors (Fig. 3).
246	

247 Discussion

Anthropic contaminants such as pesticides are considered as one of the factors threating
ecosystem sustainability, notably through interfering with direct and indirect biotic
relationships in arthropod communities (Boone and Semlitsch, 2002; Knillmann et al., 2012;
Cordeiro et al., 2014; Biondi et al. 2015; Guedes et al., 2016, 2017; Xiao et al. 2016). We
demonstrated that the presence of pesticide on wheat plants modulated both intraspecific and
interspecific competitions involving the cherry-oat aphid *R. padi* and the wheat aphid *S. avenae*.

The performance of each species under intraspecific competition conditions diverged with and without imidacloprid exposure, with *R. padi* suffering more with the insecticide, which greatly suppressed the population of this species while exhibiting only milder impact on *S. avenae*. Imidacloprid exposure relaxed intraspecific competition leading to increased rate of population growth under this condition reverting the trend of reduced population growth with increased initial density from the insecticide-free environment. In addition, imidacloprid exposure also led to a shift in the outcome of interspecific competition between *R. padi* and *S. avenae* compromising the dominance of the former species in insecticide-free
plants, while favoring the prevalence of the latter species, the wheat aphid, under imidacloprid
exposure. The mutual interference between species observed without imidacloprid
contamination was virtually nullified when the insecticide was applied. This finding is also
suggestive of the importance of interspecific competition in shaping the associated
community in contrast with the usual emphasis given to intraspecific competition (Kaplan and
Denno, 2007; Moon et al., 2010; Villemereuil and Lopez-Sepulcre, 2011).

269 Differential (acute) toxicity

The susceptibility of both aphid species to imidacloprid was different, what is likely a 270 271 contributing factor for the observed outcome of competition (Zhao et al., 2017). The concentration-mortality bioassays performed indicated that R. padi is about 3-fold more 272 susceptible to imidacloprid than S. avenae. Therefore, imidacloprid exposure should lead to 273 274 higher mortality of the former species than of the latter, but this expectation is based solely in a mortality assessment while the demographic impact of the compound is of greater 275 importance although frequently neglected (Stark and Banks, 2003; Guedes et al., 2016), 276 allowing even the recognition of potential hormesis-like stimulatory effects that may take 277 place (Guedes and Cutler, 2014). For example, low imidacloprid concentrations can exert 278 279 stimulatory effects on reproduction and immature development in the soybean aphid Aphis glycines (Qu et al. 2015). Regardless, a range of factors may determine such differential 280 susceptibility, including distinct rates of insecticide penetration, detoxification activity, and 281 even minute differences in the target site of insecticide action, but S. avenae seems to exhibit 282 higher insecticide detoxification activity than R. padi, as suggested by previous studies (Lu et 283 al., 2013; Xiao et al., 2015; Lu and Gao, 2016). 284

285 Imidacloprid impact on intraspecific competition

286 Intraspecific competition did occur in both aphid species, *R. padi* and *S. avenae*, when no

insecticide was present and as already suggested by field results from Jarosik et al. (2003). In 287 288 contrast, when aphids were exposed to the imidacloprid intraspecific competition was relaxed and the aphids exhibited higher population with higher initial population. Indeed, low initial 289 290 densities afford lower mating opportunities reducing later competition (Huston, 1979), what was enhanced with higher initial densities particularly under imidacloprid contamination. 291 292 Nonetheless, population growth was highest at the lowest initial densities of both species in 293 without imidacloprid contamination indication that densities as low as 5 insects/pot of 10 seedlings, while the highest density likely approached the carrying capacity of the 294 experimental units used. 295

296 When the intraspecific competition of both aphid species are compared, the prevalence of R. padi over S. avenae without imidacloprid contamination was nullified in the presence of 297 the insecticide. The higher acute toxicity of imidacloprid to *R. padi* causing higher mortality 298 299 in this species than in S. avenae is a likely cause for such outcome, but sublethal and transgenerational effects are also arguably playing a relevant role for this observed outcome 300 301 (Xiao et al., 2015). An aided concern is the fact that the relaxation of intraspecific competition 302 with imidacloprid exposure affords higher changes of survival and selection for insecticide resistance in both species (Cordeiro et al., 2014; Guedes et al., 2016, 2017). Nonetheless, the 303 strength of selection will probably be stronger for R. padi since it is the most susceptible 304 species (and thus subjected to stronger selection pressure for resistance). 305

306 Imidacloprid impact on interspecific competition

The sublethal insecticide concentrations are expected to interfere with not only intra-, but also with interspecific competition (Liess et al., 2013; Cordeiro et al., 2014; Guedes et al., 2016). Our study also provides support for this notion and consistent with our results of intraspecific competition for both aphid species. Again imidacloprid contamination relaxed competition reducing the final population and population growth of both species, but much more so of

R. padi, the most susceptible and previously dominant species. Even the species interference
when under competition, which is suggested by the results without insecticide contamination,
are suppressed with imidacloprid exposure, unlike suggested observations with whiteflies,
leafminers and thrips (Sun et al., 2013; Gao et al., 2014; Zhao et al., 2017). Again, both lethal
and sublethal effects on each aphid species are likely playing a role for the observed outcome
(Cordeiro et al., 2014; Xiaon et al., 2015).

318 Both species were able to co-exist under competition, regardless of sublethal imidacloprid contamination. However, the insecticide contamination shifted the species 319 dominance greatly compromising the prevalence of R. padi over S. avenae. This result 320 321 consistent with several earlier reports about the interactions among sap feeder arthropods under natural colonization (Pascual and Callejas, 2004; Qureshi and Michaud, 2005; Umina 322 and Hoffmann, 2005; Paini et al., 2008; Tapia et al., 2008; Sun et al., 2013; Zhao et al., 2017). 323 324 These reports showed that all competing species can be negatively affected by competition, and the weaker competitors will be more affected. In addition, these reports also suggest that 325 326 pesticide application may induce a shift in competitive potential of competing species, 327 possibility demonstrated by Cordeiro et al. (2014) in density-dependent and concentrationdependent experiments with grain beetles. 328

329 The findings reported here showing a shift in dominance between competing aphid species when subjected to imidacloprid-contaminated plants is consistent with the 330 intermediate disturbance hypotheses. This hypothesis was earlier developed to explain the 331 maximization of species diversity under intermediate levels of disturbance able to reduce the 332 333 abundance of the competitively dominant species (Connell, 1978; Shea et al., 2004). The rational and hypothesis was more recently used to in the context of insecticide disturbance 334 mediating competitive interactions (Cordeiro et al., 2014; Guedes et al., 2016), context 335 equality applicable to the present study with the competing aphids R. padi and S. avenae. This 336

337	is the case because a low imidacloprid concentration (LC_5) favored the weaker competing
338	species compromising the dominance of the stronger competitor, R. padi in our case. High
339	concentrations of imidacloprid would likely greatly compromise both species, while very low
340	concentrations would not affect them, but intermediate concentrations would potentially allow
341	higher diversity and a shift in ecological dominance, as reported here. The extended use of
342	imidacloprid will likely change the associated arthropod community and may favor secondary
343	pest outbreaks, particularly of S. avenae, what is a management concern and should be
344	considered when designing pest management programs.
345	
346	Acknowledgements

347 This study was financially supported by the Modern Agro-industry Technology Research
348 System (CARS-05).

349

350 Author Contributions

- A.A.H.M., N.D., and X.G. designed the experiments, A.A.H.M., X.S., and F.Y. performed the
- 352 experiments. A.A.H.M., R.N.C.G., N.D., and L.S.M. carried out the data analysis, X-W.G
- 353 contributed reagents/ materials/analysis tools, A.A.H.M., L.S.M., R.N.C.G., N.D., and X-

354 W.G. wrote the main manuscript text. All authors reviewed the manuscript

- 355
- **Competing for financial interests:** The authors declare that no competing financial interests.
- 357

358 **References**

- 359 Ali A, Desneux N, Lu YH, Wu KM. (2018). Key aphid natural enemies showing positive
- 360 effects on wheat yield through biocontrol services in northern China. Agriculture,
- 361 Ecosystems & Environment 266:1-9.

362	Barabás G., Michalska-Smith M. J., and Allesina S. (2016). The effect of intra- and
363	interspecific competition on coexistence in multispecies communities. Am Nat. 188:
364	E1-E12.
365	Bebber D. P. (2015). Range expanding pests and pathogens in a warming world. Annu. Rev.
366	Phytopathol. 53:335–356.
367	Biondi A, Desneux N, Siscaro G, Zappalà L. (2012). Using organic-certified rather than
368	synthetic pesticides may not be safer for biological control agents: selectivity and side
369	effects of 14 pesticides on the predator Orius laevigatus. Chemosphere 87:803-812.
370	Biondi A, Campolo O, Desneux N, Siscaro G, Palmeri V, Zappalà L. (2015). Life stage-
371	dependent susceptibility of Aphytis melinus DeBach (Hymenoptera: Aphelinidae) to
372	two pesticides commonly used in citrus orchards. Chemosphere 128:142-147.
373	Boone M. D. and Semlitsch R. D. (2002). Interactions of an insecticide with competition and
374	pond drying in amphibian communities. Ecol Appl 12: 307–316.
375	Bompard A, Jaworski CC, Bearez P, Desneux N. (2013). Sharing a predator: can an invasive
376	alien pest affect the predation on a local pest? Population Ecology 55:433-440.
377	Chagnon M., Kreutzweiser D., Mitchell E. A., Morrissey C. A., Noome D.A., and Van der
378	Sluijs J. P. (2015). Risks of large-scale use of systemic insecticides to ecosystem
379	functioning and services. Environ Sci Pollut Res. 22:119-134.
380	Chailleux A., Mohl E., Teixeira A., Messelink G., and Desneux N. (2014). Natural enemy-
381	mediated indirect interactions among prey species: current theories and potential for
382	enhancing biocontrol services in agro-ecosystems. Pest Manag Sci. 70: 1769–1779.
383	Cordeiro E. M. G., Correa A. S., and Guedes R. N.C. (2014). Insecticide-mediated shift in
384	ecological dominance between two competing species of grain beetles. PLoS ONE. 9:
385	e100990.
386	Damalas C. A and Eleftherohorinos I. G. (2011). Pesticide Exposure, Safety Issues, and Risk

387	Assessment Indicators. Int. J. Environ. Res. Public Health. 8: 1402-1419.
388	Del Arco A. I., Rico A., and van den Brink P. J. (2015). Effects of intra- and interspecific
389	competition on the sensitivity of Daphnia magna populations to the fungicide
390	carbendazim. Ecotoxicology. 24:1362–1371.
391	Desneux N, Fauvergue X, Dechaume-Moncharmont FX, Kerhoas L, Ballanger Y, Kaiser L
392	(2005). Diaeretiella rapae limits Myzus persicae populations following applications of
393	deltamethrin in oilseed rape. Journal of Economic Entomology 98:9-17.
394	Desneux N., Decourtye A., and Delpuech J., (2007). The sublethal effects of pesticides on
395	beneficial arthropods. Annu. Rev. Entomol. 52:81-106.
396	Duan, M. Liu Y., Yu Z., Baudry J., Li L., Wang C. and Axmacher J. C. (2016). Disentangling
397	effects of abiotic factors and biotic interactions on cross-taxon congruence in species
398	turnover patterns of plants, moths and beetles. Sci. Rep. 6:23511.
399	Duan XL, Peng X, Qiao XF, Chen MH (2017) Life cycle and population genetics of bird
400	cherry-oat aphids Rhopalosiphum padi in China: an important pest on wheat crops. J.
401	Pest Sci. 90:103-116.
402	Gao Y, Reitz S. R., Wei Q., Yu W., Zhang Z., and Lei Z. (2014). Local crop planting systems
403	enhance insecticide-mediated displacement of two invasive Leafminer Fly. PLoS
404	ONE. 9: e92625.
405	Gergs A., Zenker A., Grimm V., and Preuss T. G. (2013). Chemical and natural stressors
406	combined: from cryptic effects to population extinction. Sci. Rep. 3: 2036.
407	Gianoli E. (2000). Competition in cereal aphids (Homoptera: Aphididae) on wheat plants.
408	Environ. Entomol. 29: 213-219.
409	Guedes R.N.C, Cutler G.C. (2014) Insecticide-induced hormesis and arthropod pest
410	management. Pest Manag. Sci. 70:690-697.
411	Guedes R.N.C., Smagghe G., Stark J.D., and Desneux N. (2016) Pesticide-induced stress in

412 arthropod pests for optimized integrated pest management programs. Annu. Rev.

413 Entomol. 61: 43-62.

- Guedes R.N.C., Walse S.S., and Throne J.E. (2017) Sublethal exposure, insecticide resistance,
 and community stress. Curr. Opin. Insect Sci. 21: 47-53.
- 416 Guo L, Desneux N, Sonoda S, Liang P, Han P, Gao XW. (2013). Sublethal and
- 417 transgenerational effects of chlorantraniliprole on biological traits of the diamondback
 418 moth, *Plutella xylostella* L. Crop Protection 48:29-34.
- 419 Hazell S. P., McClintock I. A. D., and Fellowes M. D. E. (2006). Intraspecific heritable
- 420 variation in life-history traits can alter the outcome of interspecific competition among
 421 insect herbivores. Basic and Applied Ecology. 7: 215-223.
- Huston M. (1979). A general hypothesis of species diversity. The American Naturalist. 113:
 81-102.
- 424 Iwabuchi T. and Urabe J. (2012). Competitive outcomes between herbivorous consumers can
 425 be predicted from their stoichiometric demands. Ecosphere. 3:7.
- 426 http://dx.doi.org/10.1890/ES11-00253.1.
- 427 Jaworski CC, Bompard A, Genies L, Amiens-Desneux E, Desneux N. (2013). Preference and
- 428 prey switching in a generalist predator attacking local and invasive alien pests. PLoS
 429 ONE 8(12):e82231
- 430 Jaworski C. C., Chailleux A. S., Bearez P., and Desneux N. (2015). Apparent competition
- 431 between major pests reduces pest population densities on tomato crop, but not yield
 432 loss. J. Pest Sci. 88:793–803.
- Jarosik V., Honeka A., and TichopadA. (2003). Comparison of field population growths of
 three cereal aphid species on winter wheat. Plant Protect. Sci. 39: 61–64.
- 435 Jordan H. R. and Tomberlin J. K. (2017). Abiotic and biotic factors regulating inter-
- 436 Kingdom.engagementbetween insects and microbe activity on vertebrate remains.

- Insects. 8: 1-19.
- Kaplan, I. and Denno R. F. (2007). Interspecific interactions in phytophagous insects
 revisited: a quantitative assessment of competition theory. Ecology Letters 10: 977–
 994.
- 441 Knillmann S., Stampfli N. C., Noskov Y. S. Mikhail A. Beketov M. A., and Matthias Liess A.
- 442 (2012). Interspecific competition delays recovery of *Daphnia* spp. populations from
 443 pesticide stress. Ecotoxicology. 21:1039–1049.
- Lang J. M., and Benbow M. E. (2013). Species interactions and competition. Nature
 Education Knowledge. 4: 8.
- 446 LeOra Software (2006). POLO-Plus. A user's guide to probit or logit analysis. LeOra
- 447 Software, Berkeley, CA .
- Liess M. and Foit K. (2010). Intraspecific competition delays recovery of population
 structure. Aquat Toxicol. 97: 15–22.
- 450 Liess M., Foit K., Becker A., Hassold E., Dolciotti I., Kattwinkel M., and Duquesne S.
- 451 (2013). Culmination of low-dose pesticide effects. Environ. Sci. Technol. 47: 8862452 8868.
- Liu XL, Tang QL, Li YD, Mateus RC, Liang P, Gao XW (2017) Widespread resistance of the
 aphid *Myzus persicae* to pirimicarb across China, and insights on ace2 mutation
 frequency in this species. Entomol. Gen. 36:285-299
- 456 Lu Y. and Gao X. (2016). Inhibiting effects of common insecticides on carboxylesterase
- 457 activity in *Sitobion avenae* and *Rhopalosiphum padi* (Hemiptera: Aphididae) and their
 458 synergism to beta-cypermethrin. Acta Entomologica Sinica. 59: 1151-1158.
- 459 Lu Y. H., He Y. P., and Gao X. W. (2013). Comparative studies on acetylcholinesterase
- 460 characteristics between the aphids, *Sitobion avenae* and *Rhopalosiphum padi*. Journal
- 461 of Insect Science.13: 9.

462	Lu Y-H. and Gao X-W. (2009). Multiple mechanisms responsible for differential
463	susceptibilities of Sitobion avenae (Fabricius) and Rhopalosiphum padi (Linnaeus) to
464	pirimicarb. Bulletin of Entomology Research. 99: 611-617
465	Lu Y-H., Yang T., and Gao X-W. (2009). Establishment of baseline susceptibility data to
466	various insecticides for aphids Rhopalosiphum padi (Linnaeus) and Sitobion avenae
467	(Fabricius) (Homoptera: Aphididae) by the method of residual film in glass tube. Acta
468	Entomologica Sinica. 52: 52-58.
469	Lu YH, Wu KM, Jiang YY, Guo YY, Desneux N. (2012). Widespread adoption of Bt cotton
470	and insecticide decrease promotes biocontrol services. Nature 487:362-365.
471	Luo C, Li DD, Qu YY, Zhao HY, Hu ZQ (2018) Indirect effects of chemical hybridization
472	agent SQ-1 on clones of the wheat aphid Sitobion avenae. Entomol. Gen. 38:61-71
473	Marchioro, C.A., Foerster, L.A. (2011). Development and survival of the diamondback moth,
474	Plutella xylostella (L.) (Lepidoptera: Yponomeutidae) as a function of temperature:
475	effects on the number of generations in tropical and subtropical regions. Neotrop.
476	Entomol. 40, 533–541.
477	Marchioro, C.A., and Foerster, L.A., (2016). Biotic factors are more important than abiotic
478	factors in regulating the abundance of <i>Plutella xylostella</i> L., in Southern Brazil.
479	Revista Brasileira de Entomologia. 60: 328–333.
480	Miao J., Du Z. B., Wu Y. Q., Gong Z. J., Jiang Y. L., Duan Y., Li T., and Lei C. L. (2014).
481	Sub-lethal effects of four neonicotinoid seed treatments on the demography and
482	feeding behaviour of the wheat aphid Sitobion avenae. Pest Manag Sci 70: 55–59.
483	Miao J., Wu Y.Q., Yu Z. X., Duan Y. and Jiang Y. L. (2011). Comparative study of feeding
484	behaviors of Sitobion avenae, Sitobion graminum and Rhopalosiphum padi
485	(Homoptera: Aphididae) using electrical penetration graph (EPG). Acta Ecol. Sin. 31:
486	175–182.

- 487 Mohammed A. A. H., Desneux N., Fan Y., Han P., Ali A., Song DL., and Gao, XW. (2018).
- 488 Impact of imidacloprid and natural enemies on cereal aphids: Integration or ecosystem
 489 service disruption? Entomol. Gen. 37: 47-61.
- Moon D. C., Moon J., and Keagy A. (2010). Direct and indirect interactions. Nature
 Education Knowledge. 3:50.
- Morris R. J., Owen T., Lewis O. T., and Godfray H. C. J. (2004). Experimental evidence for
 apparent competition in a tropical forest food web. Nature. 428: 310-313.
- 494 Naselli M, Biondi A, Tropea Garzia G, Desneux N, Russo A, Siscaro G, Zappalà L. (2017).
- Insights on food webs associated with the South American Tomato Pinworm in
 Europe. Pest Management Science 73:1352-1357.
- 497 Oliveira E. E., Guedes R. N. C., Totola M. R., and De Marco P. Jr. (2007). Competition
 498 between insecticide-susceptible and -resistant populations of the maize weevil,
 499 *Sitophilus zeamais*. Chemosphere. 69: 17–24.
- Ortiz-Martinez SA, Lavandero B (2018) The effect of landscape context on the biological
 control of *Sitobion avenae*: temporal partitioning response of natural enemy guilds. J.
 Pest Sci. 91:41-53
- Paini D. R., Funderburk J. E. and Reitz S. R. (2008). Competitive exclusion of a worldwide
 invasive pest by a native. Quantifying competition between two phytophagous insects
 on two host plant species. Journal of Animal Ecology. 77: 184–190.
- Pascual S. and Callejas C. (2004). Intra- and interspecific competition between biotypes B
 and Q of *Bemisia tabaci* (Hemiptera: Aleyrodidae) from Spain. Bulletin of
 Entomological Research. 94: 369–375.
- Passos LC, Soares MA, Collares LJ, Malagoli I, Desneux N, Carvalho GA. (2018). Lethal,
 sublethal and transgenerational effects caused by insecticides on *Macrolophus basicornis*, predator of *Tuta absoluta*. Entomol. Gen. 38:127-143.

512	Pisa L., Goulson D., Yang E-C., Gibbons D., Sánchez-Bayo F., Mitchell E., Aebi A., van der
513	Sluijs J., MacQuarrie C. J. K., Giorio C., Long E. Y., McField M., & van Lexmond M.
514	B., and Bonmatin J-M. (2017). An update of the worldwide integrated assessment
515	(WIA) on systemic insecticides. Part 2: impacts on organisms and ecosystems.
516	Environ Sci Pollut Res. DOI 10.1007/s11356-017-0341-3.
517	Prabhaker N., Castle S. J., Naranjo S. E., Toscano N. C., and Morse J. G. (2011).
518	Compatibility of two systemic neonicotinoids, imidacloprid and amethoxam, with
519	various natural enemies of agricultural pests. J. Econ. Entomol. 104: 773-781.
520	Qu YY, Xiao D, Li JY, Chen Z, Biondi A, Desneux N, Gao XW, Song D. (2015). Sublethal
521	and hormesis effects of imidacloprid on the soybean aphid Aphis glycines.
522	Ecotoxicology 24:479–487.
523	Qureshi J. A. and Michaud J. P. (2005). Interactions among three species of cereal aphids
524	simultaneously infesting wheat. Journal of Insect Science. 5:13.
525	Reitz1 S. R. and Trumble J. T. (2002). Interspecific and intraspecific differences in two
526	Liriomyza leafminer species in California. Entomologia Experimentalis et Applicata.
527	102: 101-113.
528	Sánchez-Bayo F. (2011). Impacts of Agricultural Pesticides on Terrestrial Ecosystems.
529	Ecological Impacts of Toxic Chemicals. 63-87.
530	Savopoulou-Soultani M., Papadopoulos N. T., Milonas P., and Moyal P. (2012). Abiotic
531	factors and insect abundance. Psyche. Article ID 167420.
532	Simon-Delso N., Amaral-Rogers V., Belzunces L. P., Bonmatin J. M., Chagnon M., Downs C.,
533	Furlan L., Gibbons D. W., Giorio C., Girolami V., Goulson D., Kreutzweiser D. P.,.
534	Krupke C. H., Liess M., Long E., McField M., Mineau P., Mitchell E. A. D., Morrissey
535	C. A., Noome D. A., Pisa L., Settele J., Stark J. D., Tapparo A., Van
536	DyckH., VanPraagh J., Van der Sluijs J. P., Whitehorn P. R., and Wiemers M. (2015).

- 537 Systemic insecticides (neonicotinoids and fipronil): trends, uses, mode of action and
 538 metabolites. Environ Sci Pollut Res. 22: 5–34.
- Soares S. d. A. (2013). The role of competition in structuring ant communities: A review.
 Oecologia Australis. 17: 271-281.
- Stark J. D., Tanigoshi L., Bounfour B., and Antonelli A. (1997). Reproductive potential: It's
 influence on the susceptibility of a species to pesticides. Ecotoxicology and

543 Environmental Safety. 37: 273–279.

- Stark J.D., Banks J.E. (2003). Population-level effects of pesticides and other toxicants on
 arthropods. Ann. Rev. Entomol. 48:505-519.
- 546 Sun D-B., Liu Y-Q., Qin L., Xu J., Li F-F., and Liu S-S. (2013). Competitive displacement
- 547 between two invasive whiteflies: insecticide application and host plant effects.

548 Bulletin of Entomological Research. 103: 344–353.

- Tang L-D., Wu J-H., Ali S., and Ren S-X. (2013). Establishment of baseline toxicity data to
- 550 different insecticides for *Aphis craccivora* Koch and *Rhopalosiphum maidis* (Fitch)
- (Homoptera: Aphididae) by Glass Tube Residual Film Technique. Pakistan J. Zool.
 45: 411-415.
- 553 Tapia D. H., Troncoso A. J., Vargas R. R., Donoso R. O., and Niemeyer H. M. (2008).
- 554 Experimental evidence for competitive exclusion of *Myzus persicae nicotianae* by
- *Myzus persicae* s.s. (Hemiptera: Aphididae) on sweet pepper, *Capsicum annuum*(Solanaceae). Eur. J. Entomol. 105: 643-648.
- 557 Tuelher E.S., Silva E.H., Hirose E., Guedes R.N.C., and Oliveira E.E. (2017). Competition
- between the phytophagous stink bugs *Euchistus heros* and *Piesodorus guildinii* in
 soybeans. Pest Manag. Sci. 72: 1837-1843.
- 560 Umina P. A. and Hoffmann A. A. (2005). Competitive interactions among four pest species of
 561 Earth Mites (Acari: Penthaleidae). J. Econ. Entomol. 98: 307-316.

562	van Veen F. F. J., 1 Morris R. J., and Godfray H. C. J. (2006). Apparent competition,
563	Quantitative food webs, and the structure of phytophagous insect communities.
564	Annu.Rev. Entomol. 51: 187–208.
565	Vilca Mallqui K. S., Oliveira E. E., Guedes R. N.C. (2013). Competition between the bean
566	weevils Acanthoscelides obtectus and Zabrotes subfasciatus in common beans.
567	Journal of Stored Products Research. 55: 32-35.
568	Villemereuil P. B. and Lopez-Sepulcre A. (2011). Consumer functional responses under intra-
569	and inter-specific interference competition. Ecological Modelling. 222: 419-426.
570	Wang SY, Qi YF, Desneux N, Shi XY, Biondi A, Gao XW. (2017). Sublethal and
571	transgenerational effects of short-term and chronic exposures to the neonicotinoid
572	nitenpyram in the aphid Aphis gossypii. J. Pest Sci. 90:389-396.
573	Williams C. T. (1987). Comparison of the winter development, reproduction and lifespan of
574	viviparae of Sitobion avenae (F.) and Rhopalosiphum padi (L.)(Hemiptera: Aphididae)
575	on wheat and perennial rye grass in England. Bull. ent. Res. 77: 35-43.
576	Wu J. Y., Anelli C. M., Sheppard W. S. (2011). Sub-Lethal Effects of Pesticide Residues in
577	Brood Comb on Worker Honey Bee (Apismellifera) Development and Longevity.
578	PLoS ONE. 6: e14720.
579	Xiao D., Yang T., Desneux N., Han P., Gao X. (2015). Assessment of sublethal and
580	transgenerational effects of pirimicarb on the wheat aphids Rhopalosiphum padi and
581	Sitobion avenae. PLoS ONE. 10:e0128936. DOI:10.1371/journal. pone.0128936.
582	Xiao D, Zhao J, Guo X, Chen HY, Qu M, Zhai W, Desneux N, Biondi A, Zhang F, Wang S.
583	(2016). Sublethal effects of imidacloprid on the predatory seven-spot ladybird beetle
584	Coccinella septempunctata (Coleoptera: Coccinellidae). Ecotoxicology 25:1782-1793.
585	Zhang P., Zhang X., Zhao Y., Wei Y., Mu W., and Liu F. (2015). Effects of imidacloprid and
586	clothianid in seed treatments on wheat aphids and their natural enemies on winter

587	wheat. Pest Management Science. 2:1141-1149.
588	Zhao X., Reitz S. R., Yuan H., Lei Z., Paini D. R., and Gao Y.(2017). Pesticide-mediated
589	interspecific competition between local and invasive thrips pests. Sci. Rep. 7: 40512.
590	DOI: 10.1038/srep40512.
591	Zhu Y. C. Yao J., Adamczyk J., and Luttrell R., (2017). Feeding toxicity and impact of
592	imidacloprid formulation and mixtures with six representative pesticides at residue
593	concentrations on honey bee physiology (Apis mellifera).PLoS ONE. 12: e0178421.

Table 1. Relative toxicity of imidacloprid to two aphid species, Rhope	ılosiphum j	padi
and Sitobion avenae, after 24 hours post treatment.		

Species	n*	Slope ±	χ^2	df	LC5 (ppm)	LC50 (ppm)
		SE				
					Confidence Limits 95%	
R. padi	30	2.55±0.26	6.21	13	3.49 (2.20-4.81)	15.46 (12.91-
	0		5			18.19)
<i>S</i> .	30	2.50±0.27	7.36	13	10.22 (6.93-	46.50 (39.53-
avenae	0		7		13.39)	55.81)

* n: Number of insects per each experiment.

Figure captions

Fig. 1. Effect of initial (conspecific) density on the final population of two species of aphids, the bird cherry-oat aphid *Rhopalosiphum padi* and the English grain aphid *Sitobion avenae*, maintained in wheat seedlings contaminated or not with the neonicotinoid insecticide imidacloprid. Each symbol (\pm SE) represents the mean of 12 replicates.

Fig. 2. Effect of initial (conspecific) density on the rate of population growth of two species of aphids, the bird cherry-oat aphid *Rhopalosiphum padi* and the English grain aphid *Sitobion avenae*, maintained in wheat seedlings contaminated or not with the neonicotinoid insecticide imidacloprid. Each symbol (\pm SE) represents the mean of 12 replicates.

Fig. 3. Filled contour plots showing the effect of conspecific and heterospecific densities on the final population of two species of aphids, the bird cherry-oat aphid *Rhopalosiphum padi* and the English grain aphid *Sitobion avenae*, maintained in wheat seedlings contaminated or not with the neonicotinoid insecticide imidacloprid. The regression models predicting the reported outcomes are indicated in each plot.
Fig. 4. Filled contour plots showing the effect of conspecific and heterospecific densities on the rate of population growth of two species of aphids, the bird cherry-oat aphid *Rhopalosiphum padi* and the English grain aphid *Sitobion avenae*, maintained in wheat seedlings contaminated or not with the neonicotinoid insecticide imidacloprid.















