



## 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

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

Abd Allah A. H. Mohammed<sup>1</sup>, Nicolas Desneux<sup>2\*</sup>, Lucie S. Monticelli<sup>2</sup>, Fan Yinjun<sup>1</sup>, Xueyan Shi<sup>1</sup>, Raul N.C. Guedes<sup>3</sup>, Xiwu Gao<sup>1\*</sup>

<sup>1</sup> *Department of Entomology, College of Plant Protection, China Agricultural University, Beijing 100193, China.*

<sup>2</sup> *INRA (French National Institute for Agricultural Research), Université Côte d'Azur, CNRS, UMR 1355-7254 Institute Sophia Agrobiotech, Sophia Antipolis 06903, France.*

<sup>3</sup> *Departamento de Entomologia, Universidade Federal de Viçosa, Viçosa, Minas Gerais 36570-900, Brazil*

\*[nicolas.desneux@sophia.inra.fr](mailto:nicolas.desneux@sophia.inra.fr) (ND), [gaoxiwu@263.net.cn](mailto:gaoxiwu@263.net.cn) (XWG).

## Abstract

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 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 carried out experiments under laboratory conditions to evaluate stress imposed by the 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 grain aphid *Sitobion avenae* F. were subjected to competition on wheat seedlings under varying density combinations of both species and subjected or not to imidacloprid exposure. Intraspecific competition does take place without insecticide exposure, but so does interspecific competition between both aphid species with *R. padi* prevailing over *S. avenae*. 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 favoring *S. avenae* over *R. padi*, in contrast with the interspecific competition without imidacloprid exposure. These findings hinted that insecticides are indeed able to mediate species interaction and competition influencing community structure and raising management concerns for favoring potential secondary pest outbreaks.

**Keywords:** Intraspecific competition, interspecific competition, *Rhopalosiphum padi*, *Sitobion avenae*, imidacloprid, dominance shift.

## Introduction

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 resulting in intraspecific competition, or among individuals of different species leading to interspecific competition (Reitz and Trumble, 2002; van Veen et al., 2006; Villemereuil and Lopez-Sepulcre, 2011; Barabás et al., 2016; Naselli et al. 2016; Zhao et al., 2017).

Competition is an important community structuring phenomenon in nature (Iwabuchi and Urabe, 2012; Soares, 2013) but impact of pesticides on competition processes has been scarcely studied in agroecosystems. The few studies available suggest that such anthropic 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 community structure may be compromised as population recovery may be delayed after pesticide application(s), and species dominance may shift favoring secondary pest outbreaks (Liess and Foit, 2010; Guedes et al., 2016; 2017)

The outcome of competition varies with the competing species ranging from 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 et al. 2013; Tuelher et al. 2017), to not affecting either or even favoring at least one of them (Vilca Mallqui et al. 2013). Regardless, intraspecific competition is usually considered more important and stronger than interspecific competition (Moon et al., 2010; Villemereuil and Lopez-Sepulcre, 2011; Del Arco et al., 2015), but both need to be considered in any given scenario to assess their relative impacts. Furthermore, initial evidence is suggestive that variation in intraspecific competition can change the outcome of interspecific competition among aphids (Hazell et al., 2006).

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

competitive interactions (Gergs et al., 2013; Duan et al., 2016; Jordan and Tomberlin, 2017). Temperature, light, relative humidity and rainfall among others, are regarded as important abiotic factors for competition (Marchioro and Foerster, 2011; Savopoulou-Soultani et al., 2012; Marchioro and Foerster, 2016). Nonetheless anthropogenic abiotic stressors are also potentially important for species competition, but they are frequently neglected in such framework (Guedes et al., 2016, 2017; Zhao et al., 2017). Pesticides, and particularly 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 al. 2018), as they may promote species outbreaks through changing the arthropod community 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).

The relevance of pesticides on competition goes beyond lethal effects, as sublethal 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). Frequent and widespread use of pesticides in crops lead to an almost chronic exposure to 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 (Knillmann et al., 2012; Cordeiro et al., 2014), even less in the case of systemic pesticides 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 insecticides and specially neonicotinoids have been the target of concerns because of their 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 understanding of complex interactions taking place in agroecosystems in which neonicotinoids are frequently applied, despite that it appears essential for potentially

improving pest management programs and minimizing environmental impact of crop protection methods (Chailleux et al., 2014; Bebbber, 2015; Mohammed et al., 2018).

Systemic pesticides, notably imidacloprid, have been largely used to target the wheat pest species, particularly the bird cherry-oat aphid *Rhopalosiphum padi* L. and the English 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. 2017; Luo et al. 2018; Ali et al. 2018; Ortiz-Martinez et al. 2018). However, the relative impact of this compound in both these aphid species and their interaction remains unknown. Therefore, the present study aimed to assess the impact of the systemic (neonicotinoid) insecticide imidacloprid on intra and interspecific competition between *R. padi* and *S. avenae*. 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 interspecific competitive interaction between both aphid pest species.

## **Materials and Methods**

### **Biological materials**

Wheat seeds used in competition experiments were provided by the Zhuozhou Experimental Station of the China Agricultural University (Hebei, China). Seeds were planted in plastic pots (10 cm in diameter and 9 cm high), and all of the pots were filled with fertile soil (granularly (mm): 4.0-8.0; pH: 5.5-6.5; N mg/kg: 300-600; P<sub>2</sub>O<sub>5</sub> mg/Kg: 150-300; K<sub>2</sub>O mg/kg: 300-550; humidity: % 45-60; organic matter %  $\geq$  30). The soil was purchased from the Fangjie Huahui Yingyang Tu Company (Beijing, China). Five days after germination, the seedlings were thinned to 10 healthy wheat seedlings per pot. The colonies of cherry-oat (*R. 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

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 insecticide-free 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.

### **Insecticide**

The neonicotinoid insecticide imidacloprid was used in the competition experiments as the abiotic agent of stress. The commercial formulation of imidacloprid (Bi Chong Lin, 10 %) used was purchased from the Jiang Su Kesheng Company (Jiangsu, China). This formulation is one of the main formulations registered and used in China at the manufacture's label rate for aphid control in the wheat field (40-70 g a.i. ha<sup>-1</sup>). Concentration-mortality bioassays with this insecticide and formulation were carried out to assess its toxicity to both aphid species allowing to recognize the sublethal range based on the LC<sub>5</sub>. The commercial formulation of imidacloprid was diluted in distilled water for use in the experiments described below.

### **Insecticide bioassay**

Imidacloprid toxicity was assessed with apterous adult aphids by using the leaf dip method (Guo et al. 2013; Liu et al. 2017). Six serial dilutions (mg/L) of imidacloprid were prepared for treating the wheat seedlings (5 days old), which were dipped into the desired concentrations for 10 seconds; the seedlings were subsequently removed from the solution, 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 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 insects were then maintained under laboratory conditions at 23-25 °C temperature, 60-70% relative humidity, and 16:8 h [L:D] photoperiod. Insect mortality was recorded after 24 h exposure and the aphids were recognized as dead when failing to exhibit movement after a gentle touch with a camel's hair brush. The results obtained were subjected to probit analysis and the respective LC<sub>5</sub> was thus estimated. The estimated LC<sub>5</sub> of each aphid species was 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 LC<sub>5</sub> were subsequently used to in the competition experiments.

#### **Imidacloprid and intraspecific competition**

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

#### **Imidacloprid and interspecific competition**

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

### **Statistical analyses**

The mortality results from the concentration-mortality bioassays were subjected to probit analyses using the software PoloPlus 2.0 (LeOra software, 2006) to allow the assessment of the imidacloprid toxicity to each aphid species, which also allowed the estimates of the  $LC_5$  and  $LC_{50}$ 's. The toxicity curves were considered as significantly different when the confidence limits (95%) at their  $LC_5$  and  $LC_{50}$  values did not overlap (Prabhaker et al., 2011). The instantaneous rate of population growth ( $r_i$ ), a strong surrogate estimator of the intrinsic rate of population growth ( $r_m$ ) (Stark and Banks 2003), was calculated using the formula  $r_i = [\ln(N_j / N_i)] / Dt$ , where  $N_j$  and  $N_i$  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 statistical analyses were performed using R version 3.3.3. After checking the assumptions of normality and homoscedasticity, three-way analyses of variance using generalized linear model were carried out to test the impact of the initial aphid density (intra and interspecific competition) and the presence of insecticide on the final insect population and on the instantaneous rate of population growth ( $r_i$ ). The results of interspecific competition were 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 variables. The regressions models were obtained using the curve-fitting procedure of the software TableCurve 3D (Systat, San Jose, CA, USA). The significant regression models were

selected based on the criteria of parsimony, high F-value, and sudden increase in  $R^2$  with model complexity. The residual distributions were checked to validate parametric assumptions.

## Results

### Concentration-mortality response

The results of the leaf dip bioassays of imidacloprid toxicity to adult aphids enabled 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).  $LC_5$  values for *S. avenae* and *R. padi* were 10.22 and 3.49 ppm, respectively (Table 1), with an average  $LC_5$  for both species of 6.86 ppm (this average value was used when both species were exposed to the insecticide simultaneously i.e. during the inter-specific competition experiments). Control mortality was < 5% in all replicates.

### Imidacloprid and intra-specific competition

The presence of insecticide had a negative impact on the final population density and  $r_i$  of both aphid species 7 days after treatment ( $F_{1,132} = 1030.10$ ,  $P < 0.001$  and  $F_{1,132} = 547.14$ ,  $P < 0.001$  respectively), as were the effects of insect species and density combinations ( $F_{1,132} > 35.35$ ,  $P < 0.001$ ). The cherry-oat aphid *R. padi* exhibited steady increase in final density with increase in initial density, as did the wheat aphid *S. avenae* although always at lower densities (Fig. 1A). Such trend was however inverted when the insects were exposed to imidacloprid and the density of *R. padi* became slightly lower than *S. avenae* for the whole range of initial 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 insecticide exposure (Fig. 2A), but the reverse taking place when imidacloprid was used (Fig. 2B). At the highest density of each species, there was a convergence in population growth of

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

### **Imidacloprid and inter-specific competition**

The regression analyses assessing the final aphid populations based on their competing initial 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 density and that of *S. avenae*, although at a smaller degree (Fig. 3). The final population densities of *R. padi* reached levels above 500 insects per experimental unit at initial 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 *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 indicate interference between competing species, but with a stronger effect of *R. padi*, which is the dominant competitor when facing *S. avenae*.

Imidacloprid exposure allowed for a very different scenario imposing a drastic stress on the competition between *R. padi* and *S. avenae*. The high final populations of *R. padi* 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 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 reduced (Fig. 3). Again, the effect of heterospecific competition was significant for both species, as indicated by the respective regression models where the initial density of both species was necessary to reliably estimate the final population densities of both *R. padi* and *S. avenae*, although the influence of conspecifics was always stronger (Fig. 3).

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

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

## Discussion

Anthropic contaminants such as pesticides are considered as one of the factors threatening 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).

### **Differential (acute) toxicity**

The susceptibility of both aphid species to imidacloprid was different, what is likely a 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 susceptible to imidacloprid than *S. avenae*. Therefore, imidacloprid exposure should lead to 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 importance although frequently neglected (Stark and Banks, 2003; Guedes et al., 2016), allowing even the recognition of potential hormesis-like stimulatory effects that may take place (Guedes and Cutler, 2014). For example, low imidacloprid concentrations can exert 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 susceptibility, including distinct rates of insecticide penetration, detoxification activity, and even minute differences in the target site of insecticide action, but *S. avenae* seems to exhibit higher insecticide detoxification activity than *R. padi*, as suggested by previous studies (Lu et al., 2013; Xiao et al., 2015; Lu and Gao, 2016).

### **Imidacloprid impact on intraspecific competition**

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 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 densities afford lower mating opportunities reducing later competition (Huston, 1979), what was enhanced with higher initial densities particularly under imidacloprid contamination. Nonetheless, population growth was highest at the lowest initial densities of both species in 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 experimental units used.

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 the insecticide. The higher acute toxicity of imidacloprid to *R. padi* causing higher mortality 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 (Xiao et al., 2015). An aided concern is the fact that the relaxation of intraspecific competition 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 strength of selection will probably be stronger for *R. padi* since it is the most susceptible species (and thus subjected to stronger selection pressure for resistance).

### **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).

Both species were able to co-exist under competition, regardless of sublethal imidacloprid contamination. However, the insecticide contamination shifted the species dominance greatly compromising the prevalence of *R. padi* over *S. avenae*. This result consistent with several earlier reports about the interactions among sap feeder arthropods under natural colonization (Pascual and Callejas, 2004; Qureshi and Michaud, 2005; Umina and Hoffmann, 2005; Paini et al., 2008; Tapia et al., 2008; Sun et al., 2013; Zhao et al., 2017). 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 pesticide application may induce a shift in competitive potential of competing species, possibility demonstrated by Cordeiro et al. (2014) in density-dependent and concentration-dependent experiments with grain beetles.

The findings reported here showing a shift in dominance between competing aphid species when subjected to imidacloprid-contaminated plants is consistent with the intermediate disturbance hypotheses. This hypothesis was earlier developed to explain the maximization of species diversity under intermediate levels of disturbance able to reduce the 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 mediating competitive interactions (Cordeiro et al., 2014; Guedes et al., 2016), context equality applicable to the present study with the competing aphids *R. padi* and *S. avenae*. This

is the case because a low imidacloprid concentration (LC<sub>5</sub>) favored the weaker competing species compromising the dominance of the stronger competitor, *R. padi* in our case. High concentrations of imidacloprid would likely greatly compromise both species, while very low concentrations would not affect them, but intermediate concentrations would potentially allow higher diversity and a shift in ecological dominance, as reported here. The extended use of imidacloprid will likely change the associated arthropod community and may favor secondary pest outbreaks, particularly of *S. avenae*, what is a management concern and should be considered when designing pest management programs.

## Acknowledgements

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

## 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 experiments. A.A.H.M., R.N.C.G., N.D., and L.S.M. carried out the data analysis, X-W.G contributed reagents/ materials/analysis tools, A.A.H.M., L.S.M., R.N.C.G., N.D., and X-W.G. wrote the main manuscript text. All authors reviewed the manuscript

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

## References

Ali A, Desneux N, Lu YH, Wu KM. (2018). Key aphid natural enemies showing positive effects on wheat yield through biocontrol services in northern China. Agriculture, 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

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

Guo L, Desneux N, Sonoda S, Liang P, Han P, Gao XW. (2013). Sublethal and transgenerational effects of chlorantraniliprole on biological traits of the diamondback moth, *Plutella xylostella* L. *Crop Protection* 48:29-34.

Hazell S. P., McClintock I. A. D., and Fellowes M. D. E. (2006). Intraspecific heritable variation in life-history traits can alter the outcome of interspecific competition among insect herbivores. *Basic and Applied Ecology.* 7: 215-223.

Huston M. (1979). A general hypothesis of species diversity. *The American Naturalist.* 113: 81-102.

Iwabuchi T. and Urabe J. (2012). Competitive outcomes between herbivorous consumers can be predicted from their stoichiometric demands. *Ecosphere.* 3:7.  
<http://dx.doi.org/10.1890/ES11-00253.1>.

Jaworski CC, Bompard A, Genies L, Amiens-Desneux E, Desneux N. (2013). Preference and prey switching in a generalist predator attacking local and invasive alien pests. *PLoS ONE* 8(12):e82231

Jaworski C. C., Chailleux A. S., Bearez P., and Desneux N. (2015). Apparent competition between major pests reduces pest population densities on tomato crop, but not yield loss. *J. Pest Sci.* 88:793–803.

Jarosik V., Honeka A., and Tichopad A. (2003). Comparison of field population growths of three cereal aphid species on winter wheat. *Plant Protect. Sci.* 39: 61–64.

Jordan H. R. and Tomberlin J. K. (2017). Abiotic and biotic factors regulating inter-Kingdom engagement between insects and microbe activity on vertebrate remains.

437           Insects. 8: 1-19.

438   Kaplan, I. and Denno R. F. (2007). Interspecific interactions in phytophagous insects  
439           revisited: a quantitative assessment of competition theory. Ecology Letters 10: 977–  
440           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.

444   Lang J. M., and Benbow M. E. (2013). Species interactions and competition. Nature  
445           Education Knowledge. 4: 8.

446   LeOra Software (2006). POLO-Plus. A user's guide to probit or logit analysis. LeOra  
447           Software, Berkeley, CA .

448   Liess M. and Foit K. (2010). Intraspecific competition delays recovery of population  
449           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: 8862–  
452           8868.

453   Liu XL, Tang QL, Li YD, Mateus RC, Liang P, Gao XW (2017) Widespread resistance of the  
454           aphid *Myzus persicae* to pirimicarb across China, and insights on ace2 mutation  
455           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 *Plutella xylostella* 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.  
 490 Moon D. C., Moon J., and Keagy A. (2010). Direct and indirect interactions. *Nature*  
 491 Education Knowledge. 3:50.  
 492 Morris R. J., Owen T., Lewis O. T., and Godfray H. C. J. (2004). Experimental evidence for  
 493 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).  
 495 Insights on food webs associated with the South American Tomato Pinworm in  
 496 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.  
 500 Ortiz-Martinez SA, Lavandero B (2018) The effect of landscape context on the biological  
 501 control of *Sitobion avenae*: temporal partitioning response of natural enemy guilds. *J.*  
 502 *Pest Sci.* 91:41-53  
 503 Paini D. R., Funderburk J. E. and Reitz S. R. (2008). Competitive exclusion of a worldwide  
 504 invasive pest by a native. Quantifying competition between two phytophagous insects  
 505 on two host plant species. *Journal of Animal Ecology.* 77: 184–190.  
 506 Pascual S. and Callejas C. (2004). Intra- and interspecific competition between biotypes B  
 507 and Q of *Bemisia tabaci* (Hemiptera: Aleyrodidae) from Spain. *Bulletin of*  
 508 *Entomological Research.* 94: 369–375.  
 509 Passos LC, Soares MA, Collares LJ, Malagoli I, Desneux N, Carvalho GA. (2018). Lethal,  
 510 sublethal and transgenerational effects caused by insecticides on *Macrolophus*  
 511 *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 Dyck H., 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.

539   Soares S. d. A. (2013). The role of competition in structuring ant communities: A review.  
540           *Oecologia Australis.* 17: 271-281.

541   Stark J. D., Tanigoshi L., Bounfour B., and Antonelli A. (1997). Reproductive potential: It's  
542           influence on the susceptibility of a species to pesticides. *Ecotoxicology and*  
543           *Environmental Safety.* 37: 273–279.

544   Stark J.D., Banks J.E. (2003). Population-level effects of pesticides and other toxicants on  
545           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.

549   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)  
551           (Homoptera: Aphididae) by Glass Tube Residual Film Technique. *Pakistan J. Zool.*  
552           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  
555           *Myzus persicae* s.s. (Hemiptera: Aphididae) on sweet pepper, *Capsicum annuum*  
556           (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  
558           between the phytophagous stink bugs *Euchistus heros* and *Piesodorus guildinii* in  
559           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.



- van Veen F. F. J., Morris R. J., and Godfray H. C. J. (2006). Apparent competition, Quantitative food webs, and the structure of phytophagous insect communities. *Annu. Rev. Entomol.* 51: 187–208.
- Vilca Mallqui K. S., Oliveira E. E., Guedes R. N.C. (2013). Competition between the bean weevils *Acanthoscelides obtectus* and *Zabrotes subfasciatus* in common beans. *Journal of Stored Products Research.* 55: 32-35.
- Villemereuil P. B. and Lopez-Sepulcre A. (2011). Consumer functional responses under intra- and inter-specific interference competition. *Ecological Modelling.* 222: 419–426.
- Wang SY, Qi YF, Desneux N, Shi XY, Biondi A, Gao XW. (2017). Sublethal and transgenerational effects of short-term and chronic exposures to the neonicotinoid nitenpyram in the aphid *Aphis gossypii*. *J. Pest Sci.* 90:389-396.
- Williams C. T. (1987). Comparison of the winter development, reproduction and lifespan of viviparae of *Sitobion avenae* (F.) and *Rhopalosiphum padi* (L.) (Hemiptera: Aphididae) on wheat and perennial rye grass in England. *Bull. ent. Res.* 77: 35-43.
- Wu J. Y., Anelli C. M., Sheppard W. S. (2011). Sub-Lethal Effects of Pesticide Residues in Brood Comb on Worker Honey Bee (*Apis mellifera*) Development and Longevity. *PLoS ONE.* 6: e14720.
- Xiao D., Yang T., Desneux N., Han P., Gao X. (2015). Assessment of sublethal and transgenerational effects of pirimicarb on the wheat aphids *Rhopalosiphum padi* and *Sitobion avenae*. *PLoS ONE.* 10:e0128936. DOI:10.1371/journal.pone.0128936.
- Xiao D, Zhao J, Guo X, Chen HY, Qu M, Zhai W, Desneux N, Biondi A, Zhang F, Wang S. (2016). Sublethal effects of imidacloprid on the predatory seven-spot ladybird beetle *Coccinella septempunctata* (Coleoptera: Coccinellidae). *Ecotoxicology* 25:1782-1793.
- Zhang P., Zhang X., Zhao Y., Wei Y., Mu W., and Liu F. (2015). Effects of imidacloprid and 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, *Rhopalosiphum padi* and *Sitobion avenae*, after 24 hours post treatment.

Species	n*	Slope $\pm$ SE	$\chi^2$	df	LC5 (ppm)	LC50 (ppm)
					Confidence Limits 95%	
<i>R. padi</i>	30	2.55 $\pm$ 0.26	6.21	13	3.49 (2.20-4.81)	15.46 (12.91-
	0		5			18.19)
<i>S. avenae</i>	30	2.50 $\pm$ 0.27	7.36	13	10.22 (6.93-	46.50 (39.53-
	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. The regression models predicting the reported outcomes are indicated in each plot.

Fig. 1.

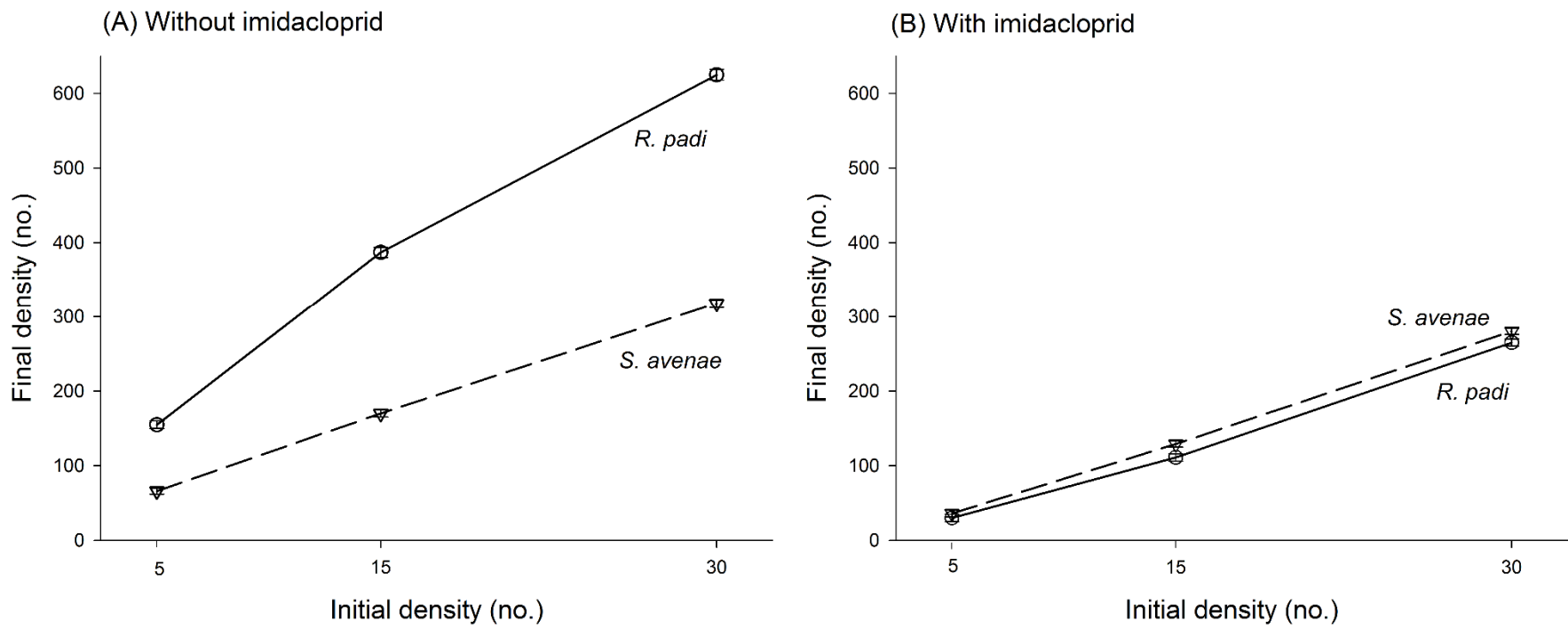


Fig. 2.

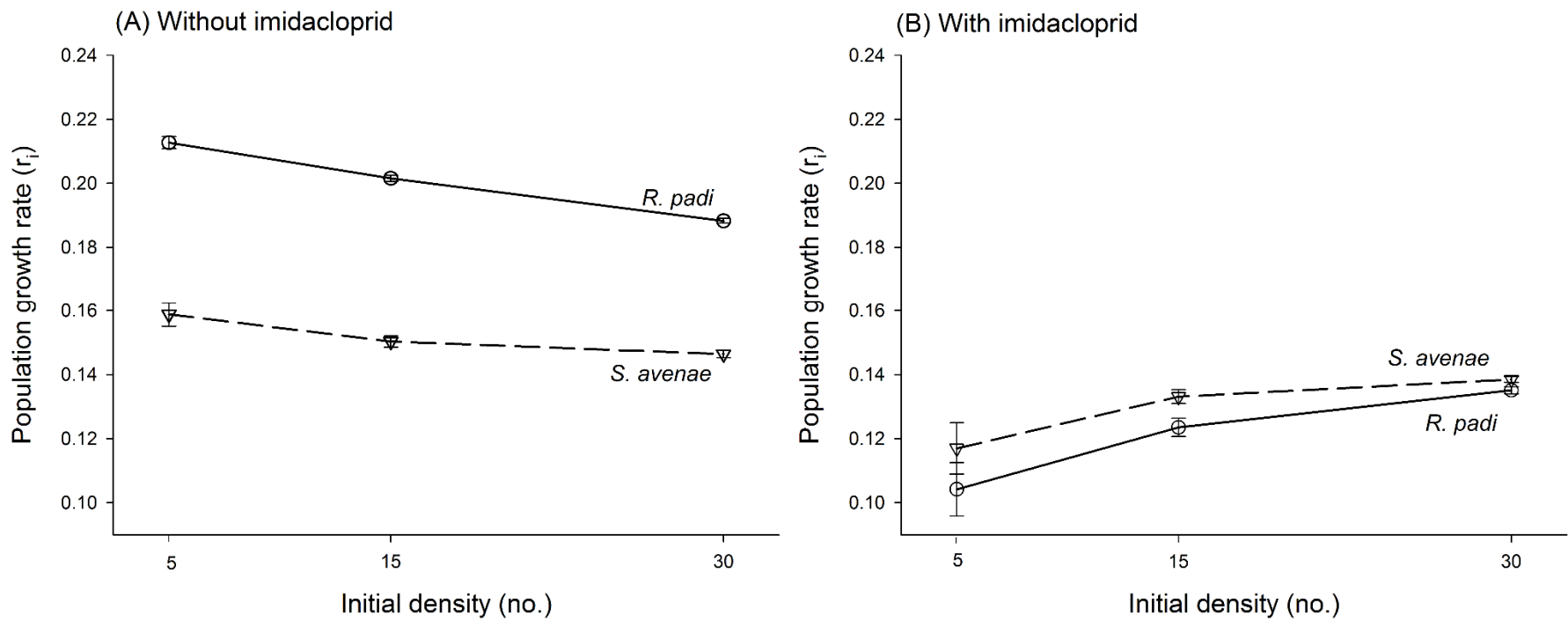


Fig. 3.

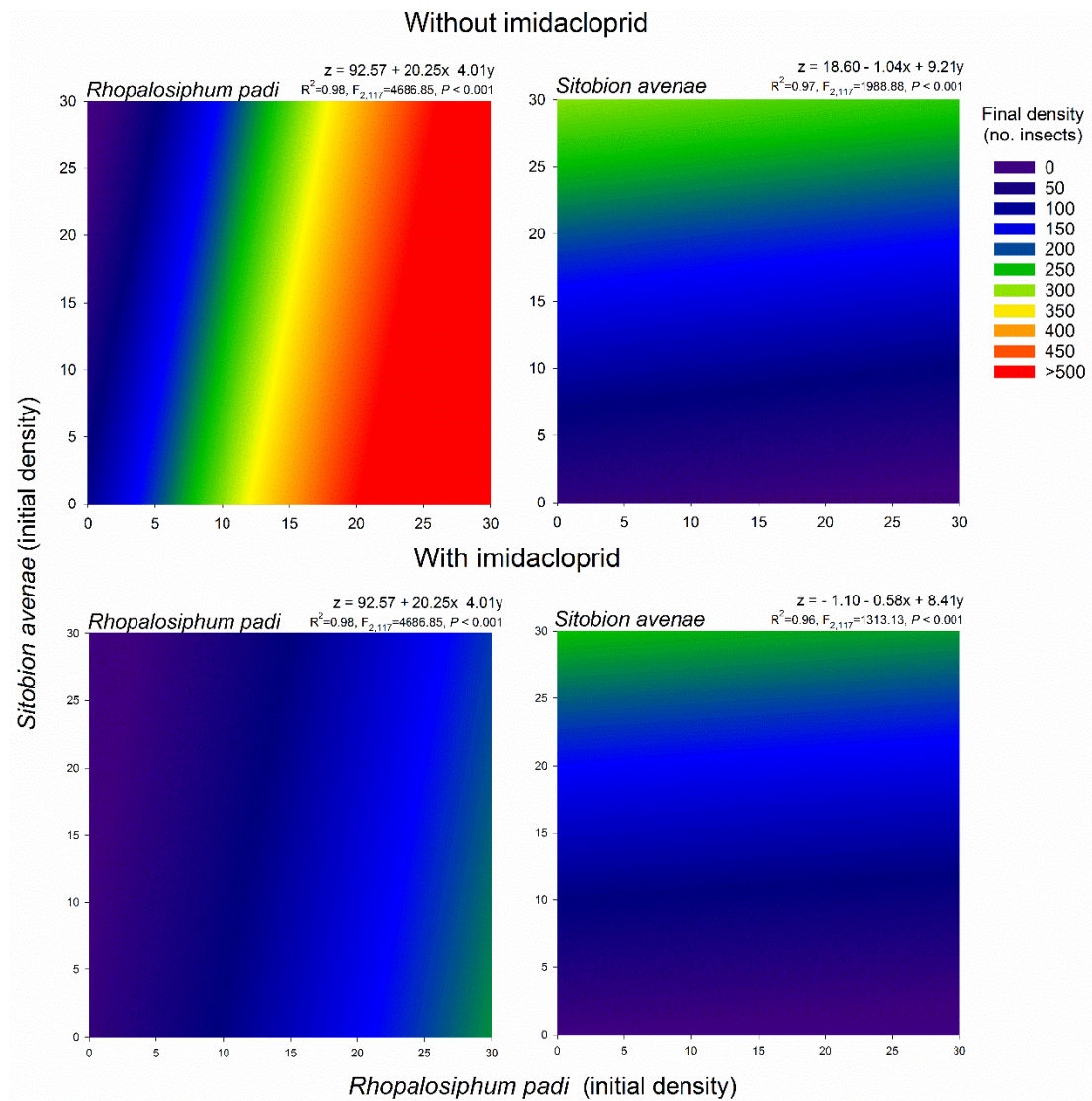


Fig. 4.

