Intraguild predation does not necessarily have negative effects on pest biological control: insights from a multiple consumer–multiple resource food web population model

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Abstract

We develop a food web population dynamical based on an experimental pest biocontrol setup consisting of thrips and aphids (pests) being consumed by two agents *Macrolophus pygmaeus* and *Orius laevigatus*, and with *O. laevigatus* being an intraguild predator of *M. pygmaeus*. By means of numerical simulations, we show that pest biocontrol disruption can be avoided depending on initial population densities of pests and agents, despite the intraguild predation (IGP) of *O. laevigatus* upon *M. pygmaeus*. This possible avoidance of pest biocontrol disruption is in accordance with the referred experimental setup and moreover, the proposed model corroborates the importance of initial densities of pests and agents in the determination of the failure or success of pest biocontrol found in this and other biocontrol experimental setups.

Keywords: pest biocontrol; greenhouse–crop system; intraguild predation; multiple consumer–multiple resource interaction; population dynamical model.

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Introduction

Generalist predators that feed on more than one species of prey have proven to be efficient biological control agents (e.g., Gardiner and Landis, 2007). Because most crops are attacked by more than one species of pest, biological control programs, especially in greenhouse crops, are increasingly based on releases of generalist predators against common greenhouse pests such as thrips, whiteflies, spider mites, aphids, and leaf miner moths (Messelink, 2012).

Despite their broad diet spectrum, generalist predators do not always control all pests (Symondson et al., 2002) and other natural enemies are needed in such situations. One approach is to release several species of generalist predators for multiple pest control. However, generalist predators are often involved in the competition for shared prey and predation upon each other (intraguild predation, IGP (Polis et al. (1989))), which can affect both their coexistence and the results of biological control.

In order to assess whether the negative effects of IGP on pest biocontrol can be mitigated in a specific biological setup, Messelink and Janssen. (2014) evaluated in an experimental study the coexistence of two generalist predatory bugs *Macrolophus pygmaeus* Rambur (Hemiptera: Miridae) and *Orius laevigatus* (Fieber) (Hemiptera: Anthocoridae) in a sweet pepper crop with two pest species as shared resources. The two pests used were the peach aphid *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) and the western flower thrips *Frankliniella occidentalis* Pergande (Thysanoptera: Thripidae), both important pests in sweet pepper. Moreover, they also found a unidirectional intraguild predation for *Orius majusculus* (Reuter) (Hemiptera: Anthocoridae) preying on *M. pygmaeus*.

Their study shows that despite being involved in intraguild predation, the two agents (predators) complemented each other in the control of the two pests.

Motivated by the experimental finding that these two agents (predators) can coexist in a sweet pepper crop, and their presence does not affect the control of the two pest species we developed a population dynamical model that can qualitatively generate this lack of pest control disruption found in the laboratory experiments carried out by Messelink and Janssen (2014).

The outline of the present work is as follows. In section 2 we present the model together with the interpretation of its variables and parameters. In section 3 we perform the numerical bifurcation analysis of the model and present the biological results in terms of pest biocontrol. In section 4 we discuss the results of the present work.

2 Methods

A multiple consumer–multiple resource food web model

Messelink and Janssen (2014) performed experiments to evaluate the co–occurrence of the generalist predators *Macrolophus pygmaeus* and *Orius laevigatus* and their control of two pests in a sweet pepper crop. Both predators prey on thrips and aphids, and *O. laevigatus* is an intraguild predator of *M. pygmaeus*. Their experimental food web is schematically shown in figure 1.

Figure 1. A food web containing multiple consumer–multiple resource interactions according to the experiment performed in Messelink and Janssen (2014). Arrows indicate predation. IGP means intraguild predation.

A continuous–time mathematical population dynamical model of the species in the food web depicted in figure 1 can take on the form:

$$\begin{aligned}
 \frac{dA}{dt} &= \underbrace{r_A A \left(1 - \frac{A}{K_A}\right)}_{\text{logistic growth of } A} - \underbrace{\left(\frac{a_{MA} A}{1 + a_{MT} h_{MT} T + a_{MA} h_{MA} A} \right) M}_{\text{multispecies functional response of agent } M \text{ upon } A} - \underbrace{\left(\frac{a_{OA} A}{1 + a_{OT} h_{OT} T + a_{OA} h_{OA} A + a_{OM} h_{OM} M} \right) O}_{\text{multispecies functional response of agent } O \text{ upon } A} \\
 \frac{dT}{dt} &= \underbrace{r_T T \left(1 - \frac{T}{K_T}\right)}_{\text{logistic growth of } T} - \underbrace{\left(\frac{a_{MT} T}{1 + a_{MT} h_{MT} T + a_{MA} h_{MA} A} \right) M}_{\text{multispecies functional response of agent } M \text{ upon } T} - \underbrace{\left(\frac{a_{OT} T}{1 + a_{OT} h_{OT} T + a_{OA} h_{OA} A + a_{OM} h_{OM} M} \right) O}_{\text{multispecies functional response of agent } O \text{ upon } T}
 \end{aligned}
 \tag{1}$$

$$\begin{aligned}
 & \underbrace{\frac{dM}{dt}}_{\text{Agent } M} = \underbrace{\left(\frac{ef_{AM}a_{MA}A + ef_{TM}a_{MT}T}{1 + p_{MT}a_{MT}h_{MT}T + p_{MA}a_{MA}h_{MA}A} \right)}_{\substack{\text{multispecies numerical} \\ \text{response of agent } M \text{ from the} \\ \text{consumption of pest } A \text{ and } T}} M - \underbrace{\left(\frac{ef_{MO}a_{OM}M}{1 + a_{OT}h_{OT}T + a_{OA}h_{OA}A + a_{OM}h_{OM}M} \right)}_{\substack{\text{multispecies numerical} \\ \text{response of agent } O \text{ from the} \\ \text{consumption (intraguild predation)} \\ \text{of agent } M}} O \\
 & - \underbrace{m_M M}_{\substack{\text{linear density} \\ \text{dependent} \\ \text{mortality} \\ \text{rate of agent } M}} - \underbrace{q_M M^2}_{\substack{\text{nonlinear density} \\ \text{dependent} \\ \text{mortality} \\ \text{rate of agent } M}} \\
 & \underbrace{\frac{dO}{dt}}_{\text{Intraguild agent } O} = \underbrace{\left(\frac{ef_{MO}a_{OM}M + ef_{AO}a_{OA}A + ef_{TO}a_{OT}T}{1 + a_{OM}h_{OM}M + a_{OT}h_{OT}T + a_{OA}h_{OA}A} \right)}_{\substack{\text{multispecies numerical} \\ \text{response of agent } O \text{ from the} \\ \text{consumption of pests } A \text{ and } T \\ \text{and the consumption (intraguild predation)} \\ \text{of agent } M}} O - \underbrace{m_O O}_{\substack{\text{linear density} \\ \text{independent} \\ \text{mortality} \\ \text{rate of agent } O}} - \underbrace{q_O O^2}_{\substack{\text{nonlinear density} \\ \text{dependent} \\ \text{mortality} \\ \text{rate of agent } O}}
 \end{aligned}$$

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124

125 A and T are the densities of the pests (prey), while O and M

126 represent the densities of the control agents (predators). The

127 definitions of the variables and the parameters of the model (1)

128 are shown in table 1.

129

130

131 Table 1 Definition of variables and parameters of the model (1)

132

Meaning	
Variables	
A	density of pest A
T	density of pest T
M	density of agent M
O	density of agent O
Parameters	
r_A	intrinsic growth rate of pest A
r_T	intrinsic growth rate of pest T
K_A	carrying capacity of pest A
K_T	carrying capacity of pest T
a_{MA}	attack coefficient of agent M on pest A
a_{MT}	attack coefficient of agent M on pest T
a_{OA}	attack coefficient of agent O on pest A
a_{OT}	attack coefficient of agent O on pest T
a_{OM}	attack coefficient of agent O on agent M
ef_{AM}	conversion coefficient from pest A to agent M
ef_{AO}	conversion coefficient from pest A to agent O
ef_{TM}	conversion coefficient from pest T to agent M
ef_{TO}	conversion coefficient from pest T to agent O
ef_{MO}	conversion coefficient from agent M to agent O
h_{MA}	manipulation time of agent M on pest A
h_{MT}	manipulation time of agent M on pest T
h_{OA}	manipulation time of agent O on pest A
h_{OT}	manipulation time of agent O on pest T
h_{OM}	manipulation time of agent O on agent M
m_M	density independent <i>per capita</i> mortality rate of agent M
m_O	density independent <i>per capita</i> mortality rate of agent O
q_M	coefficient of density dependent <i>per capita</i> mortality rate of agent M
q_O	coefficient of density dependent <i>per capita</i> mortality rate of agent O

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135 We assume a logistic growth in the pests A and T because of
136 the presumed lack of exploitative competition among them. This
137 assumption is based on another experiment where exploitative
138 competition between the pests was improbable, certainly due to
139 the large leaf size of the crop (Messelink et al., 2008).

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141 The density dependent–mortality rate of the agents M and
142 O , i.e., the expressions $q_M M^2$ and $q_O O^2$ can be associated with con–
143 specific cannibalism. For instance, control agent such as spider
144 mite of the species *Amblyseius swirski* AthiasHenriot

(Acari:Phytoseiidae) is subject to con-specific cannibalism in the early stages of their life cycle (Rasmy et al., 2004).

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In Messelink and Janssen (2014) it is experimentally shown that besides the coexistence of the two agents, the intraguild predation between these agents does not disrupt pest biological control. Therefore, regarding this experimental result, it is interesting to investigate if our proposed model (1) can yield this same result in qualitative terms. This can be verified by increasing the value of the intraguild predation attack coefficient of *O. laevigatus* upon *M. pygmaeus* (a_{OM}) in the model (1) and checking how this increase in IGP affects the densities of all populations in the equilibrium in the model (1). By having the values of the population densities we can assess whether the agents coexist and do not disrupt biocontrol (as found in the experiment). To perform this analysis, a numerical bifurcation of the model (1) as a function of a_{OM} by means of the software package XPPAUT (Ermentrout, 2002) is undertaken. In essence, this software calculates the equilibrium points of the nonlinear differential equations given by the model (1) (i.e., the numerical solutions to the system of equations given by $dA/dt=0$, $dT/dt=0$, $dM/dt=0$, and $dO/dt=0$) as one varies, for instance, the parameter a_{OM} , together with the real part of their corresponding eigenvalues. This information is gathered to draw the graphs with equilibrium population density levels and their respective stability characteristics (stable/unstable equilibrium points) displayed throughout this work. Moreover, we call attention to the fact that the choice of the parameter values of the model (1) was partially guided by an intention to create, when possible, stable dynamics in the analyzed models, avoiding thus, for instance, sustained oscillations (e.g., limit cycles). In this way, all species densities variation of the model (1) as a consequence of changes in the intensity of the intraguild coefficient attack a_{OM} can be promptly

178 read off the bifurcation diagrams without resorting to mean value
179 calculation of the species densities due to the species temporal
180 oscillations.

181

182 Results

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184 The resulting bifurcation diagram of all the involved species
185 (A , T , M , O) of the model (1) is displayed in figure 2. These
186 diagrams show the densities of the species when the intraguild
187 predation attack coefficient of *O. laevigatus* upon *M. pygmeus*
188 (a_{OM}) is increased.

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(a) *Aphids* (A)

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(b) *Thrips* (T)

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(c) *M. pygmaeus* (M)

(d) *O. laevigatus* (O)

Figure 2. A numerical bifurcation diagram of model (1) as a function of the intraguild predation attack coefficient of *O. laevigatus* upon *M. pygmaeus* (a_{OM}). Bistability occurs along the interval $0.24 < a_{OM} < 1.54$. Red lines: stable equilibrium points; black lines: unstable equilibrium points. Parameter values: $r_A=1.12$; $r_T=1.1$; $K_A=9.12$; $K_T=3.444$; $a_{OT}=0.9$; $a_{OA}=0.9$; $a_{MT}=1$; $a_{MA}=1$; $ef_{MO}=5$; $ef_{AO}=5$; $ef_{TO}=5$; $ef_{TM}=2$; $ef_{AM}=2$; $h_{OM}=2$; $h_{OT}=2$; $h_{OA}=2$; $h_{MT}=2$; $h_{MA}=2$; $m_T=0.1$; $m_O=0.1$; $q_M=0.5$; $q_O=0.5$.

208

209   Note first that the food web in figure 1 consists of two
 210 community modules (Holt, 1997) of type “two prey species that
 211 share one predator” (i.e., $A - T - M$ and $A - T - O$) which are
 212 connected also by the intraguild predation of O upon M (i.e.,
 213 coefficient a_{OM}). These two community modules ($A - T - M$ and
 214 $A - T - O$) are known to possess positive bistability (Abrams and
 215 Matsuda, 1996) (here, positive bistability is the occurrence of two
 216 different population levels in which all species can coexist).
 217 Actually, the choice of the parameter values was also guided by
 218 the creation of a positive bistability in the model (1) (as shown in
 219 figure 2) on account of the following reason: this bistability in the
 220 model (1), which occurs throughout the interval $0.24 < a_{OM} <$
 221 1.54 , can provide a two-fold explanation: (i) the red lower
 222 branch of the pests A and T may well represent pest suppression
 223 (relatively low pest levels), while (ii) the red upper branch of the
 224 pests A and T may well represent the disruption of pest control
 225 (relatively high pest levels). In a way, item (i) corroborates that
 226 predation of one agent upon the other (the intraguild predation of
 227 *O. laevigatus* upon *M. pygmaeus*) does not necessarily have
 228 negative effects on biological control of aphids and thrips
 229 (Messelink and Janssen, 2014).

230

231   Importantly, model (1) also suggests that these two
 232 outcomes in pest control (pest suppression and disruption of pest
 233 control) depend on the initial level of the populations (a
 234 consequence of the positive bistability of the model (1); see figure
 235 2). This result corroborates the importance of initial population
 236 densities in pest control (Messelink and Janssen (2014), p.4; see
 237 also observations about the importance of initial population
 238 densities in a biocontrol prey–predator experimental setup in
 239 Leman and Messelink (2014)). However, to be more precise with
 240 respect to the mentioned texts in the above references, one should

241 carry out time–series simulations of the model (1) with varying
 242 initial densities of the predators *O. laevigatus* (i.e., $O(0)$) and *M.*
 243 *pygmaeus* (i.e., $M(0)$) and check the final densities of the pests
 244 *Aphids* (A) and *Thrips* (T) so as to assess the efficiency of pest
 245 control with respect to initial densities of agents (e.g., inoculative
 246 (low levels of) /inundative (high levels of) agent releases).
 247 Nonetheless, it is important to remark that the model (1) also
 248 suggests that increasing the intraguild predation attack coefficient
 249 of *O. laevigatus* upon *M. pygmaeus* (a_{OM}) brings about the
 250 increase of both pest levels in the lower and in the upper branch
 251 of the bifurcation diagrams of figure 2.

252

253

254 Discussion

255

256 Messelink and Janssen (2014) experimentally evaluated how
 257 the co–occurrence of the generalist control agents *Macrolophus*
 258 *pygmaeus* and *Orius laevigatus* affected their control of two pests
 259 in a sweet pepper crop. Both agents prey on thrips and aphids, and
 260 *O. laevigatus* is an intraguild predator of *M. pygmaeus*. Their
 261 study provides further evidence that the use of natural enemies
 262 that can be involved in intraguild predation does not necessarily
 263 have negative effects on biological control (confirming other
 264 experimental studies). Moreover, they also mention that the
 265 mechanisms that prevent such negative effects of intraguild
 266 predation and the exclusion of one agent (predator) by the other
 267 remain elusive.

268

269 In this work, by means of simulations of a proposed
 270 theoretical food web population dynamical model describing the
 271 biotic species interactions in the mentioned experiment, we
 272 showed that the use of natural enemies that can be involved in
 273 intraguild predation does not necessarily have negative effects on

274 biological control. This result is conveyed in the model (1) by the
 275 relatively low pests' equilibrium densities in figure 2.
 276 Furthermore, from a myriad of possible biological processes, we
 277 narrowed them down to those included in the model (1) as
 278 potential candidates to explain to some extent how negative
 279 effects of intraguild predation and the exclusion of one agent
 280 (predator) by the other can be avoided in this specific intraguild
 281 food web. That is to say, perhaps conceptual
 282 (strategic/phenomenological) models (May, 2001) such as model
 283 (1) (and/or others) could shed some light to help unveil these
 284 mechanisms – at least, qualitatively– and thereby lessen their
 285 seeming elusiveness in experimental setups.

286

287 In a more general context of food web population dynamics
 288 theory, we investigated how the effects of a disturbance (in our
 289 case, an increase in the intensity of the intraguild attack
 290 coefficient a_{OM}) propagate through the species densities of a
 291 specific food web. We think that this conjunction of applied and
 292 theoretical ecology can contribute to expanding the understanding
 293 of how natural enemy–density–mediated indirect interactions may
 294 be used to enhance pest biocontrol strategies (Chailleux et al.
 295 2014).

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