

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

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8
9 **Abstract**

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

24
25 *Keywords: pest biocontrol; greenhouse–crop system; intraguild*
26 *predation; multiple consumer–multiple resource interaction;*
27 *population dynamical model.*

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37 **Introduction**

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

47

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

56

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

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

73

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

80

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

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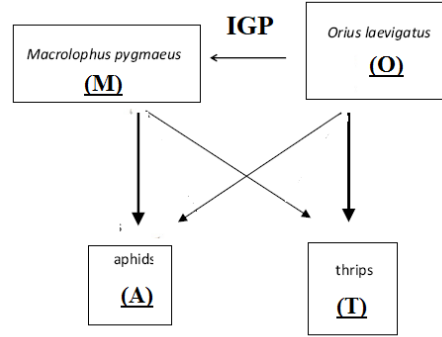
90 **2 Methods**

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92 **A multiple consumer–multiple resource food web model**

93

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



101
102 Figure 1. A food web containing multiple consumer–multiple resource
103 interactions according to the experiment performed in Messelink and
104 Janssen (2014). Arrows indicate predation. IGP means intraguild predation.

105
106 A continuous–time mathematical population dynamical
107 model of the species in the food web depicted in figure 1 can take
108 on the form:

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110

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

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

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(1)

$$\frac{dM}{dt} = \underbrace{\left(\frac{ef_{AM}a_{MA}A + ef_{TM}a_{MT}T}{1 + p_{MT}a_{MT}h_{MT}T + p_{MA}a_{MA}h_{MA}A} \right)}_{\substack{\text{multispecies numerical} \\ \text{response of agent } M \text{ from the} \\ \text{consumption of pest } A \text{ and } T}} M - \underbrace{\left(\frac{ef_{MO}a_{OM}M}{1 + a_{OT}h_{OT}T + a_{OA}h_{OA}A + a_{OM}h_{OM}M} \right)}_{\substack{\text{multispecies numerical} \\ \text{response of agent } O \text{ from the} \\ \text{consumption (intraguild predation)} \\ \text{of agent } M}} O$$

118

$$- \underbrace{m_M M}_{\substack{\text{linear density} \\ \text{dependent} \\ \text{mortality} \\ \text{rate of agent } M}} - \underbrace{q_M M^2}_{\substack{\text{nonlinear density} \\ \text{dependent} \\ \text{mortality} \\ \text{rate of agent } M}}$$

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$$\frac{dO}{dt} = \underbrace{\left(\frac{ef_{MO}a_{OM}M + ef_{AO}a_{OA}A + ef_{TO}a_{OT}T}{1 + a_{OM}h_{OM}M + a_{OT}h_{OT}T + a_{OA}h_{OA}A} \right)}_{\substack{\text{multispecies numerical} \\ \text{response of agent } O \text{ from the} \\ \text{consumption of pests } A \text{ and } T \\ \text{and the consumption (intraguild predation)} \\ \text{of agent } M}} O - \underbrace{m_O O}_{\substack{\text{linear density} \\ \text{independent} \\ \text{mortality} \\ \text{rate of agent } O}} - \underbrace{q_O O^2}_{\substack{\text{nonlinear density} \\ \text{dependent} \\ \text{mortality} \\ \text{rate of agent } O}}$$

123

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

Variables	Meaning
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

133

134

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).

140

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

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

147

148 In Messelink and Janssen (2014) it is experimentally shown
149 that besides the coexistence of the two agents, the intraguild
150 predation between these agents does not disrupt pest biological
151 control. Therefore, regarding this experimental result, it is
152 interesting to investigate if our proposed model (1) can yield this
153 same result in qualitative terms. This can be verified by increasing
154 the value of the intraguild predation attack coefficient of *O.*
155 *laevigatus* upon *M. pygmaeus* (a_{OM}) in the model (1) and
156 checking how this increase in IGP affects the densities of all
157 populations in the equilibrium in the model (1). By having the
158 values of the population densities we can assess whether the
159 agents coexist and do not disrupt biocontrol (as found in the
160 experiment). To perform this analysis, a numerical bifurcation of
161 the model (1) as a function of a_{OM} by means of the software
162 package XPPAUT (Ermentrout, 2002) is undertaken. In essence,
163 this software calculates the equilibrium points of the nonlinear
164 differential equations given by the model (1) (i.e., the numerical
165 solutions to the system of equations given by $dA/dt=0$, $dT/dt=0$,
166 $dM/dt=0$, and $dO/dt=0$) as one varies, for instance, the parameter
167 a_{OM} , together with the real part of their corresponding
168 eigenvalues. This information is gathered to draw the graphs with
169 equilibrium population density levels and their respective stability
170 characteristics (stable/unstable equilibrium points) displayed
171 throughout this work. Moreover, we call attention to the fact that
172 the choice of the parameter values of the model (1) was partially
173 guided by an intention to create, when possible, stable dynamics
174 in the analyzed models, avoiding thus, for instance, sustained
175 oscillations (e.g., limit cycles). In this way, all species densities
176 variation of the model (1) as a consequence of changes in the
177 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.

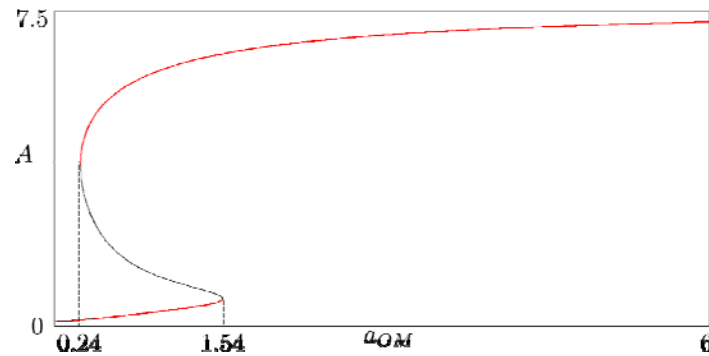
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182 **Results**

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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.

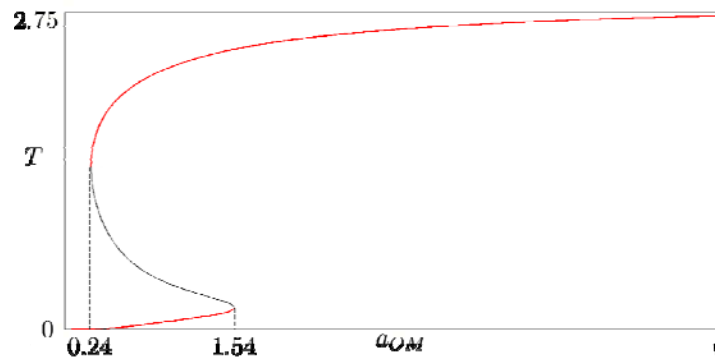
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(a) *Aphids (A)*

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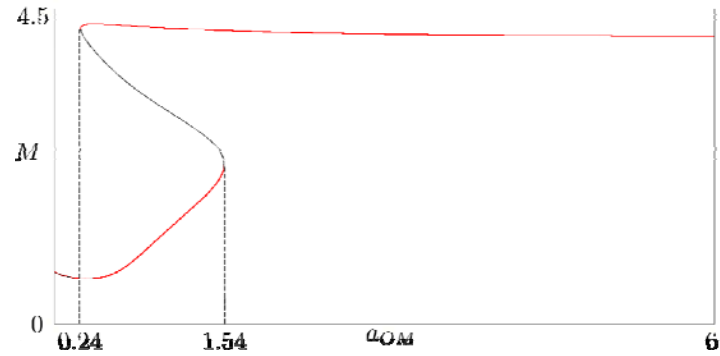


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(b) *Thrips (T)*

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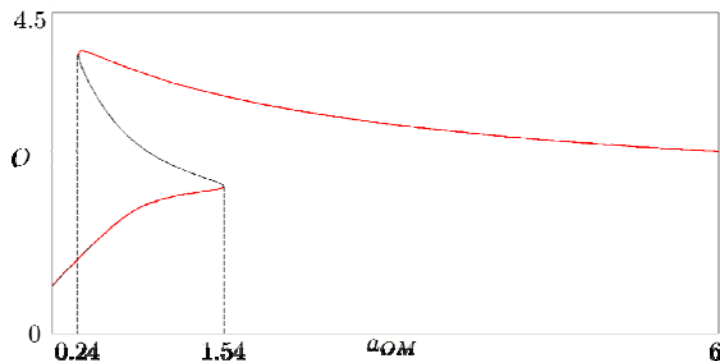


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(c) *M. pygmaeus* (M)



198

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(d) *O. laevigatus* (O)

200 Figure 2. A numerical bifurcation diagram of model (1) as a function of the
 201 intraguild predation attack coefficient of *O. laevigatus* upon *M. pygmaeus*
 202 (a_{OM}). Bistability occurs along the interval $0.24 < a_{OM} < 1.54$. Red lines:
 203 stable equilibrium points; black lines: unstable equilibrium points.

204 Parameter values: $r_A=1.12$; $r_T=1.1$; $K_A=9.12$; $K_T=3.444$; $a_{OT}=0.9$; $a_{OA}=0.9$;
 205 $a_{MT}=1$; $a_{MA}=1$; $ef_{MO}=5$; $ef_{AO}=5$; $ef_{TO}=5$; $ef_{TM}=2$; $ef_{AM}=2$; $h_{OM}=2$; $h_{OT}=2$;
 206 $h_{OA}=2$; $h_{MT}=2$; $h_{MA}=2$; $m_T=0.1$; $m_O=0.1$; $q_M=0.5$; $q_O=0.5$.

207

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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