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- 1 **Synergies and tradeoffs in natural regulation of crop pests and diseases under plant species**
- 2 **diversification**
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8 Abstract

9 It has been suggested that increasing plant species diversity (PSD) in agroecosystems at different
10 spatiotemporal scales reduces the impacts of crop pests and diseases as well as the dependence on
11 synthetic plant protection products. This principle was applied to a range of tropical case studies.
12 These studies involved various pests and pathogens with contrasting life history traits, different
13 cropping systems (a cereal crop in conservation agriculture, vegetable crops in rotational and trap
14 cropping systems, perennial crops in agroforestry) and various spatial scales of PSD deployment (field
15 and farmscape). Here we review the outcomes of these studies, and discuss the lessons learned
16 regarding synergies and tradeoffs associated with regulation effects provided by PSD. The major
17 points are:

- 18 1) results contributed to solve local crop pest and disease problems such as bacterial wilt on tomato
19 in Martinique, scarab beetles and witchweed on upland rice in Madagascar, fruitworms on tomato
20 in Martinique and okra in Niger, fruit flies on cucurbit vegetables in Reunion, mirid bugs and
21 black pod rot on cocoa in Cameroon, berry borer and leaf rust on coffee in Costa Rica;
- 22 2) the importance of cross-cutting issues regarding green manure, cover crops or companion plants
23 across case studies at the field scale involving below-ground and aerial processes, were
24 highlighted, particularly that of the within-species genetic variation of these plants;
- 25 3) based on the fruitworm/tomato case study, a dynamic and spatially-explicit individual-based
26 model was developed as a generic tool to improve understanding of system functioning by
27 assessing infestation patterns in response to main crop/trap crop relative attractiveness,
28 spatiotemporal deployment of the main crop/trap crop and insect behavioral traits;
- 29 4) tradeoffs were highlighted regarding pest and disease complex management, single-option pest
30 and disease control via several pathways based on a single PSD-deployment measure and other
31 ecosystem services and disservices at various scales.

32 Keywords: Agroforestry; Companion plant; Conservation agriculture; Cover crop; Green manure;
33 Horticulture; Life history trait; Market gardening; Modelling; Spatial scale

34 1. Introduction

35 Farmers in the tropics are faced with considerable plant protection-related risks. The outcomes of pest
36 management decisions, whether these are to take no action, to apply pesticides, or to implement other
37 management strategies, impact widely the whole food production chain. Pest and disease damage to
38 crops, as well as pesticide applications *per se*, can cause (i) food insecurity and lost income, (ii)
39 adverse effects on human and environmental health (which also affects other actors in crop value
40 chains e.g. agricultural workers and laborers, and consumers), and (iii) export restrictions due to
41 quarantine pests and diseases and maximum limits on pesticide residues (Sikora et al., 2019).

42 This high vulnerability of crops to damage by pests and diseases is mostly observed in intensive
43 monocrop production systems which have been overly simplified (Tilman et al., 2002). In these
44 systems, companion agrobiodiversity is low, and thus unable to provide supporting ecosystem services
45 such as pest and disease regulation. It has been hypothesized that the resilience of intensive cropping
46 systems to pest and disease outbreaks could be obtained through diversified plantings that approach
47 the structure and trait composition of proximate natural ecosystems, similar to those found in many
48 traditional agroecosystems (Dawson and Fry, 1998; Jackson, 2002; Lewis et al., 1997; Malézieux,
49 2012).

50 This hypothesis originated in observations that pest and disease outbreaks are typically low in natural
51 systems, and therefore, that designing agroecosystems to include high functional biodiversity may
52 preserve the ecological functions that keep pest and disease incidence low (Hooper et al., 2005;
53 Soliveres et al., 2016; Tscharrntke et al., 2005). In this context, strategic conservation of plant diversity
54 or increased plant diversity at multiple spatial and temporal scales are important (Gaba et al., 2015;
55 Malézieux et al., 2009; Tiltonell, 2014). In addition to agronomic benefits, e.g. reduced soil erosion,
56 and improved water and nutrient use by crop plants (Malézieux et al., 2009), increasing agroecosystem
57 plant diversity may enhance ecosystem services (Bommarco et al., 2013; Isbell et al., 2017), notably
58 pest and disease regulation (Deguine et al., 2008; Ferron and Deguine, 2005; Nicholls and Altieri,
59 2004). Increased agroecosystem diversity may also mitigate or alleviate risks in the face of
60 disturbances such as climatic events and price fluctuations.

61 Between 2008 and 2012, CIRAD (“Agricultural Research for Development”) and its partners
62 implemented the “Optimization of ecological mechanisms of pest and disease management for
63 sustainable improvement of agrosystem productivity” (*Optimisation des Mécanismes Ecologiques de*
64 *Gestion des bioAgresseurs pour l’Amélioration durable de la productivité des Agrosystèmes*, or
65 Omega3) project (Ratnadass et al., 2010). This project examined the impacts of increased plant species
66 diversity (PSD) on pest and pathogen population densities, and on crops. It included specific studies
67 that considered both temporal (permanent plantings and rotations) and spatial (field and farmscape)
68 interventions. Farmscape in this context refers to a small area of the landscape which has been defined
69 as “an area comprising the farm plus a 1.5 km buffer area” (Estrada-Carmona et al., 2019). The project
70 had two specific objectives: (i) to gain knowledge on ecological processes that regulate pest and
71 pathogen populations and how these could be mobilized to improve pest and disease management, and
72 (ii) to generate tools and methods for the design and evaluation of novel diversified cropping systems
73 and land use arrangements that prevent pest and pathogen outbreaks.

74 Among the eight major pathways of pest and disease regulation via increased PSD that were reviewed
75 prior to the Omega3 project implementation (Ratnadass et al., 2012a), we selected eleven biological
76 models, distributed over six case studies, representing a range of spatial scales of PSD deployment,
77 and of pest or pathogen dispersal ability and host specificity (Table 1). Amongst pest and pathogen life
78 history traits, dispersal ability and host specificity are the most amenable to manipulation via PSD.
79 This was done with a view to robustness and capacity to generalize results.

80 At the field scale, we studied the sanitizing effects of green manure, cover crops and companion plants
81 (GMCCPs) on two pest and pathogen complexes. Firstly, we studied the soil borne pathogen *Ralstonia*
82 *solanacearum* (Burkholderiaceae) which causes bacterial wilt of tomato (*Solanum lycopersicum*)
83 (Solanaceae) in Martinique. Secondly, we studied the effects of GMCCP on scarab beetles (white
84 grubs and black beetles *Heteronychus* spp.) (Coleoptera: Scarabaeidae) and witchweed (*Striga*
85 *asiatica*) (Orobanchaceae) which impact upland rice (*Oryza sativa*) (Poaceae) in Madagascar.

86 **Table 1. Description of the six Omega3 project case studies and 11 biological models, as a function of scale levels at which plant species diversity**
87 **modalities and effects translate, and a life history trait-based typology of pests and pathogens**

Case study	Pest or disease	Crop	Cropping system ¹	Spatial scale	Geographical area	Host specificity	Dispersal ability
1	Bacterial wilt	Tomato	VR	Field	Martinique	Low ²	Low ²
2	Scarab beetles	Upland rice	CA	Field	Madagascar	Medium ³	Low ⁴
	Witchweed	Upland rice	CA	Field	Madagascar	High ⁵	Low ⁵
3	Fruitworm	Tomato	VT	Field	Martinique	Low ⁶	High ⁷
	Fruitworm	Okra	VT	Field	Niger	Low ⁶	High ⁷
	Whitefly	Okra	VT	Field	Niger	Low ⁸	Medium ⁹
4	Fruit flies	Cucurbits	VT	Field	Réunion	Medium ¹⁰	High ¹⁰
5	Mirid bugs	Cocoa	AF	Field	Cameroon	Medium ¹¹	Medium ¹²
	Black pod rot	Cocoa	AF	Field	Cameroon	High ¹³	Medium ¹⁴
6	Leaf rust	Coffee	AF	Field and Farmscape	Costa Rica	High ¹⁵	High ¹⁶
	Berry borer	Coffee	AF	Farmscape	Costa Rica	High ¹⁷	Medium ¹⁸

88 ¹ VR: Vegetable rotational system; CA: Conservation agriculture system; VT: Vegetable trap cropping system; AF: Agroforestry system; ² Hayward (1991);
89 ³Paulian (1954); ⁴Glogoza et al. (1998); ⁵Runo and Kuria (2018); ⁶Fitt (1989); ⁷Moral Garcia (2006); ⁸Greathead (1986); ⁹Naranjo et al. (2010); ¹⁰Ryckewaert
90 et al. (2011); ¹¹Entwistle (1972); ¹²Leston (1973); ¹³Opoku et al. (2002); ¹⁴Ristaino and Gumpertz (2000); ¹⁵McCook (2006); ¹⁶Bowden et al. (1971);
91 ¹⁷Johannesson and Mansingh (1984); ¹⁸Decazy (1989)

92 The pest attracting effects of trap plants at field level was studied in combination with other pest
93 management pathways. These were (i) the barrier effects and conservation biological control of tomato
94 fruitworms (*Helicoverpa zea* and *H. armigera*) (Lepidoptera: Noctuidae), respectively on tomato in
95 Martinique and okra (*Abelmoschus esculentus*) (Malvaceae) in Niger (and to a lesser extent whitefly
96 (*Bemisia tabaci*) (Hemiptera: Aleyrodidae) on okra in Niger) and, (ii) a food attractant mixed with a
97 biological insecticide on cucurbit fruit flies (Diptera: Tephritidae) in Réunion. We also studied the
98 effect of distinct intercropping arrangements of cocoa (*Theobroma cacao*) (Malvaceae) and
99 companion perennials on the cocoa plant bug *Sahlbergella singularis* (Hemiptera: Miridae) and
100 *Phytophthora megakarya* (Peronosporaceae), black pod rot disease in Cameroon. Similarly, we
101 studied the effect of distinct intercropping arrangements of coffee (*Coffea* spp.) (Rubiaceae) and
102 companion perennials on *Hemileia vastatrix* (Pucciniales), the causative agent of the coffee leaf rust,
103 in Costa Rica. At the farmscape scale, we studied the effects of density and arrangement of various
104 land uses on the incidence of leaf rust, and the abundance of the coffee berry borer (*Hypothenemus*
105 *hampei*) (Coleoptera: Curculionidae) in coffee in Costa Rica.

106 Here, we present the major results of the above-mentioned case studies, emphasizing the major lessons
107 learned. These results particularly emphasize that while PSD can have important effects on pest and
108 disease regulation, different contexts can produce conflicting effects, either between pest or disease
109 regulation and agronomic performance, or among individual pest and/or pathogen species within pest
110 and pathogen complexes. A need therefore exists to manage tradeoffs or exploit synergies that underlie
111 PSD-based regulatory processes. We also discuss how modeling could be used as a tool for designing
112 and developing PSD-based cropping systems that are resilient to pest and disease outbreaks. We focus
113 on the way to optimize systems that can have antagonistic effects on pests and diseases, and how, if
114 need be, pest and disease regulating effects can be enhanced. We also consider inclusion of “mimics”
115 of PSD-based regulatory processes to address a particular pest or disease that cannot be controlled by
116 PSD *per se*.

117 **2. Major outcomes of the Omega3 project case studies**

118 References to case studies that were developed during this project and which can be consulted for
119 more details are provided in Table 2.

120 **Table 2. References of publications reporting results of the Omega3 project case studies**

Case study	Crop	Geographical area	Pest or disease	References
1	Tomato	Martinique	Bacterial wilt (<i>Ralstonia solanacearum</i>)	Deberdt et al. (2015); Deberdt et al. (2018); Diédhiou et al. (2012)
2	Upland rice	Madagascar	Scarab beetles (<i>Heteronychus</i> spp.)	Rabary et al. (2011); Rafarasoia et al. (2016)
2	Upland rice	Madagascar	Witchweed (<i>Striga asiatica</i>)	Michellon et al. (2011)
3	Tomato	Martinique	Fruitworm (Corn earworm <i>Helicoverpa zea</i>)	Rhino et al. (2014); Grechi et al. (2012)
3	Okra	Niger	Fruitworm (Tomato fruitworm <i>Helicoverpa armigera</i>)	Ratnadass et al. (2014); Yabo (2010)
3	Okra	Niger	Whitefly (<i>Bemisia tabaci</i>)	Ratnadass et al. (2014)
4	Cucurbits	Réunion	Fruit flies (Diptera : Tephritidae)	Bonnet (2010); Duhautois (2010); Atiama-Nurbel et al. (2012); Deguine et al. (2015)
5	Cocoa	Cameroon	Mirid bug (<i>Sahlbergella singularis</i>)	Babin et al. (2012); Mahob et al. (2015)
5	Cocoa	Cameroon	Black pod rot (<i>Phytophthora megakarya</i>)	Ten Hoopen et al. (2012)
6	Coffee	Costa Rica	Leaf rust (<i>Hemileia vastatrix</i>)	Avelino et al. (2012); Lopez-Bravo et al. (2012)
6	Coffee	Costa Rica	Berry borer (<i>Hypothenemus hampei</i>)	Avelino et al. (2012)

121 2.1. Sanitizing effects of GMCCPs planted as rotational crops *vis-à-vis* bacterial wilt on tomato in
122 market-gardening systems of Martinique (“case study 1, Table 1)

123 *Ralstonia solanacearum*, a quarantine organism, causes bacterial wilt that affects many crops
124 worldwide. This disease is particularly damaging to tomato in tropical and subtropical environments.
125 Since chemical control is largely ineffective and not a sustainable option for disease control (Enfinger
126 et al., 1979) in these regions, alternative management measures based on ecological processes are
127 needed. In Martinique, the importance of bacterial wilt has increased dramatically since 1999, with the
128 emergence and rapid spread of a new genotype of *R. solanacearum*, phylotype IIB/4NPB, throughout
129 the island (Deberdt et al., 2014; Wicker et al., 2007). This phylotype infects tomato cultivars
130 previously considered resistant, resulting in significant yield losses. To address this, crop species that
131 were previously used as nematode-sanitizing crops were investigated as a potential alternative
132 management method.

133 The (undesirable) ability of the emergent population of *R. solanacearum* to persist *in planta* and in the
134 rhizosphere of eight candidate crop cultivars was first evaluated under controlled conditions (growth
135 chambers) and the incidence of bacterial wilt assessed in tomato plants subsequently grown in the
136 same soil media. These candidate crops were in the families Brassicaceae (*Raphanus sativus* cv
137 Melody and *R. sativus* cv Karakter), Asteraceae (*Tagetes erecta* cv Sunset and *Tagetes patula* cv
138 Bonita) and Fabaceae (*Mucuna deeringiana* from Singapore and *M. deeringiana* cv Mucuna añã;
139 *Crotalaria juncea* cv IAC-1 and *Crotalaria spectabilis* cv Comùn). Results showed that all assessed
140 cultivars hosted *R. solanacearum* latently, but that the concentration of this pathogen in the
141 rhizosphere differed between cultivars within the same species and between species within the same
142 genus. Among the Brassicaceae and Asteraceae, the highest concentration of *R. solanacearum* was
143 found *in planta* and in the rhizosphere of *T. erecta*. The concentration of the *R. solanacearum*
144 population in the rhizosphere of *R. sativus* cv. Karakter was significantly higher than in that of *R.*
145 *sativus* cv. Melody. In Fabaceae, the *in planta* concentration of *R. solanacearum* was statistically
146 similar in all species. The concentration of the *R. solanacearum* population in the rhizosphere of *C.*
147 *juncea* cv. IAC-1 was significantly higher than that in *C. spectabilis* cv. Comùn.

148 This study conducted at nursery scale over a 45-day period showed for the first time that *C. spectabilis*
149 and *R. sativus* cv. Melody, grown prior to a tomato crop, improved tomato performance (see below),
150 with similar effects on *R. solanacearum* populations as those observed on tomato planted after a bare
151 soil precedent. Disease incidence in tomato decreased by 86% and 60% if cultivated after *R. sativus*
152 cv. Melody and *C. spectabilis*, respectively. These results indicate that *C. spectabilis* and *R. sativus* cv.
153 Melody can be used in ecological management strategies for bacterial wilt, even though no drastic
154 suppression of *R. solanacearum* population inside stem tissues and in the rhizosphere of these two
155 GMCCPs may occur (Deberdt et al., 2015).

156 Greenhouse pot experiments were then conducted to investigate the effect of the most promising plant
157 species identified from those mentioned above on soil microbial communities and their ability to
158 suppress bacterial wilt in a naturally infected soil. These plant species were: *M. deeringiana*, *C.*
159 *spectabilis*, *C. juncea*, *Allium fistulosum* (Liliaceae), *R. sativus* and *T. patula*. Each was cultivated as
160 sanitizing plants at three planting densities (bare soil control, field density and twice the field density)
161 followed by planting the same pot with a tomato crop. Tomatoes were grown in each pot as a bio-
162 indicator of bacterial wilt, after the preceding crop plants were either removed or uprooted and
163 chopped with their residues incorporated into the soil for 10 days of initial decomposition, prior to
164 planting of tomato seedlings. The incidence of plants exhibiting tomato bacterial wilt was reduced by
165 51% and 61% respectively in pots previously cultivated with *C. juncea* and *C. spectabilis*. For all the
166 plant species, bacterial wilt incidence correlated negatively with the incidence of GramN and GramP
167 bacteria and actinomycetes suggesting an antagonistic interaction between these microbial
168 communities and *R. solanacearum* populations. The only treatment that significantly reduced the
169 incidence of bacterial wilt was that with *C. juncea* which resulted in a 66% reduction in the incidence
170 of bacterial wilt compared to the bare soil control. Across all sanitizing plant treatments, however,
171 bacterial wilt incidence was negatively correlated with soil NH_4^+ level, GramN bacteria and
172 actinomycetes densities, plant root biomass and the bacteria/fungi ratio, thus suggesting significant
173 soil ecosystem impacts on disease control.

174 Overall results suggested that *C. juncea* and *C. spectabilis* have potentially important biological
175 control properties as rotational crops. Their use may result in favorable changes in microbial
176 communities that suppress tomato bacterial wilt disease (Diédhiou et al., 2012). However, most of the
177 plant species showing promise under growth chamber and greenhouse conditions lost their sanitizing
178 effect once their residues were ploughed into the soil. This could possibly be ascribed to a change in
179 the relative concentrations of microbial groups, despite an overall increase in soil microbial
180 community biomass.

181 The potential of the three Fabaceae species (*M. deeringiana*, *C. juncea* and *C. spectabilis*) to control
182 bacterial wilt was then evaluated under field conditions, without incorporation of plant residues into
183 the soil, but leaving the residues as a mulch on the soil surface. The best control was obtained with *C.*
184 *juncea* and *C. spectabilis* with a decrease of bacterial wilt incidence on tomato by 71% and 58%,
185 respectively. These results thus suggest that *C. juncea* and *C. spectabilis* could be used as sanitizing
186 plants, placed as a mulch but not incorporated, to contribute to bacterial wilt control under field
187 conditions in agroecological crop protection strategies (Deberdt et al., 2018).

188 2.2. Allelopathic effects of cover crops *vis-à-vis* upland rice pests in conservation agriculture 189 systems in Madagascar (case study 2, Table 1)

190 *Heteronychus* spp. are important pests of upland rice in the Central Highlands of Madagascar. Both
191 the adults (black beetles) and larvae (white grubs) are particularly damaging in some conservation
192 agriculture (no-till) systems. Certain species of cover crops used in conservation agriculture systems
193 may have suppressive effects on white grub and adult black beetle populations. It is thought that the
194 mechanism of suppression is *via* alteration of soil macrofauna communities or changes in status (pest
195 or beneficial) of some white grub/black beetle species, through changes in feeding strategies from
196 rhizophagous to saprophagous (Ratnadass et al., 2013; 2017).

197 Diverse cover crops were evaluated for suppression effects on white grubs within upland rice cropping
198 systems. These cultivation systems were: no-till rice with a cover crop, no-till rice without a cover
199 crop, and conventional tillage rice. The plants used as cover crops in two-year rice and cover crop(s)

200 rotations with rice were: hairy vetch (*Vicia villosa*) and rattlebox (*Crotalaria grahamiana*) (Fabaceae);
201 fodder radish (*R. sativus*) (Brassicaceae); *Brachiaria ruziziensis* x *Brachiaria brizantha* (var. Mulato)
202 (Poaceae); and a mixture of *Cleome hirta* (Capparaceae), *Tagetes minuta* and *Cosmos caudatus*
203 (Asteraceae). Fodder radish emerged as a promising tool for white grub pest management. In addition,
204 it did not reduce the diversity and abundance of soil macrofauna (Rabary et al., 2011).

205 We also conducted a laboratory study on the possible effects of adding dried plant mulch (hereafter
206 'residues') to the soil (1% of dried plant mulch + 1% of rice straw) on *Heteronychus bituberculatus*
207 larvae and adults. The residues of ten cover crop species were tested. Pigeon pea *Cajanus cajan*
208 (Fabaceae), green leaf desmodium *Desmodium intortum* (Fabaceae) and finger millet *Eleusine*
209 *coracana* (Poaceae) were used in addition to the seven cover crops mentioned above. Adding residues
210 of *C. grahamiana*, *E. coracana* and *C. caudatus* resulted in significantly higher white grub mortality
211 than in the control treatments (with 2% of rice straw), while residues of *R. sativus* had a marginally
212 significant effect. Adding residues of *C. grahamiana*, *C. caudatus*, *C. hirta*, *T. minuta* and *R. sativus*
213 significantly reduced damage caused by black beetles to rice plants (Rafaraso et al., 2016).

214 In the mid-West of Madagascar, witchweed infestation on hillsides often results in farmers having to
215 abandon cultivation of cereals such as rice or corn (*Zea mays*) (Poaceae). Various conservation
216 agriculture cropping systems were therefore tested for their witchweed-alleviating potential and
217 compared with conventional tillage practices. Most of the evaluated systems were based on the two-
218 year rice and corn rotation cycles favored by farmers. The common rice and corn rotation system with
219 conventional tillage was compared with: i) rice+*Stylosanthes* and corn+*Stylosanthes* rotation, with
220 *Stylosanthes guianensis* (Fabaceae) cv CIAT 184 used as dry mulching material for direct seeding; ii)
221 rice and corn+*B. ruziziensis*+*C. cajan* rotation, with *Brachiaria* and pigeon pea used as dry mulch; iii)
222 rice and corn+cowpea rotation, with cowpea *Vigna unguiculata* (Fabaceae) used as dry mulch; iv)
223 rice+perennial *Arachis* and corn+perennial *Arachis* rotation, with *Arachis pintoii* or *A. repens*
224 (Fabaceae). In the latter treatment, *Arachis* plants were suppressed (i.e. not killed but having above-
225 ground part desiccated by using low herbicide rates) before direct rice or corn seeding.

226 Evaluation of the suppressive effect on witchweed was based on the number of witchweed seeds
227 remaining in the soil, and number of plants parasitizing cereals at the end of the season. The best
228 control was obtained with perennial *Arachis* (*A. pintoii* or *A. repens*) and *S. guianensis*. Systems based
229 on *S. guianensis* always produced more rice than other systems. The second-best treatment was
230 cowpea rotated with corn. Surprisingly, the perennial *Arachis* treatment, which was most efficient at
231 controlling witchweed, did not result in higher yields than those recorded with the conventional tillage
232 systems. This can be ascribed to competition for water between the main crop and *Arachis* plants,
233 especially during dry years. Because this system requires a specific management knowledge, and
234 because *Arachis* seeds are difficult to source, this cropping system is seldom adopted by farmers.
235 Conversely, the high adaptability and practicality of *S. guianensis* systems make them more amenable
236 to adoption by farmers (Michellon et al., 2011). These results suggest that *R. sativus*, *C. grahamiana*
237 and *C. caudatus* on the one hand, and *S. guianensis* on the other hand, are promising pest-suppressive
238 cover crops against respectively scarab beetles in the Central Highlands and witchweed in the mid-
239 west of Madagascar.

240 2.3. Attracting and barrier effects of trap plants on *Helicoverpa* spp. fruitworms and whitefly in 241 market-gardening systems of Martinique and Niger (case study 3, Table 1)

242 The corn earworm, *H. zea*, is a major insect pest of sweet corn, cotton (*Gossypium hirsutum*)
243 (Malvaceae), and vegetable crops, particularly tomato in North and South America, including the West
244 Indies. In West Africa, the tomato fruitworm, *H. armigera*, is considered to be the most destructive
245 pest of okra (Kumar et al., 2010). As an environmentally friendly alternative management practice to
246 synthetic insecticides, we (i) tested the potential of sweet corn varieties as border trap crops, and (ii)
247 determined the optimal corn planting time so as to concentrate *H. zea* on this trap crop and divert the
248 pest away from tomato crops in Martinique. The potential of using trap crops for the management of
249 the tomato fruitworm *H. armigera*, was also evaluated in Niger on okra. In these studies, short and
250 extra-short growing season varieties of pigeon pea, sorghum (*Sorghum bicolor*) and cotton were used
251 as perimeter trap crops, and crop yield compared to those of insecticide-sprayed and unsprayed plots.

252 In Martinique, *H. zea* infestation was lower in tomato fields that had a corn plant border, and when
253 corn silk emergence was synchronized with tomato flowering compared to fields without corn borders.
254 The Sugar Jean and Java Sweet corn varieties were suitable trap crops because few larvae survived on
255 the silks and larval growth and development was poor. These two varieties, which therefore show
256 “dead-end” trap cropping properties (Shelton and Nault, 2004), could reduce the risk of *H. zea*
257 development and dispersion from corn plant borders into the tomato crop (Rhino et al., 2014).

258 In Niger, however, only a slight regulating effect on tomato fruitworm was observed in okra with an
259 extra-short growing season pigeon pea cultivar (cv ICPL 85010) planted as trap crop. This was
260 however not ascribed to the trapping function of pigeon pea but to increased top-down regulation by
261 generalist predatory spiders. Colonization by the latter was indeed significantly higher on the
262 unsprayed okra crop with extra-short growing season pigeon pea cultivar borders than on both sprayed
263 and unsprayed okra monocrops in the absence of extra-short growing season pigeon pea cultivar
264 borders (Ratnadass et al., 2014). Early-season establishment of spiders in okra plots surrounded by
265 extra-short growing season pigeon pea cultivars was itself ascribed to higher early infestation by prey
266 (leafhoppers: *Empoasca* sp.), which was most likely due to increased attractiveness of nitrogen-rich
267 okra plants associated with a legume (namely pigeon pea).

268 Besides the above-mentioned experimental efforts, a modeling approach was used to determine how
269 the deployment modalities of trap crops and commercial crops affect trap cropping efficacy. In this
270 respect, Individual Based Models (IBMs) are suitable tools to study the interplay between factors that
271 influence successful diversification strategies. IBMs are spatially explicit models with a strong
272 emphasis on the behavior of individual organisms, that have been used to study pest management
273 efficacy of agro-ecosystem diversification strategies (Fenoglio et al., 2017; Potting et al., 2005;
274 Vinatier et al., 2012). Such a modeling approach was thus applied to the management of *H. zea* by
275 means of sweet corn as a trap crop (Grechi et al., 2012) (Box 1).

Model description. The dynamic and spatially-explicit IBM, developed on the NetLogo 4.1 agent-based simulation platform (Wilensky, 1999) includes three interacting modules that describe (i) phenology of tomato and corn plants and dynamics of their attractive stages for *H. zea*, (ii) *H. zea* development, and (iii) movement and oviposition behavior of *H. zea*. Plant phenology and insect development were both based on physiological time using thermal units. The model runs at the field scale over one tomato cropping cycle and was approximated at a daily time-step. At each time-step, the following behavioral events were taken into account (Fig.1): juvenile tomato fruitworms aged and accumulated degree-days ('grow'), died at a constant stage-dependent mortality rate ('die'), and transited into successive stages ('update-stage'). Each day, adult females colonized the field and a random spatial position was assigned within the plot ('colonize the field'). Then, each moth repeated a set of behavioral actions in successive loops within the day. During one loop, the moth first determined whether or not it accepted the plant it was located on, to oviposit ('accept?'). If the moth accepted the plant, it arrested and laid eggs on it ('oviposit'), after which it moved to a new plant selected randomly within a searching area restricted to the plant itself and its neighboring plants ('area restricted search'). If the moth did not accept the plant, it flew away to search for a more suitable plant to land on ('fly'), based on its pre-alighting host recognition abilities. In that case, host selection is driven by the attractiveness of plants and restricted to those within insect perception distance. In both situations, the spatial localization of the moth was updated. The movement tendency of the moth was determined by the suitability of the plant that the moth encountered: a suitable plant induces moth arrestment and local movement, while an unsuitable plant induces continued moth flight to explore wider areas.

Simulation-based assessment of pest infestation patterns. With a more global prospect, this model is aimed to be used as a generic tool to improve our understanding of system functioning by assessing general pest infestation patterns in response to plant characteristics, the spatio-temporal deployment of commercial and trap crops, and insect behavioral traits (Fig. II). As an example we assessed pest infestation patterns in response to relative attractiveness of the commercial crop vs the trap crop, spatio-temporal planting design of the crops (Fig. IIB) and *H. zea* perception distance. For simplification, a similar probability was set for oviposition on both tomato and corn plants, assuming a same suitability of the two species for *H. zea* oviposition, and the number of females infesting the field each day was set as an input. In this way, as both endogenous and exogenous adult females are assumed to leave the field at the end of the day, the model does not account explicitly for new females emerging from the field but for an overall infestation level.

In all the above simulated cases, planting of corn trap-crops resulted in reduced infestation levels of tomato (of between 27 to 50%), compared to the control plots only planted with tomato (Fig. IIA). The simulations suggested that the border design was less effective in reducing infestation levels than the strip and patch designs. It was also suggested that the effect of border design on infestation levels mostly depended on the perception distance of the insect, while the efficacy of strip and patch designs mostly depended on relative attractiveness of plants (Fig. IIB).

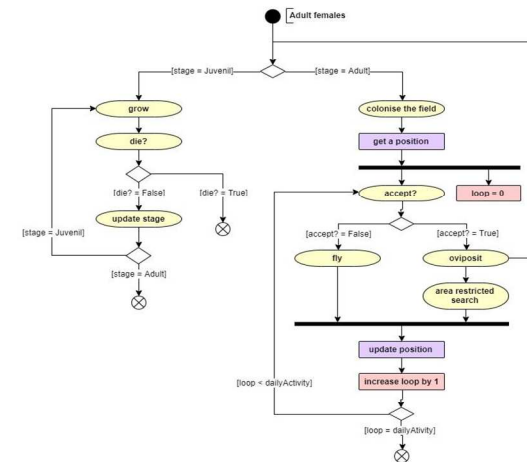


Fig. I. Flow diagram of the behavioral events for each individual at a daily time-step in the simulation model (adult behavioral events are for females only)

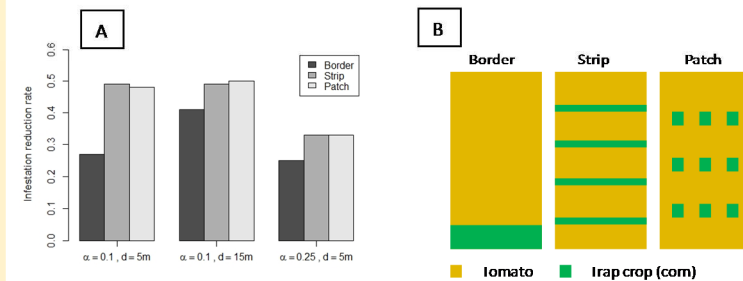


Fig. II. A) Simulated reduction rate in tomato plant infestation by tomato fruit worm according to trap-crop planting design (border, strip and patch), relative attractiveness of the commercial vs. trap-crop (α) and insect perception distance (d). Plant infestation is expressed as the number of eggs laid per tomato plant and infestation reduction rate is relative to a control plot only planted with tomato. B) Schematic representation of the three trap-crop planting designs and control plot.

276

277 **Box 1. An individual-based modeling approach to assess the efficacy of trap cropping in pest management: *Helicoverpa zea* management in tomato**

278 **field (after Grechi et al., 2012)**

279 The results of the case study on tomato in Martinique, supported by the modelling approach, suggested
280 that highly attractive sweet corn varieties with dead-end trap crop properties (e.g. Sugar Jean and Java)
281 could be used as border trap crops to control *H. zea*, via bottom-up effects. On the other hand, ICPL
282 85010, an extra-short growing season pigeon pea cultivar, could be used as perimeter trap crop to
283 control *H. armigera* on okra in Niger, via top-down effects.

284 2.4. Assisted trap cropping for cucurbit fruit fly management in Réunion (case study 4, Table 1)

285 In Réunion, fruit fly species belonging to the tribe Dacini of the family Tephritidae (Diptera) have
286 been reported as the major cause of damage to cucurbit crops for many decades, notably: *Zeugodacus*
287 *cucurbitae*, *Dacus ciliatus* and *Dacus demmerezi* (Ryckewaert et al., 2010). In order to develop
288 environmentally-friendly alternatives to the use of synthetic insecticides for tephritid management, we
289 compared the attractiveness of corn and Napier grass (*Pennisetum purpureum*) (Poaceae) as potential
290 trap plants onto which baits could be applied. This study was conducted with only two of the fly
291 species and results showed that corn, since it provided roosting sites, was more attractive to adults of
292 *Z. cucurbitae* and *D. demmerezi* than Napier grass, irrespective of fruit fly sex and sexual maturity
293 status. This study therefore showed the relevance of using corn as a trap plant onto which to apply
294 bait, e.g. GF-120® Syneïs Appât®, a spinosad-based fruit fly bait (Dow AgroSciences LLC,
295 Indianapolis, IN) for the management of cucurbit fruit fly populations (Atiama-Nurbel et al., 2012).

296 In order to study the characteristics (seasonal fluctuation, relative abundance and sex ratio) of the
297 communities of tephritid species that damage cucurbits in Réunion, the numbers of adult flies roosting
298 on corn planted within or around fields of cultivated cucurbits were recorded. Adults of the three fly
299 species spent most of their time on corn plants and their numbers on the cucurbit crop (zucchini:
300 *Cucurbita pepo*) were very low, except for a short period every day, depending on the species. While
301 males remained roosting on corn plants throughout the day, only gravid females migrated to zucchini
302 plants to lay eggs. Hourly observations showed that the three species had circadian rhythms which
303 varied according to the species. On the other hand, the three different spatial arrangements of corn
304 plantings (borders around the field, or patches, or strips within the field) were all found to be effective
305 in concentrating cucurbit fruit fly populations onto corn plants (Bonnet, 2010; Deguine et al., 2015).

306 Duhautois (2010) also analyzed the structure of the Diptera communities to assess the impact of corn
307 on non-target fly species. She focused on six families: Calliphoridae, Muscidae, Otitidae,
308 Sarcophagidae, Sepsidae and Syrphidae and found that at the regional scale, the community structure
309 was influenced by the locality, while at the field scale it was influenced by corn phenology. Beyond
310 concentrating pest fly species, corn plants harbored beneficial species such as hoverflies (Diptera:
311 Syrphidae), which are well-known pollinators and bio-indicators of agroecosystem health, with larvae
312 of some species being efficient predators of plant-sucking pests (Sarhou et al., 2005). Populations of
313 the dominant hoverfly species, *Melanostoma annulipes*, a predator of many pest species (Schmutterer,
314 1974), peaked in late March, corresponding to the flowering period of corn. Their abundance was also
315 the highest at 08:30 a.m. which is also the time of maximal corn pollen shed (Duhautois, 2010).
316 Although it was found that application of GF-120® bait resulted in attraction and mortality of dipteran
317 taxa other than tephritid flies, this was not quantified for these species (Duhautois, 2010).

318 These results suggest that corn is more suitable than Napier grass as a trap plant onto which apply the
319 adulticide bait GF-120® for cucurbit fruit fly management, either as borders around the field, or
320 patches, or strips within the field. However, a potential indirect negative effect on natural biological
321 control of other pest guilds, due to the attractiveness of GF-120® for predatory flies, was also
322 highlighted.

323 2.5. Intercropping cocoa to create barriers for the management of cocoa mirid bugs and black pod 324 rot disease in Cameroon (case study 5, Table 1)

325 The brown cocoa mirid bug, *S. singularis*, is the most harmful insect pest of cocoa in Cameroon
326 (Mahob et al., 2020), while black pod rot, caused by *P. megakarya*, is the major disease affecting this
327 crop (Ndoungue et al., 2018). Unshaded monocrop cocoa orchards are a common practice in the cocoa
328 belt of West Africa, which accounts for more than 70% of the world cocoa production. However, full-
329 sun orchards are often highly damaged by mirid bugs that feed on developing vegetative parts such as
330 green shoots, buds and young leaves (Mahob et al., 2020). Mirid bug damage lesions lead to the
331 desiccation of branch tips, cankers on branches, and premature ageing of trees which then quickly
332 become unproductive. Consequently, unshaded cocoa orchards, especially the young developing trees,

333 require intensive use of insecticides for mirid control (Mahob et al., 2014). A study was conducted to
334 assess the impact of cocoa-fruit tree intercropping on mirid bug infestation. The study focused on the
335 potential effect of using fruit trees as physical barriers to limit mirid bug infestation on cocoa during
336 the first years of plantation, when fruit trees are not yet developed enough to provide cocoa with
337 shade. Previous studies have shown that mirid bugs may use visual cues while flying in search of their
338 host (Leston, 1973) and we hypothesized that intercropping with fruit trees (which are known not to be
339 cocoa mirid bug plant hosts) may disturb mirid bug flight behavior.

340 Over two consecutive years, mirid infestation was assessed in seven four-year-old orchards located in
341 the Centre Region of Cameroon. The average orchard size was 0.3 ha. Every second row of trees in
342 these orchards consisted of fruit trees (avocado: *Persea americana*, safou: *Dacryodes edulis*, and
343 *Citrus* spp.) replacing cocoa every four plants. Original biometric methods were developed for this
344 study as follows: the spatial distribution pattern was characterized through a semivariogram analysis,
345 whereas the barrier effect of intercropped trees was analyzed with presence-absence data through joint
346 count analysis and permutation tests (Babin et al., 2012; Mahob et al., 2015). Mirid bug infestation
347 was assessed at the population peak (from June/July to October/November) through counting of
348 individuals and scoring of recent damage symptoms on cocoa pods and shoots (N'Guessan et al.,
349 2008). Results showed that mirid bug populations were strongly aggregated at small distances, but
350 damage symptoms tended to be more uniformly distributed across orchards, suggesting population
351 movements during the study period. Since no barrier effect was detected, we concluded that
352 intercropped fruit trees did not impact mirid bug movement and distribution in cocoa orchards (Babin
353 et al., 2012; Mahob et al., 2015).

354 A similar survey of black pod rot occurrence was conducted in the same young unshaded cocoa
355 orchards. Previous studies conducted in well-established orchards suggested that spatiotemporal
356 dynamics of the disease was first determined by the presence of primary inoculum in the soil (Deberdt
357 et al., 2008). Secondary inoculum would then appear and drive temporal infection at tree level,
358 through different dispersion mechanisms, including rain splash and ant tents (Ten Hoopen et al.,
359 2010). During the latter study however, infection by black pod rot was too low to reveal any impact of

360 intercropping of fruit trees on disease dynamics. Results suggested an exogenous origin of the
361 infection and dispersion through human activities, with microclimate and cocoa genetic origin as the
362 main factors explaining the persistence of the initial infection in some parts of the orchards (Ten
363 Hoopen et al., 2012).

364 These results suggest that intercropping with fruit trees had no effect on cocoa infestation by mirid
365 bugs, while such an effect (or lack of thereof) on cocoa infection by black pod rot was not evident due
366 to too low infection levels at the time of the study.

367 2.6. Effects of farmscape fragmentation on orange rust epidemics and berry borer dynamics in 368 coffee-based agroforestry systems in Costa Rica (case study 6, Table 1)

369 Coffee is affected by a number of diseases and insect pests, of which coffee leaf rust, caused by *H.*
370 *vastatrix*. and the coffee berry borer, *H. hampei* are among the major ones with a worldwide
371 distribution (Avelino et al., 2018). They are notably the main biotic stresses affecting coffee
372 production in Costa Rica, where a recent study on landscape effects on pest dynamics may help to
373 develop more sustainable management programs (Avelino et al., 2012).

374 In a first study, coffee berry borer abundance in coffee tree plots was found to be positively correlated
375 with the proportion of coffee area in the farmscape at a distance of 150 m around the plots. Negative
376 correlations were obtained with other land uses, specifically forest, pasture and sugar cane. Since the
377 coffee berry borer is a monophagous pest, large extensions of connected coffee tree areas probably
378 increased the likelihood of flying individuals locating new coffee berries for colonization. The latter is
379 especially important after coffee harvest, when coffee berries are rare. Finding new berries to infest
380 and survive on during the post-harvest period supports and sustains pest populations and high
381 infestation levels and damage in the subsequent season. In this study, fragmenting of the farmscape
382 with forests or pastures that adversely affected the borer host location process was associated with a
383 noted reduction in pest abundance.

384 However, fragmenting coffee farmscapes with pasture yielded higher incidences of coffee leaf rust
385 (peak correlation at a distance of 200 m). We hypothesize that wind turbulence, produced by low-

386 wind-resistance land uses such as pasture, favored removal of coffee leaf rust spore clusters from host
387 surfaces, resulting in increased epidemics (Avelino et al., 2012).

388 These results demonstrated that what is conceived as a barrier for one species may be conducive to the
389 survival of another. It is therefore necessary to take into account the whole crop pest and pathogen
390 complex to ensure efficient management. In this case, fragmenting coffee farmscapes with forest
391 patches was suggested to limit coffee berry borer abundance, without favoring coffee leaf rust.

392 Another study was conducted to quantify shade tree effects on coffee leaf rust in *Erythrina*
393 *poeppigiana* (Fabaceae)-based agroforestry systems. Shade tree effect on coffee leaf rust is an
394 example of conflicting effects that certain environmental conditions may provide in terms of
395 management of pests or diseases. On the one hand, shade helps to reduce leaf receptivity to the
396 pathogen by preventing leaf exposure to radiation and high fruit loads, but, at the same time, shade
397 may provide appropriate microclimate conditions for pathogen development. In order to quantify the
398 individual effects of these antagonistic pathways, which are combined under natural conditions, these
399 two factors were dissociated by manually homogenizing fruit loads under shade and in full sunlight
400 conditions. Under each light regime, fruiting nodes were removed from coffee plants in order to obtain
401 four fruit load levels (zero, 150, 250 and 500 fruiting nodes per coffee plant).

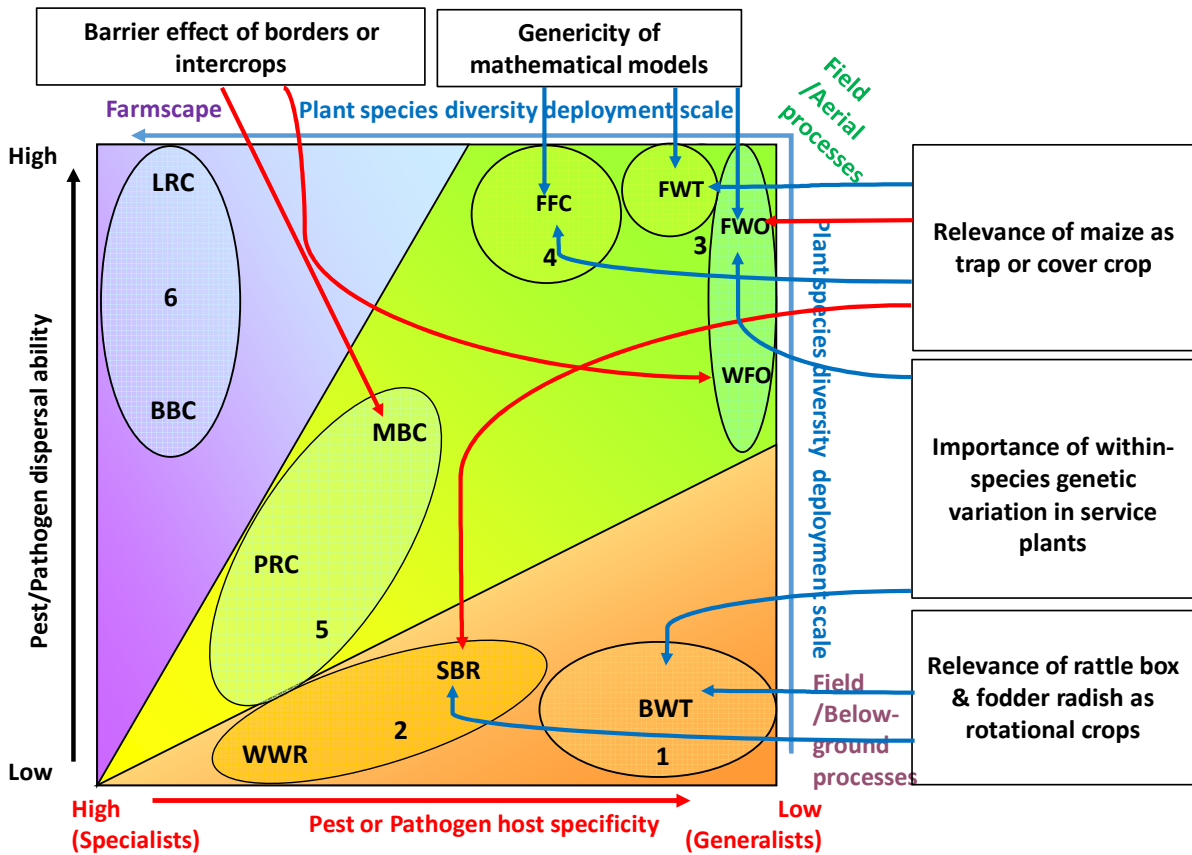
402 As expected, the intensity of the coffee leaf rust disease increased as fruit load per tree increased
403 (28.9% increase in incidence and 129.2% increase in disease severity on plants with 500 fruiting
404 nodes, as compared to plants with no fruits). With homogenous fruit loads, the intensity of the coffee
405 leaf rust disease was greater under shady conditions, with a 21.5% increase in incidence and a 22.4%
406 increase in severity. Two mechanisms were suggested. First, we found a dilution effect due to host
407 growth, i.e. the continuous appearance of new healthy leaves in the system. The number of new leaves
408 and new leaf area was 25.2% and 37.5% greater, respectively, in full sunlight conditions. Second, the
409 microclimate was more conducive to coffee leaf rust under shade, due to lower intra-day temperature
410 variations and higher leaf wetness. Shade, as expected, has antagonistic effects on coffee leaf rust:

411 reduction of the disease due to reduced fruit load vs increased disease severity due to microclimatic
412 conditions that favor the pathogen (Avelino et al., 2012; Lopez-Bravo et al., 2012).

413 These results suggest that fragmenting coffee farmscapes with forest patches could limit coffee berry
414 borer abundance without favoring coffee leaf rust, while shade (e.g. in *E. poeppigiana*-based
415 agroforestry systems) has antagonistic effects on coffee leaf rust, namely reduced disease intensity due
416 to reduced fruit load vs increased disease severity due to favorable microclimatic conditions.

417 **3. Major lessons learned in terms of PSD-based pest and disease regulation effects with** 418 **emphasis on synergies and tradeoffs**

419 Studies conducted under the Omega3 project yielded results of different natures demonstrating the
420 complex nature of agroecological interventions for pest and disease control. One of the integrative
421 objectives of the project was to document context specific pest and disease regulation processes, and
422 verify whether generalizable principles could be elevated. Several of the case studies demonstrated
423 that locally adapted pest and disease regulation impacts exist and that these can be effective (section
424 2). Synergies and tradeoffs highlighted in the project are discussed in the following sections, and
425 some of them are summarized in Fig. 1.



427

428 **Figure 1.** Positioning of the reported case studies (cf. Table 1 for numbering and abbreviations),
 429 as a function of scale levels at which plant species diversity modalities and effects are deployed
 430 (field level via below-ground processes: bottom right triangle; field level via aerial processes:
 431 central kite; farmscape level: top left triangle), and a life history trait-based typology of pests
 432 and disease-causative pathogens (host specificity and dispersal ability), with some transversal
 433 synergies or tradeoffs highlighted. *Blue arrow: positive regulatory effect on target pest/pathogen-*
 434 *crop system (synergy/genericity highlighted); Red arrow: negative (or absence of) effect (tradeoff*
 435 *requirement highlighted).*

436 3.1. Lack of beneficial effect of PSD deployment on some targeted pests and diseases

437 Unsurprisingly, due to high variability across systems studied, we found no evidence of generic
 438 relationships between PSD and pest and disease suppression impacts, since there were instances where
 439 anticipated pest and disease reduction effects of PSD practices were not evident. For instance,

440 although we expected a barrier effect (physical obstruction) against whiteflies provided by trap crops
441 in the Niger subcase study (See § 2.3), Ratnadass et al. (2014) reported that late-maturing pigeon-pea
442 and sorghum in particular did not have any effect on whitefly density. Similarly, trap crops did not
443 affect leafhopper infestation, which turned out to be a benefit overall (See § 3.5), or at least not a
444 disservice, since these less injurious early-season pests triggered a regulatory effect on a later
445 occurring/highly damaging fruit pest (tomato fruitworm), via top-down pathways involving spiders.
446 Conversely, in the case of the assisted trap cropping for cucurbit fruit fly management in Réunion,
447 predatory flies were attracted by GF-120[®] bait (Duhautois, 2010), highlighting a potential indirect
448 negative effect on natural biological control of other pest guilds, e.g. aphids and whiteflies.

449 In the case of cocoa-based agroforestry systems, no effect of intercropping with fruit trees was
450 observed (particularly no barrier effect on mirid bugs) in our study. It should be also noted that
451 conflicting effects were actually highlighted in similar studies, e.g. weaver ants and other ant species
452 acting as both black pod rot disseminators and predators of plant bugs on the one hand, and shade both
453 facilitating black pod rot infection and negatively affecting infestation by mirid bugs on the other hand
454 (Babin et al., 2010; Bagny Beilhe et al., 2018; Gidoïn et al., 2014; Tadu et al., 2014). However, ants
455 could also help pollinating cocoa (Toledo-Hernández et al., 2017).

456 In the case of coffee-based agroforestry systems, a positive relationship between shade and leaf rust
457 due to favorable microclimatic conditions and absence of a dilution effect was highlighted at plot
458 scale. Antagonistic effects were observed in the case of the coffee berry borer when the
459 entomopathogenic fungus *Beauveria bassiana* was applied (Sanchez et al., 2013), possibly because
460 shade trees favored the coffee berry borer as well as its natural enemy. The lack of effects of increased
461 PSD or barrier crops in more complex and diverse environments such as the coffee production systems
462 in this study could possibly be ascribed to the already high diversity in these agroforests. Such effects
463 have been found at the landscape level, e.g. Batáry et al. (2011) reported that local agroecological
464 management practices had strongest impacts in simple compared to already diverse, ecologically
465 complex landscapes.

466 We did however observe that cropping systems were frequently robust *vis-à-vis* new invasive or
467 emerging pests and pathogens. This is for example, the case of the emergent ecotype of *R.*
468 *solanacearum* (Phyl IIB/seq4NPB) (Deberdt et al., 2014; Wicker et al., 2007) associated with certain
469 rotation crops. This also holds true, as shown in other studies, for new fruit fly invaders such as
470 *Bactrocera dorsalis* (Diptera: Tephritidae) on the Indian Ocean Islands (De Villiers et al., 2016), or of
471 lepidopteran pests such as the fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in
472 Africa and adjacent islands (Harrison et al., 2019; Midega et al., 2018).

473 3.2. Genericity/overarching nature of results obtained on GMCCPs

474 Some overarching results of the above-mentioned case studies considered the effects of several
475 GMCCPs across soil and field scales, and stressed the importance of the genotypic aspect for
476 GMCCPs, beyond deployment of main crop genetic diversity (Tooker and Franck, 2012), which was
477 neither addressed in this project nor in an earlier review (Ratnadass et al., 2012a). The case study on
478 trap cropping for control of *Helicoverpa* spp. highlighted the specificity of agricultural contexts in
479 Martinique and Niger, *e.g.* sweet corn was ruled out under dry conditions in Niger (Yabo, 2010).
480 Similarly, in Madagascar, plants adapted to the ecology where witchweed thrives are not the same as
481 those species found in High Plateaus region of Madagascar where scarab beetles are the main
482 problems. Table 3 shows some overarching results regarding some GMCCPs across case studies at the
483 field scale.

484 The main aspects determining pros and cons of these GMCCPs are:

- 485 • their susceptibility to either abiotic stresses (*e.g.* case of susceptibility of corn to drought, of *C.*
486 *spectabilis* to waterlogging causing stem rot) or biotic stresses (*e.g.* case of susceptibility of most
487 rattlebox (*Crotalaria*) species to the mirid bug, *Moissonia importunitas* (Ratnadass et al., 2018;
488 2020);
- 489 • the importance of the within-species genetic variation of GMCCPs (*e.g.* rattlebox species and
490 fodder radish cultivars for bacterial wilt regulation on the one hand, and corn and pigeon-pea
491 cultivars for tomato fruitworm regulation on the other hand);

492 • their status as alternate hosts of pests (*e.g.* corn and Brachiaria ruled out of conservation
493 agriculture systems in Madagascar *vis-à-vis* scarab beetles and witchweed, while it is not the case
494 for some GMCCPs in rotations *vs* bacterial wilt (although all species host *R. solanacearum* at least
495 latently), and to a lesser extent with sweet corn on the tomato fruitworm (due to ‘dead-end’
496 regulation) or pigeon-pea (due to ease of manual management of the target pest on the same).

497 **Table 3. Literature references on pros and cons of some GMCCPs* evaluated across some Omega3 project case studies**

Case studies (Crops- Areas-Pests/ Diseases)	GMCCPs	Upland rice		Tomato			Zucchini
		Madagascar		Martinique		Niger	Réunion
		Effect ¹	Witchweed	Scarab beetles	Bacterial wilt	Fruitworm	Fruitworm
Rattlebox: <i>Crotalaria</i> spp.	(+)	Grubben and Denton 2004 ² Gacheru and Rao 2005 ²	Rafarasoia et al. 2015 ³	Deberdt et al. 2015 ³ Diédhiou et al. 2012 ³	na ⁴	na	na
	(-)	na	na	na	na	na	na
Fodder radish: <i>Raphanus sativus</i>	(+)	na	Rafarasoia et al. 2015 ³ Rabary et al. 2011 ³	Deberdt et al. 2015 ³	na	na	na
	(-)	na	na	na	na	na	na
Corn: <i>Zea mays</i>	(+)	na	na	na	Rhino et al. 2014 ³	na	Atiama-Nurbel et al. 2012 ³ Bonnet 2010 ³
	(-)	Husson et al. 2008 ⁵	Vayssière 1946 ⁵	na	na	Yabo 2010 ⁶	na

498 * GMCCPs: green manure, cover crops and companion plants

499 1. (+): Positive effect; (-): Negative effect

500 2. Positive effect potentially applicable to project case studies based on literature

501 3. Positive effect documented in the Omega3 project

502 4. No reference available

503 5. Negative effect potentially applicable to Omega3 project case studies based on literature

504 6. Negative effect documented in the Omega3 project

505 3.3. Genericity/overarching nature of mathematical methods used

506 This project also highlighted the complementary use of models with field trials as a tool for designing
507 and developing PSD-based cropping systems that are resistant/tolerant to pest and disease attacks,
508 particularly to optimize systems that can have antagonistic effects on pests and diseases. A specific
509 IBM model based on the tomato/corn earworm biological model can in the future be extended to
510 cucurbit fruit fly modeling, provided adequate parameterization. The latter model was also used to
511 compare the efficiency of pest or disease regulatory services provided by trap crop patches, borders
512 and strips, in terms of spatial design. This model can also be adapted to the Niger tomato fruitworm
513 case study, by including the perimeter trap crop design (see Potting et al., 2005).

514 3.4. Synergies in terms of pest and disease complex management by PSD-deployment measures

515 Crop rotation strategies were observed to provide valuable regulatory effects on pests and diseases in
516 the relevant case studies of this project. Some plant species provided allelopathic effects against soil-
517 borne pests and diseases and nematicidal plants (e.g. some rattlebox and fodder radish
518 species/cultivars: Aydin and Mennan, 2018; Wang et al., 2002) were found to have sanitizing effects
519 against soil-borne bacteria (e.g. against tomato bacterial wilt: Deberdt et al., 2015; 2018). Some plant
520 species also provided insecticidal effects (e.g. against scarab beetles: Rafaraso et al., 2016).

521 Based on the experience from Martinique, *Crotalaria* spp. could also be evaluated for their potential to
522 provide bacterial wilt control on potato in Madagascar (Ravelomanantsoa et al., 2018). Conversely,
523 based on the experience from Madagascar, *Crotalaria* spp. could also be evaluated for their potential
524 as a management tool against the Taro black beetle (*Tomarus ebenus*) (Scarabaeidae: Dynastinae)
525 (Robin, 2008) in Martinique.

526 Similarly, *Crotalaria* spp. could be used for bacterial wilt control in market gardening systems in
527 Réunion. However, care should be taken to use the right genotype since rattlebox is also highly
528 susceptible to the mirid bug, *M. importunitas*, which is an important pest in Réunion (Ratnadass et al.,
529 2018; 2020). On the other hand, some *Crotalaria* spp., e.g. *C. brevidens* could also be evaluated as
530 cover crops to control witchweed via induction of suicidal germination (Gacheru and Rao, 2005;

531 Grubben and Denton, 2004) in cereal-based conservation agriculture systems in the Midwest region of
532 Madagascar. Since the genus *Crotalaria* includes 702 species (Le Roux et al., 2013), there are still
533 many studies to be conducted to determine whether there are also other species that could provide
534 regulatory effects but that are not susceptible to mirid bugs.

535 Sweet corn was found to be an effective trap crop for *H. zea* (Rhino et al., 2014; 2016), while field
536 corn was found adequate for assisted push-pull against vegetable fruit flies in the cucurbit-based
537 cropping systems of Réunion (Deguine et al., 2015). Corn might therefore have potential for use in the
538 management of *Neoceratitis cyanescens* (Diptera: Tephritidae) in irrigated tomato-based cropping
539 systems in Réunion (Brévault et al., 2008). The use of corn as a component of a management strategy
540 for *Bactrocera dorsalis* in mango orchards should also be investigated further. In addition, in drier
541 environments, sorghum and pigeon pea could also be used, as was done in okra-based systems for *H.*
542 *armigera* in Niger (Ratnadass et al., 2014). However, the effectiveness of sorghum and pigeon pea as a
543 barrier crop against whitefly (*B. tabaci*) was not established. It is further suggested that genotypes
544 other than those of forage sorghum be evaluated for their nematicidal properties (Dover et al., 2004).
545 Similarly, rather than extra-short duration pigeon-pea cultivars, longer-season and taller cultivars
546 should be preferred, since they are more likely to act as physical barriers.

547 Corn was ruled out as a rotational crop in upland rice-based cropping systems (Ratnadass et al., 2017)
548 since it is an alternate host for both scarab beetles and witchweed. However, corn may provide
549 possible indirect positive effects to control witchweed, along with other weeds, via the physical barrier
550 effect of its residues in conservation agriculture systems (Ranaivoson et al., 2018). In this respect,
551 further studies confirmed the potential of *S. guianensis* for witchweed and non-parasitic weed control
552 in Malagasy conservation agriculture systems (Ranaivoson et al., 2018; Randrianjafizanaka et al.,
553 2018; Rafenomanjato, 2018). However, a recent study highlighted a clear tradeoff between corn yield
554 and the biomass production of *S. guianensis*, highlighting the need for careful and timely management
555 of this perennial legume to avoid interspecific competition with the cereal crop (Rodenburg et al.,
556 2020).

3.5. Synergies in terms of control of single pest or pathogen species *via* several pathways based on single PSD-deployment measures

GMCCP biomass productions were observed to provide valuable regulatory effects of some soil-borne pests and pathogens in this study. Different pests and pathogens were observed to be regulated *via* different pathways. For example, increased percentage of ground cover was observed to provide weed suppression (Ranaivoson et al., 2018), while the numbers of some scarab beetle species were suppressed because of GMCCP-related changes in macrofauna communities and the status of scarab beetle species (Ratnadass et al., 2013; 2017).

Bacterial wilt on tomato may be regulated both *via* biocidal effects (Deberdt et al., 2012) and *via* antagonistic microbial community mobilization due to GMCCP practices (Diédhiou et al., 2012). Also, for some sanitizing species such as *C. spectabilis*, bacterial wilt on tomato may be regulated through a symbiotic effect caused by arbuscular mycorrhizal fungi (AMF) brought by the sanitizing plant. Chave et al. (2017) similarly demonstrated that the association of AMF (*Rhizophagus irregularis* MUCL 41833) with tomato seedlings delayed the appearance of bacterial wilt disease symptoms caused by *R. solanacearum* phytotype IIB/4NPB. Conversely, *R. solanacearum* did not affect root colonization by the AMF within the 16 days of the experiment, suggesting that the AMF fungus was able to reduce bacterial wilt, probably by eliciting defense mechanisms in the plant. This strategy could possibly also be used to manage witchweed (Lendzemo et al., 2006).

This project also highlighted the efficacy of certain intercropping/trap cropping strategies against some aerial pests. For example, biocidal/bottom-up effects (e.g. growth inhibition effect of corn silks on the tomato fruitworm) and top-down effects, e.g. predators like ladybugs (Coleoptera: Coccinellidae) on corn (Rhino et al., 2014; 2016) and pirate bugs (Hemiptera: Anthocoridae) and spiders on pigeon-pea (Ratnadass et al., 2014) were reported. Indirect effects (*via* food webs) such as the attraction of spiders into okra fields *via* perimeter pigeon-pea growing (Ratnadass et al., 2014) were highlighted.

The latter example highlighted the need to consider possible tradeoffs, between the prevention of infestation of the main vegetable crop by certain less important pests or the encouragement thereof.

583 This can be achieved, for example, by allowing early-season, less injurious sap- or mesophyll-feeding
584 pests into crop fields, in anticipation of a regulatory effect on later occurring highly damaging fruit
585 pests (e.g. tomato fruitworm), via top-down pathways involving generalist predators. This may be put
586 in perspective with studies on tripartite trophic interactions between weaver ants, scale insects and
587 fruit flies on different host tree species (Olotu et al., 2013; Thurman et al., 2019; van Mele et al.,
588 2009), or mirid bugs on cocoa in West Africa (Bagny Beilhe et al., 2018; Bisseleua et al., 2017) and
589 Australia (Forbes and Northfield, 2017).

590 3.6. Synergies or tradeoffs with respect to other ecosystem services or disservices (at the 591 farm/cropping system level)

592 Soil improvement (via atmospheric Nitrogen fixation), is one of the objectives of the use of legume
593 cover crops such as *Crotalaria* spp. Some species of the same genus can also be used for food, e.g. *C.*
594 *brevidens* (Abukutsa-Onyango, 2007). This is also true for pigeon-pea when used as trap crops, since
595 pods can still be used even if partly damaged, unlike okra or tomato fruits.

596 Such a valorization of trap crop products occurs in Niger in the case of pigeon-pea seeds, while no
597 such valorization is possible with sweet corn cobs in Martinique. On the other hand, it is precisely
598 because sweet corn is not commonly grown that it can be proposed to farmers for cultivation as a
599 “sacrificial crop”, and harvested seed could still be used, e.g. as poultry feed (Rhino et al., 2014).
600 Ranaivoson et al. (2017) have shown that much of the expected function of cover plant biomass
601 depends on the amount of biomass left on the ground. However, with the notable exception of
602 *Crotalaria* spp., due to its containing toxic pyrrolizidine alkaloids (Williams and Molyneux, 1987)
603 almost all the plants used as cover crops, particularly in the Omega 3 project, are also valuable forage
604 plants. In the context of family farming in sub-Saharan Africa, this biomass generally has a high
605 economic value as livestock fodder (Naudin et al., 2015). While farmers may experience an almost
606 certain gain in terms of livestock fodder, this may not always be the case in terms of pest control.
607 Furthermore, the seeding of cover crops requires a cost in time and money in an already-constrained
608 agricultural context.

609 In addition to soil fertility enhancement, pigeon-pea borders may play a role in wind erosion
610 alleviation. Similarly, legume trees used in agroforestry systems (e.g. *Erythrina poeppigiana*, but also
611 other Fabaceae like *Leucaena leucocephala* or *Albizzia lebeck*) contribute both to soil fertility
612 enhancement and reduced soil erosion.

613 In the reported studies, we have highlighted the importance of identification of tradeoffs and gains in
614 GMCCP implementation on pest and disease management. Tradeoffs should be determined between
615 allelopathic effects on witchweed of GMCCPs used in cereal-based conservation agriculture systems
616 and competition for water with the main crop in mid-elevation areas (e.g. *Arachis*, *Desmodium*, which
617 are more adapted to conservation agriculture systems in higher altitude/rainfall areas). In this regard,
618 inspiration could be found in the “Climate-Smart Push-Pull Technology” approach (Khan et al., 2017),
619 which was adapted from the earlier and highly successful “Push-Pull” technology (Cook et al., 2007)
620 to address challenges provided by climate change. These adaptations implied that water-demanding
621 trap crops and intercrops (e.g. respectively Napier grass and Silverleaf desmodium) were replaced by
622 more drought-tolerant species (e.g. such as *Brachiaria* (cv Mulato) as trap crop and Greenleaf
623 desmodium as intercrop) (Cheruiyot et al., 2018a), with the same pest-regulating effects (Cheruiyot et
624 al., 2018b).

625 Environmental limitations to establishment and growth of trap crops are important and should be
626 considered in planning of habitat management strategies such as increased PSD. For example, trap
627 crops such as corn which has high water and soil fertility requirements can be grown wherever such
628 resources are not limited (e.g. in Martinique). However, alternate trap crops which are drought tolerant
629 and/or self-sufficient in nitrogen (e.g. sorghum, pigeon-pea) should be used wherever these resources
630 are scarce. Trap crops such as pigeon-pea and corn (cf. Martinique, Niger, Réunion) furthermore
631 contribute to biodiversity conservation, particularly of natural enemies of pests and may provide a
632 natural pest regulation service to the whole farm (Deguine et al., 2015; Ratnadass et al., 2014; Rhino
633 et al., 2014).

634 Another example is the role that intercropped plants like shade trees may play in cocoa pollination
635 ecology. In West African countries, cocoa yields hardly exceed a quarter of their potential. There are
636 many reasons for this, one of which could be inadequate pollination. Cocoa flowers are thought to be
637 almost exclusively pollinated by midges of the family Ceratopogonidae (Diptera), largely from the
638 genus *Forcipomyia* (Toledo-Hernández et al., 2017). These insects prefer humid habitats where they
639 breed in moist litter on the ground. Several studies have shown that adding organic matter to cocoa
640 litter improves pollination and fruit set. By diversifying litter sources and increasing humidity in full-
641 sun cocoa, plant diversification may thus improve pollination and consequently yield (Adjaloo et al.,
642 2013; Claus et al., 2018). In addition, Toledo-Hernández et al. (2017) suggested that plant
643 diversification, through habitat diversification, may enhance the role of other neglected groups of
644 cocoa pollinators, such as ants, that could contribute to cocoa pollination.

645 3.7. Tradeoffs that occur at other levels in the production system, landscape scale and/or crop 646 value chain

647 Possible tradeoffs include for example the acceptance of lower production levels vs premium prices
648 due to certification (e.g. Organic Agriculture; Ethical Coffee labels: Perfecto et al., 2005; Tschardtke
649 et al., 2015; Waldron et al., 2015). However, while there is a potential market for organic tomato in
650 Martinique, no such market exists in Niger for okra (Ratnadass, 2020). Similarly, there are
651 opportunities for agroecotourism (Asare et al., 2014) in Martinique or in Réunion (Deguine et al.,
652 2015) but less so in Africa. On the other hand, potential for organic or ethical cocoa or coffee
653 production labels exists for West African or Costa Rican agroforestry systems (Ayenor et al., 2004;
654 Babin, 2018).

655 As mentioned above, some GMCCPs can be valued for their market value *per se*, e.g. *Allium*
656 *fistulosum* (“Onion péyi”) in Martinique, which was reported to be a sanitizing plant used for
657 controlling bacterial wilt on tomato caused by *R. solanacearum* (Deberdt et al., 2012). Similar markets
658 can be further developed for aromatic/medicinal companion plants in Martinique, as was suggested for
659 the “push” or “pull” components of horticultural “push-pull” systems (Cook et al., 2007). This was
660 accomplished in Cuba with *Plectranthus* and *Ocimum* species, since the time of the US trade embargo

661 which started at the beginning of the Revolution, and especially during the ‘Special Period’ (1990-
662 1991) after the collapse of imports of petroleum, agrochemicals and farm machinery from the Soviet
663 bloc (Acosta de la Luz, 2001; Altieri and Toledo, 2011).

664 In addition to adaptation to climate change, mitigation thereof may also be an incentive to deploy
665 PSD-based pest and disease management strategies within agroecosystems. This might be of particular
666 importance in relation to the carbon sequestration market (particularly for conservation agriculture,
667 agroforestry and push-pull systems: Corbeels et al., 2019). Actually, beyond the carbon sequestration
668 aspect of PSD-based cropping systems, any crop protection measure *per se* contributes to climate
669 change mitigation, as reduction of pest and disease-associated losses reduces the need for excessive
670 input applications and unnecessary CO₂ emissions linked with their production (Lamichhane et al.,
671 2015).

672 As for agroforestry systems, PSD which is deployed partly in view of pest or disease alleviation for
673 the farmer’s benefit, also contributes to watershed services (Allinne et al., 2016), for example
674 improvement of water quality in dam reservoirs of Costa Rica (Gomez-Delgado et al., 2011). Benefits
675 other than mere limitation of soil water erosion were reported by Ratnadass et al. (2012b), who
676 indicated significant reduction in pollution levels of run-off water in conservation agriculture systems
677 in Madagascar (Ratnadass et al., 2012b). Another example of the additional benefits of PSD in terms
678 of limiting soil erosion and providing pest management services is that by Van den Berg (2006) and
679 Van den Berg et al. (2003), who suggested the planting of Vetiver grass (*Chrysopogon zizanioides*)
680 (Poaceae), which is commonly used as soil erosion management measure, for managing corn and rice
681 stem borers.

682 Finally, other important aspects to keep in mind with regard to using PSD as a pest and disease
683 management tool are the potential invasiveness of some GMCCPs, and their potential to host other
684 pests and diseases that may become economically important. In this respect, some specific rules for
685 their selection, as those proposed in the tomato bacterial wilt case study in Martinique (Deberdt et al.,
686 2018) should be followed, which could be used in other locations, particularly in islands where there is

687 a risk with invasive plants. The importance of several pests and diseases, as well as disease vectors
688 that occur on plants that could be used as service plants in PSD systems have been reported by Van
689 den Berg et al. (2001), and should not be overlooked (Ratnadass et al., 2018; 2020).

690 4. Conclusions

691 The Omega3 project presented in this review yielded results of different natures and each case study
692 contributed to resolving local problems. For example, sanitizing crops for managing bacterial wilt on
693 tomato in Martinique were identified and direct-seeding/mulch-based cropping systems were shown to
694 reduce scarab beetle and witchweed numbers on upland rice in Madagascar. The potential of using
695 trap cropping systems to control fruitworms on tomato in Martinique and on okra in Niger was
696 reported and the suppressive effects of landscape fragmentation on coffee berry borer and orange leaf
697 rust on coffee in Costa Rica, highlighted. However, this project also indicated that PSD deployment
698 *per se* does not provide positive pest regulatory services; for example, no effects were observed on the
699 cocoa mirid bug/brown pod rot case study in Cameroon.

700 A dynamic and spatially-explicit individual-based model was developed based on the
701 fruitworm/tomato subcase study described above. This model will in the future be used as a generic
702 tool to study pest and disease infestation patterns in response to plant characteristics as well as
703 spatiotemporal deployment of commercial and trap crops, which will eventually lead to a better
704 understanding of agroecosystem functioning.

705 Results also highlighted cross-cutting issues regarding plants used as green manure, cover crops or
706 companion plants (GMCCP) in conservation agriculture and market gardening case studies (at the
707 field scale), and stressed the importance of within-species genetic variation of these GMCCP species.
708 It is important to realize that tradeoffs exist when pest management tools such as PSD management is
709 used to manage a complex of pests and diseases. A single pest or disease control tool may affect the
710 pest/pathogen complex through several pathways and may also influence other ecosystem services or
711 disservices at various scales.

712 A major conclusion of this set of studies is that PSD strategies can be effective, but they are largely
713 context dependent. Successful application of PSD as a pest and disease management tool thus requires
714 clear understanding of generalizable agroecological principles (Wezel et al., 2009), and a capacity to
715 adapt and apply those principles in specific contexts. The constantly changing nature of crop, pest and
716 disease interaction also calls for capacity to adapt practices to change, and possibly to deploy multiple
717 control measures and processes simultaneously.

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738 **Author contribution**

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