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Synergies and tradeoffs in natural regulation of crop pests and diseases under plant species diversification

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Abstract

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

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

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

1. Introduction

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

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

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

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

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

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

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 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]

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

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

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

2. Major outcomes of the Omega3 project case studies

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

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 (*Ralstonia solanacearum*)	Deberdt et al. (2015); Deberdt et al. (2018); Diédhiou et al. (2012)
2	Upland rice	Madagascar	Scarab beetles (*Heteronychus* spp.)	Rabary et al. (2011); Rafarasoa et al. (2016)
2	Upland rice	Madagascar	Witchweed (*Striga asiatica*)	Michellon et al. (2011)
3	Tomato	Martinique	Fruitworm (Corn earworm *Helicoverpa zea*)	Rhino et al. (2014); Grechi et al. (2012)
3	Okra	Niger	Fruitworm (Tomato fruitworm *Helicoverpa armigera*)	Ratnadass et al. (2014); Yabo (2010)
3	Okra	Niger	Whitefly (*Bemisia tabaci*)	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 (*Sahlbergella singularis*)	Babin et al. (2012); Mahob et al. (2015)
5	Cocoa	Cameroon	Black pod rot (*Phytophthora megakarya*)	Ten Hoopen et al. (2012)
6	Coffee	Costa Rica	Leaf rust (*Hemileia vastatrix*)	Avelino et al. (2012); Lopez-Bravo et al. (2012)
6	Coffee	Costa Rica	Berry borer (*Hypothenemus hampei*)	Avelino et al. (2012)

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

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

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

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

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

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

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

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

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

Diverse cover crops were evaluated for suppression effects on white grubs within upland rice cropping systems. These cultivation systems were: no-till rice with a cover crop, no-till rice without a cover crop, and conventional tillage rice. The plants used as cover crops in two-year rice and cover crop(s) rotations with rice were: hairy vetch (*Vicia villosa*) and rattlebox (*Crotalaria grahamiana*) (Fabaceae); fodder radish (*R. sativus*) (Brassicaceae); *Brachiaria ruziziensis* x *Brachiaria brizantha* (var. Mulato) (Poaceae); and a mixture of *Cleome hirta* (Capparaceae), *Tagetes minuta* and *Cosmos caudatus* (Asteraceae). Fodder radish emerged as a promising tool for white grub pest management. In addition, it did not reduce the diversity and abundance of soil macrofauna (Rabary et al., 2011).

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

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

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

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

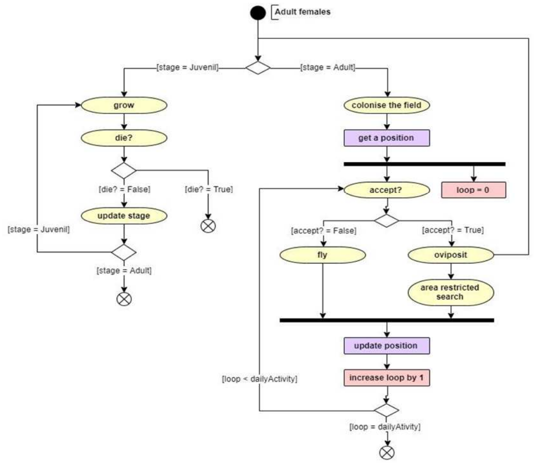
The corn earworm, *H. zea*, is a major insect pest of sweet corn, cotton (*Gossypium hirsutum*) (Malvaceae), and vegetable crops, particularly tomato in North and South America, including the West Indies. In West Africa, the tomato fruitworm, *H. armigera*, is considered to be the most destructive pest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

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

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

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



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)

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).

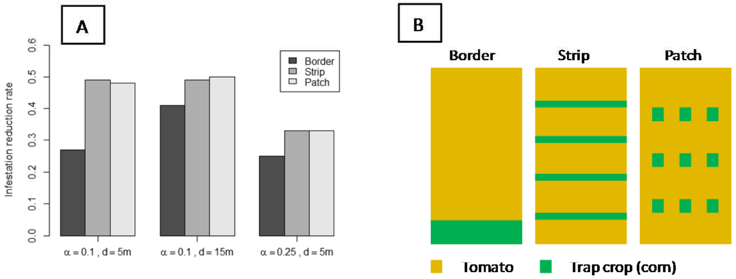


Fig. II. A) Simulated reduction rate in tomato plant infestation by tomato fruit worm according to trap-crop planting design (border, strip and patch), relative attractiveness of the commercial vs. trap-crop (α) and insect perception distance (d). Plant infestation is expressed as the number of eggs 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.

Box 1. An individual-based modeling approach to assess the efficacy of trap cropping in pest management: *Helicoverpa zea* management in tomato field (after Grechi et al., 2012)

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

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

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

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

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

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

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

The brown cocoa mirid bug, *S. singularis*, is the most harmful insect pest of cocoa in Cameroon (Mahob et al., 2020), while black pod rot, caused by *P. megakarya*, is the major disease affecting this crop (Ndoungue et al., 2018). Unshaded monocrop cocoa orchards are a common practice in the cocoa belt of West Africa, which accounts for more than 70% of the world cocoa production. However, full-sun orchards are often highly damaged by mirid bugs that feed on developing vegetative parts such as green shoots, buds and young leaves (Mahob et al., 2020). Mirid bug damage lesions lead to the desiccation of branch tips, cankers on branches, and premature ageing of trees which then quickly become unproductive. Consequently, unshaded cocoa orchards, especially the young developing trees, require intensive use of insecticides for mirid control (Mahob et al., 2014). A study was conducted to assess the impact of cocoa-fruit tree intercropping on mirid bug infestation. The study focused on the potential effect of using fruit trees as physical barriers to limit mirid bug infestation on cocoa during the first years of plantation, when fruit trees are not yet developed enough to provide cocoa with shade. Previous studies have shown that mirid bugs may use visual cues while flying in search of their host (Leston, 1973) and we hypothesized that intercropping with fruit trees (which are known not to be cocoa mirid bug plant hosts) may disturb mirid bug flight behavior.

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

A similar survey of black pod rot occurrence was conducted in the same young unshaded cocoa orchards. Previous studies conducted in well-established orchards suggested that spatiotemporal dynamics of the disease was first determined by the presence of primary inoculum in the soil (Deberdt et al., 2008). Secondary inoculum would then appear and drive temporal infection at tree level, through different dispersion mechanisms, including rain splash and ant tents (Ten Hoopen et al., 2010). During the latter study however, infection by black pod rot was too low to reveal any impact of intercropping of fruit trees on disease dynamics. Results suggested an exogenous origin of the infection and dispersion through human activities, with microclimate and cocoa genetic origin as the main factors explaining the persistence of the initial infection in some parts of the orchards (Ten Hoopen et al., 2012).

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

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

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

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

However, fragmenting coffee farmscapes with pasture yielded higher incidences of coffee leaf rust (peak correlation at a distance of 200 m). We hypothesize that wind turbulence, produced by low-wind-resistance land uses such as pasture, favored removal of coffee leaf rust spore clusters from host surfaces, resulting in increased epidemics (Avelino et al., 2012).

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

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

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

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

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

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

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

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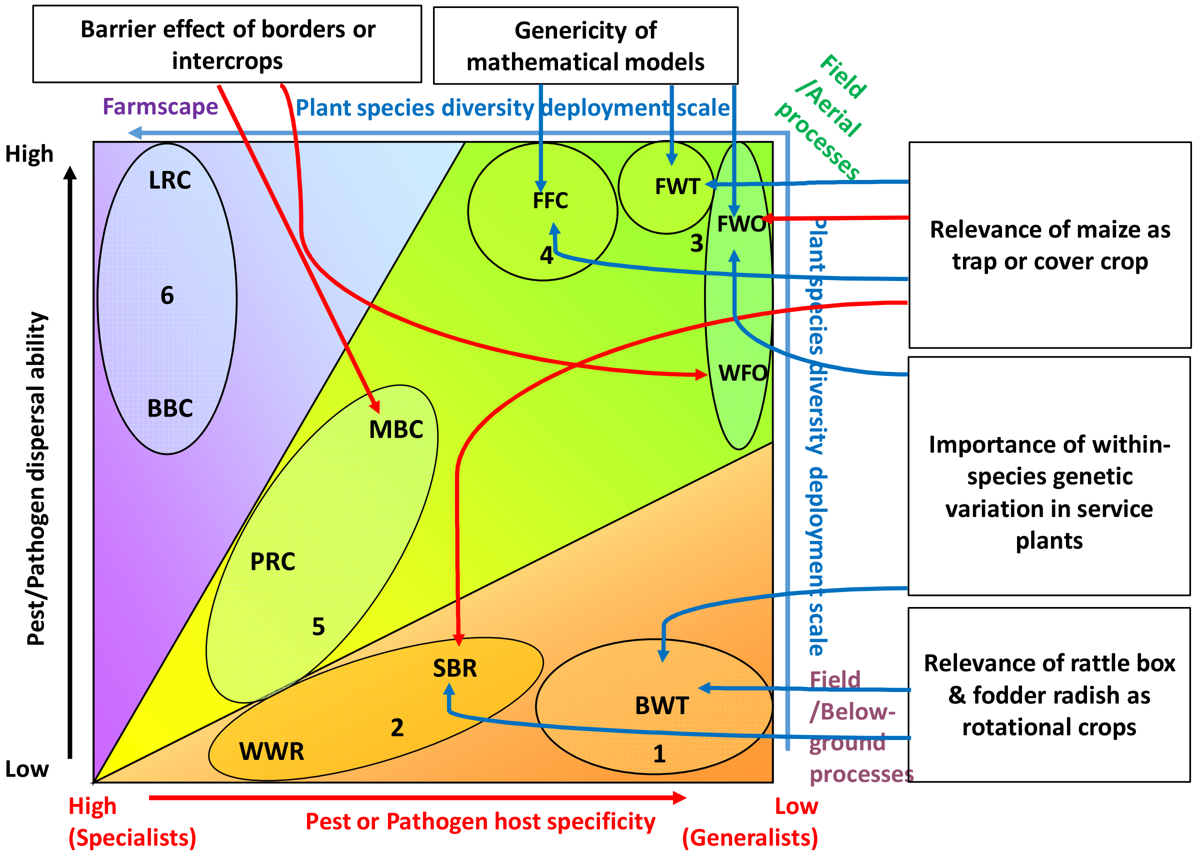

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Figure 1. Positioning of the reported case studies (cf. Table 1 for numbering and abbreviations), as a function of scale levels at which plant species diversity modalities and effects are deployed (field level via below-ground processes: bottom right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

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

Unsurprisingly, due to high variability across systems studied, we found no evidence of generic relationships between PSD and pest and disease suppression impacts, since there were instances where anticipated pest and disease reduction effects of PSD practices were not evident. For instance, although we expected a barrier effect (physical obstruction) against whiteflies provided by trap crops in the Niger subcase study (See § 2.3), Ratnadass et al. (2014) reported that late-maturing pigeon-pea and sorghum in particular did not have any effect on whitefly density. Similarly, trap crops did not affect leafhopper infestation, which turned out to be a benefit overall (See § 3.5), or at least not a disservice, since these less injurious early-season pests triggered a regulatory effect on a later occurring/highly damaging fruit pest (tomato fruitworm), via top-down pathways involving spiders. Conversely, in the case of the assisted trap cropping for cucurbit fruit fly management in Réunion, predatory flies were attracted by GF-120® bait (Duhautois, 2010), highlighting a potential indirect negative effect on natural biological control of other pest guilds, *e.g.* aphids and whiteflies.

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

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

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

3.2. Genericity/overarching nature of results obtained on GMCCPs

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

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

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

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

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	Fruit flies
Rattlebox: *Crotalaria* spp.	(+)	Grubben and Denton 2004[2] Gacheru and Rao 2005[2]	Rafarasoa 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: *Raphanus sativus*	(+)	na	Rafarasoa et al. 2015[3] Rabary et al. 2011[3]	Deberdt et al. 2015[3]	na	na	na
	(-)	na	na	na	na	na	na
Corn: *Zea mays*	(+)	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

* GMCCPs: green manure, cover crops and companion plants

1. (+): Positive effect; (-): Negative effect
2. Positive effect potentially applicable to project case studies based on literature
3. Positive effect documented in the Omega3 project
4. No reference available
5. Negative effect potentially applicable to Omega3 project case studies based on literature
6. Negative effect documented in the Omega3 project

3.3. Genericity/overarching nature of mathematical methods used

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

As mentioned above, some GMCCPs can be valued for their market value *per se*, e.g. *Allium fistulosum* ("Onion péyi") in Martinique, which was reported to be a sanitizing plant used for controlling bacterial wilt on tomato caused by *R. solanacearum* (Deberdt et al., 2012). Similar markets can be further developed for aromatic/medicinal companion plants in Martinique, as was suggested for the "push" or "pull" components of horticultural "push-pull" systems (Cook et al., 2007). This was accomplished in Cuba with *Plectranthus* and *Ocimum* species, since the time of the US trade embargo which started at the beginning of the Revolution, and especially during the ‘Special Period’ (1990-1991) after the collapse of imports of petroleum, agrochemicals and farm machinery from the Soviet bloc (Acosta de la Luz, 2001; Altieri and Toledo, 2011).

In addition to adaptation to climate change, mitigation thereof may also be an incentive to deploy PSD-based pest and disease management strategies within agroecosystems. This might be of particular importance in relation to the carbon sequestration market (particularly for conservation agriculture, agroforestry and push-pull systems: Corbeels et al., 2019). Actually, beyond the carbon sequestration aspect of PSD-based cropping systems, any crop protection measure *per se* contributes to climate change mitigation, as reduction of pest and disease-associated losses reduces the need for excessive input applications and unnecessary CO_2 emissions linked with their production (Lamichhane et al., 2015).

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

Finally, other important aspects to keep in mind with regard to using PSD as a pest and disease management tool are the potential invasiveness of some GMCCPs, and their potential to host other pests and diseases that may become economically important. In this respect, some specific rules for their selection, as those proposed in the tomato bacterial wilt case study in Martinique (Deberdt et al., 2018) should be followed, which could be used in other locations, particularly in islands where there is a risk with invasive plants. The importance of several pests and diseases, as well as disease vectors that occur on plants that could be used as service plants in PSD systems have been reported by Van den Berg et al. (2001), and should not be overlooked (Ratnadass et al., 2018; 2020).

4. Conclusions

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

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

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

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

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The authors declare that there is no conflict of interest

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