

RESEARCH ARTICLE

Local species-specific effect of trees and shrubs on the incidence of the millet head miner, *Heliocheilus albipunctella* (Lepidoptera, Noctuidae)

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Abstract

1. Understanding the interactions between crop pests, natural enemies and semi-natural habitats in agricultural landscapes is crucial for developing ecology-based pest management in agroecosystems.
2. In the present study, we investigated the local-scale species-specific effect of tree and shrub cover and diversity on the incidence and natural pest regulation of the millet head miner (MHM), *Heliocheilus albipunctella* (Lepidoptera: Noctuidae) de Joannis and subsequent grain losses in a tree-crop agroforestry system in Senegal.
3. To this purpose, we monitored a network of 60 millet fields with variable tree and shrub species composition within a 50-m radius buffer around the centre of millet fields.
4. The proportion of egg-infested panicles increased with the area covered by baobabs (*Adansonia digitata*) but decreased with that of soapberry trees (*Balanites aegyptiaca*). Baobabs and apple-ring acacias (*Faidherbia albida*) locally increased pest incidence and associated grain loss, likely by providing favourable microhabitats for MHM and limiting the impact of larval parasitoids, respectively. In contrast, bush-willow shrubs (*Combretum micranthum*) increased egg parasitism, but not enough to disrupt the relationships between crop colonization, pest incidence and yield loss. Furthermore, Shannon's diversity index had no measurable influence on pest dynamics, suggesting that species identity and functional traits are more important than diversity per se.
5. These findings underline the importance of careful selection of tree and shrub species in agroforestry design strategies for optimizing the delivery of multiple ecosystem services. Integrating tree functional traits, seasonal canopy dynamics and spatial scale considerations is key to enhancing ecosystem services such as biological control in tree-crop agroforestry systems.

KEYWORDS

Africa, conservation biological control, crop pest, natural enemies, tree-crop agroforestry, yield loss

Ahmadou Sow and Julien Winkelmann should be considered joint first authors.

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INTRODUCTION

Crop pests are major impediments to agricultural production, particularly in tropical areas where they pose a permanent threat to food security (Riegler, 2018). Predictions indicate that their impact could be exacerbated by climate change, through the expansion of their geographic range, an increase in the number of generations, or changes in their interaction with host plants and natural enemies (Skendžić et al., 2021), resulting in total crop losses in worst-case scenarios (Deutsch et al., 2018; Nguru & Mwongera, 2023). In the same line, agricultural intensification and land use changes that contribute to habitat fragmentation could reduce the diversity and abundance of natural enemies, thereby affecting natural pest regulation and crop yield losses (Zhao et al., 2016). The reliance on the use of pesticides is not the response, due to detrimental negative impacts on taxonomical and functional biodiversity and related ecosystem services, such as natural pest regulation, which directly benefit agricultural production and food security challenges (Grab et al., 2018; Rusch et al., 2016). Finding agroecological solutions inspired by natural processes is essential for promoting sustainable pest management and reconciling modern agriculture with biodiversity conservation (Brévault & Clouvel, 2019). One of the multiple levers is conservation biological control, which promotes the restoration or protection of habitats favourable to natural enemies of pests in the agricultural landscape, through less disruptive farming systems (e.g., fewer pesticides) or the provision of complementary resources (Gurr et al., 2017; Zaviezo & Muñoz, 2023). This is particularly true for predators and parasitoids, whose effectiveness depends largely on the composition (e.g., abundance and diversity of semi-natural vegetation) and configuration (e.g., connectivity between habitats) of the agricultural landscape (Rusch et al., 2013; Soti et al., 2019; Sow et al., 2022; Zhang et al., 2021). However, semi-natural habitats can also benefit pests (Laterza et al., 2023; Sow et al., 2022; Tamburini et al., 2020). Therefore, it is often difficult to generalize about the effect of semi-natural habitats on pest management, partly due to the inconsistent response of natural enemies and pests to the heterogeneity of the agricultural landscape (Delaune et al., 2021; Karp et al., 2018; Tschamtké et al., 2016). Understanding how pests and their natural enemies interact with their habitats and resources, from the field to the landscape scale, is thus fundamental to design field-scale to area-wide pest management strategies.

In West Africa, the millet head miner (MHM), *Heliocheilus albipunctella* (de Joannis) (Lepidoptera, Noctuidae), is a major constraint to increasing pearl millet crop (*Pennisetum glaucum*, Poaceae) yields (Gahukar & Ba, 2019; Sow et al., 2018). Moths emerge from the soil one to two months after the beginning of the rainy season. After mating, females lay eggs in the millet panicle on the silk of the flower involucre or under stamens, but also on the floral peduncles or on the spine (Nwanze & Harris, 1992). Newborn and young larvae (1–7 days old larvae) perforate glumes and consume flowers, while the older ones (8–18 days old larvae) cut off the floral peduncles (Gahukar, 1984; Vercambre, 1978), thus preventing grain formation. Outbreaks of the MHM are observed almost every year, and yield

losses of up to 85% can occur (Gahukar & Ba, 2019). In Senegal, in the absence of any insecticide application by farmers, millet production relies on pest regulation by natural enemies (Bhatnagar, 1987; Payne et al., 2011; Sow et al., 2019, 2020). In addition, Sow et al. (2020) reported that grain losses dramatically increased when panicles were not accessible to natural enemies, including arthropods, but also birds and bats, confirming their net contribution to pest regulation. In the same line, Soti et al. (2019) showed that natural pest regulation of the MHM increased with the abundance of trees and the diversity of vegetation in the landscape around millet fields. In another study in the same area, Sow et al. (2022) showed that pest regulation provided by natural enemies could also be amplified by the abundance of trees at a local scale. However, additional studies are still needed to capture the species-specific and local effect of trees and shrub species on the performance of conservation biological control of the MHM.

In the present study, we investigated the local-scale species-specific effect of tree and shrub cover on crop colonization by the MHM (egg or first-instar larvae on panicles), pest incidence (second to fourth-instar larvae on panicles), natural pest regulation by arthropod natural enemies (egg and larval parasitism and predation) and in return grain losses, in a tree-crop agroforestry system in Senegal. To this purpose, we monitored these indicators across a network of millet fields, with variable tree and shrub species composition within a 50-m radius buffer around the centre of millet fields. We hypothesized that the increasing area covered by species-specific trees or shrubs and the Shannon's diversity of trees and shrubs would positively affect natural pest regulation and decrease pest incidence and subsequent grain loss. Results are discussed in the light of the manipulation of non-crop habitats, particularly regarding the role of tree and shrub species, which could contribute to improving the performance of biological control of the MHM populations and reduce crop damage, by providing a range of resources to natural enemies.

METHODS

Study area and design

The study was carried out in the Bambey area (14°42'30.1" N, 16°28'58.8"W) located in the Peanut basin in Senegal (Figure 1a). This area is under the influence of a Sahelian climate with rainfall going up from 400 to 600 mm from July to September. Millet, peanut and to a lesser extent cowpea and roselle are the main rainfed crops. The landscape is a mosaic of crops in tree-crop agroforestry systems that are mainly composed of apple-ring acacias (*Faidherbia albida*), acacias (e.g., *Acacia seyal* and *A. mellifera*), soapberry trees (*Balanites aegyptiaca*) and baobabs (*Adansonia digitata*).

Five clusters of six millet fields (Figure 1a) were selected in 2019 and 2020 according to a gradient of tree and shrub cover, in terms of abundance and diversity, within a 50-m radius buffer around millet fields (Figure 1b). Millet plots were not necessarily the same from one year to the next because of rotation with legumes, but in such case,

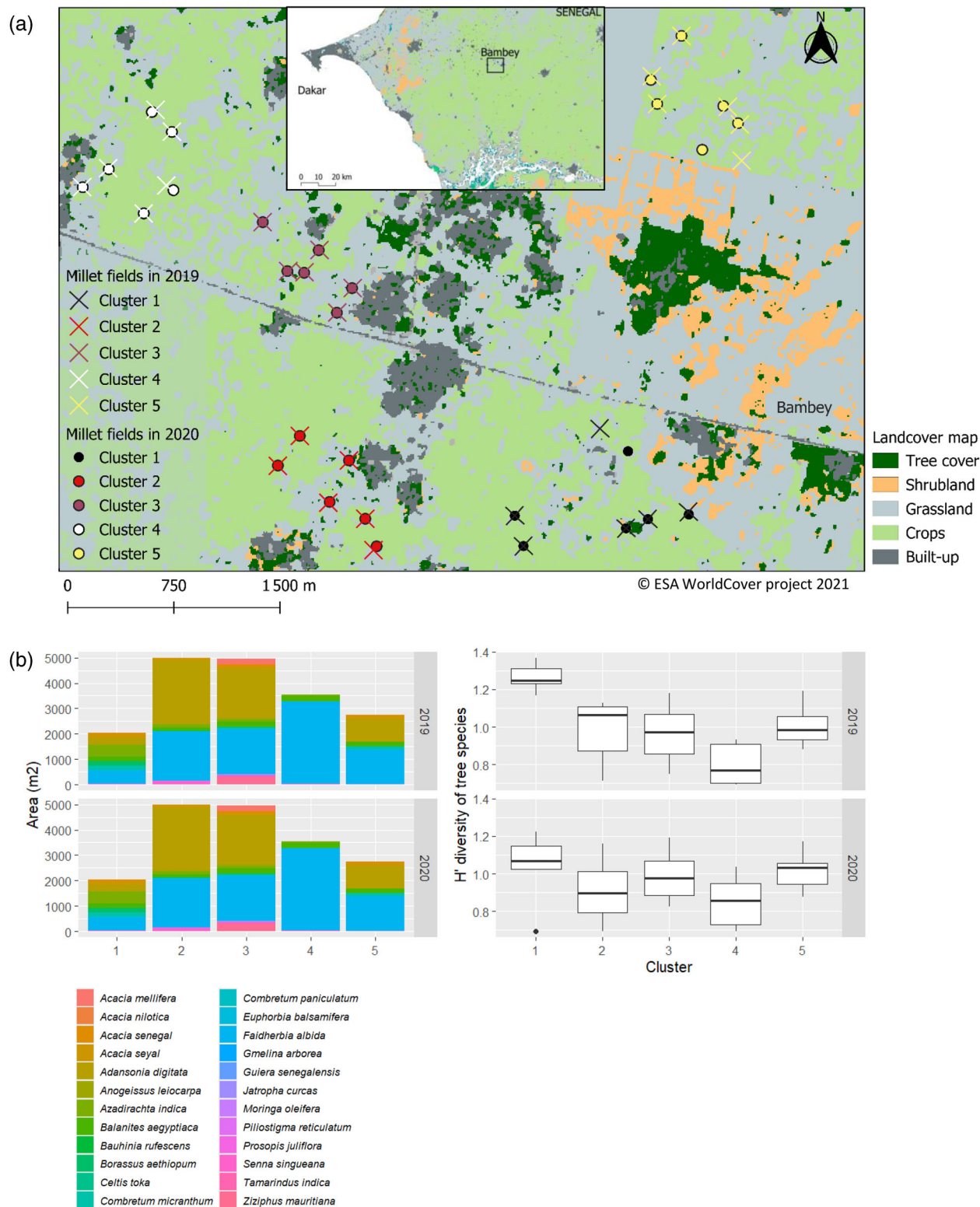


FIGURE 1 (a) Map of the 60 millet fields in the study area (Bambeý, Senegal). (b) Mean area of land cover categories (trees, shrubs, grasses, crops and built-up) and H' tree species diversity at a 50 m radius around millet fields.

we selected the nearest millet plot. This buffer size was chosen in order to assess the local effect of the semi-natural vegetation on pest incidence and natural pest regulation in millet fields, with an exhaustive census of tree and shrub species, which is not possible over large

areas. The average size of the focal millet fields was 0.4 ha (0.1–1.3). Clusters were distant in average 2.2 km (0.9–3.5) from each other, whereas fields within each cluster were distant in average 498 m (100–1030). In every millet field, one central 10 × 10 m yield plot was

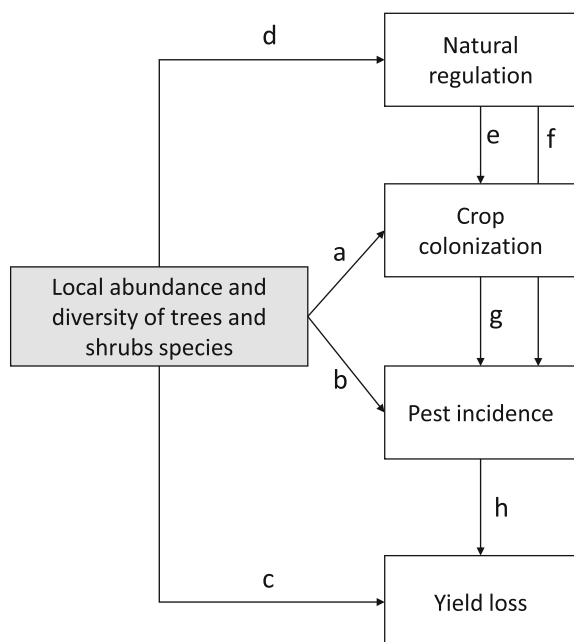


FIGURE 2 Conceptual model constructed following ecologically based hypotheses: The local abundance and diversity of tree and shrub species decrease crop colonization (a), pest incidence (b) and grain loss (c), but increase pest regulation by natural enemies (b), thus contributing to the reduction of pest incidence in millet crops (e, f) and the direct effect of crop colonization on pest incidence (g), thus reducing the grain yield loss (h).

set up for the assessment of damage on panicles due to the MHM and grain losses (Figure 2).

Local tree and shrub cover and diversity

Tree and shrub patches within the 50-m radius buffer around sampling plots were individually identified at the species level and georeferenced using the iGIS mobile application v.8.4.6 (QGIS Development Team, 2019). A land cover map, where polygonal vectors represented tree and shrub patches, was then produced. Two local metrics were calculated using QGIS (v.3.10.0): the area covered by tree and shrub species patches and the Shannon's diversity index (H') of tree and shrub species, using the following formula: $H' = -\sum P_i(\ln P_i)$, where P_i is the proportion of cover of tree or shrub species i at the 50-m radius around sampling plots. Clusters showed a substantial variability in the abundance and Shannon's diversity (H') of tree and shrub species land cover (Figure 1b). Twenty-four tree and shrub species were identified in the 50-m radius buffer around the centre of sampling fields (Appendix S1: Figure S1).

MHM crop colonization, incidence and damage

The abundance of the MHM was monitored on 40 panicles randomly selected within the focal fields along four rows at the proximity of

yield plots. Egg and first-instar larvae counting, as an indicator of 'crop colonization' by the MHM, was performed based on a round trip inspection of panicles between floral initiation and female flowering stages. Second to fourth-instar larva counting, as an indicator of 'pest incidence' was performed 18 days later by the inspection of the entire panicle on the same rows at the grain filling stage. At panicle maturity, 8 days later, when MHM larvae had completed their development, damage caused by the MHM (number, length and width of mines) was recorded on 40 panicles from different plants randomly selected in the central yield plots. We calculated the damaged area (cm^2) by multiplying the length and width of mines. Then, based on allometric relationships established on healthy millet panicles of different sizes and varieties (Appendix S1: Figure S2), we inferred the percentage of grain weight loss (Thiaw et al., 2017).

Biocontrol services index

The biological control of the MHM immature stages was evaluated by experimentally excluding natural enemies from naturally infested millet panicles, according to Soti et al. (2019). Six replicates were set up in each field. In each replicate, three panicles (<2 m away from each other) at the female flowering stage were selected, as early stages of panicle development (up to female flowering) are preferred for MHM egg laying. One panicle was protected using a mesh bag (15×70 cm) to exclude natural enemies and paired with one open panicle as a control and another open non-infested panicle (checked for egg presence and cleaned when necessary) to estimate potential further egg laying. The percentage of grain loss was estimated at 18 days after panicle flowering, as described above. A biocontrol services index (BSI) adapted from Gardiner et al. (2009) and Soti et al. (2019) was then calculated for each millet field, by using the following formula:

$$BSI = \frac{\sum_{p=1}^n \frac{GLP_p - (GLO_p - (\frac{GL_p}{3}))}{GLP_p}}{n} \times 100,$$

where GLP is the percentage of grain loss on protected panicles, GLO is the percentage of grain loss on open panicles, GL is the percentage of grain loss on non-initially infested open panicles (to take into account oviposition occurring after setting up of mesh bags), p the replicate number and n is the number of replicates for a given millet field. The resulting BSI varies from 0 to 100, with values increasing as the level of biological control increases.

Parasitism

MHM eggs and larvae were collected from 40 different panicles randomly selected along four rows of millet at the proximity of yield plots (different from the two rows dedicated to assessment of pest incidence) at panicle emergence and grain filling, respectively; then reared in the laboratory for monitoring of parasitism (Sow et al., 2018). A

total of 1478 eggs (10–32 per millet field) were collected, sorted in small pillboxes and incubated at room temperature ($30 \pm 3^\circ\text{C}$) up to larval hatching or emergence of parasitoids, away from sunlight, to reproduce natural conditions. A total of 2160 larvae (36 per millet field) were randomly collected from panicles and individually incubated at room temperature ($25 \pm 2^\circ\text{C}$) in 12-well culture plates (Fisher Scientific, France) filled with artificial diet (Southland Products, USA) up to pupation or emergence of parasitoids (Sow et al., 2019). We calculated parasitism rates as the ratio of the number of parasitized eggs or larvae to the number of hatched eggs or live larvae (Sow et al., 2019). All parasitoids' species were identified by specialists or using taxonomic keys (e.g., Delvare & Aberlenc, 1989; Huddleston & Walker, 1988; Zack, 1999). Identifications were checked by comparing them with specimens already identified (Sow et al., 2018, 2019, 2022) and held in the reference collections at CBGP (Centre de Biologie pour la Gestion des Populations, Montpellier, France).

Statistical analyses

Statistical analyses were performed in two steps: (1) preselection of best local tree and shrub cover and diversity variables and (2) assessment of the effect of selected variables on crop colonization, pest incidence, natural regulation and grain loss. The effect of 'year' on variables representing crop colonization, pest incidence, grain loss and natural pest regulation was assessed using Student's *t*-test. All statistical analyses were conducted using the R software v.4.4.0 (R core Team, 2024). Dataset and R code were available at the Dryad data repository (<https://doi.org/10.5061/dryad.sj6mf40>) (Sow et al., 2025).

Partial least squares regression (PLS-R) was used to examine the relative importance of local variables (area covered by tree and shrub species patches and Shannon's diversity of trees and shrubs species) on crop colonization (mean number of eggs and first-instar larvae per panicle), pest incidence (mean number of second to fourth-instar larvae per panicle), components of natural regulation (BSI, egg parasitism rate, larval parasitism rate) and grain loss. PLS-R calculates latent variables defined as a linear combination of explanatory variables that maximize the variance explained in the response variables (Wold et al., 2001). Explanatory and response variables were centred and reduced to give all variables equal weight and to simplify the expected variance partitions for each predictor (Quinn & Keough, 2022). The validity of the PLS-R model was assessed using the following indices: (R²Y) the proportion of variance in the dependent variable explained by the model and (Q²) the proportion of variance in the response predicted by the model obtained by a cross-validation procedure. The strength of the relationship between each predictor and the dependent variable was illustrated by the importance of the variable in the projection (VIP) described by Chong and Jun (2005). The VIP was calculated as the sum of the influence of the predictor variables on all dimensions of the model divided by the total variation explained by the model. Variables with a VIP > 0.8 were considered the most relevant and significant for predicting the dependent

variable (Tenenhaus, 1998) (see Appendix S2: Figure S1). We performed PLS-R models using the 'pls' package (Mevik & Wehrens, 2007).

We then fitted a piecewise structural equation model (P-SEM) to infer the relationship between local variables, crop colonization, natural pest regulation, pest incidence at grain filling stage and resulting damage or grain loss, using the 'piecewiseSEM' R package (Lefcheck, 2016). Compared with the traditional variance covariance-based SEM, the P-SEM is a more powerful and flexible approach because it incorporates non-normal distributions, hierarchical nesting and random effects (Lefcheck, 2016). We constructed six sub-models following ecologically based assumptions. Each model was fitted by appropriate generalized linear mixed model (GLMM), distribution type and link function: binomial for proportions (logit) and Poisson for count data (log), using the 'MuMIn', 'nlme' and 'Mass' R packages. We tested the multicollinearity between landscape variables using the variance inflation factor (VIF) (Smith et al., 2009) (see Appendix S2: Table S1). Only predictors with non-significant inter-correlations (VIF < 2) were included in the final model (see Appendix S2: Table S1). We included a nested-random effect 'cluster/plot' and random effect 'year' in each model. Crop colonization, pest incidence and grain loss variables were log-transformed. We evaluated the overall fit of the piecewise SEM using Shipley's test of *d*-separation, Fisher's *C* statistic and AIC (Shipley, 2009). We calculated the direct, indirect and total effects of the SEM model using the 'SemEff' package with 1000 bootstraps (Mark, 2024) (see Appendix S2: Table S1). The absence of spatial autocorrelation between clusters was checked for each response variable by using the Moran's *I* Index (Moran, 1950), using 'ape' R package (Paradis & Schliep, 2019) (see Appendix S2: Table S2).

RESULTS

Crop colonization

The mean number of eggs per panicle was lower in 2019 (0.6) than in 2020 (1.4) ($t = -5.4$, $df = 40.1$, $p < 0.001$) (Figure 3a). The area covered by baobabs (*A. digitata*) within a 50-m radius buffer around the sampling plot positively affected crop colonization when considering the proportion of infested panicles as the response variable (Table 1; Figure 4). Conversely, the proportion of infested panicles decreased with the importance of the area covered by soapberry trees (*B. aegyptica*) (Table 1; Figure 4), though no significant negative correlation between the abundance of baobabs and soapberry trees was observed. The abundance of other tree and shrub species and egg parasitism rate did not affect crop colonization (Table 1; Figure 4).

Pest incidence and grain loss

The mean number of larvae per panicle was also lower in 2019 (1.2) than in 2020 (2.7) ($t = -7.5$, $df = 39.6$, $p < 0.001$) (Figure 3b). Consequently, grain loss due to the MHM was significantly lower in 2019

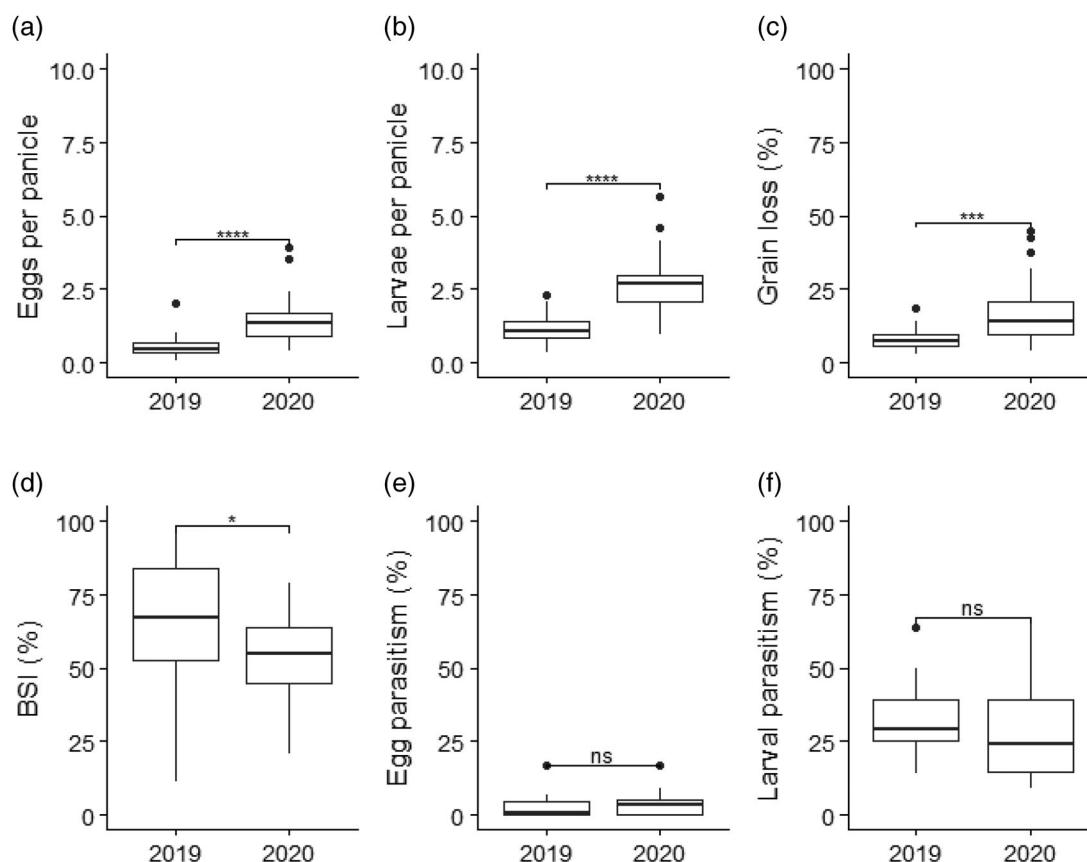


FIGURE 3 Boxplots of (a) mean number of eggs per panicle, (b) mean number of larvae per panicle, (c) grain loss (%), (d) biocontrol services index (%), (e) egg parasitism (%) and (f) larval parasitism (%) in the 2019 and 2020 field surveys. The statistical difference between years was assessed using a Student *t*-test. *****p* < 0.0001; ****p* < 0.001; ***p* < 0.01; **p* < 0.05. 'ns' no significant.

(7.8%) than in 2020 (16.8%) ($t = -4.4$, $df = 33.6$, $p < 0.0001$), but it was highly variable among sampling plots (2.9%–44.6%) (Figure 3c). Pest incidence and resulting grain loss were positively affected by the area covered by baobabs and apple-ring acacias (*F. albida*) in and around millet fields (Table 1; Figure 4). No effect of Shannon's diversity of trees and shrubs on pest incidence or grain loss was observed. A significant top-down effect of crop colonization on yield loss via pest incidence was observed (Table 1; Figure 4).

Natural pest regulation

Natural regulation of the MHM evaluated through the exclusion of natural enemies from naturally infested panicles (BSI) was higher in 2019 (64.1%) than in 2020 (53.0%) ($t = 2.2$, $df = 51.9$, $p < 0.05$), but highly variable across sampling plots (11.1%–79.1%) (Figure 3d). Egg parasitism was relatively low in 2019 (3.4%) and 2020 (3.5%) ($t = -1.1$, $df = 57.8$, $p = 0.250$) and weakly variable across sampled fields (0%–16.7%) (Figure 3e). All parasitoids that emerged from eggs were identified as *Trichogrammatoidea armigera* Manjunath (Hymenoptera, Trichogrammatidae). Larval parasitism was relatively high in 2019 (32.6%) and 2020 (28.1%) ($t = 1.3$, $df = 50.8$, $p = 0.19$) but highly variable among sampling plots (8.8%–66.7%) (Figure 3f). A

high prevalence of other parasitoids such as *Copidosoma primulum* Mecet (Hymenoptera, Encyrtidae) and *Schoelanelle sahelensis* Huddleston & Walker (Hymenoptera, Braconidae) was observed with 39.0% and 56.0% of the parasitized larvae, respectively (Appendix S1; Table S1).

No effect of the area of tree or shrub species or Shannon's diversity of tree and shrub species on the BSI was observed. However, egg parasitism increased with the area covered by bushwillow shrubs (*Combretum micranthum*) within a 50-m radius around the centre of millet fields (Table 1; Figure 4), whereas a negative effect of the area covered by apple-ring acacias (*A. albida*) on larval parasitism was observed. No effect of natural pest regulation on crop colonization, pest incidence or grain loss was observed (Table 1; Figure 4).

DISCUSSION

In the present study, we studied the local species-specific effect of tree and shrub cover on crop colonization by the MHM, pest incidence, natural pest regulation by arthropod natural enemies and in return millet grain losses in a tree-crop agroforestry system in Senegal. We hypothesized that the increasing area covered by species-specific trees or shrubs and the Shannon's diversity of trees

TABLE 1 Bootstrapped, standardized path coefficients of direct, indirect and total causal relationships of the piecewise structural equation model (P-SEM).

Response variables	Predictors	Direct	Indirect	Total	<i>p</i>
Crop colonization	<i>A. digitata</i>	0.23	0.00	0.23	0.036
	<i>B. aegyptiaca</i>	−0.20	0.00	−0.20	0.044
	<i>F. albida</i>	0.12	0.00	0.12	0.295
	Egg parasitism	0.10	0.00	0.10	0.348
Pest incidence	<i>A. digitata</i>	0.15	0.05	0.20	0.030
	<i>F. albida</i>	0.12	0.04	0.16	0.040
	Crop colonization	0.23	0.00	0.23	0.030
	BSI	−0.11	0.00	−0.11	0.243
	Larval parasitism	−0.02	0.00	−0.02	0.846
BSI (%)	<i>A. digitata</i>	0.00	0.00	0.00	0.985
	<i>B. aegyptiaca</i>	0.12	0.00	0.12	0.393
	<i>F. albida</i>	−0.06	0.00	−0.06	0.663
	<i>A. senegal</i>	0.15	0.00	0.15	0.319
	<i>A. seyal</i>	−0.14	0.00	−0.14	0.308
	<i>A. indica</i>	0.04	0.00	0.04	0.788
Egg parasitism (%)	<i>A. digitata</i>	−0.04	0.00	−0.04	0.176
	<i>F. albida</i>	−0.03	0.00	−0.03	0.338
	<i>A. seyal</i>	−0.03	0.00	−0.03	0.159
	<i>A. indica</i>	−0.05	0.00	−0.04	0.292
	<i>C. micranthum</i>	0.05	0.00	0.05	0.031
Larval parasitism (%)	<i>A. digitata</i>	0.02	0.00	0.02	0.314
	<i>F. albida</i>	−0.15	0.00	−0.15	0.896
Grain loss (%)	<i>A. digitata</i>	0.17	0.14	0.31	0.038
	<i>F. albida</i>	0.02	0.13	0.15	0.040
	Pest incidence	0.69	0.00	0.69	0.001
	BSI	−0.03	−0.11	−0.13	0.661

Note: Negative values represent negative relationships and positive values represent positive relationships. Significant relationships for total effect ($p < 0.05$) are in bold.

and shrubs would positively affect natural pest regulation and decrease pest incidence and subsequent grain loss.

Our analysis revealed a species-dependent effect of trees and shrubs on the MHM crop colonization, incidence and natural regulation. Crop colonization increased with the abundance of baobabs, but decreased with the abundance of soapberry trees, in a 50 m radius buffer around the centre of the millet fields. These results confirm those obtained by Sow et al. (2020) in the same area who showed that crop colonization increased with the abundance of baobabs, but decreased with the abundance of soapberry trees at a local scale (100 m radius buffer around the centre of the millet fields). It is possible that soapberry trees promote MHM moth predation by providing refuges for insectivorous vertebrates (e.g., birds and bats) and invertebrates (e.g., spiders) during the rainy season. However, the dense canopy of baobab trees likely provides shelter and a favourable microclimate that allows MHM moths to rest during the day and lay their eggs on nearby millet panicles at night. Pest incidence and resulting grain loss were also positively affected by the area covered by baobabs, indicating a cascading effect of crop

colonization on yield loss via pest incidence. This indicates that natural pest regulation was not sufficient to disrupt this cascading effect (linear to non-linear relationship). Natural regulation of the MHM over the two-year monitoring period was, however, generally high (BSI > 50.0% and larval parasitism of around 30%) and similar to that reported in previous studies in the same area (Soti et al., 2019; Sow et al., 2020), but they may not be suitable indicators of overall natural pest regulation. Also, no effect of tree and shrub abundance on the BSI was observed, suggesting that the local scale may not be relevant to capture the effect of semi-natural habitats. Soti et al. (2019) showed that natural pest regulation of the MHM, estimated through the BSI, increased with the abundance of trees and the diversity of vegetation in the landscape scale, that is, 1750m around millet fields.

Surprisingly, the area covered by apple-ring acacias in and around millet fields also increased pest incidence and resulting grain loss. As it was also observed that MHM larval parasitism decreased with the area covered by this tree species, it can be hypothesized that they are poor habitats for natural enemies, especially parasitoids (Sipos &

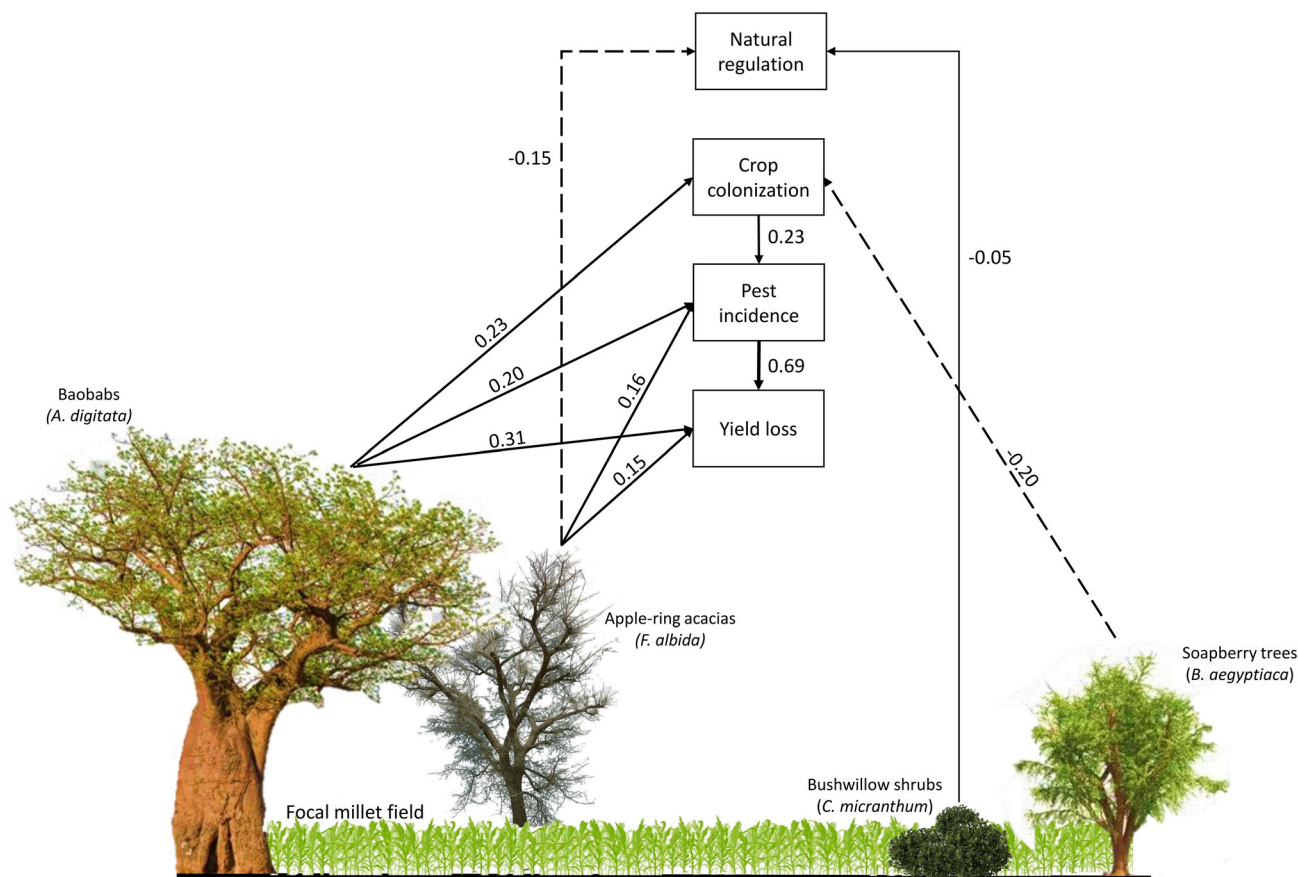


FIGURE 4 Piecewise structural equation model (P-SEM). Single-headed arrows represent causal relationships. Complete lines represent significant positive relationships, and dotted lines represent significant negative relationships ($p < 0.05$). The number along the arrows are bootstrapped standardized path coefficients. Crop colonization and pest incidence are built from 'mean egg per panicle' and 'mean larva per panicle' variables, respectively. The latent variable 'Natural regulation' include egg and larval parasitism and the BSI.

Kindlmann, 2013). Indeed, this tree species has the unique characteristic of shedding its foliage at the start of the rainy (i.e., cropping) season. However, apple-ring acacias play a vital role for crops growing under their canopy, particularly millet, as they compete to a small degree for light, water or nutrients during the cropping season and bring nitrogen to the soil under their canopy (Bayala et al., 2012; Haskett et al., 2019). Interestingly, we showed that the local abundance of bushwillow shrubs (here, *Combretum micranthum*) significantly increased egg parasitism. This result supports that of Sow et al. (2022) carried out in the south of the groundnut basin (Niore du Rip), who showed that, at a local scale (250 m around millet fields), MHM egg parasitism increased with the area covered by rangelands, mainly composed of shrubs. In the present study, no effect of Shannon's diversity of trees and shrubs on crop colonization, pest incidence or natural pest regulation at a local scale was observed.

CONCLUSION

This study highlights the species-specific effects of trees and shrubs on MHM dynamics and associated grain losses in millet-based

agroforestry systems in Senegal. The presence and abundance of certain woody species influenced crop colonization, pest incidence, natural pest regulation and yield loss in contrasting ways. Baobabs and apple-ring acacias increased pest incidence and associated grain loss, likely by providing favourable microhabitats for MHM or limiting the impact of larval parasitoids. In contrast, bushwillow shrubs may enhance egg parasitoid activity by offering refuges or other ecological resources. More research on insect-plant interactions is needed to improve our knowledge on the reasons why such trees or shrubs affected pest incidence or parasitism, wherein other species like acacias did not. Although overall natural pest regulation was high (BSI > 50%, larval parasitism ~30%), it was insufficient to prevent cascading effects from colonization to yield loss in fields dominated by certain tree species. Furthermore, Shannon's diversity index had no measurable influence on pest dynamics, suggesting that species identity and functional traits are more important than diversity per se.

On an applied perspective, it is clear that farmers have a critical role to conserve or restore non-crop habitats within agricultural landscapes, particularly beneficial trees (e.g., soapberry trees) and shrubs (e.g., bushwillow), to improve the management of the MHM and reduce yield losses through conservation biological control. For

example, based on our results, moving the millet fields further away from the baobab parks and combining more soapberry trees (*B. aegyptiaca*) and bushwillow shrubs (*C. micranthum*) within apple- acacia tree parks (*F. albida*) would benefit both soil fertilization and MHM suppression. These findings underline the importance of careful selection of tree and shrub species in agroforestry design strategies for optimizing the delivery of multiple ecosystem services. Integrating tree functional traits, seasonal canopy dynamics and spatial scale considerations is key to enhancing ecosystem services such as biological control in tree-crop agroforestry systems.

AUTHOR CONTRIBUTIONS

Ahmadou Sow: Data curation; formal analysis; methodology; visualization; writing – original draft; writing – review and editing. **Julien Winkelmann:** Conceptualization; data curation; formal analysis; methodology; validation; writing – review and editing. **Alexandre Aebi:** Conceptualization; project administration; supervision; validation; writing – review and editing. **Thierry Brévault:** Conceptualization; funding acquisition; methodology; supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in “DryAd” at <https://doi.org/10.5061/dryad.tjq2bw9z>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Figure S1. Number of tree and shrubs species inventoried in and around the 60 focal millet fields.

Figure S2. Allometric relationships between the grain surface damaged by millet head miner larva (gallery) and the corresponding grain weight loss (%), from 50 healthy pearl millet panicles of different sizes and varieties (Thiaw et al., 2017).

Table S1. Parasitoid species and parasitism rate (%) recovered from the 2160 larvae collected from the 60 focal millet fields (2019–2020).

Appendix S2: Figure S1. Variable importance value of landscape variables for each targeted variable using partial least squares regression. The variables with variable in the projection >0.8 (red line) were include in the structural equation model.

Table S1. Bootstrapped, standardized path coefficients of direct, indirect and total causal relationships of structural equation models (piecewise SEM). Negative values represent negative relationships and positive values represent positive relationships. The collinearity of landscape variable were tested using the variance inflation factor (VIF). Significant results ($p < 0.05$) are highlighted in bold. Rm.: R marginal. Rc.: R conditional. GoF: Global goodness-of-fit of Fisher's C test with $p = 0.747$ and on 62 degrees of freedom.

Table S2. Summary of the Moran's I test output for evaluating the spatial autocorrelation between clusters of millet fields for each response variable.

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