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2 **Birds and bats contribute to natural regulation of the millet head miner in tree-**
3 **crop agroforestry systems**

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17

18 **Abstract**

19 A better understanding of environmental factors driving natural pest regulation is a major challenge for
20 designing sustainable cropping systems. The objective of the present study was to assess the association
21 between vegetation openness in traditional tree-crop agroforestry systems in Senegal, richness and

22 abundance of vertebrates including insectivorous birds and bats, and their contribution to the natural
23 regulation of crop pests. The millet head miner (MHM), *Heliocheilus albipunctella* (Lepidoptera,
24 Noctuidae), a major constraint to increasing millet crop productivity in sub-Saharan Africa, was selected
25 as a model system. Ten sites separated by at least one km from each other were selected in a 100 km²
26 study area in the Peanut basin in Senegal. In each site, a pair of millet fields distant from at least 100 m
27 each was selected according to a gradient of vegetation openness within a 100-m radius buffer with
28 sampling plot (5 x 5 m) at the center. Nine insectivorous bird and bat species were recorded in millet
29 fields over the 2017 cropping season and their predator status was confirmed by direct observation or
30 DNA detection in fecal samples. Grain losses were reduced when panicles were accessible to birds and
31 bats, confirming their net contribution to pest regulation. At a local scale, tree diversity and vegetation
32 openness were important predictors of the abundance of insectivorous village weaver birds and grey-
33 headed sparrows, respectively. Some tree species (soapberry trees and neems) indirectly contributed to
34 natural regulation of the MHM likely by providing refuges to insectivorous vertebrates whereas other
35 tree species (baobabs) provided disservices as possible refuges for the MHM moths. Further research is
36 needed to better understand relationships between tree cover, food web interactions and natural pest
37 suppression, so that specific conservation measures such as habitat management can be designed to
38 improve pest control.

39

40 **1. Introduction**

41 During the last decades, worldwide losses of biodiversity have occurred at an unprecedented rate and
42 agricultural intensification has been a major driver (Cardinale et al., 2012; Philpott et al., 2008; Tilman et
43 al., 2002; Wilby and Thomas, 2002). The dramatic land use changes include the simplification of
44 agricultural landscapes by deforestation and monoculture and the extensive use of agricultural inputs
45 such as broad-spectrum insecticides to control crop pests, with detrimental impact on ecosystem health

46 (Tscharrntke et al., 2005; Barzman et al., 2015). Along with the loss of functional biodiversity, particularly
47 biological control agents, such cultivated ecosystems have become more and more susceptible to pest
48 outbreaks. This is particularly pregnant in southern contexts where arthropod pests pose a permanent
49 threat to food security (Garrity et al., 2010). New models for crop protection are needed to reduce the
50 dependence of agricultural systems on pesticides that stimulate ecological processes of natural
51 regulation of crop pests (Brévault and Clouvel, 2019). One approach is to use the benefits of agroforestry
52 systems to enhance or restore functional biodiversity (here, natural enemies of crop pests) to boost
53 ecosystem services such as biological control of crop pests. A meta-analysis conducted by Pumarino et al.
54 (2015) showed that agroforestry practices generally result in higher abundance of natural enemies of
55 pests, lower pest abundance and less plant damage in perennial crops (e.g., coffee, cocoa and plantain)
56 but not in annual crops (e.g., maize, rice and beans). However, studies carried out in Kenya showed that
57 abundance of stem borers was significantly lower in *Leucaena leucocephala* (Lam.) (Fabales,
58 Mimosaceae) alley cropping than in a maize monocrop (Ogol et al., 1999).

59 Among natural enemies of crop pests, vertebrates including insectivorous bats and birds can provide
60 valuable ecosystem services such as suppression of insect pests (Maas et al., 2013; Maine and Boyles,
61 2015; Pejchar et al., 2018). By protecting crops through feeding on herbivorous pests, they can provide
62 substantial increases in crop yields (Bael et al., 2008; Karp et al., 2013) and a true alternative to chemical
63 insecticides (Bianchi et al., 2006; Tscharrntke et al., 2012). The abundance and diversity of semi-natural
64 habitats within agricultural landscapes, particularly trees, has the potential to increase the abundance
65 and diversity of birds and bats (Harvey et al., 2006; Redlich et al., 2018) and thus natural regulation of
66 crop pests (e.g., nesting and breeding site, alternative preys). However, birds and bats can also
67 negatively impact natural regulation of crop pests by consuming natural enemies of crop pests, i.e., intra-
68 guild predation (Grass et al. 2017; Tschumi et al., 2018). On the other hand, trees can also benefit pests
69 by providing food and refuges (Schroth et al., 2000). More research is thus needed on ecological issues

70 to better understand how tree-crop agroforestry systems can contribute to enhance ecosystem services
71 such as biological control of crop pests. Although a substantial body of research has been performed on
72 the role of bats and birds in perennial cropping systems such as coffee plantations (Bael et al., 2008), few
73 studies have focused on annual cropping systems as an unstable mosaic of habitats (Kennedy and Storer,
74 2000). More research is thus needed to deepen our knowledge of the life system of insectivorous birds
75 and bats including seasonal population dynamics (e.g., breeding cycles, migration), multitrophic
76 interactions within food webs (e.g. intraguild predation; see Grass et al., 2017), and temporal suitability
77 of habitats in agricultural landscapes (Maas et al., 2016).

78 Agricultural landscapes in the “Peanut basin” in Senegal (West Africa) are generally structured by
79 traditional agroforestry parkland systems (AFS), in which trees (mainly apple-ring acacias, *Faidherbia*
80 *albida*) (Fabales, Fabaceae) are distributed in cultivated fields (Seyler, 1993). Even though the impact of
81 those trees on soil fertility has been widely demonstrated, their effect on crop pests and biological
82 control has been poorly studied (Hadgu et al., 2009; Umar et al., 2013). At the landscape scale, they offer
83 a greater diversity of ecological niches in time and space than a simple mosaic of annual crops. The pearl
84 millet, *Pennisetum glaucum* (L.) R. Br. (Cyperales, Poaceae), is the main annual crop in those agricultural
85 systems. However, a key insect pest, the millet head miner (MHM) (*Heliocheilus albipunctella* de Joannis)
86 (Lepidoptera, Noctuidae) is a permanent threat for increasing crop yields (Gahukar, 1984; Sow et al.,
87 2018; Vercambre, 1978). Moths emerge from the soil one to two months after the beginning of the rainy
88 season. After mating, females lay eggs in the millet panicle on the silk of the flower involucre or under
89 stamens, but also on the floral peduncles or on the spine (Nwanze and Harris, 1992). The young larvae
90 perforate the glumes and consume flowers, while the older ones cut off the floral peduncles (Gahukar,
91 1984; Vercambre, 1978), thus preventing grain formation. In the absence of any insecticide application
92 by farmers, millet production relies on pest regulation by natural enemies (Bhatnagar, 1987; Nwanze and
93 Sivakumar, 1990; Sow et al., 2019, 2017). A two-year monitoring of 90 millet fields and their surrounding

94 landscape (2000 m-buffer around millet fields) showed that abundance of trees at the landscape scale
95 significantly increased natural regulation of the MHM (Soti et al., 2019). Using high throughput molecular
96 tools, the food web structures and ecological processes underlying natural regulation of crop pests by
97 arthropods were documented and a large diversity of parasitoids and predators among arthropods were
98 identified (Sow et al., 2018).

99 In the present study, we investigated the contribution of vertebrates, particularly insectivorous birds and
100 bats, to the natural regulation of the MHM in tree-crop agroforestry systems in Senegal. We
101 hypothesized that (i) abundance and diversity of trees at a local and landscape scale enhance the
102 abundance and diversity of insectivorous birds, and that (ii) abundance and diversity of insectivorous
103 birds at a local scale reduce pest incidence. We used satellite and drone imagery, remote sensing and
104 geographical information system (GIS), to map and quantify the abundance and diversity of trees species
105 at local and landscape scale around a set of 20 millet fields. Pest incidence and grain loss were evaluated
106 by direct field observations on millet panicles while natural regulation was assessed using exclusion
107 cages. In addition, the abundance and diversity of birds and bats was monitored in and around millet
108 fields and fecal samples were collected to check for the presence of the MHM based on DNA analyses.
109 Results are discussed in the light of relationships between tree diversity and abundance, role of
110 vertebrates in food webs (ecosystem services vs. disservices) and biological control of crop pests for the
111 deployment of ecologically-intensive cropping systems.

112

113 **2. Materials and Methods**

114 **2.1. Study area**

115 The field survey was conducted in 2017 in the northern area of the "Peanut basin", near Bambey
116 (14°43'0.79"N ; 16°30'5.56"O) in Senegal. This area is under the influence of a Sudano-Sahelian climate

117 with a short rainy season (400-600 mm) from July to October (monsoon). The landscape is composed of
118 tree-crop agroforestry systems mainly including apple-ring acacias (*Faidherbia albida*), soapberry trees
119 (*Balanites aegyptica*; Sapindales, Zygophyllaceae), baobabs (*Adansonia digitata*; Malvales,
120 Bombacaceae), tamarinds (*Tamarindus indica*; Fabales, Caesalpiniaceae) and red acacias (*Acacia seyal*;
121 Fabales, Fabaceae). Crops mainly include staple crops such as pearl millet, peanuts, and cowpea.

122 **2.2. Study design**

123 A total of 10 sites distant from at least one km each other (Fig. 1) were selected across the landscape
124 (100 km²) according to the land-use proportion of tree cover (2.8-8.7%) at a landscape scale (one-km
125 radius buffer around millet fields), following previous treatment of very high resolution satellite imagery
126 (Soti et al., 2018). In each site, two millet fields distant from at least 100 m each were selected according
127 to vegetation openness (open vs. closed) within a 100-m radius buffer with sampling plot (5 x 5 m) at the
128 center. The minimum-maximum distance between paired sampling points was 100 m (Fig. 1). Sampling
129 points captured a large variation in the abundance (number of trees and land-use proportion of tree
130 cover) and diversity (SHDI) of trees (Table 1). Tree cover around sampling plots (100-m radius buffer) was
131 mainly composed of *A. indica*, *B. aegyptiaca*, *F. albida*, and *A. digitata* (Table 1). Situations of closed
132 vegetation were mostly found around “compound” (close-to-home) millet fields with high abundance of
133 neems, whereas “bush” millet fields presented more open vegetation (Fig. S1).

134

135 **2.3 Landcover mapping**

136 Drone photogrammetry and object-based image analysis procedures were used to characterize each site
137 following the method described in Sarron *et al.* (2018). Briefly, each site was overflown using a UAV (DJI
138 Mavic Pro, DJI Inc, China) in order to compute a high resolution orthomosaic (1.30 cm.pixel⁻¹) and a
139 Canopy Height Model (CHM) using a photogrammetry procedure. The two layers were then analysed in

140 eCognition Developer 9 software (Trimble Geospatial, Munich, Germany) through an object-based
141 classification workflow to obtain land cover maps. These landcover maps contained 5 object classes:
142 millet crops, bare soil, trees, grasslands, and building (Fig. 1). Tree species were manually identified
143 within the 100-m radius buffer (photointerpretation) and corrections were made when needed. Land
144 cover maps were expressed as geospatial vectors with each object, including the delineated trees,
145 corresponding to a geolocalized polygon and described in an adjunct database (.shapefile format) to be
146 imported in GIS and processed in Fragstats software (McGarigal and Marks, 1995) for spatial analysis.

147 **2.4. Data collection**

148 The incidence of the MHM was monitored in the 20 sampling plots by counting eggs on 25 randomly
149 selected panicles at panicle emergence. Counting is done with a round trip on the surface of the panicle
150 with a fine forceps. Females of the MHM usually lay their eggs on emerging panicles up to the male
151 flowering stage, between involucre bristles and glumes.

152 At the male flowering stage of millet, i.e. after completion of egg development, sampling plots were
153 divided into two subplots of each 2.5 x 5 m. One subplot designated bird enclosure, while the other
154 served as control. Bird enclosures (2.5 m height) were built with wooden frames covered with a
155 polyethylene nylon mesh (25 x 25 mm cell size) that allowed predatory arthropods to enter but that
156 excluded birds. In each cage, eight panicles were protected with a mesh bag to exclude natural enemies,
157 while 16 other panicles were left open (without mesh bag) to exclude only birds. The same design was
158 reproduced outside the cage in the second subplot with eight panicles protected with a mesh bag to
159 exclude natural enemies, and 16 other panicles left open as a control. As a result, a total of 960 panicles
160 were monitored in the study design. Damages caused by the MHM (number and length of mines) were
161 recorded from each panicle just before harvest, i.e., 21 days later. Conversion of damages to grain losses
162 was done using allometric relations (Thiaw et al., 2017).

163 Field monitoring of birds and bats was performed on the five sites located in the southern part of the
164 study area, over a period of 15 days (3 days in each site) from millet grain filling to maturity.
165 Observations of birds were carried out around sampling plots in the morning (7.00 to 9.00 am UTC) and
166 in the late afternoon (4.30 to 6.30 pm UTC). The species and food diet (millet grain vs. MHM larvae) of
167 birds observed on millet panicles were recorded. Bird abundance in millet fields was calculated by using
168 the frequency of occurrence (C) proposed by Linsdale (1928). Bird species were identified using the
169 "Guide of West African birds" (Borrow and Demey, 2015). Bats were counted at regular time intervals (5
170 min) at dusk (from 6.30 to 7.40 pm UTC).

171 **2.5. Analysis of fecal samples**

172 To check the predation of the MHM by vertebrates, fecal samples of the village weaver (*Ploceus*
173 *cucullatus*; Passeriformes, Ploceidae) and the Mauritian tomb bat (*Taphozous mauritanum*; Chiroptera,
174 Emballonuridae) were collected during 24 hours by using a plastic tarpaulin placed under nesting trees,
175 neem (*Azadirachta indica*; Sapindales, Meliaceae) and palm trees (*Borassus aethiopum*; Arecales,
176 Arecaceae), respectively. Samples were collected at three millet phenological stages corresponding to
177 successive development of the immature stages of the MHM: (1) panicle emergence to female flowering
178 for eggs, (2) panicles with grains at the milk stage for the 1st and 2nd instar larvae, and (3) panicles with
179 grains at the dough stage for 3rd and 4th instar larvae, from late August to late September. A total of 80
180 and 92 fecal samples for birds and bats, respectively, were individually collected using clean cotton buds
181 and placed in 2-ml microtubes with silica-gel granules to absorb moisture and prevent the development
182 of molds and DNA degradation. Detection of the MHM in fecal samples was performed by amplification
183 of the 133 bp fragment of cytochrome c oxidase I (COI mini-barcode, Gillet et al., 2015) and sequencing
184 on a MiSeq Illumina platform (Appendix A).

185 **2.6. Statistical analyses**

186 The R program (version 3.6.1) was used for statistical analyses (R Core team, 2014). We used generalized
187 linear models (*glm* function from the *MASS* package) to test the effect of bird abundance and diversity
188 on pest incidence (including the number of eggs per panicle and grain loss). Models were fitted using the
189 appropriate distribution type and link function: binomial for proportion of infested panicles or grain loss
190 (link = logit), and Poisson for abundance (count data, link = log). We then tested with the same type of
191 models the effect of tree cover at a local and landscape scale on the abundance and diversity of birds,
192 and on pest incidence. Multi-model inference approach was performed to examine the relative
193 importance of each explanatory variable (Burnham and Anderson, 2002). The *MuMIn* package was used
194 to perform model selection and model averaging. Akaike weights were calculated according to the
195 Akaike information criterion (AICc) which is a bias-corrected version of the AIC recommended in analyses
196 where the sample size is small relative to the number of fitted parameters (Burnham and Anderson,
197 2002; Rusch et al., 2011; Soti et al., 2019). The indirect effect of natural enemy exclusion (three
198 treatments: mesh bag, cage, and open as control) on grain loss was analysed using a linear mixed model
199 (*lmer* function in the *lme4* package) with site as a random effect to account for the variation due to this
200 factor. Multiple post-hoc comparisons were carried out with Tukey contrasts using the *glht* function from
201 the *multcomp* package.

202 **3. Results**

203 **3.1. Abundance and diversity of insectivorous birds and bats**

204 Sampling points captured a large variation in the abundance (number) and diversity (SHDI) of observed
205 birds (Table 1). A total of eight insectivorous birds belonging to five families (Corvidae, Passeridae,
206 Ploceidae, Pycnonotidae and Sturnidae) were observed in millet fields (Table 2). The grey-headed
207 sparrow (*Passer griseus*, Passeriformes, Passeridae), the village weaver (*P. cuculatus*), and the little
208 weaver (*Ploceus luteolus*; Passeriformes, Ploceidae) were the most frequently observed species (Table 2).

209 The frequency of occurrence of the five other bird species observed was very low (<3%). Direct field
210 observations showed that the encountered bird species were omnivorous (both granivorous and
211 insectivorous), except *Lamprotornis pulcher* (Muller) (Passeriformes, Sturnidae) which was observed
212 feeding exclusively on insects. We identified two bat species foraging around millet sampling plots: a
213 frugivorous species, the African straw-colored fruit bat (*Eidolon helvum*; Chiroptera, Pteropodidae) and
214 an insectivorous species, the Mauritian tomb bat (*T. mauritanus*) (Table 2).

215 Using a metabarcoding approach, we successfully detected DNA sequences of the MHM in fecal samples
216 of the village weaver bird and the Mauritian tomb bat. The frequency of detection of the MHM DNA in
217 fecal samples from village weavers indicated that these birds primarily feed on late instar larvae (Fig. 2).
218 Detection of the MHM DNA in bats indicated that they feed on MHM moths (egg oviposition period) and
219 probably also on late instar larvae.

220 **3.2. Effect of tree cover on insectivorous birds**

221 The diversity of trees was the most important predictor explaining the abundance of birds observed in
222 and around millet sampling plots (Fig. 3A). The abundance of birds increased with the diversity of trees in
223 a 100-m radius around sampling plots. The abundance of the village weavers followed the same trend,
224 whereas the abundance of the grey-headed sparrow was negatively correlated to the abundance of trees
225 (Fig. 3B, 3C). No effect of tree cover on the abundance or diversity of birds was detected at a landscape
226 scale (1000 and 1750-m radius buffer around sampling points). Direct field observations showed that
227 palm trees served as preferential nesting site for the Mauritian tomb bat.

228 **3.3. Effect of insectivorous vertebrates on pest incidence**

229 The MHM incidence in millet fields was generally high (53.4% egg-infested panicles, 96% damaged
230 panicles), but variable among fields (24-80% egg-infested panicles, 87-100% damaged panicles). Grain
231 losses due to the MHM varied from 9.7 to 29.3% among sampling plots (Table 1). The abundance and

232 diversity of birds did not contribute significantly in explaining pest incidence levels (Fig. 4). Grain loss was
233 significantly reduced when panicles were accessible to arthropods only (-17.4%), and even more (-35.7%)
234 when they were accessible to both arthropods and birds (Fig. 5).

235 **3.4. Effect of tree cover on MHM incidence**

236 The abundance of baobabs at a local scale, i.e., 100-m radius buffer around sampling plots, increased
237 MHM egg infestation on panicles and grain losses (Fig. 6). Conversely, the abundance of soapberry trees
238 in the same area decreased egg infestation and grain losses, whereas the abundance of neems
239 decreased egg infestation only (Fig. 6). Egg infestation and grain loss did not depend on the abundance
240 or diversity of trees at a landscape scale.

241 **4. Discussion**

242 Among natural enemies of crop pests, vertebrates including insectivorous bats and birds can provide
243 valuable ecosystem services such as suppression of insect pests, particularly in agroforestry systems
244 (Karp et al., 2013, 2016; Maas et al., 2013; Maine and Boyles, 2015). However, they can also disrupt
245 natural pest regulation by intraguild competition with predatory arthropods in agroecosystems (Grass et
246 al., 2017; Martin et al., 2013). In the present study, we investigated the association between vegetation
247 openness, richness and abundance of insectivorous birds and bats, and their contribution to the natural
248 regulation of the MHM in tree-crop agroforestry systems in Senegal.

249 The exclusion of natural enemies including arthropods and vertebrates from millet panicles showed that
250 grain losses significantly decreased when panicles were accessible to arthropods only, and even more
251 when they were accessible to both arthropods and birds. We did not observed significant damage on
252 millet panicles due to seed predation by granivorous birds. The vertebrate predatory community was
253 composed of eight bird species of Passeriformes mostly represented by weavers (*Ploceus* spp.) and
254 sparrows (*Passer griseus*). Direct field observations showed that encountered bird species were both

255 granivorous and insectivorous, except *L. pulcher*, which was observed feeding exclusively on insects. Two
256 bat species were seen foraging in the surrounding environment of millet sampling plots: a frugivorous
257 species, the African straw-colored fruit bat (*Eidolon helvum*) and an insectivorous species, the Mauritian
258 tomb bat (*Taphozous mauritanus*). The analysis of fecal samples of birds and bats indicated that village
259 weavers primarily fed on late instar larvae, whereas bats fed on MHM moths (egg oviposition period)
260 and probably also on late instar larvae. According to Goodman et al. (2007), the Mauritian tomb bat is a
261 nocturnal hunter, with moths as preferred food, though during daylight hours they can occasionally prey
262 upon butterflies and termites. The Mauritian tomb bat possibly contributes more than birds to the
263 natural regulation of MHM populations, because unlike birds, insectivorous bats can feed on a large
264 quantity of moths (Kingdon, 1974), thus limiting egg-laying on millet panicles. Birds can exert high
265 predation on MHM larvae during the reproductive season to feed their chicks. Contrary to adults who
266 feed mainly on seeds to which they add insects, chicks feed exclusively on insects including lepidopteran
267 larvae (Bruggers et al., 1985; Petersen et al., 2007).

268 The abundance and diversity of natural habitats in agroforestry systems is a key factor for the
269 conservation of natural enemies, particularly vertebrates in agricultural landscapes (Bianchi et al., 2006;
270 Holland et al., 2016; Rusch et al., 2016). The positive impact of trees species richness on bats and
271 insectivorous birds communities in agricultural landscape has been demonstrated (Harvey et al., 2006).
272 In our study, the abundance of birds (all species together) was positively related to the diversity of trees
273 around millet sampling plots. Populations of village weavers showed the same trend, whereas grey-
274 headed sparrows were preferentially observed in open habitats. Village weavers are gregarious (Collias
275 and Collias, 1970) and their colonies settle a few weeks after the start of the rainy season, just before the
276 emergence of millet panicles (Bruggers et al., 1985). They build their nests on different tree species
277 (mainly neems, palm trees, and balanites) located near residential areas and forage in neighbor millet
278 fields to collect insects, particularly late instar larvae on panicles at the time of chick breeding. Unlike the

279 village weaver, the grey-headed sparrow is solitary and it can be encountered in a wide range of open
280 habitats, including open woodlands and human habitation. No effect of tree cover was detected at a
281 landscape scale (1000 and 1750-m radius buffer around sampling points), indicating short-distance
282 interaction of insectivorous birds with the surrounding landscape. Direct field observations showed that
283 palm trees served as preferential nesting site for the Mauritian tomb bat. The species is characterized by
284 very effective hunting aptitudes including excellent vision, nocturnal hunting, echolocation of prey, and
285 fast flight (Fenton, 1990; Dengis, 1996), which make it an excellent predator of noctuid moths. Their
286 hunting season coincides with the moment when MHM females leave their shelter sites at dusk to lay
287 eggs on millet heads. Our field observations revealed that this generalist predator was able to hunt
288 insects under the street lights in villages, in addition to its ability to hunt effectively in total darkness (A.
289 Sow, unpublished data).

290 When addressing the effect of tree cover on the incidence of MHM, we found that relative contribution
291 of trees to natural pest regulation was probably species-dependent. In the present study, we observed a
292 negative effect of the abundance of soapberry trees and neems on egg infestation. As these trees are
293 often used as nesting sites by village weaver colonies, MHM moths could have been deterred from
294 resting on such trees, as the analysis of fecal samples indicated that those birds primarily feed on late
295 instar larvae. An alternative hypothesis is that soapberry trees and neems offer refuges for other natural
296 enemies groups capable of affecting pest incidence through the direct consumption of eggs (e.g.,
297 predatory arthropods) or moths (e.g., bats). On the other hand, the presence of certain tree species can
298 negatively affect crop yield by increasing the population density of the pest (Schroth et al., 2000). This is
299 possibly the case for baobabs, as our results showed that MHM incidence (egg infestation on panicles
300 and grain losses) increased with baobab density at a local scale. Baobabs could provide resources for
301 insect pests, such as refuges and food.

302 **5. Conclusion**

303 The present study provides key information on hypotheses addressed about the link between abundance
304 and diversity of trees at a local and landscape scale and the abundance and diversity of insectivorous
305 birds and bats, and their net contribution to natural pest control and reduction of millet grain loss. At a
306 local scale, the abundance of insectivorous village weaver birds increased with tree diversity whereas
307 that of grey-headed sparrows decreased with the abundance of trees. Results also showed that trees
308 indirectly contribute to natural regulation of the MHM likely by providing refuges to insectivorous
309 vertebrates (e.g., palms/bats or neems/village weavers). However, other tree species can provide
310 disservices as refuges for pests (e.g., baobabs/MHM moths). To capture the variability of such natural
311 pest regulation and the effects of environmental perturbations (climate, land use, deforestation,
312 pesticides, etc.), it would be relevant to carry out this study on a pluriannual scheme. More research is
313 also needed to deeply examine the links between tree species (habitats), natural enemies (taxonomic
314 and functional traits of communities), pest regulation (e.g., intraguild predation, temporal dynamics) and
315 crop yield. This should assist the design of specific conservation measures such as habitat management
316 to promote conservation biological control. Next steps include farmer-participatory approaches to
317 design farmscapes fostering natural pest regulation.

318

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324 **Competing interests**

325 The authors declare no competing interests.

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471 **Appendix A. Supplementary Data**472 **Figure S1**473 **Figure captions**

474 **Figure 1.** Map of the 20 paired millet sampling plots within the study area (Bambey, Senegal). Example
475 (on the right) of a digitized landscape around one sampling plot.

476 **Figure 2.** Detection rate (%) of the millet head miner DNA in bird (*Ploceus cucullatus*) and bat (*Taphozous*
477 *mauritanus*) fecal samples collected at different phenological stages of the millet crops corresponding to
478 the presence of different development stages of the millet head miner (moths and eggs, moths and early
479 instar larvae, late instar larvae). Bars represent the 95% confidence intervals (CI95).

480 **Figure 3.** Relative importance of the abundance and diversity of trees (at a 100-m radius buffer around
481 sampling plots) in explaining variation of (A) the abundance of birds, (B) the abundance of the grey-
482 headed sparrow, and (C) the abundance of the village weaver. Variables were ranked according to their
483 sum of Akaike weights, which are the probabilities that the given predictor would appear in the best
484 fitting model. Black bars indicate the most important variables. Estimated parameter values and their
485 their standard error (SE) are presented on the right of each bar.

486 **Figure 4.** Relative importance of the abundance and diversity of birds (at a 100-m radius buffer around
487 sampling plots) in explaining variation of (A) egg infestation and (B) grain losses due to the millet head
488 miner (MHM). Variables were ranked according to their sum of Akaike weights ($w + (j)$), which are the
489 probabilities that the given predictor would appear in the best fitting model. Estimated parameter values
490 and their standard error (SE) are presented on the right of each bar.

491 **Figure 5.** Grain loss (%) on egg-infested panicles (i) covered with a mesh bag to exclude natural enemies,
492 (ii) covered with a polyethylene nylon mesh (25 x 25 mm cell size) to exclude vertebrates but not
493 predatory arthropods or parasitoids, or (iii) exposed to both parasitoids, predatory arthropods and
494 vertebrates (open panicles). Means followed by different letters are significantly different (post hoc
495 Tukey test). Mean grain (\pm SE) loss: mesh bag ($26.3 \pm 1.4\%$), cage ($21.7 \pm 1.3\%$) and open control ($16.9 \pm$
496 1.1%).

497 **Figure 6.** Relative importance of the abundance and diversity of trees (at a 100-m radius buffer around
498 sampling plots) in explaining variation of (A) egg infestation and (B) grain losses due to the millet head
499 miner (MHM). Variables were ranked according to their sum of Akaike weights ($w + (j)$), which are the
500 probabilities that the given predictor would appear in the best fitting model. Black bars indicate the most
501 important variables. Estimated parameter values and their standard error (SE) are presented on the right
502 of each bar.

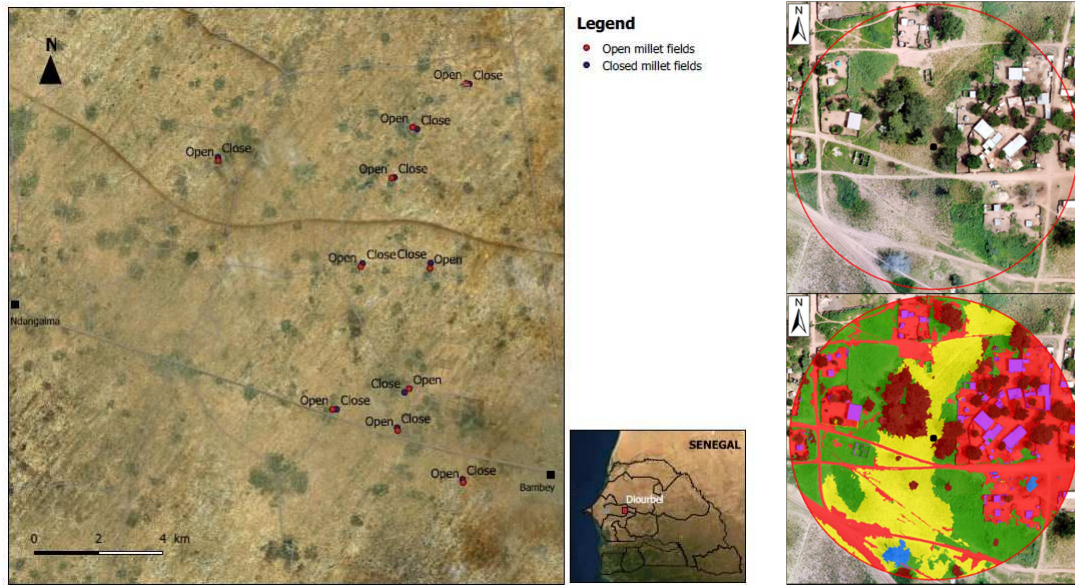
Table 1. Tree cover and diversity, bird abundance and diversity, and pest incidence of the 20 sampling plots in the study area. Tree cover is characterized at the local (100-m radius buffer around sampling plots) and landscape scale (1-km radius buffer around sampling plots).

Variables		Range (min-max)	Mean \pm CI95
Tree cover			
At a local scale	Tree cover (%)	3.5-18.3	9.3 \pm 1.8
	Number of trees	21-94	52.3 \pm 9.3
	Number of <i>Azadirachta indica</i>	0-53	15.8 \pm 6.5
	Number of <i>Balanites aegyptiaca</i>	0-29	13.4 \pm 3.2
	Number of <i>Faidherbia albida</i>	2-18	8.2 \pm 1.9
	Number of <i>Adansonia digitata</i>	0-31	8.3 \pm 3.7
	Number of <i>Borassus aethiopium</i>	0-7	1.3 \pm 0.8
	Tree SHDI	0.9-1.7	1.3 \pm 0.1
At a landscape scale	Tree cover (%)	2.8-8.7	5.7 \pm 1.0
Bird abundance and diversity			
	Number of birds per sampling plot	1-83	49 \pm 18
	Bird SHDI	0.0-1.3	0.9 \pm 0.3
Pest incidence			
	Egg infested panicles (%)	24.0-80.0	53.4 \pm 6.8
	Number of eggs per panicle	0.4-3.8	1.9 \pm 0.4
	Damaged panicles (%)	86.7-100	96.2 \pm 1.9
	Grain loss (%)	9.7-29.3	16.9 \pm 2.1

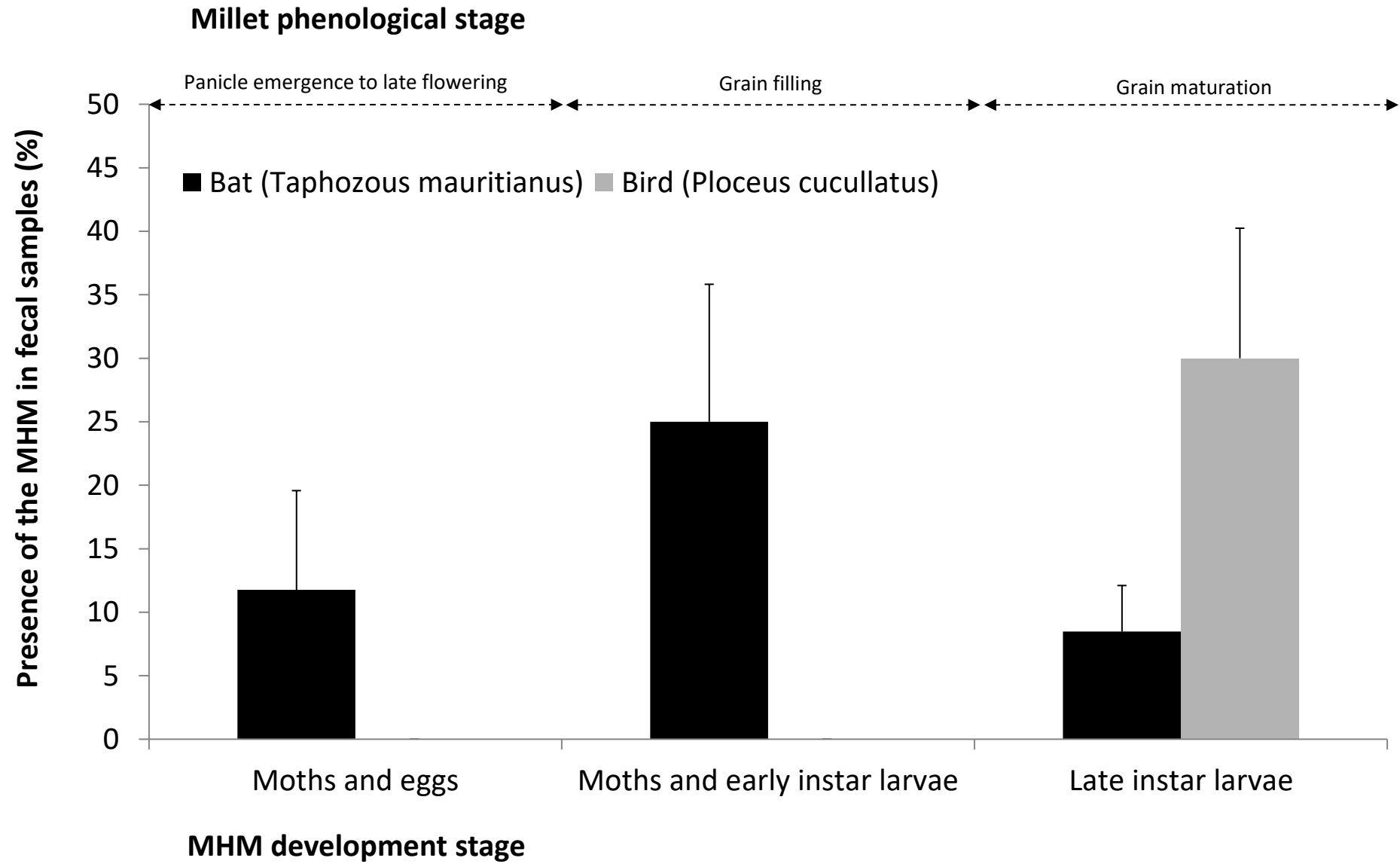
Table 2. Inventory of major birds and bats observed in millet-based agroecosystems in the North of the Peanut basin in Senegal.

Order Family	Common name	Latin name	Food diet	Frequency of occurrence (%)	Relative abundance (%)	*Predat ion evidenc e on MHM by direct observa tions. **Pred ation evidenc e on MHM confirm ed by molecul ar
Passeriformes						
Corvidae	African piapiac	<i>Ptilostomus afer</i> (Swainson, 1837)*	I/G	0.4	1.5	
Passeridae	Grey-headed sparrow	<i>Passer griseus</i> (Vieillot, 1817)*	I/G	32.5	42.6	
Ploceidae	Village weaver	<i>Ploceus cucullatus</i> (Statius Müller, PL, 1776)**	I/G	34.2	37.4	
	Little weaver	<i>Ploceus luteolus</i> (Lichtenstein, MHK, 1823)*	I/G	17.1	12.3	
Pycnonotidae	Common bulbul	<i>Pycnonotus barbatus</i> (Desfontaines, 1789)*	I/G	2.5	1.9	
Sturnidae	Long-tailed glossy starling	<i>Lamprotornis caudatus</i> (Statius Müller, 1776)*	I/G	0.4	3.3	
	Chestnut-bellied starling	<i>Lamprotornis pulcher</i> (Müller, 1776)*	I	0.8	0.4	
	Lesser blue-eared starling	<i>Lamprotornis chloropterus</i> (Swainson, 1838)*	I/G	0.8	0.6	
Chiroptera						
Pteropodidae	African straw-colored fruit bat	<i>Eidolon helvum</i> (Kerr, 1792)**	F	-	-	
Emballonuridae	Mauritian tomb bat	<i>Taphozous mauritanus</i> (E. Geoffroy, 1818)**	I	-	-	

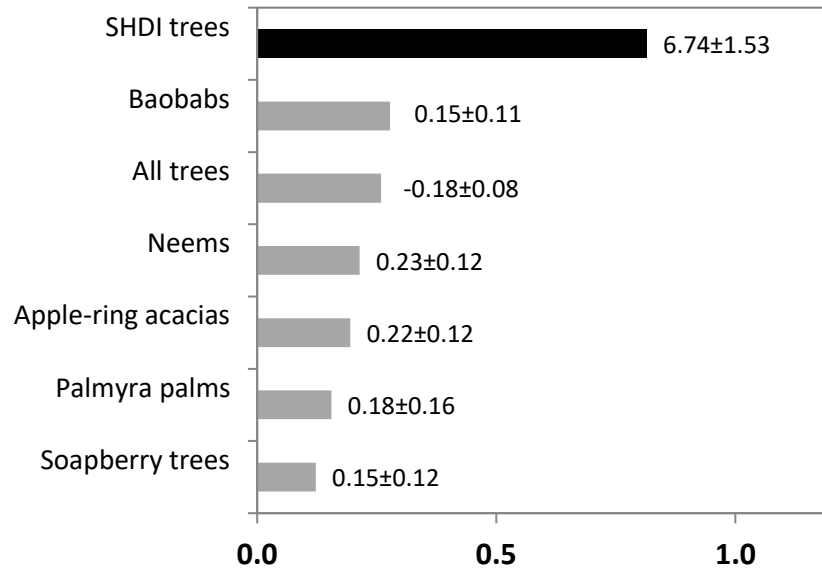
analysis. I: insectivorous. F: frugivorous. G: granivorous.



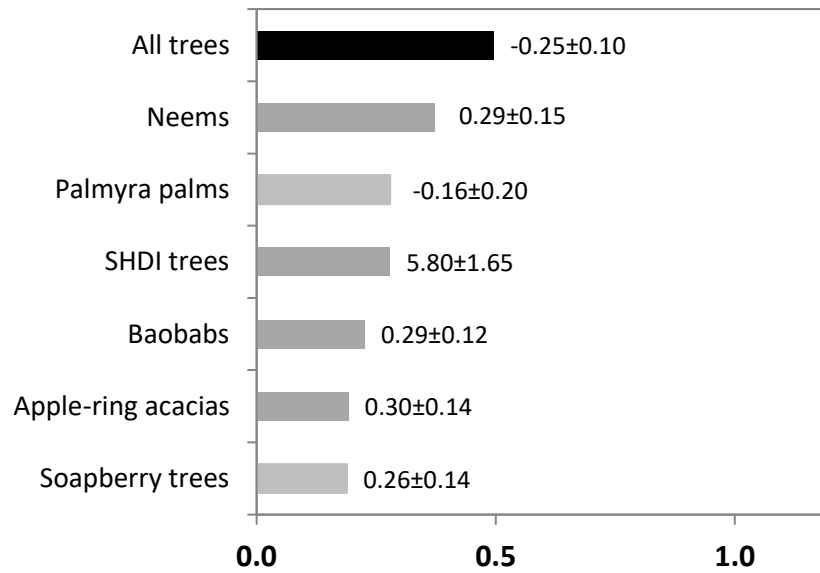
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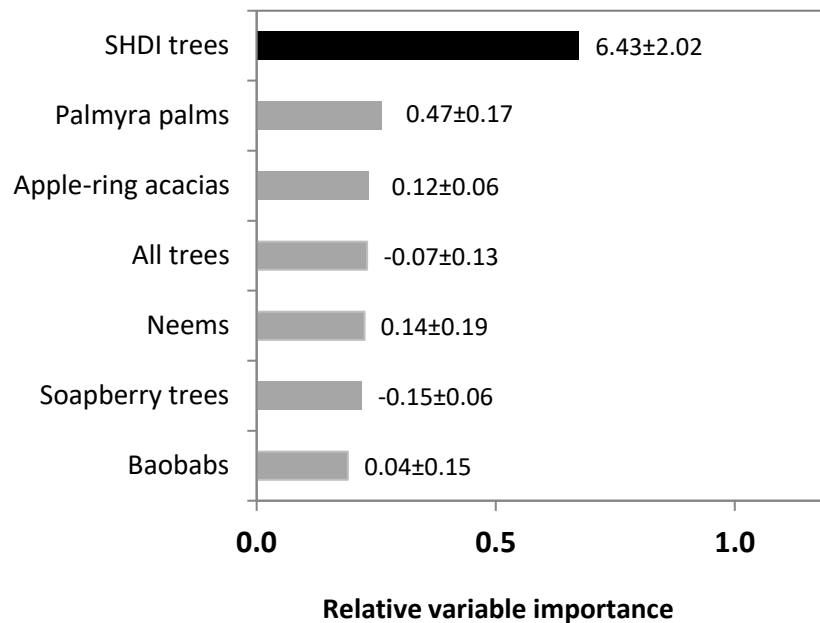
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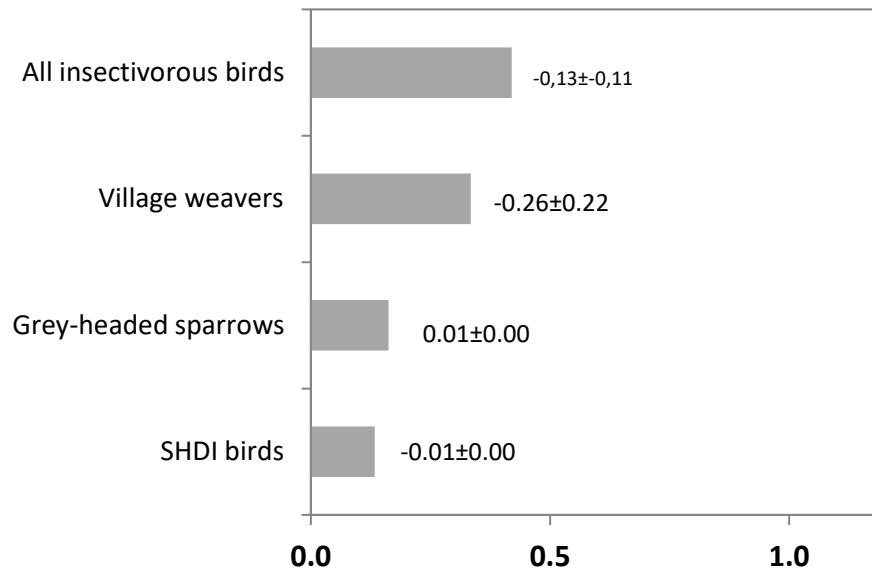


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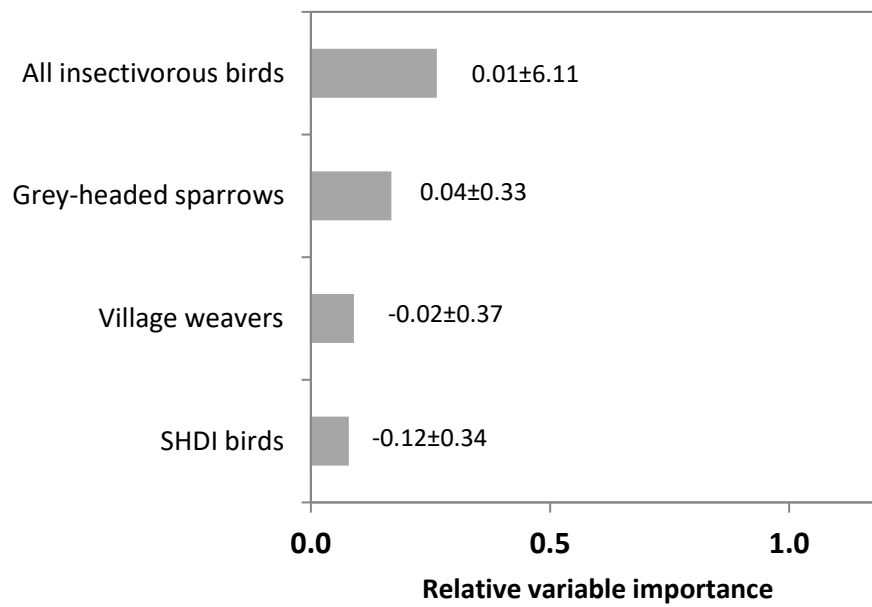


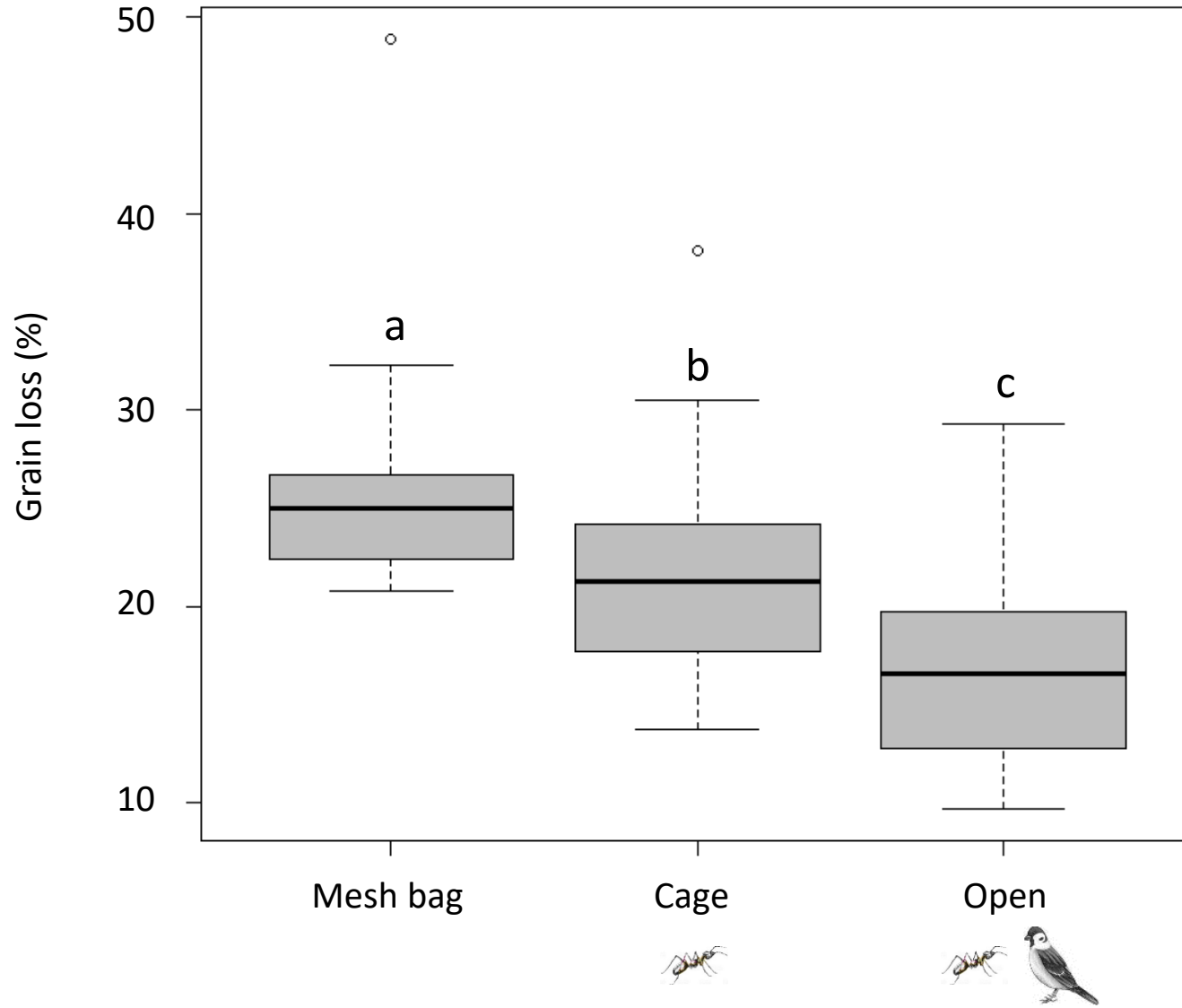
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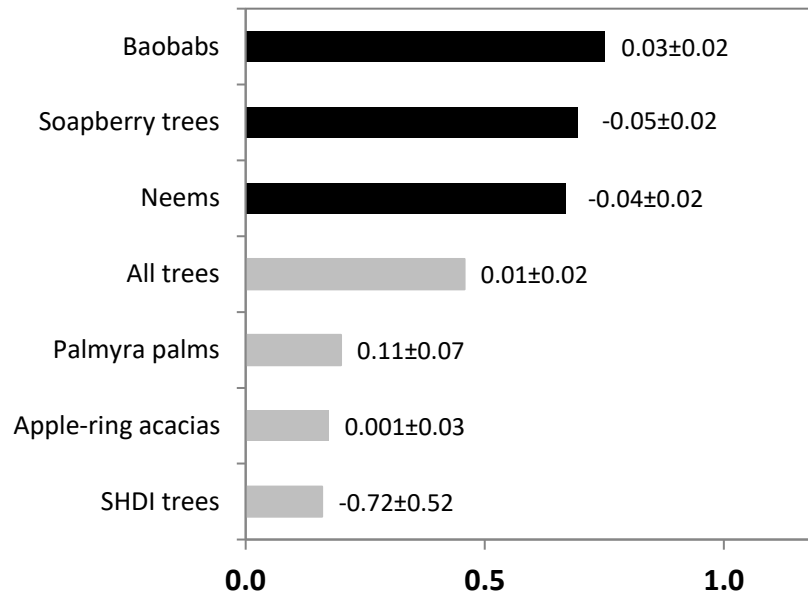


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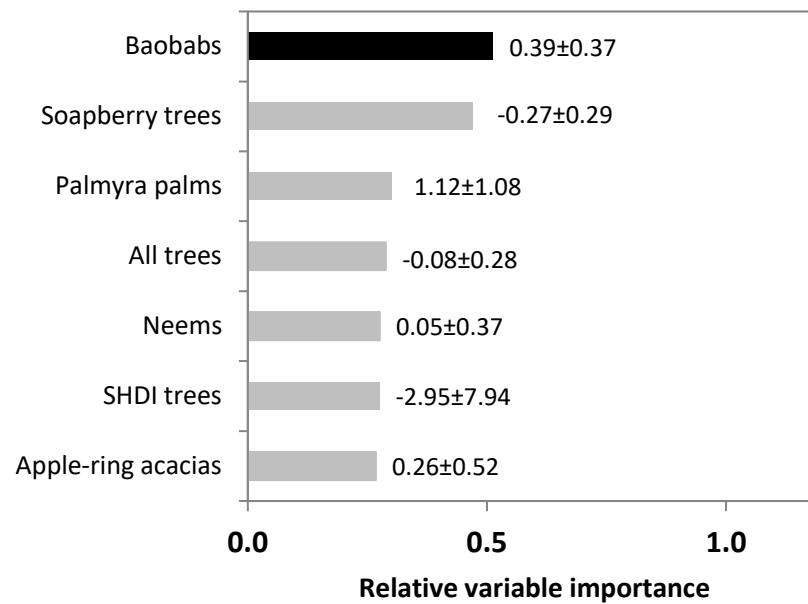




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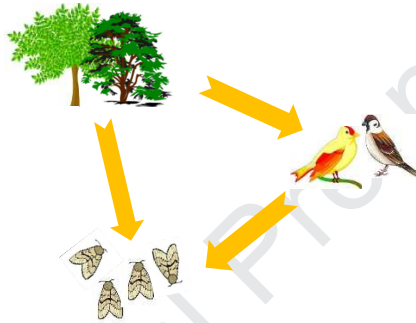


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Highlights

- Vertebrates, including birds and bats, are effective predators of the millet head miner.
- They contribute to natural pest control and reduction of millet grain loss.
- The abundance of insectivorous birds is enhanced by tree diversity at a local scale.
- The contribution of trees for natural pest control is species-dependent. Trees can serve as refuges for pest (eg. baobab/moths) and predators (eg. palm tree/bats or neem/village weavers).



Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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