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1 **Arthropod diversity is governed by bottom-up and top-**
2 **down forces in a tropical agroecosystem**

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13
14 Running headline: Bottom-up and top-down forces in an agroecosystem

15 **Abstract**

16 Understanding the factors underlying biodiversity patterns is crucial to develop sustainable
17 agroecosystems conserving diversity and the services it provides. This topic has been
18 addressed by several authors in biodiversity experiments. Yet, despite this knowledge, multi-
19 trophic approaches and large spatial scales remain scarce to confirm the results of the studies.
20 The aim of our study was to identify multi-trophic interactions between arthropod trophic
21 guilds in a tropical agroecosystem, while taking the effects of farming practices and landscape
22 complexity into account. To do so, we conducted an experiment in 10 mango orchards on
23 Reunion Island during three consecutive years. In each orchard, we monitored arthropod
24 diversity in two different plots: one plot which maintained customary farming practices and
25 one plot where conservation biological control practices were applied. We used structural
26 equation models to identify the variables that affected the abundance and diversity of different
27 arthropod trophic guilds in two strata in mango orchards: the surface of the ground vs. the
28 mango tree canopy.

29 Links were found to be weak at the trophic guild abundance level on both the surface of the
30 ground and in the mango tree canopy. Conversely, biodiversity mediated complex bottom-up
31 and top-down interactions, including diversity cascades, which differed significantly between
32 the strata. A remarkable difference in the forces affecting herbivore and predator diversity
33 was observed. Herbivore diversity was controlled by top-down forces on the ground, whereas
34 predator diversity was controlled by bottom-up forces in the canopy.

35 These results demonstrate that biodiversity depends on both top-down and bottom-up effects
36 in the tropical agroecosystem community studied here. Interaction directions indicate that
37 conservation biological control based on diverse plant community in ground cover can be an
38 effective lever to foster parasitoid diversity, but not for predatory diversity.

39

40 *Key-words:* ecosystem functioning, food web, landscape, mango, plant diversity, species

41 richness

42 **1. Introduction**

43

44 The relationship between biodiversity and ecosystem functioning is of major interest in
45 community ecology, especially since it became known that biodiversity is being lost at
46 unprecedented rates (Wilson, 1985). Most studies show that biodiversity is positively
47 correlated with several ecosystem processes and functions, in particular with primary
48 productivity (Hooper et al., 2005; Loreau et al., 2001). To investigate ecosystem functioning
49 beyond primary productivity and to understand biodiversity-ecosystem functioning
50 relationships, ecologists are increasingly using multi-trophic approaches and a food web
51 perspective (Cardinale et al., 2009; Duffy et al., 2007; Hines et al., 2015; Thébault and
52 Loreau, 2006; Thompson et al., 2012). The majority of studies have considered the effect of
53 plant diversity on diversity or on the abundance of arthropods at higher trophic levels. Meta-
54 analyses have shown that the diversity of primary producers increases the diversity of both
55 primary (Balvanera et al., 2006) and secondary consumers (predators) Castagneyrol and
56 Jactel (2012). At the same trophic level, species can be grouped in trophic guilds depending
57 on the resource they use and how they use it (Morin, 2011). However, few studies that aimed
58 at understanding the forces explaining species diversity took the network of interactions
59 among trophic guilds into account. Studies are thus needed to bridge this gap because, among
60 these interactions, diversity may influence and be influenced by two opposing forces: the top-
61 down control of resources by consumers, and the bottom-up control of consumers by
62 resources (Hairston, Smith et al., 1960; Hunter and Price, 1992; Leroux and Loreau, 2015).

63

64 The mechanisms underlying bottom-up effects between plants and primary consumers, or
65 between primary consumers and secondary consumers, are modulated by the degree of
66 specialisation of consumers, resource productivity and/or resource density. As explained by

67 the *resource specialization hypothesis*, when consumer species are specialists, increasing
68 resource diversity may lead to higher consumer diversity (Cook-Patton et al., 2011; Haddad et
69 al., 2009). According to the *more individuals hypothesis*, increasing productivity of resources
70 increases consumer abundance and diversity (Cook-Patton et al., 2011; Haddad et al., 2009;
71 Srivastava and Lawton, 1998). Resource density also promotes diversity by attracting
72 generalist consumers, a common phenomenon in plant-herbivorous arthropod systems
73 (Eveleigh et al., 2007). Compared with bottom-up effects, the top-down effects of biodiversity
74 are not well understood. These effects imply consumer diversity has an impact on diversity at
75 lower trophic levels. For instance, some studies have shown that the diversity of secondary
76 consumers reduces the diversity of primary consumers (Dyer and Letourneau, 2003; Pearson
77 and Dyer, 2006). However, one would expect that species diversity among consumers would
78 increase resource diversity. Top-down control can increase resource diversity when it is
79 exerted by one or a few consumer species through a mechanism known as *keystone predation*
80 (Chesson, 2000; Paine, 1966, 1974). *Keystone predation* can even influence non-adjacent
81 trophic levels through a top-down trophic cascade (Bruno and O'Connor, 2005; Byrnes et al.,
82 2006; Oksanen et al., 1981; Persson et al., 1992; Schmitz, 2003). In view of the mechanisms
83 described above, one would expect arthropod diversity to be shaped by the existence of top-
84 down and bottom-up forces between trophic guilds at adjacent and non-adjacent trophic
85 levels.

86

87 Knowledge of the multitrophic interactions explaining diversity patterns is still limited. In
88 plant-aphid-parasitoid communities, Petermann et al. (2010) tested the existence of direct and
89 indirect (cascade) bottom-up effects between plant diversity, aphids and their parasitoids.
90 These authors provided evidence for a strong bottom-up cascading effect: host plant richness
91 increased aphid richness, which increased primary parasitoid richness and, in turn, hyper-

92 parasitoid richness. Four other studies tested the direction of effects (one-way dependencies
93 as bottom-up or top-down forces) between trophic guilds or trophic levels. In an endophytic
94 community, Dyer and Letourneau (2003) showed distinct functioning in two sympatric food
95 webs: the detrital food web was influenced mainly by bottom-up diversity cascades, and the
96 “living” food web was affected by top-down trophic cascades. In grasslands, Pearson and
97 Dyer (2006) showed that the direction of forces between plants, herbivores and enemies
98 varied with the type of management (grazed and irrigated vs. not grazed and not irrigated).
99 The most comprehensive study of multi-trophic interactions was conducted by Scherber et al.
100 (2010), who tested one-way dependencies between several trophic guilds belonging to three
101 trophic levels in a grassland experiment. Their results concerning the aboveground strata
102 showed that plant diversity had a positive bottom-up effect on herbivore abundance, which in
103 turn influenced predator and parasitoid abundances. More recently, Schuldt et al. (2017)
104 confirm the bottom-up control of above ground community web in a subtropical forest. Since
105 these are the results of biodiversity experiments conducted at small scales with controlled and
106 standardised manipulations of biodiversity at a single trophic level, they need to be tested in
107 more realistic contexts (Brose and Hillebrand, 2016), as conducted by Barnes et al. (2017).

108

109 Understanding the factors that influence biodiversity and biodiversity functions in
110 agroecosystems is critical to develop more sustainable agroecosystems (Duru et al., 2015;
111 Gaba et al., 2014). The study of biodiversity effects on multi-trophic interactions in
112 agroecosystems requires taking the influence of farming practices and the landscape context
113 into account. Farming practices can influence biodiversity, in particular through the use of
114 pesticides (Geiger et al., 2010; Rusch et al., 2010) and through the management of the plant
115 community (weeding and habitat manipulation, respectively; Dassou and Tixier, 2016;
116 Holland et al., 2016). Most studies have compared the effects of organic vs. conventional

117 farming, and meta-analyses showed that organic farming increased species richness in several
118 groups including plants and arthropods (Henckel et al., 2015; Schneider et al., 2014; Tuck et
119 al., 2014). At the landscape scale, landscape complexity enhances the diversity of pests and of
120 their natural enemies (Chaplin-Kramer et al., 2011). In their meta-analysis, Gonthier et al.
121 (2014) stressed that different types of organisms respond differently at field and landscape
122 scales.

123

124 The main goal of the present study was to understand how biodiversity controls multi-trophic
125 interactions in mango orchards on Reunion Island. Mango is one of the most widely grown
126 fruits in tropical areas worldwide and the results of our study may help manage their
127 associated pests. We used structural equation models (SEM) to test simultaneously (i) how the
128 species richness of six arthropod trophic guilds are related, and (ii) how farming practices (
129 insecticide spraying frequencies and within field plant diversity) and landscape complexity
130 influence the species richness of these trophic guilds. The same analyses were conducted on
131 the abundance data of each trophic guild to distinguish mechanisms driven by the abundance
132 or by the diversity of each. Analyses were performed independently of the two strata, (the
133 mango tree canopy and the surface of the ground), where we expected to observe the effects
134 of different processes due to differences in their complexity (simple and complex
135 respectively).

136 **2. Materials and Methods**

137 *2.1. Study area and sampling protocol*

138 The study was conducted between 2012 and 2014, in 10 mango orchards (hereafter “sites”) on
139 the west coast of Reunion Island (Indian Ocean) with different landscape. The mango
140 orchards belong to the network of Biophyto experimental project (www.biophyto.org). We
141 employed both surveys and experimental approaches. At each site, we monitored two types of
142 plots: one in which customary farming practices were used and the other in which
143 conservation biological control practices were applied from 2012 to 2014. Conservation
144 biological control practices imply no use of insecticides, and enhanced plant diversity in the
145 ground cover. As explained below, customary farming practices and conservation biological
146 control practices varied between sites, resulting in varying plant diversity and insecticide
147 applications at plot level. This is why the type of farming practice was not included as
148 explanatory variable in our analyses; instead, we used variables that derive from these
149 practices, i.e. plant diversity and insecticide applications. To study multi-trophic interactions
150 using a multiscale approach, we conducted “snapshot” field sampling once a year in August
151 during the mango flowering season. On these occasions, we collected arthropods, plants and
152 landscape data over a period of three weeks. Surveys of farmers by partners involved in the
153 Biophyto project provided dates of insecticide treatments for each plot.

154

155 *2.2. Farming practices*

156 We considered two indicators of farming practices, insecticide spraying frequencies and
157 within field plant diversity. Insecticide spraying frequencies were calculated for a period of
158 two months before the beginning of arthropod sampling. Plant diversity surveys were
159 conducted one week before the beginning of arthropod sampling. Plants were identified along
160 transects established between two rows of mango trees and perpendicular to them. The

161 abundance of each species along each transect was considered as the sum of the occupied
162 portions of transects. Plant diversity was estimated at the plot scale using the same
163 methodology as for arthropod diversity in Jacquot et al. (2017).

164

165 2.3. Landscape complexity

166 Each year, crops and semi-natural habitats were mapped within a circle with a 400 m radius
167 from the centre of each plot, using field observations, aerial photographs (IGN 2013) and
168 ArcGIS v. 10.3. We used a scale of 400 m because both natural enemies and pests have been
169 found to respond to landscape at this spatial scale (Chaplin-Kramer et al., 2011). We
170 measured landscape complexity with two commonly used metrics (Gonthier et al., 2014;
171 Tschardt et al., 2005): the Shannon diversity index of land use types using *fragstat* v. 4.2.1
172 and the proportion of semi-natural habitats measured with *raster* and *fragstat* package in *R*.

173

174 2.4. Arthropod communities

175 Arthropod communities were sampled in two distinct strata in each orchard: in the mango tree
176 canopy and on the surface of the ground. Arthropods on the ground were sampled with pitfall
177 traps and by suction using. Samples were collected by suction along the same transects along
178 which the plants were identified. Arthropods living in the mango trees were collected in the
179 canopy using suction sampling. For a detailed description of the sampling methods, see
180 Jacquot et al. (2017). All the arthropods collected were identified to morphospecies or
181 morphotype levels. Next, we assigned arthropod species to trophic guilds according to data
182 from the literature. In this study, we considered six trophic guilds: detritivores (detritivores,
183 scavengers, fungivores and micro-herbivores), herbivorous pests of mango (hereafter pests),
184 non-pest herbivores (hereafter herbivores), parasitoids, predators (strict predators, feeding
185 only on other arthropods), omnivores (feeding on other arthropods and on plants and/or

186 detritus). Hyperparasitoids and top-predators were scarce and were thus not considered in our
187 study. For each trophic guild, we used the observed species richness and abundance of each
188 sample as the variables of interest.

189

190 *2.5. Structural equation models*

191 Statistical analyses were conducted independently for four types of models, i.e. for each
192 stratum (ground vs. canopy) we used structural equation models (SEM) on either abundances
193 or on the diversity of all arthropod trophic guilds (log-transformed data). In both strata,
194 abundances and diversities of trophic guilds were defined by latent variables. In the tree
195 canopy stratum, these latent variables depended on the data corresponding to samples
196 collected by suction in the mango tree canopy; on the surface of the ground, these latent
197 variables depended on data from pitfall traps and samples collected on the ground by suction.
198 We considered the two strata separately, assuming that different processes occurred in each
199 stratum despite possible movement of species between strata. The temporal aspect of the
200 dataset was managed at the level of latent variables through a general autocorrelation structure
201 (see Appendix S1). All latent variables were assumed to be spatially auto-correlated,
202 following an exponentially decreasing correlation based on Euclidean distance between sites.

203 We used SEMs because they make it possible to decipher the direct and indirect effects
204 (Grace et al., 2010) which occur in our network of arthropod trophic guilds, farming practices
205 and landscape metrics. We considered a maximum of 12 relationships between the six
206 arthropod trophic guilds, assuming that there was no direct relationship between trophic
207 guilds of primary consumers (Fig. 1). In addition, we studied the effects of four “extrinsic
208 variables” (plant diversity, frequency of insecticide spraying and the two-landscape metrics)
209 on each trophic guild, corresponding to a maximum of 24 combinations of “extrinsic effects”.
210 We did not take into account the effect of landscape complexity on plant diversity, as a meta-

211 analysis showed that, in agroecosystems, plants are influenced by local management but not
212 by landscape complexity (Gonthier et al., 2014) so we assumed that, in our system, the plant
213 communities were mainly dependent on farming practices.

214 Another important goal of our analysis was to identify one-way statistical dependencies
215 between arthropod trophic guilds, which required comparisons of SEMs with different
216 directions of statistical relationship between dependent variables. However, testing all
217 possible models and sub-models would represent a total of 12,754,584 models to run. To
218 constrain the number of models to be tested, for each stratum, we ran only models with a
219 small number of variables (“reduced” models) and with many variables (“nearly full”
220 models). “Reduced” models were composed of two one-way statistical dependencies between
221 trophic guilds and two extrinsic effects. “Nearly full” models were composed of 12 one-way
222 statistical dependencies between trophic guilds and 22 extrinsic effects (among 24). To
223 manage the massive amounts of outputs from these models, we conducted the analysis for
224 each stratum in several stages (summarized hereafter and detailed in Appendix S2). We ran all
225 the selected models calculate their BIC weight of each model and evidence ratio (ER and
226 ER_{null}) of each parameter. Then for the kind of models (“reduced” or “nearly full”) showing
227 the lowest BIC, we ran models with $\Delta BIC < 5$ to get posteriors of parameters, and we used
228 model averaging to compute coefficient estimates and credibility intervals. In our results, we
229 considered an effect as credible if it was highly plausible ($ER/ER_{null} > 2$) and if it had a
230 model-averaged 95% credibility interval which did not overlap zero.

231

232 The models were run on the *Southgreen Bioinformatic platform* (CIRAD, Montpellier,
233 France, <http://www.southgreen.fr/>), using JAGS software (Plummer, 2003) to perform Gibbs
234 sampling and the function *jags* in R package *R2jags* (Su and Yajima, 2012) as an interface to
235 R. Three Markov chain Monte Carlo (MCMC) chains of 50,000 iterations were simulated,

236 with a burn-in period of 30,000 iterations. Convergence of MCMC chains was ensured by
237 checking that the potential scale reduction factor was between 1.0 and 1.1 for each parameter
238 at the end of the burn-in period (Gelman and Shirley, 2011). All our analyses used *R* 3.1.0 (R
239 Development Core Team 2014) and *JAGS* 4.4.0. An example of *JAGS* code for our models is
240 provided in the Appendix S3.

241 **3. Results**

242 *3.1. Composition of arthropod communities*

243 In total, we collected 126,753 arthropods, of which 109,079 individuals belonging to 504
244 species (four classes and 22 orders) were identified and assigned to one of the six trophic
245 guilds (see Tables S1 and S2 in Supporting Information). The composition of the trophic
246 guilds of secondary consumers was similar in the two strata, parasitoids were mainly
247 composed of Hymenoptera, predators mainly consisted of spiders, and omnivores were
248 mainly composed of ants. Four insect pests of mango inflorescences were recorded in both
249 strata. The non-pest herbivores were mainly composed of Coleoptera, Hemiptera and
250 Thysanoptera species. Lastly, detritivores were mainly composed of Diptera and Blattodea on
251 mango tree canopy, Amphipoda, Collembola and Isopoda on the surface of the ground.

252

253

254 *SEM based on the diversity of the trophic guilds*

255 When we modelled the diversity of trophic guilds on the surface of the ground, the lowest
256 BIC among structural equation models was obtained with “reduced” models ($\Delta\text{BIC} = 216$
257 between the best model from both guilds). Based on “reduced” models, model parameters
258 with ER/ER_{null} higher than 2 were the effects of herbivores on parasitoids, of parasitoids on
259 omnivores, of predators on detritivores and herbivores, as well as the effect of frequency of
260 insecticide spraying on omnivores, and the effects of plant diversity and the proportion of
261 semi-natural habitats on herbivores (Table 1). Model averaging was conducted on the
262 “reduced” models with a delta BIC (difference between the BIC of a model and the BIC of
263 the smallest BIC) below 5 (corresponding to 404 models). From the six model parameters
264 with ER/ER_{null} higher than 2, only four had an average 95% posterior estimate interval which
265 did not overlap zero (Fig. 2, Table 1). Thus, on the surface of the ground, the results of

266 structural equation models showed that neither the frequency of insecticide spraying, nor the
267 landscape complexity metrics influenced the species richness of trophic guilds. However, the
268 species richness of plants had a positive effect on the species richness of herbivorous
269 arthropods. Regarding statistical links among trophic guilds, herbivore richness had a positive
270 effect on parasitoid richness. By contrast, predator richness had a strong positive top-down
271 effect on herbivore richness and a weak positive top-down effect on detritivore richness. Pest
272 and omnivore richness were not explained by other trophic guild diversity and did not explain
273 other trophic guild diversity.

274

275 Concerning diversity data within the mango tree canopy, the best BIC among all the SEMs
276 tested was found among the “nearly full” models, with 157 fewer units of BIC than “reduced”
277 models. Parameters with $ER/ER_{null} > 2$ were only interactions between trophic guilds: the
278 effects of detritivores and herbivores on parasitoids, predators and omnivores, the effect of
279 predators on pests and the effect of parasitoids on pests (Fig. 2, Table 1). Model averaging
280 was applied to the “nearly full” models with a delta BIC below 5 (corresponding to 2,607
281 models). Of the eight model parameters with $ER/ER_{null} > 2$, four had a model-averaged 95%
282 credibility interval that did not overlap zero (Fig. 2, Table 1). No landscape or agricultural
283 practice variables explained the richness of the trophic guilds. In contrast to what was shown
284 for diversity on the surface of the ground, herbivore richness had a positive bottom-up effect
285 on predator and omnivore richness, albeit weaker in the case of omnivores. Detritivore
286 richness had a positive bottom-up effect on parasitoid richness. The only top-down effect in
287 this stratum was the positive effect of predator richness on pest richness.

288

289 *3.2. SEM based on abundances of trophic guilds*

290 On the surface of the ground, the SEM explaining abundances of trophic guilds with the best
291 BIC found among the “reduced” models, with 206 fewer BIC units than the best “nearly full”
292 model. Model averaging was applied to the “reduced” models with a delta BIC below 5
293 (corresponding to 6,612 models). Based on “reduced” models, the only effect with ER/ER_{null}
294 > 2.72 was the positive effect of detritivore abundance on predator abundance, and its average
295 posterior was significantly different from 0 (Fig. 2, Table 1). Concerning data on the mango
296 tree canopy, the SEM of abundances of trophic guilds did not have any model parameter with
297 $ER > 2$ among “reduced” or “nearly full” models. Thus, we considered that there was no
298 effect between the abundances of trophic guilds within the canopy. In both strata, no effect of
299 farming practices and landscape complexity indicators were likely and significantly different
300 from 0.

301 **4. Discussion**

302 Our results show positive bottom-up and top-down effects among trophic guilds in each
303 stratum (in the mango tree canopy and on the surface of the ground). According to BIC-based
304 SEM selection, no interaction between diversities of trophic guilds within secondary
305 consumers seems likely. Among farming practices and landscape indicators, the positive
306 effect of plant diversity on herbivore diversity was the only significant effect. Concerning the
307 abundances of trophic guilds, only one relationship between trophic guilds (detritivores on
308 predators on ground surface) was significant.

309

310 Plant diversity influenced diversity in arthropod communities only on the surface of the
311 ground. In this stratum, plant diversity had a direct positive effect on herbivore diversity, but
312 plant diversity had no direct effect on the diversity of secondary consumer trophic guilds. Our
313 results differ from the results of studies in which consumer trophic guilds were considered
314 independently. In those studies, plant diversity was reported to increase the diversity of both
315 herbivores and secondary consumers in grassland experiments (Haddad et al., 2009; Hertzog
316 et al., 2016; Scherber et al., 2010; Ebeling et al., 2018; Zhao et al., 2018), and these results
317 were confirmed in a meta-analysis by (Dassou and Tixier, 2016). In our system, even if plant
318 diversity did not directly affect secondary consumers, plant diversity positively affected
319 parasitoid diversity through herbivore diversity. This bottom-up diversity cascade has already
320 been found in studies which assessed plant-aphid-parasitoid interactions using path analysis
321 (Petermann et al., 2010), and in plant-herbivore-enemy systems in which predators and
322 parasitoids were considered together, (Pearson and Dyer 2006). In contrast, in our study, no
323 plant diversity cascade was found for predator diversity, the herbivore-predator relationship
324 being top-down rather than bottom-up. To our knowledge, only one study has simultaneously
325 tested the direct and indirect effects of plant diversity on higher trophic levels, in that

326 particular case on the abundance of parasitoïds, predators and omnivores (Scherber et al.,
327 2010). These authors provided evidence for two different bottom-up diversity cascades, one in
328 which plant diversity increased the abundance of parasitoïds and predators aboveground, and
329 the other in which plant diversity increased the abundance of belowground predators.

330

331 On the surface of the ground, the relationships between herbivore diversity and two guilds of
332 secondary consumers went in opposite directions: the herbivore-parasitoïd relationship was
333 bottom-up, while the herbivore-predator relationship was top-down. Differences in the degree
334 of resource specialisation of the species comprising these two trophic guilds could explain
335 this contrast. This would be consistent with the *resource specialisation hypothesis* (Cook-
336 Patton et al., 2011; Haddad et al., 2009; Hutchinson, 1959). parasitoïds are mainly composed
337 of specialist consumers which parasitize a few host species, whereas predators are mainly
338 composed of generalist consumers (i.e. spiders). Increasing resource diversity (here
339 herbivores) could increase the number of specifically associated herbivore species leading to
340 an increase in the number of specifically associated parasitoïd species. On the other hand,
341 generalist consumers (here predators) would be less sensitive to a bottom-up effect of
342 herbivore diversity, resources for which they are not particularly specialised. Our results have
343 strong implications for conservation biological control in mango orchards. Farming practices
344 that promote plant diversity in ground cover can foster parasitoïd diversity, but not predator
345 diversity.

346

347 The link between herbivore and predator diversity was the only feature common to the two
348 strata, but in opposite directions, with a top-down relationship on the surface of the ground
349 and a bottom-up direction in the canopy. These results are in line with the *enemies hypothesis*
350 (Root, 1973), which predicts that natural enemies of herbivores are more abundant and

351 control herbivore populations more efficiently in complex systems (diverse plant
352 communities) than in simple systems (monocultures). In our study, the two strata
353 corresponded to these two systems. The surface of the ground is a complex stratum with
354 numerous plant species and detritus. Predators have a top-down effect not only on herbivore
355 diversity but also on detritivore diversity. Conversely, the canopy stratum is simpler in
356 comparison, as it is composed of mango leaves and branches, and is quite independent of the
357 surface of the ground, as shown by the absence of a plant diversity effect.

358

359 In our study, the only top-down effect on the mango tree canopy was the positive effect of
360 predator diversity on pest diversity. This top-down control contrasts with the bottom-up
361 relationship between predator diversity and non-pest herbivore diversity. Herbivorous pests
362 spend more time on mango inflorescences, because oviposition and larval development occur
363 there, and also because of their feeding behaviour (sap, cell-content and/or tissue feeders),
364 implying that herbivorous pests would be more exposed to predation than non-pest
365 herbivores. Non-pest herbivores mainly come to mango tree canopies to feed on nectar and
366 pollen. Our results have implications for pest control because we found that predator diversity
367 increased pest diversity. Higher pest diversity could increase damage to the crop, a
368 speculation which is in agreement with the results of the meta-analysis which showed that the
369 increasing species richness of a trophic guild allows more complete depletion of its resources
370 (Cardinale et al., 2006). For example, in a study in the Andes, pest diversity increased damage
371 to potato crops (Dangles et al., 2009). On the contrary, a higher diversity of pest species was
372 shown to increase the biological control of pests in greenhouse cucumber, by increasing the
373 density of predators (Messelink et al., 2010). Another example showed that a plant faced with
374 damage caused by multiple pest species could even increase their yield in compensatory
375 reaction to the damage (oilseed rape; Gagic et al. 2016). To advance pest control based on

376 natural enemy diversity, future studies will need to characterise the relationship between pest
377 diversity and damage to mango inflorescences and, more broadly, to identify the factors
378 which influence communities of natural enemies and of pest communities. The bottom-up
379 diversity cascade from plant to parasitoïd diversity suggests that promoting within field plant
380 diversity could be a lever for conservation biological control.

381

382 The three top-down controls of biodiversity occurring across strata were positive effects of
383 predator diversity. Predation by single species is known to promote the diversity of the
384 consumed community through keystone predation (Menge et al., 1994; Paine, 1966, 1974;
385 Terborgh, 2015). In particular, generalist predators could promote coexistence between
386 species through higher predation on the more competitive species, thus equalizing fitness
387 between prey species (Chesson 2000). Here we document for the first time, the positive
388 effects of generalist predator diversity on the diversity of primary consumers. Consumer
389 diversity is also known to increase resource consumption and consumer abundance (Cardinale
390 et al., 2006). We seem to observe this feature, on the surface of the ground, for the
391 relationship between detritivore and predator. Indeed, predator diversity increased detritivore
392 diversity, and in turn, the abundance of detritivores increased the abundance of predators.

393

394 Our results did not reveal any effect of the frequency of insecticide spraying, landscape
395 diversity or of the percentage of semi-natural habitats in the surrounding landscape. The
396 absence of an insecticide effect is probably due to the fact that insecticide treatments were
397 limited to a few plots. The absence of landscape complexity effects could be due to
398 limitations of our study design and the particularity of our system. Firstly, we used a pre-
399 existing network of plots in which the proximity of the plots may have prevented the
400 detection of such effects. Secondly, the chosen landscape radius and metrics may not

401 represent a landscape effect in our system. Thirdly, species in our system may not be sensitive
402 to landscape, as sensitivity to landscape is notably influenced by the dispersal ability of a
403 species (Kormann et al., 2015; Tschardt et al., 2005). Finally, we acknowledge that our
404 method of analysis comprised a limited set of variables. Future studies should include extra
405 exogenous variables, and should divide the community into more trophic guilds, and perhaps
406 include dispersal traits. A complementary method to understand the relative importance of
407 bottom-up, top-down, intra-trophic levels and exogenous variables for all consumer trophic
408 guilds, could be to use a multivariate approach based on trophic guild composition (Rzanny,
409 Kuu, & Voigt, 2013).

410

411 **5. Conclusions**

412 Complex bottom-up and top-down biodiversity effects are at play in mango orchard food
413 webs. The mechanism involved appears to be mainly based on resource specialisation by
414 consumers and the complexity of the strata. Our study confirms that multi-trophic approaches,
415 with tests of interaction directions, are essential to understand arthropod biodiversity in
416 agroecosystems. From the point of view of application, our results showed that plant diversity
417 in the ground cover can be a lever to promote parasitoid diversity, but not predator diversity.

418

419 **Authors' contributions**

420 MJ, JPD and PT conceived the study and designed the methodology; MJ, DM and BD
421 collected the data; MJ and FM analysed the data; MJ led the writing of the manuscript. All
422 authors contributed critically to the drafts and gave their final approval for publication.

423

424

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705 **Supplementary material**

706 Additional Supporting Information can be found in the online version of this article.

707

708 **Appendix S1.** Time series management in SEM.

709 **Appendix S2.** Methods of model selection and multi-model inference.

710 **Appendix S3.** Schematic representation and JAGS code for an example model.

711 **Table S1.** Abundance and species richness of arthropods in the mango canopy.

712 **Table S2.** Abundance and species richness of arthropods on the surface of the ground.

713

714

715 **Figure captions**

716

717 **Figure 1: Path diagram of the multi-trophic interactions tested in structural equation**
718 **models.** Double-head arrows show that we tested the two directions of each interaction. Black
719 arrows show interactions within trophic levels, grey arrows show interactions across trophic
720 levels. SEM included the effects of plant richness, frequency of insecticide spraying and the
721 two landscape metrics on each trophic guild, but these effects are not shown to facilitate
722 readability.

723

724 **Figure 2: Food webs on the surface of the ground and mango tree canopy biodiversity.** A
725 and B: diversity of arthropod trophic guilds in the tree canopy and on the surface of the
726 ground, respectively. C and D: abundances of arthropod trophic guilds in the tree canopy and
727 on the surface of the ground, respectively. The number next to the arrows is the model-
728 averaged standardised mean of the parameters, which are all positive. Boxes showing the
729 frequency of insecticide spraying and landscape metrics are not included, because they were

730 unlikely and/or not significantly different from zero. The evidence ratio (ER/ER_{null}), model-
731 averaged posterior mean and 95% credibility interval (CI) for all parameters are reported in
732 Table 1.

733

734 **Table 1: Ratio of ER to ER_{null} and model-averaged parameter estimates (95% credibility**
735 **interval) for the structural equation models of the two strata for each metric (diversity**
736 **and abundance).** “Reduced” or “nearly full” indicates the types of model selected for the
737 calculation of ER and posteriors (with the lowest BIC; see Methods). “Reduced” models were
738 composed of two one-way statistical dependencies between trophic guilds and two extrinsic
739 effects; “nearly full” models were composed of 12 one-way statistical dependencies between
740 trophic guilds and 22 extrinsic effects. Parameter with $ER/ER_{null} > 2$ are in bold, parameter
741 posteriors significantly different from zero are underlined. Empty cells indicate posteriors not
742 estimated by model averaging, because the variables were absent from the set of “best”
743 models used for model averaging (diversity on the surface of the ground) or because model
744 averaging was not conducted if no variables showed $ER/ER_{null} > 2$ for the model type
745 (abundances in the canopy).

Trophic groups/ tested influence of...	Diversities of trophic groups				Abundances of trophic groups			
	Canopy ("Nearly full")		Ground surface ("reduced")		Canopy ("reduced")		Ground surface ("reduced")	
	ER/ER _{null}	Posteriors	ER/ER _{null}	Posteriors	ER/ER _{null}	Posteriors	ER/ER _{null}	Posteriors
Detritivores								
Parasitoids	0,21	0.47 (0.39 to 1.51)	0,10	-0.31 (-0.91 to 0.32)	1,20	.	0,62	0.11 (-0.59 to 1.07)
Predators	0,26	0.45 (0.33 to 1.85)	190,96	0.49 (0.09 to 1.85)	1,35	.	2,61	0.56 (0.13 to 1.55)
Omnivores	0,19	0.45 (0.33 to 2.12)	0,00	.	1,14	.	0,70	-0.19 (-1.17 to 0.82)
Insecticides	1,04	-0.31 (-1.29 to 0.50)	0,52	-0.02 (-0.25 to 0.12)	1,10	.	0,96	-0.16 (-0.81 to 0.25)
Plant diversity	1,04	0.42 (-0.37 to 1.42)	0,40	0.07 (-0.07 to 0.46)	1,04	.	0,82	0.37 (-0.19 to 1.35)
Landscape semin. diversity	0,99	-0.27 (-1.22 to 0.52)	1,21	-0.1 (-0.59 to 0.21)	1,04	.	1,16	-0.47 (-1.35 to 0.04)
Landscape diversity	0,96	-0.49 (-1.50 to 0.27)	0,50	-0.06 (-0.28 to 0.07)	1,22	.	1,06	-0.23 (-0.93 to 0.29)
Herbivores								
Parasitoids	0,22	.	1,13	0.64 (0.15 to 1.66)	1,26	.	0,77	0.77 (0.18 to 1.91)
Predators	0,25	0.69 (0.97 to 1.63)	4,99	1.03 (0.29 to 2.24)	0,45	.	1,10	0.77 (0.19 to 1.87)
Omnivores	0,26	0.78 (0.78 to 3.59)	0,03	-0.18 (-0.35 to 1.15)	0,66	.	0,89	0.23 (-0.81 to 1.53)
Insecticides	0,80	-0.04 (-0.87 to 0.73)	1,15	-0.06 (-0.69 to 0.4)	0,98	.	0,99	-0.02 (-0.69 to 0.67)
Plant diversity	1,29	1.26 (0.44 to 2.41)	2,69	0.79 (0.16 to 1.89)	0,91	.	1,02	0.75 (0.2 to 1.83)
Landscape semin. diversity	1,01	-0.49 (-1.46 to 0.25)	3,52	-0.65 (-1.72 to 0.08)	1,00	.	1,03	-0.49 (-1.4 to 0.11)
Landscape diversity	1,02	0.22 (-0.56 to 1.06)	1,08	-0.02 (-0.74 to 0.6)	0,98	.	0,99	0.02 (-0.67 to 0.81)
Pests								
Parasitoids	1,64	0.13 (-0.95 to 1.27)	0,00	.	1,41	.	0,83	-0.47 (-1.53 to -0.04)
Predators	2,11	0.82 (0.09 to 2.04)	0,00	.	1,46	.	1,08	-0.46 (-1.47 to -0.04)
Omnivores	4,14	-0.33 (-1.50 to 0.78)	0,00	.	1,15	.	0,45	0.35 (-0.26 to 1.47)
Insecticides	1,02	-0.40 (-1.95 to 1.15)	0,44	0 (-0.22 to 0.22)	1,02	.	1,02	-0.05 (-0.54 to 0.33)
Plant diversity	1,42	0.62 (-0.98 to 2.16)	0,39	-0.15 (-0.67 to 0.03)	0,97	.	1,10	-0.3 (-1.08 to 0)
Landscape semin. diversity	1,07	0.14 (-1.39 to 1.64)	0,58	0.22 (0.06 to 0.6)	1,00	.	1,14	0.39 (0.08 to 1.3)
Landscape diversity	1,17	-0.25 (-1.78 to 1.24)	0,35	-0.09 (-0.51 to 0.1)	1,03	.	1,03	-0.14 (-0.74 to 0.16)
Parasitoids								
Detritivores	4,87	0.83 (0.04 to 2.02)	0,32	0.51 (-0.58 to 2)	0,86	.	0,73	0.06 (-0.49 to 0.87)
Herbivores	4,61	0.31 (-1.03 to 1.64)	2,00	1.06 (0.26 to 2.34)	1,55	.	0,67	0.65 (0.14 to 1.76)
Pests	0,61	-0.05 (-0.86 to 0.78)	0,11	-1.11 (-1.91 to 0.26)	1,48	.	0,83	-0.74 (-1.77 to -0.06)
Predators	1,06	1.01 (0.24 to 2.26)	0,01	.	1,34	.	0,99	0.49 (0.04 to 1.5)
Omnivores	1,59	0.47 (-0.43 to 1.64)	0,04	.	0,40	.	1,07	0.58 (-0.02 to 1.84)
Insecticides	1,19	-0.23 (-1.65 to 1.18)	1,47	-0.33 (-1.31 to 0.32)	0,98	.	0,88	-0.23 (-0.99 to 0.3)
Plant diversity	1,04	0.07 (-1.40 to 1.53)	0,49	0.61 (0.09 to 1.7)	0,92	.	0,79	0.59 (0.12 to 1.63)
Landscape semin. diversity	1,06	-0.60 (-2.03 to 0.81)	0,78	0.33 (-0.27 to 1.29)	1,06	.	1,03	-0.08 (-0.85 to 0.71)
Landscape diversity	0,97	0.71 (-0.84 to 2.13)	0,80	0 (-0.93 to 0.96)	0,95	.	0,95	0.42 (-0.02 to 1.37)
Predators								
Detritivores	3,83	0.19 (-0.9 to 1.31)	0,59	0.82 (0.18 to 2.05)	0,96	.	8,73	0.89 (0.2 to 2.11)
Herbivores	3,95	1.12 (0.09 to 2.42)	0,01	.	0,49	.	0,72	0.63 (0.12 to 1.66)
Pests	0,47	0.42 (-0.09 to 1.44)	0,47	-0.1 (-0.99 to 0.77)	1,31	.	0,63	-0.74 (-1.82 to 0.11)
Parasitoids	0,94	0.98 (0.25 to 2.16)	0,00	.	1,06	.	0,63	0.51 (0.05 to 1.54)
Omnivores	1,33	0.26 (-0.74 to 1.45)	0,00	.	0,70	.	0,47	-0.4 (-1.21 to 1.87)
Insecticides	1,08	0.52 (-0.79 to 1.95)	1,10	-0.09 (-0.65 to 0.33)	1,06	.	1,02	-0.16 (-0.76 to 0.23)
Plant diversity	1,37	0.44 (-0.98 to 1.88)	0,95	0.59 (0.12 to 1.53)	0,94	.	0,69	0.67 (0.13 to 1.73)
Landscape semin. diversity	0,90	0.19 (-1.21 to 1.62)	0,63	-0.68 (-1.59 to -0.08)	1,00	.	0,70	-0.39 (-1.19 to 0.07)
Landscape diversity	1,07	0.41 (-1.07 to 1.86)	1,32	0.12 (-0.48 to 0.84)	0,99	.	0,90	0.25 (-0.29 to 1.04)
Omnivores								
Detritivores	5,20	0.06 (-0.74 to 0.93)	0,00	.	0,76	.	0,87	-0.08 (-0.7 to 0.57)
Herbivores	3,78	0.78 (0.05 to 1.92)	0,04	.	0,77	.	0,42	0.5 (0.08 to 1.6)
Pests	0,24	-0.59 (-1.61 to 0.09)	0,88	-0.2 (-1.27 to 0.99)	1,26	.	0,69	-0.25 (-1.01 to 0.42)
Parasitoids	0,63	0.37 (-0.26 to 1.35)	4,08	0.32 (-1.1 to 1.46)	0,35	.	0,17	0.69 (0.39 to 2.33)
Predators	0,75	0.19 (-0.49 to 1.13)	0,00	.	0,92	.	0,76	-0.15 (-0.9 to 0.55)
Insecticides	0,75	-0.89 (-2.08 to 0.11)	2,55	0 (-0.72 to 0.75)	0,83	.	1,01	-0.13 (-0.7 to 0.27)
Plant diversity	0,65	-0.51 (-1.75 to 0.70)	0,40	-0.09 (-0.68 to 0.69)	0,93	.	1,72	0.4 (0.07 to 1.29)
Landscape semin. diversity	0,77	0.56 (-0.50 to 1.78)	1,54	0.03 (-0.79 to 0.88)	1,04	.	0,99	0.46 (0.03 to 1.42)
Landscape diversity	1,01	0.31 (-0.87 to 1.50)	0,33	0.1 (-0.36 to 0.74)	1,02	.	1,06	-0.01 (-0.64 to 0.68)