



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



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### ABSTRACT

Understanding the factors underlying biodiversity patterns is crucial to develop sustainable agroecosystems conserving diversity and the services it provides.

The aim of our study was to identify multi-trophic interactions between arthropod trophic guilds in a tropical agroecosystem, while taking the effects of farming practices and landscape complexity into account. To do so, we conducted an experiment in 10 mango orchards on Reunion Island during three consecutive years. In each orchard, we monitored arthropod diversity in two different plots: one plot which maintained customary farming practices and one plot where conservation biological control practices were applied. We used structural equation models to identify the variables that affected the abundance and diversity of different arthropod trophic guilds in two strata in mango orchards: the surface of the ground vs. the mango tree canopy.

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

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

### 1. Introduction

The relationship between biodiversity and ecosystem functioning is of major interest in community ecology, especially since it became known that biodiversity is being lost at unprecedented rates (Diaz et al., 2019). Most studies show that biodiversity is positively correlated with several ecosystem processes and functions, in particular with primary productivity (Hooper et al., 2005; Loreau et al., 2001). To investigate ecosystem functioning beyond primary productivity and to understand biodiversity-ecosystem functioning relationships, ecologists are increasingly using multi-trophic approaches and a food web perspective (Cardinale et al., 2009; Duffy et al., 2007; Hines et al., 2015; Thébault

and Loreau, 2006; Thompson et al., 2012). The majority of studies have considered the effect of plant diversity on diversity or on the abundance of arthropods at higher trophic levels. Meta-analyses have shown that the diversity of primary producers increases the diversity of both primary (Balvanera et al., 2006) and secondary consumers (predators; Castagnérol and Jactel, 2012). At the same trophic level, species can be grouped in trophic guilds depending on the resource they use and how they use it (Morin, 2011). However, few studies that aimed at understanding the forces explaining species diversity took the network of interactions among trophic guilds into account. Studies are thus needed to bridge this gap because, among these interactions, diversity may influence and be influenced by two opposing forces: the top-down

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control of resources by consumers, and the bottom-up control of consumers by resources (Hairston, Smith et al., 1960; Hunter and Price, 1992; Leroux and Loreau, 2015).

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

Knowledge of the multitrophic interactions explaining diversity patterns is still limited. In plant-aphid-parasitoid communities, Petermann et al. (2010) tested the existence of direct and indirect (cascade) bottom-up effects between plant diversity, aphids and their parasitoids. These authors provided evidence for a strong bottom-up cascading effect: host plant richness increased aphid richness, which increased primary parasitoid richness and, in turn, hyper-parasitoid richness. Four other studies tested the direction of effects (one-way dependencies as bottom-up or top-down forces) between trophic guilds or trophic levels. In an endophytic community, Dyer and Letourneau (2003) showed distinct functioning in two sympatric food webs: the detrital food web was influenced mainly by bottom-up diversity cascades, and the "living" food web was affected by top-down trophic cascades. In grasslands, Pearson and Dyer (2006) showed that the direction of forces between plants, herbivores and enemies varied with the type of management (grazed and irrigated vs. not grazed and not irrigated). The most comprehensive study of multi-trophic interactions was conducted by Scherber et al. (2010), who tested one-way dependencies between several trophic guilds belonging to three trophic levels in a grassland experiment. Their results concerning the above-ground strata showed that plant diversity had a positive bottom-up effect on herbivore abundance, which in turn influenced predator and parasitoid abundances. More recently, Schuldt et al. (2017) confirmed the bottom-up control of an aboveground community web in a subtropical forest. Since these are the results of biodiversity experiments conducted at small scales with controlled and standardised manipulations of biodiversity at a single trophic level, they need to be tested in more realistic contexts (Brose and Hillebrand, 2016), as conducted by Barnes et al. (2017).

Understanding the factors that influence biodiversity and biodiversity functions in agroecosystems is critical to develop more sustainable agroecosystems (Duru et al., 2015; Gaba et al., 2014). The study of biodiversity effects on multi-trophic interactions in agroecosystems requires taking the influence of farming practices and the landscape context into account. Farming practices can influence

biodiversity, in particular through the use of pesticides (Geiger et al., 2010; Rusch et al., 2010) and through the management of the plant community (weeding and habitat manipulation, respectively; Dassou and Tixier, 2016; Holland et al., 2016). Most studies have compared the effects of organic vs. conventional farming, and meta-analyses showed that organic farming increased species richness in several groups including plants and arthropods (Henckel et al., 2015; Schneider et al., 2014; Tuck et al., 2014). At the landscape scale, landscape complexity enhances the diversity of pests and of their natural enemies (Chaplin-Kramer et al., 2011). In their meta-analysis, Gonthier et al. (2014) stressed that different types of organisms respond differently at field and landscape scales.

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

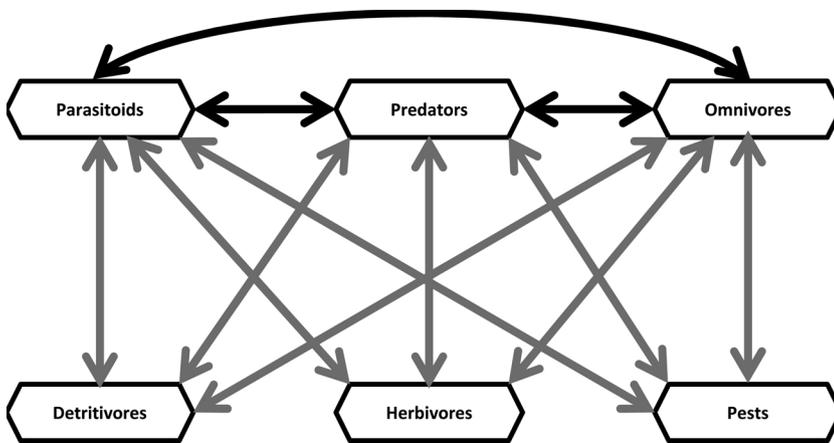
## 2. Materials and methods

### 2.1. Study area and sampling protocol

The study was conducted between 2012 and 2014, in 10 mango orchards (hereafter "sites") on the west coast of Reunion Island (Indian Ocean) with different landscape. The mango orchards belong to the network of Biophyto experimental project (<http://www.agriculture-biodiversite-oi.org/Biophyto>). We employed both surveys and experimental approaches. At each site, we monitored two types of plots: one in which customary farming practices were used and the other in which conservation biological control practices were applied from 2012 to 2014. The average size of plots was 1404 m<sup>2</sup>, with an average intra-site distance of 89.3 m, and an average inter-site distance of 46 km. Conservation biological control practices imply no use of insecticides, and enhanced plant diversity in the ground cover (no use of herbicides, seeding of herbaceous plants, spray irrigation). As explained below, customary farming practices and conservation biological control practices varied between sites, resulting in varying plant diversity and insecticide applications at plot level. This is why the type of farming practice was not included as an explanatory variable in our analyses; instead, we used variables that were derived from these practices, i.e. plant diversity and insecticide applications. To study multi-trophic interactions using a multiscale approach, we conducted "snapshot" field sampling once a year in August during the mango flowering season. On these occasions, we collected arthropods, plants and landscape data over a period of three weeks. Surveys of farmers by partners involved in the Biophyto project provided dates of insecticide treatments for each plot. Variations between sites concerning landscape, plant diversity and frequency of insecticide spraying are detailed in Appendix S1 in Supporting information.

### 2.2. Farming practices

We considered two indicators of farming practices, insecticide spraying frequencies and within field plant diversity. Insecticide spraying frequencies were calculated for a period of two months before the beginning of arthropod sampling. Plant diversity surveys were



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

conducted one week before the beginning of arthropod sampling. Plants were identified along transects established between two rows of mango trees and perpendicular to them. The abundance of each species along each transect was considered as the sum of the occupied portions of transects. Plant diversity was estimated at the plot scale using the same methodology as for arthropod diversity in Jacquot et al. (2017).

### 2.3. Landscape complexity

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

### 2.4. Arthropod communities

Arthropod communities were sampled in two distinct strata in each orchard: in the mango tree canopy and on the surface of the ground. Arthropods on the ground were sampled with pitfall traps (diameter: 12 cm) and by suction sampling (reverse leaf blower STIHL BG56, with an oval nozzle: 14.5 × 10 cm). Each year, eight pitfall traps were placed in plots during one week. Suction samples were collected along the same transects along which the plants were identified. Transects were perpendicular to rows of mango trees and equal to the distance between rows ( $6.8 \pm 1.0$  linear meters on average). On average,  $25.3 \pm 1.1$  linear meters were sampled per 1000 m<sup>2</sup>. Arthropods living in the mango trees were collected in the canopy using suction sampling on 1 m<sup>2</sup> of canopy at each of the four cardinal points. The number of sampled trees was proportional to the plot area (on average  $3.75 \pm 0.2$  trees per 1000 m<sup>2</sup>). For a detailed description of the sampling methods, see Jacquot et al. (2017). All the arthropods collected were identified to morphospecies or morphotype levels. Next, we assigned arthropod species to trophic guilds according to data from the literature. In this study, we considered six trophic guilds: detritivores (detritivores, scavengers, fungivores and micro-herbivores), herbivorous pests of mango (hereafter pests), non-pest herbivores (hereafter herbivores), parasitoids, predators (strict predators, feeding only on other arthropods), omnivores (feeding on other arthropods and on plants and/or detritus). Hyperparasitoids and top-predators were scarce and were thus not considered in our study. For each trophic guild, we used the observed species richness and abundance of each sample as the variables of interest.

### 2.5. Structural equation models

Statistical analyses were conducted independently for four types of models, i.e. for each stratum (ground vs. canopy) we used structural equation models (SEM) on either abundances or on the diversity of all arthropod trophic guilds (log-transformed data). In both strata, abundances and diversities of trophic guilds were defined by latent variables. In the tree canopy stratum, these latent variables depended on the data corresponding to samples collected by suction in the mango tree canopy; on the surface of the ground, these latent variables depended on data from pitfall traps and samples collected on the ground by suction. We considered the two strata separately, assuming that different processes occurred in each stratum despite possible movement of species between strata. The temporal aspect of the dataset was managed at the level of latent variables through a general auto-correlation structure (see Appendix S2 in Supporting information). All latent variables were assumed to be spatially auto-correlated, following an exponentially decreasing correlation based on Euclidean distance between sites.

We used SEMs because they make it possible to decipher the direct and indirect effects (Grace et al., 2010) which occur in our network of arthropod trophic guilds, farming practices and landscape metrics. We considered a maximum of 12 relationships between the six arthropod trophic guilds, assuming that there was no direct relationship between trophic guilds of primary consumers (Fig. 1). In addition, we studied the effects of four “extrinsic variables” (plant diversity, frequency of insecticide spraying and the two-landscape metrics) on each trophic guild, corresponding to a maximum of 24 combinations of “extrinsic effects”. We did not take into account the effect of landscape complexity on plant diversity, as a meta-analysis showed that, in agroecosystems, plants are influenced by local management but not by landscape complexity (Gonthier et al., 2014) so we assumed that, in our system, the plant communities were mainly dependent on farming practices.

Another important goal of our analysis was to identify one-way statistical dependencies between arthropod trophic guilds, which required comparisons of SEMs with different directions of statistical relationship between dependent variables. However, testing all possible models and sub-models would represent a total of 12,754,584 models to run. To constrain the number of models to be tested, for each stratum, we ran only models with a small number of variables (“reduced” models) and with many variables (“nearly full” models). “Reduced” models were composed of two one-way statistical dependencies between trophic guilds and two extrinsic effects. “Nearly full” models were composed of 12 one-way statistical dependencies between trophic guilds and 22 extrinsic effects (among 24). To manage the massive amounts of outputs from these models, we conducted the analysis for each stratum in several stages (summarized hereafter and detailed in Appendix S3 in Supporting information). We ran all the selected models;

we calculated their BIC weight and evidence ratio ( $ER$  and  $ER_{null}$ ) of their parameters. Then for the kind of models (“reduced” or “nearly full”) showing the lowest BIC, we ran models with  $\Delta BIC < 5$  to get posteriors of parameters and we used model averaging to compute coefficient estimates and credibility intervals (Burnham and Anderson, 2002). In our results, we considered an effect as credible if it was highly plausible ( $ER/ER_{null} > 2$ ) and if it had a model-averaged 95% credibility interval which did not overlap zero (Massol et al., 2007).

The models were run on the *Southgreen Bioinformatic platform* (CIRAD, Montpellier, France, <http://www.southgreen.fr/>), using JAGS software (Plummer, 2003) to perform Gibbs sampling and the function *jags* in R package *R2jags* (Su and Yajima, 2012) as an interface to R. Three Markov chain Monte Carlo (MCMC) chains of 50,000 iterations were simulated, with a burn-in period of 30,000 iterations. Convergence of MCMC chains was ensured by checking that the potential scale reduction factor was between 1.0 and 1.1 for each parameter at the end of the burn-in period (Gelman and Shirley, 2011). All our analyses used R 3.1.0 (R Development Core Team 2014) and JAGS 4.4.0. An example of JAGS code for our models is provided in the Appendix S4 in Supporting information.

### 3. Results

#### 3.1. Composition of arthropod communities

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

#### 4. SEM based on the diversity of the trophic guilds

When we modelled the diversity of trophic guilds on the surface of the ground, the lowest BIC among structural equation models was obtained with “reduced” models ( $\Delta BIC = 216$  between the best model from both guilds). Based on “reduced” models, model parameters with  $ER/ER_{null}$  higher than 2 were the effects of herbivores on parasitoids, of parasitoids on omnivores, of predators on detritivores and herbivores, as well as the effect of frequency of insecticide spraying on omnivores, and the effects of plant diversity and the proportion of semi-natural habitats on herbivores (Table 1). Model averaging was conducted on the “reduced” models with a delta BIC (difference between the BIC of a model and the BIC of the smallest BIC) below 5 (corresponding to 404 models). From the six model parameters with  $ER/ER_{null}$  higher than 2, only four had an average 95% posterior estimate interval which did not overlap zero (Fig. 2, Table 1). Thus, on the surface of the ground, the results of structural equation models showed that neither the frequency of insecticide spraying, nor the landscape complexity metrics influenced the diversity of trophic guilds. However, plant diversity had a positive effect on herbivore diversity. Regarding statistical links among trophic guilds, herbivore diversity had a positive effect on parasitoid diversity. By contrast, predator diversity had a strong positive top-down effect on herbivore diversity and a weak positive top-down effect on detritivore diversity. Pest and omnivore diversity were not explained by other trophic guild diversity and did not explain other trophic guild diversity.

Concerning diversity data within the mango tree canopy, the best BIC among all the SEMs tested was found among the “nearly full”

models, with 157 fewer units of BIC than “reduced” models. Parameters with  $ER/ER_{null} > 2$  were only interactions between trophic guilds: the effects of detritivores and herbivores on parasitoids, predators and omnivores, the effect of predators on pests and the effect of parasitoids on pests (Fig. 2, Table 1). Model averaging was applied to the “nearly full” models with a delta BIC below 5 (corresponding to 2607 models). Of the eight model parameters with  $ER/ER_{null} > 2$ , four had a model-averaged 95% credibility interval that did not overlap zero (Fig. 2, Table 1). No landscape or agricultural practice variables explained the diversity of the trophic guilds. In contrast to what was shown for diversity on the surface of the ground, herbivore diversity had a positive bottom-up effect on predator and omnivore diversity, albeit weaker in the case of omnivores. Detritivore diversity had a positive bottom-up effect on parasitoid diversity. The only top-down effect in this stratum was the positive effect of predator diversity on pest diversity.

#### 4.1. SEM based on abundances of trophic guilds

On the surface of the ground, the SEM explaining abundances of trophic guilds with the best BIC found among the “reduced” models, with 206 fewer BIC units than the best “nearly full” model. Model averaging was applied to the “reduced” models with a delta BIC below 5 (corresponding to 6612 models). Based on “reduced” models, the only effect with  $ER/ER_{null} > 2.72$  was the positive effect of detritivore abundance on predator abundance, and its average posterior was significantly different from 0 (Fig. 2, Table 1). Concerning data on the mango tree canopy, the SEM of abundances of trophic guilds did not have any model parameter with  $ER > 2$  among “reduced” or “nearly full” models. Thus, we considered that there was no effect between the abundances of trophic guilds within the canopy. In both strata, no effect of farming practices and landscape complexity indicators were likely and significantly different from 0.

### 5. Discussion

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

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

**Table 1**

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

	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
<b>Detritivores</b>								
Parasitoids	0.21	0.47 (0.39–1.51)	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 (0.33–1.85)	<b>190.96</b>	<b>0.49 (0.09–1.85)</b>	1.35	.	<b>2.61</b>	<b>0.56 (0.13–1.55)</b>
Omnivores	0.19	0.45 (0.33–2.12)	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)
<b>Herbivores</b>								
Parasitoids	0.22	.	1.13	0.64 (0.15–1.66)	1.26	.	0.77	0.77 (0.18–1.91)
Predators	0.25	0.69 (0.97–1.63)	<b>4.99</b>	<b>1.03 (0.29–2.24)</b>	0.45	.	1.10	0.77 (0.19–1.87)
Omnivores	0.26	0.78 (0.78–3.59)	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 (0.44–2.41)	<b>2.69</b>	<b>0.79 (0.16–1.89)</b>	0.91	.	1.02	0.75 (0.2–1.83)
Landscape semin. diversity	1.01	–0.49 (–1.46 to 0.25)	<b>3.52</b>	<b>–0.65 (–1.72 to 0.08)</b>	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)
<b>Pests</b>								
Parasitoids	1.64	0.13 (–0.95 to 1.27)	0.00	.	1.41	.	0.83	–0.47 (–1.53 to –0.04)
Predators	<b>2.11</b>	<b>0.82 (0.09–2.04)</b>	0.00	.	1.46	.	1.08	–0.46 (–1.47 to –0.04)
Omnivores	<b>4.14</b>	<b>–0.33 (–1.50 to 0.78)</b>	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 (0.06–0.6)	1.00	.	1.14	0.39 (0.08–1.3)
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)
<b>Parasitoids</b>								
Detritivores	<b>4.87</b>	<b>0.83 (0.04–2.02)</b>	0.32	0.51 (–0.58 to 2)	0.86	.	0.73	0.06 (–0.49 to 0.87)
Herbivores	<b>4.61</b>	<b>0.31 (–1.03 to 1.64)</b>	<b>2.00</b>	1.06 (0.26–2.34)	1.55	.	0.67	0.65 (0.14–1.76)
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 (0.24–2.26)	0.01	.	1.34	.	0.99	0.49 (0.04–1.5)
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)
<b>Predators</b>								
Detritivores	<b>3.83</b>	<b>0.19 (–0.9 to 1.31)</b>	0.59	0.82 (0.18–2.05)	0.96	.	<b>8.73</b>	<b>0.89 (0.2–2.11)</b>
Herbivores	<b>3.95</b>	<b>1.12 (0.09–2.42)</b>	0.01	.	0.49	.	0.72	0.63 (0.12–1.66)
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 (0.05–1.54)
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 (0.12–1.53)	0.94	.	0.69	0.67 (0.13–1.73)
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)
<b>Omnivores</b>								
Detritivores	<b>5.20</b>	<b>0.06 (–0.74 to 0.93)</b>	0.00	.	0.76	.	0.87	–0.08 (–0.7 to 0.57)
Herbivores	<b>3.78</b>	<b>0.78 (0.05–1.92)</b>	0.04	.	0.77	.	0.42	0.5 (0.08–1.6)
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)	<b>4.08</b>	<b>0.32 (–1.1 to 1.46)</b>	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)	<b>2.55</b>	<b>0 (–0.72 to 0.75)</b>	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 (0.07–1.29)
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 (0.03–1.42)
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)

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

On the surface of the ground, the relationships between herbivore

diversity and two guilds of secondary consumers went in opposite directions: the herbivore-parasitoid relationship was bottom-up, while the herbivore-predator relationship was top-down. Differences in the degree of resource specialisation of the species comprising these two trophic guilds could explain this contrast. This would be consistent with the *resource specialisation hypothesis* (Cook-Patton et al., 2011; Haddad et al., 2009; Hutchinson, 1959). Parasitoids are mainly composed of

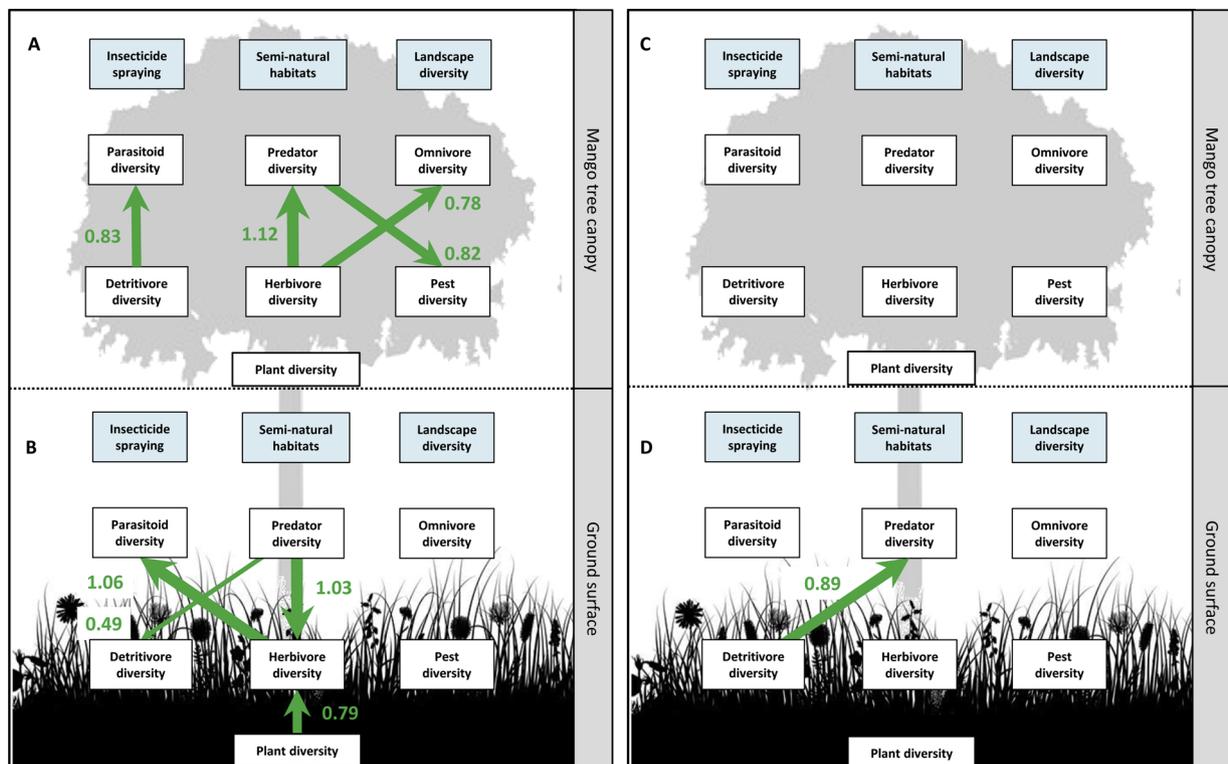


Fig. 2. Food webs on the surface of the ground and mango tree canopy biodiversity. (A and B) diversity of arthropod trophic guilds in the tree canopy and on the surface of the ground, respectively. (C and D) abundances of arthropod trophic guilds in the tree canopy and on the surface of the ground, respectively. The number next to the arrows is the model-averaged standardised mean of the parameters, which are all positive. The evidence ratio ( $ER/ER_{null}$ ), model-averaged posterior mean and 95% credibility interval (CI) for all parameters are reported in Table 1.

specialist consumers which parasitize a few host species, whereas predators are mainly composed of generalist consumers (i.e. spiders). Increasing resource diversity (here herbivores) could increase the number of specifically associated herbivore species leading to an increase in the number of specifically associated parasitoid species. On the other hand, generalist consumers (here predators) would be less sensitive to a bottom-up effect of herbivore diversity, resources for which they are not particularly specialised. Our results have strong implications for conservation biological control in mango orchards. Farming practices that promote plant diversity in ground cover can foster parasitoid diversity and associated regulation service. In contrast, predator diversity would not be promoted by diverse ground covers, while it is positively correlated with predation service (Jacquot et al., 2017). Future studies should evaluate which agroecological farming practice can enhance predator diversity.

The link between herbivore and predator diversity was the only feature common to the two strata, but in opposite directions, with a top-down relationship on the surface of the ground and a bottom-up direction in the canopy. These results are in line with the *enemies hypothesis* (Root, 1973), which predicts that natural enemies of herbivores are more abundant and control herbivore populations more efficiently in complex systems (diverse plant communities) than in simple systems (monocultures). In our study, the two strata corresponded to these two systems. The surface of the ground is a complex stratum with numerous plant species and detritus. Predators have a top-down effect not only on herbivore diversity but also on detritivore diversity. Conversely, the canopy stratum is simpler in comparison, as it is composed of mango leaves and branches, and is quite independent of the surface of the ground, as shown by the absence of a plant diversity effect.

In our study, the only top-down effect on the mango tree canopy was the positive effect of predator diversity on pest diversity. This top-down control contrasts with the bottom-up relationship between predator diversity and non-pest herbivore diversity. Herbivorous pests

spend more time on mango inflorescences, because oviposition and larval development occur there, and also because of their feeding behaviour (sap, cell-content and/or tissue feeders), implying that herbivorous pests would be more exposed to predation than non-pest herbivores. Non-pest herbivores mainly come to mango tree canopies to feed on nectar and pollen. Our results have implications for pest control because we found that predator diversity increased pest diversity. Higher pest diversity could increase damage to the crop, a speculation which is in agreement with the results of the meta-analysis which showed that the increasing species richness of a trophic guild allows more complete depletion of its resources (Cardinale et al., 2006). For example, in a study in the Andes, pest diversity increased damage to potato crops (Dangles et al., 2009). In contrast, a higher diversity of pest species was shown to increase the biological control of pests in greenhouse cucumber, by increasing the density of predators (Messelink et al., 2010). Another example showed that a plant faced with damage caused by multiple pest species could even increase their yield in compensatory reaction to the damage (oilseed rape; Gagic et al., 2016). To advance pest control based on natural enemy diversity, future studies will need to characterise the relationship between pest diversity and damage to mango inflorescences and, more broadly, to identify the factors which influence communities of natural enemies and of pest communities. The bottom-up diversity cascade from plant to parasitoid diversity suggests that promoting within field plant diversity could be a lever for conservation biological control.

The three top-down controls of biodiversity occurring across strata were positive effects of predator diversity. Predation by single species is known to promote the diversity of the consumed community through keystone predation (Menge et al., 1994; Paine, 1966, 1974; Terborgh, 2015). In particular, generalist predators could promote coexistence between species through higher predation on the more competitive species, thus equalizing fitness between prey species (Chesson, 2000). Here we document for the first time that generalist predator diversity

promoted the diversity of primary consumers (herbivores, detritivores and mango pests).

The key role of predation seems to be confirmed by the loop observed between detritivore and predator trophic groups on the surface of the ground. High predator diversity would ensure a high predation and thus high detritivore diversity. Such increased resource consumption, allowed by predator diversity (Cardinale et al., 2006), would increase the abundance of predators explaining positive bottom-up effect between detritivore and predator abundance.

Our results did not reveal any effect of the frequency of insecticide spraying, landscape diversity or of the percentage of semi-natural habitats in the surrounding landscape. The absence of an insecticide effect is probably due to the fact that insecticide treatments were limited to a few plots. The absence of landscape complexity effects could be due to limitations of our study design and particularity of our system. Firstly, we used a pre-existing network of plots in which the proximity of the plots may have prevented the detection of such effects. Secondly, the chosen landscape radius and metrics may not represent a landscape effect in our system. Thirdly, species in our system may not be sensitive to landscape, as sensitivity to landscape is notably influenced by the dispersal ability of a species (Kormann et al., 2015; Tschardt et al., 2005). Finally, we acknowledge that our method of analysis comprised a limited set of variables. Future studies should include extra exogenous variables, and should divide the community into more trophic guilds, and perhaps include dispersal traits. A complementary method to understand the relative importance of bottom-up, top-down, intra-trophic levels and exogenous variables for all consumer trophic guilds, could be to use a multivariate approach based on trophic guild composition (Rzanny et al., 2013).

## 6. Conclusions

Complex bottom-up and top-down biodiversity effects are at play in mango orchard food webs. The mechanism involved appears to be mainly based on resource specialisation by consumers and the complexity of the strata. Our study confirms that multi-trophic approaches, with tests of interaction directions, are essential to understand arthropod biodiversity in agroecosystems. From the point of view of application, the bottom-up diversity cascade from plant to parasitoid diversity suggests that promoting plant diversity in ground cover could be a lever for biological control in mango orchards. By contrast, predator diversity would be insensitive to this farming practice.

## Authors' contributions

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

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## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agee.2019.106623>.

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