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Shade trees decrease pest abundances on brassica crops in Kenya

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Abstract Agroforestry practices may mitigate the current loss of biodiversity and ecosystem services due to deforestation and agricultural intensification. To examine the effects of agroforestry on the ecosystem service of pest regulation, we assessed pest abundances and biological control potential in shaded and open kale (*Brassica oleracea* L. *acephala*) fields in Western Kenya. Specifically, we compared the abundance of pest aphids and caterpillars, ground-dwelling ants, spiders and predatory beetles, and examined aphid parasitism rates, predation rates on diamondback moth eggs, attack rates on surrogate caterpillars and bird predation on aphids. Shade trees effectively reduced abundances of aphids, caterpillars and increased abundances of spiders and predatory beetles, but neither affected ant abundances, or predation and parasitism rates. Our results suggest that presence of shade trees can decrease pest abundances, but that this is not only due to improved biological control by natural enemies but also due to microclimatic conditions affecting pest performance and bottom-up processes such as changes in plant quality and soil conditions. We encourage studies exploring simultaneously how top-down and bottom-up processes affect pest regulation in agroforestry settings.

Introduction

Increased cover of agricultural land-use, occurring mainly at the expense of natural habitats, and agricultural intensification are primary causes for the current biodiversity loss and degradation of ecosystem services (Foley et al. 2005). Decreasing biodiversity is likely to trigger a negative feedback on agricultural production, which could decrease agricultural yields in the long-term (Matson et al. 1997). A change towards more sustainable practices, including improved management of ecosystem services, is thus required (Bommarco et al. 2013).

Agroforestry is a land management practice whereby woody perennials are planted together with crops and/or livestock (Lundgren 1982). It can enhance several ecosystem services, including pest regulation (Schroth et al. 2000; Tscharntke et al. 2011; Pumariño et al. 2015; Kuyah et al. 2016). The

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increased habitat complexity in agroforestry plantations compared to monocultures has the potential to increase natural predator and parasitoid populations by providing shelter and alternative food sources (Landis et al. 2000). The dispersal of natural enemies through agricultural landscapes can also be affected by the presence, size, composition and spatial arrangement of agroforestry patches (Dunning et al. 1992). Many studies have shown that landscape complexity and presence of trees in agricultural habitats can improve regulation of specific pests (Bianchi et al. 2006; Tscharntke et al. 2011; Pumariño et al. 2015) in both temperate and tropical climates, with crops as diverse as cabbage and coffee, and with natural enemies ranging from vertebrates (birds and bats) to invertebrates (parasitic wasps, ants, hoverflies and spiders) (e.g. Bianchi et al. 2006; Tscharntke et al. 2011; Bisseleua et al. 2013; Alignier et al. 2014). However, implementation of perennial agroforestry practices can also reduce opportunities for pest regulation achieved through disturbances, such as crop rotations or tillage (Schroth et al. 2000). Other mechanisms such as modification of micro-climate or changes in crop nutritional value can also explain differences in pest regulation between agroforestry and conventional practices (Schroth et al. 2000).

Kale (*Brassica olearacea* L. var. *acephala*, Brassicaceae) is an important food crop in Western Kenya, with 80% of Kenyan crucifers consumed locally (Salasya and Burger 2010). Crucifers are known to host more pests than most other crops. Aphids (Hemiptera: Aphididae) and moth caterpillars, including the diamondback moth *Plutella xylostella* L. (Lepidoptera: Plutellidae), are among the most abundant pests in Kenyan brassica crops (Kibata 1997; Badenes-Perez and Shelton 2006; Ndang'ang'a et al. 2013). These pests are mainly managed with insecticides, which are used by at least 80% of all Kenyan farmers producing crucifers (Nyambo et al. 1996; Badenes-Perez and Shelton 2006). The cost of such insecticides average 14.1% of the total production costs and can thus be a burden for small-scale farmers (Badenes-Perez and Shelton 2006). Most of the insecticides used in Kenya are also known to have a high negative environmental impact (Badenes-Perez and Shelton 2006). Development of more sustainable pest management practices in this system is therefore needed.

Here, we assess the effect of presence of shade trees on pest regulation in kale fields of Western Kenya. We examine pest abundances (aphids and free-feeding caterpillars) and biological control potential by estimating bird predation on aphids and caterpillars, egg predation by ground-dwelling arthropods and predator attack rates on surrogate caterpillars. We also assessed aphid parasitism rates and activity-density of ground-dwelling predators. We hypothesized that fields surrounded by shade trees would experience higher pest predation and parasitism rates and host higher abundances of predators compared to sun exposed fields, while sun exposed fields would host higher abundances of pests.

Materials and methods

Study site

The study was conducted in the Trans-Nzoia district in Western Kenya (Fig. 1a), approximately 15 km east of Kitale town (01°00'N 35°00'E). The area is located at 1800–1900 m a.s.l. and with a mean annual temperature of 19 °C. The average yearly rainfall is 1000–1200 mm, of which the majority falls during one rainy season, from mid-March to October (Jaetzold et al. 2006).

We carried out the work at the settlements Botwa, Hututu, Wehoya, Yuya and Sinoko (Fig. 1b). Agroforestry practices have been promoted in these settlements by the NGO Vi-Agroforestry since the 1980 s, and the landscape structure is characterised by a landscape dominated by small agricultural fields, homesteads and scattered trees. The trees grown on the farms are both native and exotic species providing fruits, timber and nitrogen-fixation. In this region, maize is the main crop, sometimes inter-cropped with beans. Small plots with kale are grown by most farmers. All farmers had used chemical pesticides at least once on their kale fields, but the frequency of pesticide-use varied among farms and was independent of shading conditions.

Study design

We selected one study field from each of four farms per settlement (i.e., 20 fields in total), with a minimum distance of 100 m between each field and within
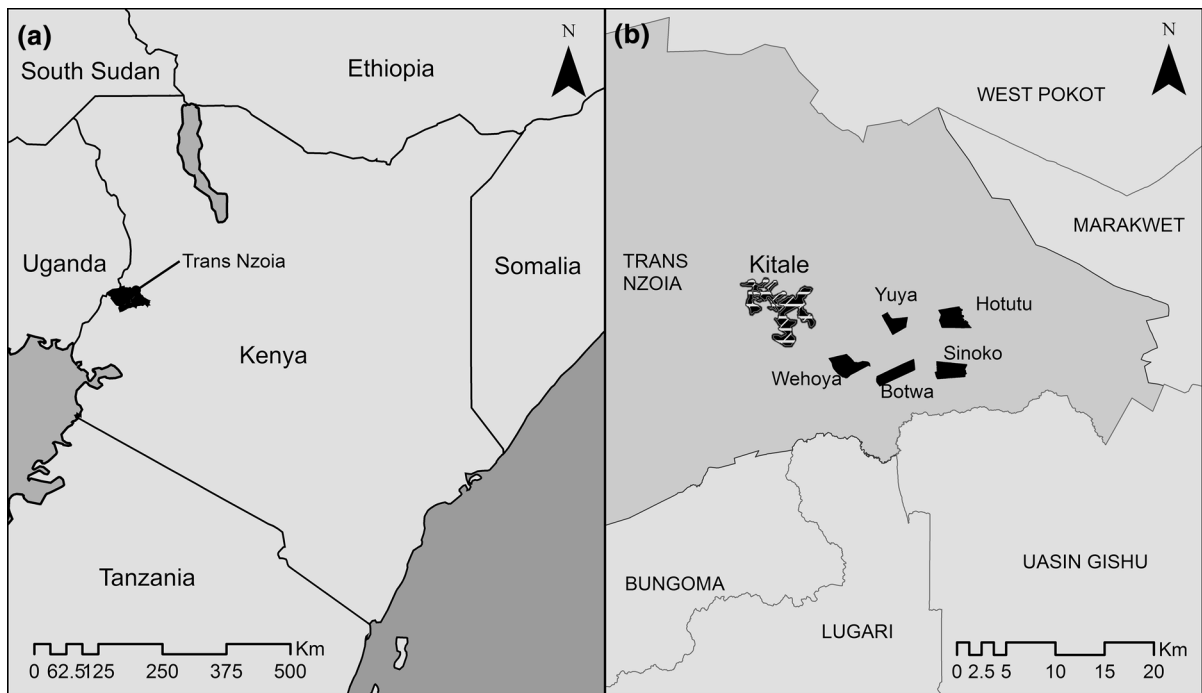
Fig. 1 Map of **a** the Trans Nzoia region within Kenya and **b** the five studied settlements (Botwa, Sinoko, Hotutu, Wehoya and Yuya) within the Trans Nzoia region and in relation to Kitale town. Two fields with shade trees and two without were assessed in Botwa, Sinoko and Wehoya, whereas three shaded and one open field were assessed in Hotuto and Yuya
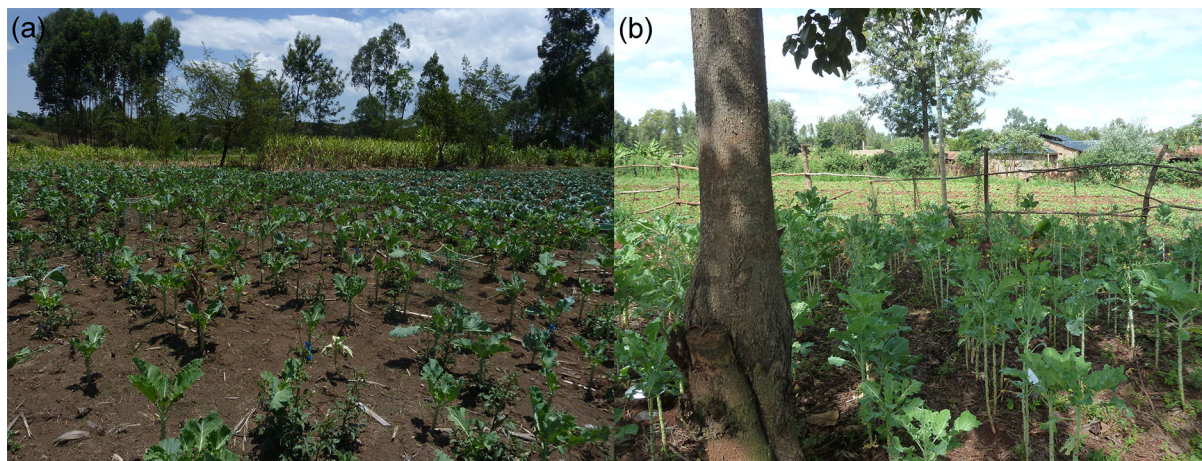
Fig. 2 Illustration of the two treatments: **a** an open field, in Hotutu, and **b** a field surrounded by shade trees, in Yuya

landscapes of similar complexity. The selected fields, of sizes varying from 20 to 100 m², all contained kale crops approximately 40–50 cm high throughout the experiment.

Each selected field was classified as being either shaded by trees or open during most of the hours of the day, by pre-classifying them visually during a first visit and confirming the categorisation after a minimum of five visits during data collection. Two fields in Botwa, Sinoko and Wehoya and one in Hotuto and Yuya, amounting to a total of eight fields, were not surrounded by any shading trees and were thus considered open. The twelve remaining fields had shade trees planted at close to regular intervals around

the perimeter and, in six cases, trees were present within the field as well (Fig. 2). Shade trees were at least 2 m high and in most cases had overarching branches. The trees consequently shaded the crops during most of the day. The tree species at the perimeter and within the fields included gum trees (Eucalyptus spp.), riverhemps (Sesbania spp.), avocado trees (Persea americana), palm trees (Arecea spp.), silky oaks (Grevilla robusta) and banana trees (Musa spp.). None of the fields were shaded by buildings or by any artificial shading systems such as nets. The order at which the fields were sampled was random, with shaded and open sites sampled within the same time intervals. All fieldwork was conducted in March and April 2014.

Pest and predator densities

At each field, the number of foliage-dwelling pests was assessed.

The number of aphids per leaf was counted on two occasion with a minimum of 12 days between counts on randomly chosen kale plants interspersed with at least 1 m. The first count took place from 6th–28th March and included one leaf per plant from a maximum of 50 plants or up to a maximum of 1000 aphids across plants, at which point the count ended at the end of the leaf where 1000 aphids had been counted (mean no. of leaves counted $\pm$ SE, 42.2 ± 2.8). The second count, took place from 7th–23rd April, following the same rules of counting up to 1000 aphids or the 50th leaf, but covered a whole plant instead of one leaf per plant, and a minimum of five plants per field.

Moth caterpillars, the only other invertebrate pest observed during the study, was counted simultaneously with aphids during their second count.

The activity-density and composition of ground-dwelling predatory invertebrates was monitored by placing four pitfall traps once in each field for 48 h, on March 25th to April 24th. The traps consisted of 850 ml plastic buckets dug down to ground level, with funnels and soap water to stop arthropods from escaping. We selected the three most common groups of ground-dwelling predators for analysis: ants (Hymenoptera: Formicidae), spiders (Arachnida: Araneae) and predatory beetles (rove and ground beetles; Coleoptera: Carabidae and Staphylinidae).

Parasitism and predation

As parasitoid wasps are known to be effective aphid biocontrol agents (Schmidt et al. 2003), aphid parasitism rate was estimated by counting alive and parasitized (mummified) aphids twice in each field, simultaneously with the pest abundance assessment previously described.

As a proxy for predation rates by ground-dwelling predators, diamondback moth egg clusters were placed on the ground in each field and removal rates were recorded after 24 h. The moth eggs were obtained from the International Centre for Insect Physiology and Ecology (ICIPE) in Nairobi. They were collected 27th–28th March in Nairobi, were received on 1st April in Kitale and kept at $+ 8$ °C until used in the experiment on 4th April (the experiment was run at all sites on the same day). Clutches of 10 (± 3) eggs were glued (UHU Super Glue liquid Ultra fast) on white 1×10 cm plastic labels. Five egg clutches were placed in each field with a minimum distance of 1 m between each clutch and attached to the ground with toothpicks, following the method described by Sandhu et al. (2008). One of the five clutches was enclosed within a 15×15 cm mesh cage (1×2 mm mesh size) as a control for desiccation and ambient egg survival without predators. All clutches were protected from rain by a round plastic cover (Ø 23 cm).

As bird predation has been found to reduce aphid populations, constrain parasitism and reduce plant damage by free-feeding caterpillars in other systems (Hooks et al. 2003; Martin et al. 2013; Ndang'ang'a et al. 2013), these variables were assessed by performing a bird exclusion experiment. Four pairs of kale plants per field were randomly selected. One plant from each pair was covered with a cage (45 cm $\times$ 45 cm $\times$ 55 cm, nylon bird mesh, mesh size 4 cm) and one was left uncaged as a control. The minimum distance between plants in each pair was 1 m and between pairs it was 2 m. On each plant, three top leaves and three bottom leaves were selected for assessing pest abundance. Living and mummified aphids were counted on half of the leaves and plant damage by chewing arthropods was estimated on the other half. The proportion of leaf damage was visually estimated with the following scale: 0, 0–10, 10–25, 25–50, 50–75 and 75–100%. Leaf herbivory and aphid numbers were assessed before placing the cages and

after the 7-day experimental period. The experiment was conducted twice on different plants with a minimum of 5 days' interval between the trials, with the first trial from 11th–28th March and the second from 1st–18th April.

Attack rates on caterpillars were estimated by placing out one surrogate caterpillar on each of ten randomly selected plants per field (each plant a minimum of 1 m apart). The caterpillars were made of non-toxic green plasticine (brand Pilens plastilina), $\sim$ 40 mm in length and 3–5 mm in diameter. Surrogate caterpillars have been successfully used for predation assessments in other systems and the method has been found efficient for comparing relative attack rates between different habitats (e.g. Loiselle and Farji-Brener 2002; Howe et al. 2009). The experiment was conducted twice on different plant individuals, with a minimum of 12 days' between the trials, with the first running 11th–28th March, and the second 1st–23rd April. Attack marks were recorded after 7 days. All marks were recorded in the field using a $10\times$ magnifying glass and were photographed for later identification. Attack marks were identified according to Howe et al. (2009) and Tvardikova and Novotny (2012). Data was summarized as presence/absence of marks for each predatory group, namely birds, predatory beetles, rodents and parasitoids, on each surrogate caterpillar. The disappearance rate of caterpillars was relatively low, with an average of 6.25% and a maximum of 30%. Non-recovered caterpillars were excluded from the analysis.

Statistical analysis

Before testing the effect of shade trees, we examined whether bird predation had an effect on aphid abundance, aphid parasitism rates and plant damage with a Mann–Whitney nonparametric test. The impact of bird predation on aphid populations was then quantified as the difference in aphid population growth rate between treatments with birds present and birds excluded. The aphid growth rate was estimated by the linear regression between day and $\log_e$ of the number of aphids per leaf, with the following formula: $\Delta r = r_{(\text{exclusion cages})} - r_{(\text{open plants})}$ (Östman et al. 2001). Leaves with no aphids on them at the start of the experiment were excluded from the analysis.

To test whether ground-dwelling arthropods were predating on moth eggs, we compared disappearance rates of caged and open egg clusters with Mann–Whitney nonparametric tests using SPSS v.20 (IBM Corp. 2011).

To test the effect of shade trees on different response variables related to pest control, we fitted generalized linear mixed-effect models (lme4 package, Bates et al. 2015) with the statistical program R v.3.3.2 (R Core Team 2017). The response variables, all averaged at field level, included the number of aphids per leaf, the abundances of free-feeding caterpillars and activity density of predators (ants, spiders, predatory beetles analysed separately and spiders and predatory beetles pooled), egg predation rates, the impact of bird predation on aphid population growth rate (Δr), the proportion of surrogate caterpillars attacked by predatory beetles, birds, rodents and parasitoids, and aphid parasitism rate. Models with all possible combinations of the following random variables were fitted: sampling date, pesticide use during the experiment and use of mulching practices, the two latter nested within settlement. For response variables expressed as proportions we used models with a binomial error distribution with an observation level vector to adjust for over-dispersion (Bolker et al. 2009). For variables expressed as counts we used a negative binomial distribution and for Δr and the log-transformed number of aphids per leaf we used a gaussian distribution (Table 1). For each response variable, we then used a model simplification procedure to select the models that best explained the variation of the data, by comparing all models according to the Akaike Information Criterion adjusted for small sample size (AICc) with the aictab function (AICcmodavg package, Mazerolle 2016). Competing models were those with a difference in AICc relative to the best AICc score (ΔAICc) equal to or lower than two.

Results

Invertebrate population surveys

We counted a total of 24,352 aphids and 40 free-feeding moth caterpillars on the plants. The presence of shade trees significantly reduced mean aphid abundance (p = 0.00002 and p = 0.00003 respectively for the two competing best-fit models, Table 1,

Table 1 Error distribution, random variables included and statistical output for each of the best-fitting generalized linear models testing the effect of shade on pest and natural enemy abundances, parasitism and predation

Response variable	Error distribution	Random variable(s)	Estimate	SE	Z value	p value
Pest abundances						
Aphids per leaf, model 1	Gaussian (log-transformed)	Sampling date	− 1.2398	0.2899	(t value) − 4.2765	0.00002***
Aphids per leaf, model 2	Gaussian (log-transformed)		− 1.2967	0.3132	(t value) − 4.1397	0.00003***
Caterpillars	Negative binomial	Sampling date	− 1.0245	0.3927	− 2.609	0.00908**
Predator abundances						
Ants	Negative binomial	Sampling date	0.4334	0.3262	1.329	0.184
Spiders	Negative binomial	Sampling date	0.5766	0.3074	1.876	0.0607
Predatory beetles	Negative binomial	Sampling date	0.8248	0.7269	1.135	0.256
Pooled spiders and predatory beetles, model 1	Negative binomial	Sampling date	0.6014	0.2508	2.397	0.0165*
Pooled spiders and predatory beetles, model 1	Negative binomial	Pesticide	0.7370	0.2550	2.890	0.00385**
Aphid parasitism rates	Binomial	Pesticide, observation level factor	0.0654	0.4099	0.16	0.873
Moth egg removal rates	Binomial	Observation level factor	− 0.05836	0.22678	− 0.257	0.797
Bird predation on aphids, model 1	Gaussian	Sampling date	0.009355	0.067950	(t value) 0.138	0.890
Bird predation on aphids, model 2	Gaussian	Mulching	0.02141	0.06621	(t value) 0.323	0.890
Surrogate caterpillar attacks by						
Birds, model 1	Binomial	Observation level factor	0.2659	0.2848	0.934	0.35
Birds, model 2	Binomial	Sampling date	0.2740	0.2872	0.954	0.34
Invertebrates	Binomial	Sampling date	0.01846	0.2503	0.074	0.941
Rodents (model 1)	Binomial	Observation level factor	0.8694	0.6669	1.304	0.192
Rodents (model 2)	Binomial	Sampling date	0.8774	0.6757	1.299	0.194
Parasitoids (model 1)	Binomial	Observation level factor	0.04351	0.54839	0.079	0.937
Parasitoids (model 2)	Binomial	Sampling date	0.04674	0.46901	0.100	0.921

* $p < 0.05$; ** $p < 0.01$; *** $P < 0.001$

Fig. 3a) as well as the abundances of caterpillars ($p = 0.00908$, Table 1, Fig. 3b).

In total, 2081 ants, 222 spiders and 48 rove and ground beetles were caught in the pitfall traps. Shade did not affect the abundance of any of the ground-dwelling predator groups when analysed individually, but significantly increased the pooled abundance of spiders and predatory beetles ($p = 0.0165$ and $p = 0.00385$ respectively for the two competing best-fit models, Table 1, Fig. 4), with a potential

impact of pesticide use as the latter was retained as a random variable improving model fit.

Parasitism and predation

For estimating aphid parasitism rate, we recorded a total of 24,352 living and mummified aphids on the plants. The overall parasitism rate was very low, 0.91%. It was not affected by shade, but pesticide use

Fig. 3 Number per field of **a** aphids per leaf (n = 40), with each dot representing the average number per leaf per field, and **b** moth caterpillars (n = 20), with each dot representing the total abundance per field, in open and shaded fields. Boxes show median and interquartile ranges for each site type, with the whiskers extending to 1.5 of the interquartile range
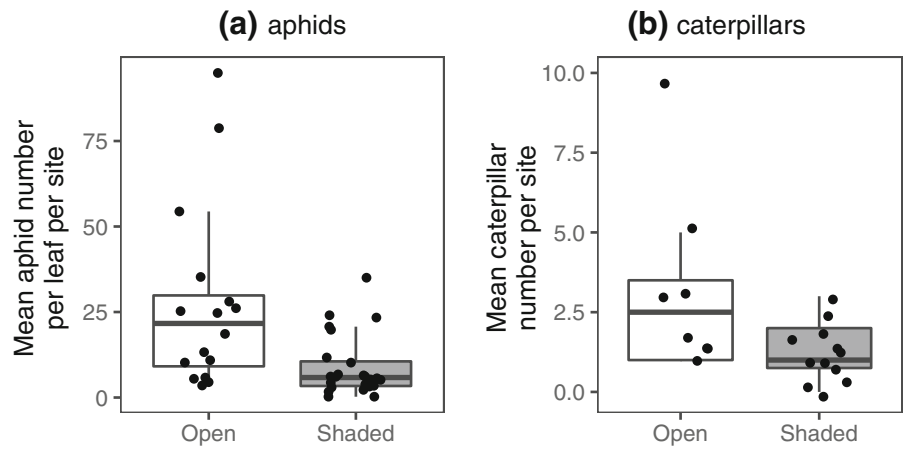
Fig. 4 Activity density per field of **a** ants (n = 20), **b** spiders (n = 20) and **c** predatory beetles (n = 20) and pooled spiders and predatory beetles (n = 20) in open and shaded fields. Each dot represents the total activity density in a field, boxes show median and interquartile ranges for each site type, with the whiskers extending to 1.5 of the interquartile range
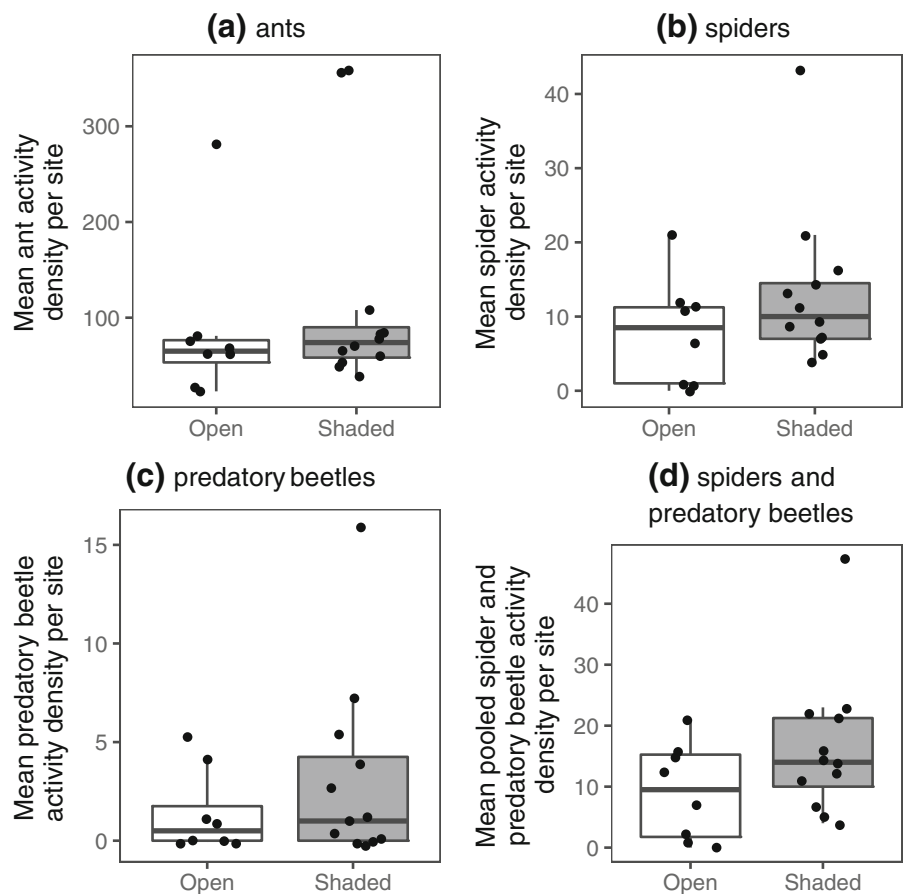
was retained as a random variable improving the model fit (Table 1, Fig. 5).

The difference between disappearance of eggs in caged control treatments and in open treatments indicated significant predation by ground-dwelling pre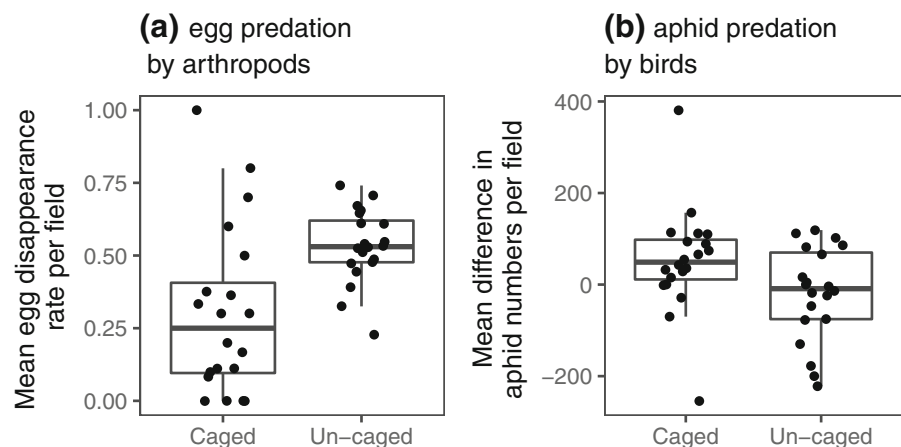dators (Mann–Whitney, U = 485.5, n = 100, p = 0.001), with the egg disappearance rate being 56.6% higher in the un-caged treatments (Fig. 6a). However, shade did not explain the variation in egg disappearance rates (Table 1, Fig. 7a). The exclusion
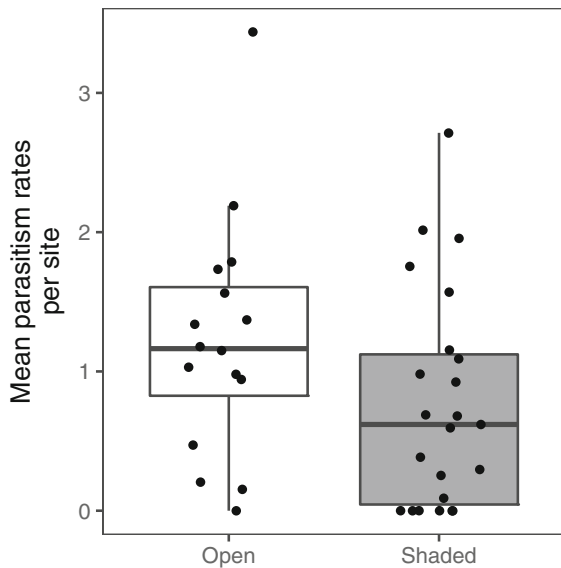
Fig. 5 Aphid parasitism rate (n = 40) in open and shaded fields. Each dot represents the average parasitism rate of a field, boxes show median and interquartile ranges for each site type, with the whiskers extending to 1.5 of the interquartile range

of birds from kale plants increased aphid abundance (Mann–Whitney, U = 10,355.5, n = 313, p = 0.018; Fig. 5b), but had no effect on herbivore-related leaf damage or on aphid parasitism rates. Bird predation on aphids was not affected by shade trees (Table 1, Fig. 7b). Surrogate caterpillars were most commonly attacked by invertebrate predators (mean ± SE proportion of caterpillars, 0.254 ± 0.024), followed by birds (0.171 ± 0.020), parasitoids (0.055 ± 0.012) and finally by rodents (0.034 ± 0.007). Attacks on surrogate caterpillars were not affected by shade (Table 1, Fig. 8).

Discussion

Our study demonstrated that presence of shade trees, inside or directly adjacent to kale fields, can reduce aphid and caterpillar pest populations on kale and increase abundances of ground-dwelling predators. However, we found no direct evidence that biological control was affected by shade, as neither predation- nor parasitism rates were affected by the presence of shade trees. This indicates that biological control by natural enemies was not the only mechanism behind reduced pest populations when shade trees were present, but that effects of microclimate on pest performance and bottom-up effects on pests, such as via changes in plant quality or soil conditions, were likely to have been important as well.

### Effect of shade on biological control

We found no effects of shade on predation rates and aphid parasitism rates in agroforestry systems compared to monocultures, thus not supporting several previous studies finding increased aphid parasitism rates (Alignier et al. 2014) and bird predation rates (e.g. Perfecto et al. 2004; Karp et al. 2013) in agroforestry systems, compared to monocultures. However, we did find that pooled abundances of ground-dwelling predatory beetles and spiders increased with shade. Although not a direct assessment of predation pressure, this increase in activity density of certain groups of natural enemies is consistent with most other studies (Pumariño et al. 2015) and indicates that biological control might still be part of the explanation between the reduced pest

Fig. 6 a Egg disappearance rate (n = 100) and **b** differences in aphid numbers (n = 313) in un-caged and caged treatments. Each dot represents the average disappearance rate per field and difference in numbers per field, boxes show median and interquartile ranges for each site type, with the whiskers extending to 1.5 of the interquartile range

Fig. 7 **a** Egg disappearance rate (n = 20), **b** bird predation rate (n = 36) in open and shaded fields. Each dot represents the disappearance rate per field and difference in numbers per field, boxes show median and interquartile ranges for each site type, with the whiskers extending to 1.5 of the interquartile range
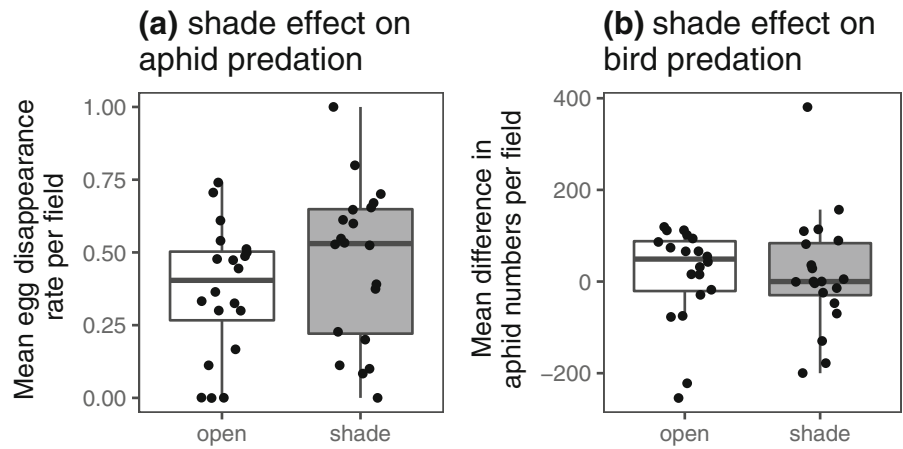
Fig. 8 Number of attacks on surrogate caterpillars by **a** birds (n = 40), **b** invertebrates (n = 40), **c** rodents (n = 40), and **d** parasitoids (n = 40) in shaded and open fields. Each dot represents the number of attacks per field, boxes show median and interquartile ranges for each site type, with the whiskers extending to 1.5 of the interquartile range
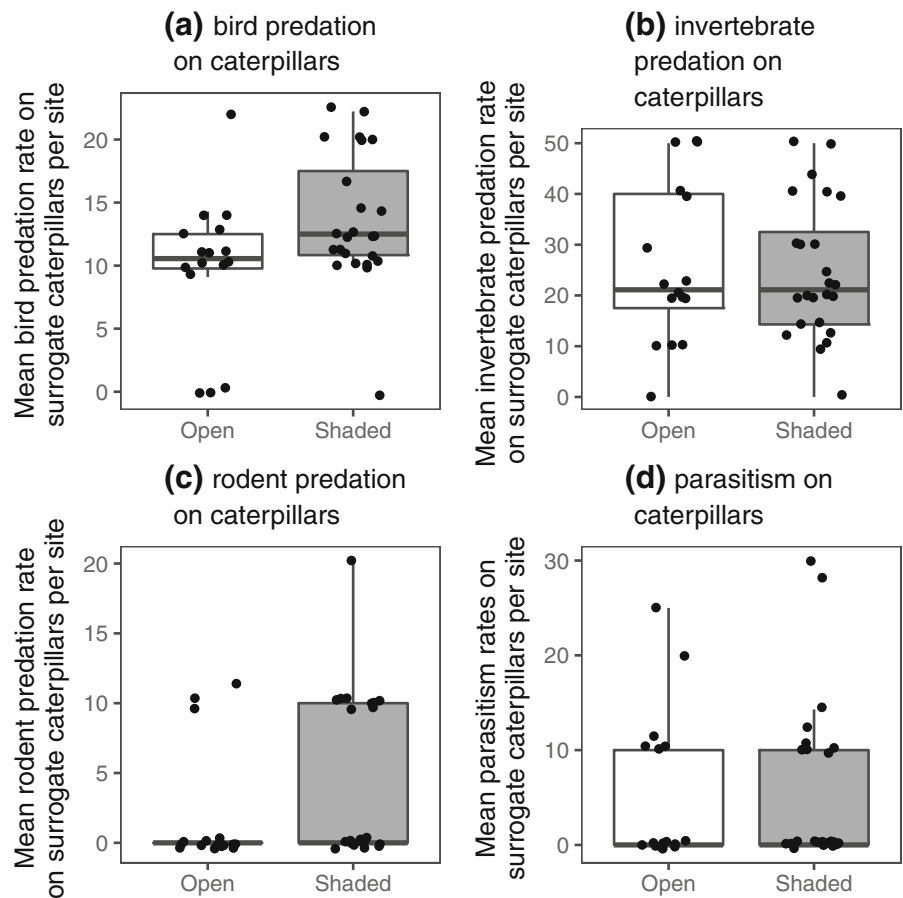
abundances in shady conditions. It should be noted however, that all our estimates of abundances and predation rates were snap-shots, and longer-term studies will be critical to properly evaluate the importance of biological control in this system.

Moreover, the incorporation of more precise measures of pesticide use could be relevant as it affected both pooled predator abundances and parasitism rates in our study and is known to have strong effects on biocontrol services in general (Geiger et al. 2010).

Microclimatic and bottom-up effects of shade on pests

Because no conclusive effect of shade on biological control potential was detected, it is likely that other factors also contributed to the reduction in pest numbers. Shade induces changes in microclimate, which can have direct effects on invertebrate physiology and thereby regulate their populations. For example, invertebrate reproductive rates are usually lower in cooler conditions, and may also be affected by humidity (Burgess et al. 1996; Chaplin-Kramer and Kremen 2012). Moreover, most insects, including aphids, use olfactory cues to locate their host plants. Incorporation of trees in agroecosystems modifies wind speed and direction, and this may influence the crop's olfactory signals for pest host location (Rao et al. 2000; Moser et al. 2009).

Furthermore, the decreased temperature and increased humidity under shaded conditions can have an impact on plant quality and palatability, which may influence pest abundances. Shade can decrease the rate of photosynthesis (Sleeman and Dudley 2001), alter plant biomass, plant height, leaf area and protein content, and alter plant chemical composition (Olsson et al. 1998; Sleeman and Dudley 2001; Barber and Marquis 2011). Chemical changes induced by shade include the decrease in phenolic compounds, known to be important for plant defence (Barber and Marquis 2011). Shade trees may also modify a crop's nutritional quality by either depleting soil nutrients following competition between crops and trees or by increasing fertilization by nitrogen-fixing trees (Rao et al. 2000). Plant nutritional quality can also be altered by decreased water stress induced by shading (Barber and Marquis 2011). Low water stress can decrease the soluble nitrogen content in brassica crops, while nitrogen is often a limiting factor for population growth of many insect pests (Burgess et al. 1996).

Effects of bird predation on pests

In our study, avian predation decreased aphid abundance, but had no effect on leaf damage by chewing herbivores. This result may seems surprising, as birds are known to decrease free-feeding caterpillar abundances and their leaf damage in kale agroecosystems (Hooks et al. 2003; Ndang'ang'a et al. 2013). However, similarly significant avian predation on aphids

has been observed in kale fields of other regions of Kenya, yet only during the dry season (Ndang'ang'a et al. 2013). This difference in predation pressure with relation to the season cautions that effects found in a single season such as with our study can not necessarily be generalised as year-round mechanisms.

Despite the beneficial effect of birds in reducing aphid abundances, the avian fauna is often considered harmful by local farmers, because some bird species are considered as pests, feeding on cereals and vegetables and spreading weeds and diseases (Chitere and Omolo 1993). Showing that birds can reduce pest damage by predation is thus of importance for promoting bird conservation.

Conclusion

This study provided further evidence that agroforestry can be used to regulate crop pests (Schroth et al. 2000; Pumariño et al. 2015), as presence of shade trees reduced populations of both aphids and caterpillars on kale. However, in contrast to many other studies, our work found no conclusive evidence of more effective biological control by natural enemies in shady habitats (although abundances of ground-dwelling predators did increase with agroforestry practices). Direct effects of changes in microclimate on pest physiology as well as bottom-up effects mediated by changes in plant or soil quality were likely also part of the mechanism behind pest reduction—although they were not explicitly measured in our study. Further research is needed to disentangle more clearly the relative importance of top-down and bottom-up mechanisms behind the often observed reductions in pest populations under agroforestry management, and to assess how these effects vary within and among seasons.

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