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Complementary ecosystem services provided by pest predators and pollinators increase quantity and quality of coffee yields

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Wild animals substantially support crop production by providing ecosystem services, such as pollination and natural pest control. However, the strengths of synergies between ecosystem services and their dependencies on land-use management are largely unknown. Here, we took an experimental approach to test the impact of land-use intensification on both individual and combined pollination and pest control services in coffee production systems at Mount Kilimanjaro. We established a full-factorial pollinator and vertebrate enclosure experiment along a land-use gradient from traditional homegardens (agroforestry systems), shaded coffee plantations to sun coffee plantations (total sample size = 180 coffee bushes). The exclusion of vertebrates led to a reduction in fruit set of *ca* 9%. Pollinators did not affect fruit set, but significantly increased fruit weight of coffee by an average of 7.4%. We found no significant decline of these ecosystem services along the land-use gradient. Pest control and pollination service were thus complementary, contributing to coffee production by affecting the quantity and quality of a major tropical cash crop across different coffee production systems at Mount Kilimanjaro.

1. Introduction

The productivity of crops depends on an intricate interplay of farming practices, abiotic conditions and ecosystem services provided by natural species communities [1]. However, in agricultural practice, the different components of such interplay still receive unequal attention. While the cost–benefit analyses of human inputs into cropping systems are easily assessable, the valuations of ecosystem services are less obvious and often neglected when new farming strategies are adopted [2]. Indeed, intensification of land use is often considered as the only possibility to meet the food demands of growing human populations. However, an impoverishment of biotic communities in the course of local land-use intensification may reduce the natural functionality of agricultural systems. Such decline requires costly human interventions that can further accelerate the loss of animal-mediated ecosystem services [3,4].

Two important ecosystem services that contribute to crop productivity and food security are pollination and natural pest control [5,6]. About two-thirds of all crop species benefit from cross-pollination by developing higher fruit sets and/or higher fruit quality [6,7]. Pollination also increases yield stability and maintains the genetic variability of crops, which counteracts inbreeding depression and facilitates resistance to environmental changes [8]. Pest predation, in contrast, enhances crop productivity indirectly: approximately 35–40% of potential crop yields worldwide

are destroyed by pests, including herbivorous insects [9,10]. Herbivores either damage the used parts of crops directly or induce resource allocations in plants. For example, leaf damage by herbivorous pests may result in reduced fruit and seed set [11]. Birds and bats, preying upon herbivorous pests, can directly reduce pest infestation rates and thus indirectly increase crop productivity [12–14].

Ecosystem services provided by pollinators and pest predators in agricultural production systems can be either additive or synergistic [15]. In the case of additive effects, pollinators and pest predators affect the same yield parameter (e.g. fruit set), but independently of each other, or they affect different yield parameters (e.g. fruit set and fruit quality), resulting in complementary effects of both guilds on crop production. However, there may also be interacting effects between pollinators and predators. Low levels of pest control can reduce pollination services owing to altered floral displays or herbivore-induced changes in plant volatile components that are avoided by pollinators [16]. Likewise, some seed predators preferentially attack cross-pollinated ovules, counteracting positive pollinator effects. Therefore, the top-down control of seed predators can stabilize positive pollination effects [15]. Such scenarios can lead to combined effects of multiple ecosystem services that are different from those of individual services.

Ecosystem services provided by pollinators and pest predators are known to be negatively affected by local land-use intensification [17,18]. For instance, loss of habitat structure by tree removal or frequent ploughing reduces the number of suitable nesting sites for animals [19]. Herbicides diminish plant diversity and thus the resource diversity for bees [20]. Regular insecticide application affects abundances of insect pollinators [21] and decreases the amount and temporal stability of food resources for insect predators such as birds and bats. Also, mass-flowering events or high biomass turnover rates, which are characteristic of intensively managed cropping systems, provide temporally unstable food and nesting resources [22], while the use of machines and increased human activity on these farms disturb mating, breeding and foraging activities [23]. The consequent loss of diversity poses serious threats to ecosystem services, as modified animal communities may be functionally impoverished [24,25].

While the effects of both pollinators and insect predators on crop performance are comparatively well understood, very few studies investigate ecosystem service synergies, i.e. interactions between functional groups and consequences for yield quantity and quality in a land-use context [15,26,27]. In this study, we investigated the impact of increased management intensity on single and combined contributions of pollinators and vertebrate pest predators to the productivity of coffee in three farming systems on Mount Kilimanjaro, Tanzania. *Coffea arabica* is a self-pollinating crop that can benefit from insect pollination by developing higher fruit set, heavier fruits and fewer seed aberrations [28]. The most important flower visitors are social bees (*Apis mellifera* (Apidae: Apini) and stingless bees (Apidae: Meliponini)), followed by solitary bees, syrphids and butterflies [29]. Birds and bats have been shown to reduce herbivore numbers and herbivory rates in natural systems [13], as well as coffee-specific pest species [14,30,31], but the consequences for fruit set and fruit quality of coffee are still a matter of debate (but see [14]). Ecosystem services provided by pollinators and vertebrates are threatened by the local intensification of farming practices on Mount Kilimanjaro. The cash crop coffee, which was traditionally planted in complex

agroforestry systems (Chagga homegardens), is now mainly produced in simplified monocultures under shade trees or at full sunlight exposure. Such habitat changes could affect pollinator and pest predator populations, with consequences for the stability of single and combined ecosystem services. Against this background, we address the following questions:

- (i) What are the single and combined effects of pest control agents and pollinators on coffee production?
- (ii) How do differently managed coffee production systems influence the magnitude of ecosystem services provided by insect predators and pollinators?

2. Material and methods

(a) Study area and study sites

The study was conducted from September 2011 to November 2012 on the southern slopes of Mount Kilimanjaro, Tanzania, at elevations between 1120 and 1660 m.a.s.l. We selected four 50 × 50 m study sites for each of three coffee (*C. arabica*) production systems: traditionally managed homegardens (HOM), shaded coffee plantations (SHA) and sun coffee plantations (SUN). The distance between study sites ranged from 0.48 to 45.56 km (2.96 to 40.05 km between study sites of the same production system). Homegardens are agroforestry systems with a diverse mixture of forest vestiges and fruit trees covering the most important cash, crops coffee and banana (*Musa* spp.), which are planted within a variety of intercrops. Canopy cover averages 80% in these systems. On shaded coffee plantations, coffee is planted in monocultures under shade trees, with a canopy cover of around 30%, whereas in sun coffee plantations coffee is grown in monoculture at full sunlight exposure.

In all management systems, farmers were requested to continue their usual farming practice during the study period: pruning was conducted once per harvest season in all systems. In homegardens, insecticides and fungicides were irregularly applied depending on the infestation rate and income level of farmers. Weeds were removed manually. On shaded and sun coffee plantations, regular, intensive pesticide and fungicide spraying was applied on the whole farm. Weeds were either controlled by herbicides (on two SHA sites and on three SUN sites), grass cutting (one SHA and one SUN) or manual weeding (one SHA). During the dry seasons (December–March, June–October), all plantations were frequently irrigated with sprinklers, while homegardens were supplied by traditional water channel systems.

(b) Study design

On each study site, we selected three clusters of four coffee bushes (minimum distance between clusters: approx. 15–20 m; see electronic supplementary material, S1a). Within clusters, we selected four bushes of similar size and with comparable bud status and applied to each bush one of the following treatments: (i) open control, (ii) pollinator enclosure, (iii) vertebrate enclosure and (iv) combined pollinator and vertebrate enclosure (figure 1). As pre-experiments revealed that the less conspicuous pollinator enclosures were often damaged by farmers during pruning, harvest or pesticide treatments, we selected three additional coffee bushes per study site outside of clusters and installed pollinator enclosure treatments and control twigs to supplement pollinator treatment bushes within clusters (see electronic supplementary material, S1a). To exclude pollinators, we used transparent gauze bags (mesh size: 0.39 × 0.77 mm) that were pulled over two randomly selected twigs with closed flower buds. Gauze bags were stretched with strings to avoid insect pollination from outside the nets and waterlogging. Two twigs served as open controls to directly contrast them to the pollinator enclosure treatment on

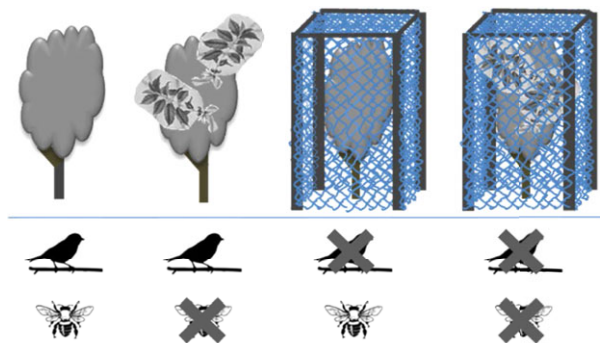


Figure 1. Experimental set-up. From the left to the right: open control, pollinator enclosure, vertebrate enclosure, combined pollinator and vertebrate enclosure (see the electronic supplementary material, figure S1a for more details). (Online version in colour.)

the hierarchical level of the coffee bush (see electronic supplementary material, S1a).

Vertebrates were excluded from two whole coffee bushes by cultivation guard net cubes (approx. $2 \times 2 \times 2$ m, mesh size 30×30 mm). One of the vertebrate enclosures was combined with one pollinator enclosure treatment (combined enclosure). Vertebrate enclosure nets were checked at least every two weeks and repaired or replaced if necessary. One coffee bush per cluster without any treatment was selected as an open control (figure 1). On both vertebrate enclosures and controls, we marked two twigs for fruit parameter assessment. A more detailed description of the experimental set-up is illustrated in the electronic supplementary material, S1a and S1b.

(c) Pollinator visitation rates

During coffee blossom, we selected coffee twigs with open coffee flowers (mean \pm s.e. number of coffee flowers per twig = 66 ± 2.9) and recorded in 10 min observation intervals all flower visitations by honeybees (*A. mellifera*) and 'other pollinators', including wild bees, syrphid flies and butterflies. We repeated observations on at least 16 coffee bushes per study site, including bushes of all treatments. Pollinator visitation rates were calculated by dividing the numbers of visits of honeybees and other pollinators, respectively, by the number of observed flowers. Neither vertebrate enclosure cubes nor the presence of pollinator enclosures on a tree negatively affected flower visitation rates on open twigs (see electronic supplementary material, S2).

(d) Fruit parameter and herbivory assessment

One week after coffee blossom, pollinator enclosures were removed to avoid exclusions of leaf and fruit herbivores that oviposit during early fruit set on the respective twigs. We counted the numbers of flowers with withered petals on all marked twigs. Buds that were not open by that time were manually removed and not counted. Six weeks after coffee blossom, we counted the number of early fruits per marked twig and related it to the number of flowers (hereafter, early fruit set). Fruits were counted again six months after the coffee blossom, as by that time fruits were harvestable on the first plots. The chance of further fruit loss on other plots was low, as fruit drop in Arabica coffee takes place in the first three months after blossoming [32]. Fruits of the same bush and twig treatment were pooled and related to both the corresponding numbers of flowers (hereafter, late fruit set) and number of early fruits (hereafter, fruit retention rate), respectively (see Statistics for more details). After fruit ripening, coffee berries of all treatments were harvested. For 15 randomly selected fruits per bush and twig treatment, we assessed fruit weight and infestation rates with the coffee berry borer (*Hypothenemus hampei*), a pest insect that drills ripening seeds for mating and oviposition (see electronic supplementary

material, S3). Herbivory rates were determined for each coffee bush by estimating the proportion of leaf damage for 30 randomly selected leaves of different age classes before the installation of vertebrate enclosures and six months later.

(e) Statistical analyses

We analysed the effect of enclosure treatments on early fruit set, late fruit set and fruit retention rate with generalized linear mixed effects models ('lmer' function in package 'lme4' [33]). The total numbers of flowers (and fruits) differed enormously between study sites. Therefore, we used a two-vector response variable for fruit set and retention rate, consisting of the number of harvestable fruits (success) and the number of 'dropped fruits' (failures, i.e. number of flowers (or early fruits) – number of harvestable fruits) for which we assumed a binomial error distribution [34]. We tested treatment and coffee production system effects on early and late fruit set and retention rate with pollinator enclosure (PollEx), vertebrate enclosure (VertEx) and production system (HOM, SHA, SUN) and all possible interactions as fixed factors. To meet the hierarchical structure of the study design, we added study site, cluster, bush and twig as nested random effects. Overdispersion of the data was corrected by adding an observation-level random effect [33]. Presence/absence of the coffee berry borer was analysed in the same way (see electronic supplementary material, S3). Impacts of VertEx, PollEx, production system and all possible interactions on fruit weight were investigated with linear mixed effects models, because the error distribution of this response variable followed a normal distribution. To meet the nested study design, we averaged fruit weight per treatment and included study site, cluster and bush as nested random effects ('lme' function in package 'nlme' [35]). For model simplification, we performed likelihood ratio tests and removed all terms that were not statistically significant [34].

We tested whether the exclusion of vertebrates influenced coffee production via altered herbivory levels on coffee bushes by fitting two linear mixed effects models with vertebrate enclosure, production system and its interaction as fixed factors, study site and cluster as random factors, and averaged herbivory per tree before and six months after the enclosures as response variables (see electronic supplementary material, S4). The influences of production system on visitation rates of 'honeybees' and 'other pollinators' were analysed with linear mixed effect models, with study site as a random factor. Models were simplified using likelihood ratio tests. All statistical analyses were conducted with the software R v. 2.14.2 for Windows [36].

3. Results

Pollinators and vertebrates increased coffee productivity complementarily by affecting different fruit parameters. Vertebrate enclosure had an effect on fruit quantity: early fruit set, fruit retention rate (see electronic supplementary material, S5) and late fruit set were significantly higher on bushes that were accessible to flying vertebrates than on vertebrate enclosures (table 1 and figure 2). By contrast, pollinators had no effect on fruit quantity parameters (table 1). Both the threefold interaction between treatments and production system, and the twofold interaction effects (PollEx \times VertEx and VertEx \times production system) on fruit set were not significant and thus not included in the minimal adequate model (table 1). We measured late fruit set reductions on an average of 9.0% under vertebrate enclosures. Also herbivory rates were affected by the six-month vertebrate enclosure: before the enclosure treatment, herbivory rates did not differ between coffee bushes (see electronic supplementary material, S4). However, six months

Table 1. Production system-dependent influence of pest control and pollination on *C. arabica* fruit set and fruit weight, respectively. Output of (generalized) mixed effects models with fruit set and fruit weight as response variables and vertebrate exclusion (VertEx), pollinator exclusion (PollEx), production system and their interactions as explanatory variables (full models). After model simplification, VertEx (in case of fruit set) or PollEx (in case of fruit weight) remained the only explaining variables in the models (simplified models). Significance codes: ** $p < 0.01$; * $p < 0.05$.

fixed effects	full model				simplified model			
	nDF	dDF	test statistics	p	nDF	dDF	test statistics	p
late fruit set			χ^2				χ^2	
VertEx	1	—	4.73	0.030*	1	—	4.89	0.027*
PollEx	1	—	0.17	0.682				
production system	2	—	6.04	0.049*				
VertEx \times PollEx	1	—	0.34	0.557				
VertEx \times production system	2	—	3.91	0.142				
PollEx \times production system	2	—	1.51	0.470				
VertEx \times PollEx \times production system	2	—	1.00	0.608				
fruit weight			F				F	
VertEx	1	90	0.13	0.724				
PollEx	1	78	8.84	0.004**	1	83	8.93	0.004**
production system	2	9	0.48	0.636				
VertEx \times PollEx	1	78	1.55	0.217				
VertEx \times production system	2	90	0.84	0.434				
PollEx \times production system	2	78	0.63	0.534				
VertEx \times PollEx \times production system	2	78	1.13	0.329				

after enclosure installation, leaf herbivory rates were significantly higher under vertebrate enclosures in homegardens and unshaded plantations than on control bushes to which vertebrates had access (figure 3). The infestation of berries with the fruit borer *H. hampei* was not affected by treatments and production system (see electronic supplementary material, S3; averaged infestation rates 1.53%).

Fruit quality was affected by pollinator exclusion, but not by vertebrate exclusion: fruit weight decreased on average by 7.4% when pollinating insects were excluded from coffee flowers (table 1 and figure 2). Both threefold and twofold interaction effects (VertEx \times PollEx, PollEx \times production system) on fruit weight were not significant (table 1).

The composition of flower visitors shifted along the land-use gradient: visitation rates of honeybees (*A. mellifera*) drastically increased with land-use intensity, resulting in 3.4 times higher honeybee visitation rates on sun plantations than in homegardens. Interestingly, in homegardens more than one-third of flower visitations were by other pollinators than *A. mellifera*. In total, flower visitation rates by other pollinators were 8.2 times higher in homegardens than in sun plantations (figure 3; electronic supplementary material, S2b).

4. Discussion

(a) Complementary contribution of pest control agents and pollinators to coffee production

We showed that both vertebrate pest predators and pollinators contribute to coffee production at Mount Kilimanjaro by

affecting different yield parameters, i.e. fruit quantity (fruit set) and fruit quality (fruit weight), respectively. As both fruit set and fruit weight increase coffee farmers' total yield, the conservation of ecosystem services provided by pollinators and flying vertebrates may be of considerable economic importance. The exclusion of birds and bats resulted in an increase in herbivory and, importantly, also in a reduction of fruit set by an average of 9.0%. The effectiveness of birds and bats in controlling arthropod abundance, pest infestation rates and herbivory has been shown on coffee farms [13,14,30,31]; however, the consequences of such changes for economically relevant fruit parameters are rarely documented (but see [14]). We suggest that the increase in herbivory rates under the enclosures partly explained the reduction of fruit set, as herbivory pressure can trigger resource allocation from reproductive to vegetative organs of plants [37]. However, as the increase in herbivory was only weak, we assume that changes in arthropod assemblages (e.g. an increase in leaf-sucking insects [27]) under vertebrate enclosures additionally affected fruit set. In addition to vertebrates, parasitoid wasps are known as important agents controlling herbivores on coffee plants [38], whose contribution to coffee production could not be analysed in this study. Future studies should incorporate this important group in experiments to assess the total benefit of natural biota for agricultural production.

Self-compatible *C. arabica* profited from insect cross-pollination by developing, on average, 7.4% heavier fruits on open pollinated twigs than on self-pollinated twigs. An effect of cross-pollination of a similar order of magnitude has been shown in the few other studies that considered not only fruit set but also fruit weight of coffee in their analyses

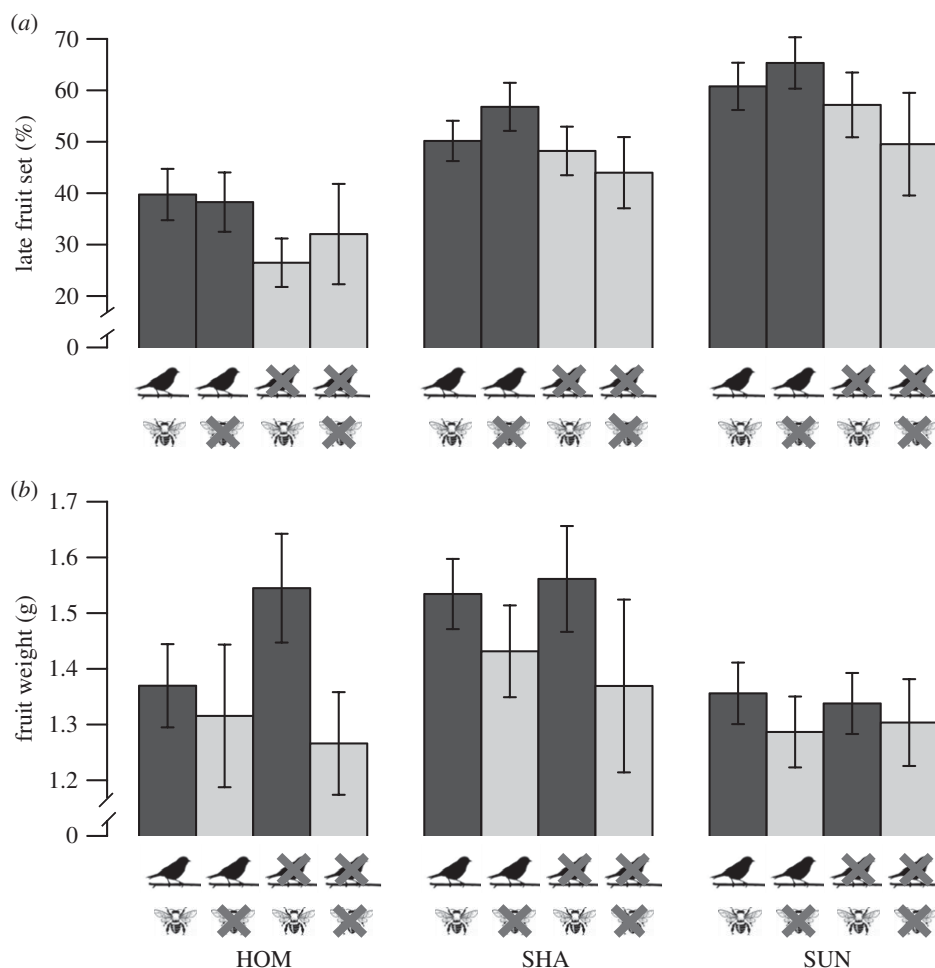


Figure 2. Effects of single and combined vertebrate and pollinator exclusions on late fruit set and fruit weight of *C. arabica* in different production systems (home-gardens (HOM), shaded plantations (SHA), sun plantations (SUN)). Statistics are presented in table 1 and the electronic supplementary material, S6. Vertebrate pest predation, but not pollination, positively influenced fruit set (a). By contrast, pollination, but not pest predation, resulted in increased fruit weights (b). Bar colours in each panel indicate which treatments were lumped in the course of model simplification. Please note that fissures were applied to y-axes for better effect resolutions.

[39,40]. Increased pollen loads and higher genetic pollen diversity have been proposed to influence the seed weight of self-compatible plants, but detailed information about the physiological mechanisms are still missing [40]. Seed size (which is correlated with seed weight) is of special economic interest as it does not only increase the total yield but also has a crucial impact on the quality and price of coffee. To our surprise, pollinators did not affect fruit set, which is inconsistent with the results of other studies investigating pollinator dependencies of coffee [39,41], though not uncommon for self-compatible plants like *C. arabica* [42]. Ngo *et al.* [29] proposed that effects of pollinator exclusions differ between locations or coffee varieties [29]. Indeed, most previous studies were conducted in the Neotropics or Asia, but not in Africa, where coffee originates [32].

We did not find interaction effects between pollination and pest control. These results suggest that, in *C. arabica*, the effect of pollination on fruit weight is independent of the pest control level and, *vice versa*, cross-pollination does not alter the effect of pest control on fruit set. We suggest that, in coffee, physiological mechanisms triggered by herbivory (e.g. resource allocations) are not linked to the pollination-dependent physiological pathways affecting fruit quality, which might explain independencies. However, by installing vertebrate and pollinator exclusions only shortly before flowering, we *a priori* excluded some interaction mechanisms that are

explained by increased herbivory immediately before or during flowering (e.g. floral tissue damage diminishing the attractiveness of flowers to pollinators) [16]. Furthermore, unconsidered pest control agents (like parasitoids) could interact with pollination services.

(b) Effects of local land-use intensity on ecosystem services

Against expectations, we found no significant effect of land-use intensity on the ecosystem services provided by pollinators and pest predators. Sun coffee plantations are currently embedded in a tessellated and still diverse landscape at Mount Kilimanjaro and may benefit from high connectivity to structurally more complex habitats, such as homegardens, shaded plantations and forests, which provide nesting sites and stable food resources for pest predators and pollinators [28]. Mobile animals have been proposed to increase their foraging ranges in intensified systems, which can additionally buffer potential ecosystem service declines [43]. Interestingly, we detected a shift in the composition of flower visitors along the land-use gradient: mass-flowering events on sun plantations attracted only very few other coffee flower visitors than *A. mellifera*, while in homegardens more than one-third of flower visitations were from wild pollinators. Despite variable total flower visitation rates, pollination services were stable in all production systems.

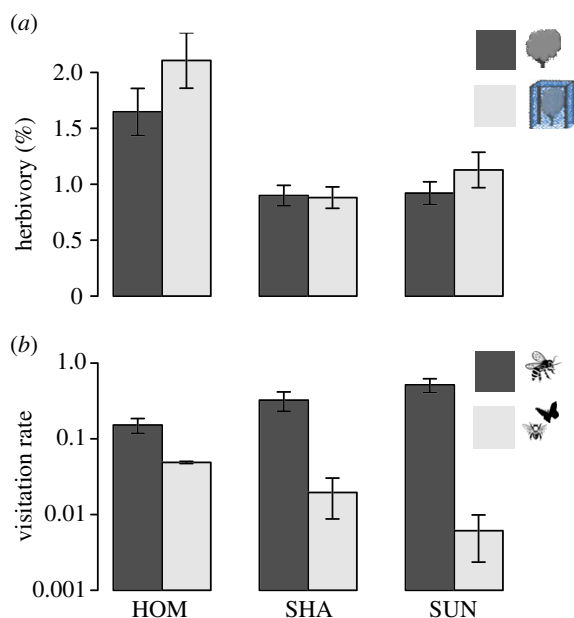


Figure 3. Herbivory and pollinator visitation rates at Arabica coffee in different production systems. (a) Shows averaged leaf herbivory (%) on open controls (dark bars) and under vertebrate exclusions (light bars) six months after exclusion installation. (b) Presents averaged coffee flower visitation rates (i.e. averaged number of pollinator visits per flower) of honeybees (*A. mellifera*) (dark bars) and 'other pollinators', including wild bees, butterflies and syrphid flies (light bars) during 10 min observation intervals. Statistics are presented in the electronic supplementary material, S4b (herbivory) and S2b (visitation rates). Note, log-transformation of the y -axis in (b). (Online version in colour.)

Either there is no pollinator-limitation along the land-use gradient or the services provided by a few wild pollinators can fully replace pollination service by more abundant honeybees [44]. This suggests that management forms that support wild

pollinators are both productive and less sensitive than systems relying on single, managed pollinator species (honeybees), as pollination services are stabilized under varying environmental conditions [8]. This is supported by Ricketts, who showed that wild pollinators can compensate drastic *Apis* declines by stabilizing visitation rates on coffee farms that are near to tropical forest fragments, but not on isolated farms [45]. Further expansions of sun coffee plantations that isolate intensified systems from more natural systems may therefore reduce the stability of ecosystem services, with potential negative effects for crop productivity.

We showed that the complementary ecosystem services provided by pest predators and pollinators support the productivity of a major tropical cash crop, *C. arabica*. Land-use intensification does not influence these ecosystem services at Mount Kilimanjaro; however, shifts in the composition of pollinator visitors raise concern about the stability of ecosystem services in intensified systems. Optimization of ecosystem services in agricultural landscapes thus requires not only knowledge of multiple ecosystem services operating in parallel, but also of management strategies that reliably match the demands of the wild animals providing these services.

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