Basic and Applied Ecology 73 (2023) 51–61

Contents lists available at ScienceDirect

Basic and Applied Ecology

journal homepage: www.elsevier.com/locate/baae

RESEARCH PAPER

The importance of shrubland and local agroecological practices for pumpkin production in sub-Saharan smallholdings

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ARTICLE INFO

Keywords:
agroecology
florivory
flower herbivory
pest management
pollination
pollinator limitation
pumpkin fruit set
smallholder agroecosystems
soil management
tropical agriculture

ABSTRACT

Land-use and local field management affect pollinators, pest damage and ultimately crop yields. Agroecology is implemented as a sustainable alternative to conventional agricultural practices, but little is known about its potential for pollination and pest management. Sub-Saharan Africa is underrepresented in studies investigating the relative importance of pests and pollinators for crop productivity and how this might be influenced by surrounding landscapes or agroecological practices. In Malawi, we selected 24 smallholder farms differing in landscape-scale shrubland cover, implementation of manual pest removal as an indicator of an agroecological pest management practice, and the number of agroecological soil practices employed at the household level, such as mulching, intercropping and soil conservation tillage. We established pumpkin plots and assessed the abundance and richness of flower visitors and damage of flowers (florivory) caused by pest herbivores on flowers. Using a full-factorial hand pollination and exclusion experiment on each plot, we investigated the relative contribution of pollination and florivory to pumpkin yield. Increasing shrubland cover decreased honeybee abundance but increased the abundance and richness of non-honeybee visitors. Manual removal of herbivores considered to be pests reduced flower visitors, whereas more agroecological soil management practices increased flower visitors. Neither shrubland cover nor agroecological management affected florivory. Pollinator limitation, but not florivory, constrained pumpkin fruit set, and increasing visitor richness decreased the relative differences between hand- and animal-pollinated flowers. We recommend improved protection of shrubland habitats and increasing agroecological soil practices to promote pollinator richness on smallholder farms.

Introduction

Land-use change, through the conversion of (semi-)natural habitats and the intensification of agricultural practices, is a major driver of biodiversity loss worldwide (IPBES, 2019; Newbold et al., 2015). Crop productivity is dependent on ecosystem services provided by biodiversity, such as pollination and pest control. The abundance and richness of biodiversity and their associated ecosystem services are related to the composition of the landscape surrounding crop fields (Martin et al., 2019a): for example, loss of semi-natural habitats surrounding crop fields and the intensification of agriculture can reduce the abundance and richness of pollinators (Kennedy et al., 2013) and can increase the abundance of pests (Tamburini et al., 2020). The links between land-use, biodiversity, ecosystem services and crops are relatively understudied in tropical landscapes cultivated by smallholder farmers compared to temperate landscapes, particularly in sub-Saharan Africa (Otieno et al., 2020; Vanlauwe et al., 2014). Low-income farmers often lack the means to counteract lowered productivity with costly synthetic inputs, and are

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https://doi.org/10.1016/j.baae.2023.10.004
Received 22 March 2023; Accepted 27 October 2023
Available online 30 October 2023

vulnerable to the impacts of biodiversity loss and the decline of associated ecosystem services (Rasmussen et al., 2018).

Smallholders grow a variety of pollinator-dependent crops essential for food security or income, such as legumes, squashes, coffee and cacao (Klein et al., 2007). Consequently, smallholder farmers depend at least partially on pollinators for their livelihoods (Chaplin-Kramer et al., 2014; IPBES, 2016). Insufficient crop visitation by pollinators can result in pollinator limitation – with sub-optimal fruit or seed set or reductions in the nutritional and commercial value of crops as a consequence (Klatt et al., 2014; Wilcock & Neiland, 2002). Crop pollinator limitation is a widespread phenomenon and has been reported from the USA (e.g., Reilly et al. 2020), Europe (e.g., Bartomeus et al. 2014; Holland et al. 2020), South America (e.g., Chacoff et al. 2008), and India (e.g., Basu et al. 2011). Although some studies have compared pollinated to pollinator-excluded crops in sub-Saharan Africa (e.g., Vogel et al., 2021) and pollinator limitation has been reported in the region (Sawe et al., 2020), sub-Saharan Africa lacks representation in the literature on the consequences of land-use change on crop pollinators and pollination services (Otieno et al., 2020).

In addition to pollinator limitation, pest damage can constrain crop yield. Compared to pollinators, the landscape drivers of insect pest abundance and damage are less consistent between studies as responses are modulated by species traits (Tamburini et al., 2020). Florivorous pests may be of particular importance for pollinator-dependent crops as damage to the flowering structures may prevent fruit set altogether or prevent proper development of fruit (McCall & Irwin, 2006). Potentially, pest abundance can benefit from landscapes low in semi-natural habitat as agricultural landscapes host high covers of suitable host (crop) plants. In addition, landscapes low in semi-natural habitats may have a lower abundance and richness of natural enemies (Chaplin-Kramer & Kremen, 2012) Despite evidence suggesting that pollinators and pests interactively shape yield (Lundin et al., 2013; Tamburini et al., 2019), pollination and herbivory are more commonly studied in isolation and rarely focus on florivory. Determining the relative importance of florivory and pollination to a crop in the smallholder context is needed to focus management efforts.

Insects may additionally be directly impacted by management choices of farmers. The abundance and richness of beneficial insects may be enhanced by an agroecological (hereafter “agroecology”) compared to conventional agriculture (Bengtsson et al., 2005). Agroecology aims to harness ecological processes whilst minimising the dependency on synthetic inputs such as synthetic fertiliser and pesticides (Wezel et al., 2020). Diversifying agroecological soil practices, such as intercropping, mulching and soil conservation tillage, has numerous social and agronomic benefits for smallholders (Rosset & Alteiri, 2017). In particular diversifying agroecological soil practices benefits smallholder food security (Bezner Kerr et al., 2021) and climate change adaptation (Snapp et al., 2021). Emerging evidence also suggests co-benefits of diversified agroecological soil management on the abundance of pollinating taxa such as butterflies (Vogel et al., 2023a), but it is so far unknown if diversified agroecological soil practices can also lead to improved yield outcomes of pollinator-dependent crops.

In addition to soil management, pest management is a major priority for farmers and motivates the use of synthetic pesticides. Pesticides have numerous disadvantages such as reduced efficacy with continued use (Ekström & Ekbom, 2011; Krauss et al., 2011). In principle, agroecological pest management should avoid these problems (Wezel et al., 2020). A specific agroecological pest management practice is manual removal or squashing of perceived pests. In contrast to chemical pest control, a common assumption is that targeted manual pest removal should not affect non-pest organisms such as pollinators. At the same time, however, the ecological knowledge of farmers on which insects are pests, and which are potentially beneficial, may be limited (Enloe et al., 2021). Especially pollinators that occur as larvae on crops, such as syrphid flies and butterflies, may be mistaken by farmers for larviform pests. For example, increasing agroecological pest control practices has been found to negatively impact a common butterfly (Vogel et al., 2023a). Before the practice is widely encouraged and implemented as a sustainable alternative, it is important to confirm that manual pest removal is effective at reducing flower damage without negatively affecting flower visitors.

In our study region in Malawi, pumpkin (Cucurbitaceae: *Cucurbita pepo*) is valued by smallholders for consumption and sale in local markets (Chagomoka et al., 2013). As a monoecious crop, pumpkin is completely pollinator-dependent (Klein et al., 2007) – but being non-native to our study region, it is unknown which insects are common pumpkin flower visitors. Pumpkin in Malawi is affected by numerous florivorous pest species, though leaf beetles (Chrysomelidae) are considered the most important (Kapeya & Maulana, 2003). Malawi lies in the biodiverse Miombo woodland ecoregion (Ribeiro et al., 2020), but woody shrubland habitats in Malawi are rapidly declining (Chirambo & Mitembe, 2014), with unknown consequences for crop visitation by flower visitors and pests. In fact, it is unknown if either of these factors constrains pumpkin productivity in Malawi. Therefore, we conducted a full-factorial exclusion experiment assessing the relative importance of florivory (bagged vs. unbagged flowers) and pollination (hand, animal and unpollinated flowers) across smallholder farms spanning independent gradients of shrubland cover and the implementation of agroecological practices to test the following predictions:

(1) The surrounding landscape and agroecological management practices affect insect activity in pumpkin fields. We expect (a) the abundance and richness of pumpkin flower visitors to increase, and florivory to decrease with increasing shrubland cover in the landscape, (b) manual pest removal to decrease florivory but leave flower visitors unaffected, and (c) that increasing the number of agroecological soil management practices to increase the abundance and richness of flower visitors while not affecting florivory.
(2) The surrounding landscape and agroecological management practices affect pumpkin yield. We expect that pumpkin fruit set, seed set, and fruit size and weight (a) to increase with increasing shrubland cover in the landscape, (b) to increase with manual pest removal, and (c) to increase with an increasing number of agroecological practices.
(3) The pollination and exclusion experiment affects pumpkin yield (fruit set, seed set, and fruit size and weight) of treated flowers. We expect (a) unpollinated flowers (bagged before flowering) to have no yield, (b) animal-pollinated and unbagged flowers (exposed to florivory) to have the lowest yield, (c) hand-pollinated and unbagged flowers to have an intermediate yield, and (d) hand-pollinated and bagged flowers (not exposed to florivory) to have the highest yield.
(4) If yield differences between treated flowers are detected, these differences depend on flower visitors and florivory. We expect that (a) in fields with a lower abundance and richness of flower visitors, yield differences between hand- and animal-pollinated flowers will be higher (indicating pollinator limitation), and that (b) in fields with high florivory, we expect that yield differences between bagged (excluded) and unbagged flowers will be larger.

Materials and methods

Site selection

This study was part of a broader transdisciplinary and participatory research project aimed at understanding the dynamics between land-use, agroecological practices, biodiversity and ecosystem services in Mzimba District, northern Malawi (Kpienbaareh et al., 2022). In October 2019, we selected 24 smallholder households with varying agroecology implementation who agreed to participate in the study (see Appendix A:

Fig. S1). Sites were at least 2 km apart to avoid overlap within 1 km radii. Maize (the main staple food) and tobacco (the main cash crop) are the dominant crops in this region. Farms in this region are typically small, ranging from 0.5 to 1.4 hectares (FAO, 2018). Additionally, each household differed in the implementation of agroecological practices. As an indicator agroecological pest management practice, we investigated manual pest removal, which half the households implemented. The agroecological soil management practices included were: soil conservation landscaping (such as terracing or pit planting), planting of vetiver grass hedges, mulching, legume intercropping, incorporation of legume residues, application of compost, application of animal manure, and agroforestry (Table S1: see *Pest and soil management survey* below, for details).

Selected households were located along a gradient of shrubland cover ranging from ~10–71 % cover in a 1 km radius (Fig. S2). We chose 1 km radii as this is a commonly applied scale in ecological studies focusing on landscape effects (Martin et al., 2019a), and covers the foraging ranges of most pollinators (Steffan-Dewenter et al., 2002). Details on how the surrounding landscape cover was quantified are provided in Supporting Information 1 (see Appendix A). Shrublands in the study region are characterised by natural vegetation typical for the Miombo woodland ecoregion (Fig. S3; Ribeiro et al. 2020). As these shrubland habitats are not effectively managed and protections unenforced, they are affected by activities such as grazing, charcoal production and the collection of firewood (Gumbo et al., 2018). Malawi is located in the seasonal tropics, with a distinct rainy season from approximately late November to April, which is also the main growing season for crops (Gama et al., 2014).

Six of the participating households owned honeybee hives, but the presence of these hives was not correlated with semi-natural habitat cover, manual pest removal, or agroecological soil management practices (Table S2) and did not affect honeybee abundance on our plots (linear model: $F = 0.25$, $p = 0.624$). Hives were not located next to pumpkin fields, nor on neighbouring fields, and were traditional hives (Fig. S4), which are hung in trees where they are potentially colonised by a honeybee colony. In our study region, the majority of honeybees are wild-nesting (Requier et al., 2019).

Field preparation

Each farmer was provided with the same local variety of pumpkin seed sourced from a local market. We established a 2×15 m plot in October 2019 and farmers sowed between mid-December 2019 to mid-January 2020, with a density of three seeds every metre, in two rows across the plot. Plots were rain-fed only and not irrigated, in line with typical management in the region. Farmers only used organic compost (called "Bokashi") (Quiroz & Céspedes, 2019), applied twice during the growing season. Soil preparation and sowing were done by farmers using a hand-hoe, as per usual practice. All day-to-day field management activities, including the use of manual pest management (see *Pest and soil management survey* below, for details), were managed by the smallholder farmers themselves.

Hand pollination and exclusion experiment

In each pumpkin patch, we marked a minimum of 8 to 19 female flowers, with a mean of 12 (SD ± 3.66) flowers. Female flowers can be easily distinguished from male flowers before blooming by the presence of ovaries that look like a small pumpkin below the petals, which the male flowers lack (Fig. S5). We aimed to use flowers of different plant individuals. Of these marked flowers, 2-5 remained open (animal pollination and florivory), 2-5 were hand pollinated (N pollination, florivory), 2-5 were hand pollinated and covered with an organza mesh bag (supplementary pollination, no florivory) and 2-5 were covered with a mesh bag just before blooming with no further treatment (all insects excluded). Flowers were hand-pollinated by depositing pollen from a male flower (the donor) from the same plot onto a female flower using a soft paint brush. Mesh bags were removed after fruit set or when flowers withered, and the fruit was left to develop as normal. All flowers received were treated between the 13th of February and the 3rd of March 2020. For consistency, all manipulations in the hand pollination and exclusion experiment were performed by the same researcher (1st author of the study).

Flower visitor recordings

Flower visitors were assessed in three rounds of transects on each plot between the 13th of February and the 10th of March. At each transect round, we walked 3 subtransects of 5 minutes per 5 m, covering the full 15×2 m plot with random walks. We considered an insect morphospecies a flower visitor if we had previously seen at least one individual contacting the reproductive parts of the pumpkin flower. The same individual was not counted twice, even if it visited multiple flowers. As the density of individual flower visitors was usually quite low, it was possible to track the movements of individual insects. Being well known nectar and/or pollen feeders, we considered bees, syrphids and tabanids as flower visitors. We also observed flower visitation by oil beetles (Meloidae) and leaf beetles (Chrysomelidae), but we considered these as flower herbivores as they were actively feeding on flowering structures (Fig. S6). Few other flower visitors were observed. Flower visitors that were not identifiable in the field were captured with an insect net and pinned for later identification. Flies were identified to family using the key in Marshall et al., (2017)and separated by morphospecies, whereas bees were identified to genus and (morpho)species using the keys in Michener (2007) and Eardley et al. (2010). Captured flower visitors are stored in the Biocentre at the University of Würzburg. All transects and flower visitor identification were performed by the first author of the study to prevent sampling bias. As pumpkin flowers close in the afternoon, all transects were walked between 08:00 and 15:00. The order in which sites were visited was randomised for each round of visits. The total observation time at each plot was 45 min.

Flower density, damage, and yield assessment

During each transect walk, we counted all open pumpkin flowers in the plot. Male and female flowers were counted separately. At each visit we also checked all flowers for damage and counted the number of flowers that exhibited (traces of) florivory, defined as feeding damage to the flowering structures. Damage to the petals was recorded separately from damage to the reproductive parts of the flowers, but we summed both damage types for analysis. All tagged flowers were monitored until harvest or abortion of fruits. First, we recorded whether fruit set had occurred. Second, when the fruits were harvest-ready, we weighed pumpkins, measured the girth (circumference at widest axis), and counted the number of seeds per fruit. In our subsequent analyses, we distinguish between "early fruit set" and "harvestable fruit set". Early fruit set included all flowers that developed a fruit, as we assume initial fruit development to be a direct consequence of pollination. Harvestable fruit set excluded any of these fruits that were not suitable for consumption or sale, for any reason, such as later abortion, rot, or damage by rodents (Fig. S7). All yield data was collected by the same researchers (2nd and 3rd authors of this study).

Pest and soil management survey

To assess the implementation of manual pest removal and soil agroecological management practices on the farms on which our pumpkin fields were located, we performed structured interviews with farmers from the 8th to 26th of March 2020. Respondents had the study explained to them and gave informed consent prior to answering questions. We asked questions about agroecological practices performed for up to three fields per farm. The questions were posed as a yes or no question (i.e.,

did you perform x practice on this field?). In addition, farmers were asked if they performed any additional practices that were not prompted in our survey. The questions were asked only to the adults of the household (men or women) who directly managed the plots. As a pest management practice, 12 of the 24 farmers reported squashing or physically removing pests, both of which we consider manual pest removal. We asked about the use of other pest management practices (for example, the use of botanical extracts) but very few reported using these methods. None of the farmers reported using synthetic pesticides on their farms. We did not instruct farmers to apply additional pest management practices, as it was not the aim of this study to encourage pest management by smallholders. Farmers reported on the following nine practices that aimed to maintain soil quality (hereafter: "soil management practices"), individual soil management practices were practiced by one up to 13 households (Table S1). These practices are the same as reported by smallholders from the same study area a year earlier (Vogel et al., 2023b), and farmers did not report any additional soil management practices. We conducted a total of 24 interviews, one for each farm on which data were collected. To obtain a single value for the diversification of soil management implementation on each farm, we used a cumulative number of soil practices adopted by the farming household, which we hereafter name "number of agroecological soil management practices". The Institutional Review Board of Cornell University for Human Subjects Research reviewed and approved the research study design (protocol 1811008425).

Statistical analysis

All data analyses were performed using R version 4.1.0 (R Core Team, 2021). Since the predictors: shrubland cover and the number of agroecological soil practices (hereafter "soil practices") were in different units of measurement, we standardized them using z-scores. Although there was variation in the number of flowers across plots, we could not detect any effect of landscape nor management on flower number (Table 1).

Effects of landscape and agroecology on flower vistors and florivory

We tested the effect of three predictors on flower visitor abundance and richness: shrubland cover, the implementation of manual pest removal, and soil practices. There were no strong correlations between these predictors (Table S2). For the overall abundance of all flower visitors, honeybees, non-honeybees (bees and flies together), bees excluding honeybees ("other bees"), and flies, we summed across all transects per site and tested them against our predictors in a negative binomial model using the function 'glm.nb' from the 'MASS' package (Venables & Ripley, 2002). We tested the effect of the predictors on cumulative visitor richness using a generalized linear model with Poisson distribution using the function 'glm'. In all models, we used log-transformed flower abundance as an offset to account for the local attractiveness of the pumpkin fields due to differences in flower abundance. Flower abundance was log-transformed to fit the Poisson or negative binomial distributions (log-distributions) of the responses. To assess the effects of the predictors on the proportion of damaged flowers per field, we summed the values of damaged and undamaged flowers across the three transects and calculated the proportion of damaged flowers. We implemented a generalised linear model with a Beta distribution using the function 'glmmTMB' from the 'glmmTMB' package (Brooks et al., 2017). As models with beta distributions can only handle responses within the open interval between 0 and 1, we added 0.001 to the proportional damages in all fields in order to achieve model convergence.

Effects of exclosure treatments, landscape and agroecology on pumpkin yield

We assessed the effects of hand pollination and exclusion treatment, shrubland cover, soil practices and manual pest removal on pumpkin yield metrics. We excluded the negative control (bagged before flowering), since this treatment only produced fruit in a single case. Since no other flower visitor-excluded flower produced fruit, we considered this measurement potentially erroneous, and a single replicate was not sufficient to be included in statistical models. For the other treatments, the

Table 1
Model results of flower abundance, flower visitor and florivory responses to shrubland cover and agroecological practices. Bold p-values indicate a significant response.

Response	Predictors	Chi^2	p-value	DF_{num}/DF_{den}	R^2	Model type
Flower abundance	Shrubland cover [%]	1.24	0.266	1/22	0.08	GLM with a negative binomial distribution
	Manual pest removal	0.06	0.802	1/21		
	Number of soil practices	0.02	0.895	1/20		
Total abundance of flower visitors	Shrubland cover [%]	8.04	**0.005**	1/22	0.19	GLM with a negative binomial distribution
	Manual pest removal	6.55	**0.011**	1/21		
	Number of soil practices	11.72	**<0.001**	1/20		
Non-honeybee abundance	Shrubland cover [%]	52.16	**<0.001**	1/22	0.67	GLM with a negative binomial distribution
	Manual pest removal	19.04	**<0.001**	1/21		
	Number of soil practices	47.99	**<0.001**	1/20		
Honeybee abundance	Shrubland cover [%]	9.41	**0.002**	1/22	0.17	GLM with a negative binomial distribution
	Manual pest removal	4.73	**0.030**	1/21		
	Number of soil practices	7.64	**0.006**	1/20		
Other bee abundance	Shrubland cover [%]	8.43	**0.004**	1/22	0.35	GLM with a negative binomial distribution
	Manual pest removal	0.19	0.658	1/21		
	Number of soil practices	18.28	**<0.001**	1/20		
Fly abundance	Shrubland cover [%]	41.01	**<0.001**	1/22	0.60	GLM with a negative binomial distribution
	Manual pest removal	25.84	**<0.001**	1/21		
	Number of soil practices	27.82	**<0.001**	1/20		
Visitor richness	Shrubland cover [%]	1.33	**<0.001**	1/22	0.64	GLM with Poisson distribution
	Manual pest removal	4.29	**0.038**	1/21		
	Number of soil practices	23.99	**<0.001**	1/20		
Proportion florivory	Shrubland cover [%]	0.12	0.727	1/22	0.02	GLM with a Beta distribution
	Manual pest removal	0.44	0.507	1/21		
	Number of soil practices	0.00	0.990	1/20		

DF_{num}: numerator degrees of freedom; DF_{den}: denominator degrees of freedom; GLM: generalised linear model

yield metrics tested were: (1) early fruit set, defined as the proportion of treated flowers successfully developing a fruit, (2) harvestable fruit set defined as the proportion of treated flowers successfully developing a fruit suitable for harvest; seed set, defined by the number of seeds per treated flower, given successful harvestable fruit set, (3) fruit weight in grams, and (4) fruit size in cm, using the circumference of its widest point. Using the 'glmer' function from the 'lme4' package we used binomial mixed effects models to test the proportion of flowers that set fruit, as well as the proportion of harvestable fruit set against treatment, shrubland cover (and its interaction with treatment), the manual pest control and soil practices, using plot as a random factor, as the treatments were nested within the plots. Using the 'lmer' function, we tested the mean seed set per fruit, mean fruit weight and mean fruit size against treatment, shrubland cover (and its interaction with treatment), as well as manual pest removal and soil practices in separate linear mixed effects models for each yield parameter, using plot as a random factor (Bates et al., 2015). If significant differences in the exclusion treatment were detected, pairwise comparisons between treatments were made using the 'lsmeans' function from the 'emmeans' package (Lenth et al., 2021). For all models including both shrubland cover and soil practices, we additionally tested for an interactive effect between shrubland cover and soil practices (Table S3). However, no such interactive effects were found.

Effects of flower visitors and florivory on pumpkin yield

To analyse the effects of flower visitors and florivory on yield, we tested these in linear mixed effects models against z-transformed visitor density (number of flower visitors/ number of female flowers), visitor richness and florivory proportion, all in interaction with treatment, with plot as a random effect. Again, we analysed proportions using binomial distribution and fruit quality metrics using Gaussian distributions. There were no strong correlations between the three predictors (Table S4). Finally, we calculated the relative difference between the hand-pollinated and florivory excluded treatment and the hand-pollinated and florivory treatment, as well as the relative difference between the hand-pollinated and florivory excluded treatment and the animal-pollinated treatment within a single field. We then analysed the effects of visitor density, visitor richness and florivory proportion on these relative differences using a linear model.

All models were validated for the assumptions of normality, distributions (of residuals) and heteroscedasticity. Models were visually validated using the 'check_model' function from the 'performance' package. Individual assumptions of co-linearity were checked using the 'check_collinearity' function (maximum accepted Variance Inflation Factor = 2.5 between predictors), and model dispersion was checked using the 'check_overdispersion' function from the 'performance' package (Lüdecke et al., 2021). For visualization, we plotted predicted values from the model with unscaled predictors using the 'ggemmeans' function from the 'ggeffects' package (Lüdecke, 2018).

Results

Across the sampling period, we collected 622 flower visitors belonging to 11 bee (morpho)species and 5 fly morphospecies (Table S5). *Apis mellifera,* the honeybee, was the dominant flower visitor on our sites, with 565 individuals (90.8 % of total observations) recorded, followed by syrphid flies (28 individuals of 4 morphospecies, 4.5 % of total observations). Of the 199 female flowers included in the experiment (excluding the negative control, which produced a single fruit), 103 (~52 % of flowers) set fruit. In total, 85 (~83 % of set fruits, ~43 % of flowers) of these fruits could be harvested, while 18 could not be harvested since 15 were lost to fungal rot, 2 eaten by mice and 1 damaged too strongly by a hailstorm after early fruit set. Of the flowers included in the exclusion experiment, only two experienced florivory during the initial flowering stages. Overall, the mean proportion of damaged flowers in the fields ranged from 0 to 35 %, with only three fields experiencing over 10 % damage.

Effects of landscape and agroecology on flower visitors and florivory

We found a decline in overall visitor abundance of approximately 60 % (Fig. S8A), but a doubling of visitor richness (Fig. 1G) from the lowest to the highest shrubland cover. The abundance pattern was almost exclusively driven by the negative relationship between the shrubland cover and *A. mellifera* abundance (Fig. 1A). The increase in species richness was due to an increase in non-honeybee visitors with increasing shrubland cover (Fig. 1D).

The use of manual pest removal nearly halved the mean overall visitor abundance from ~28 to ~16 (Fig. S8B). Manual pest removal also reduced visitor richness from approximately 2.6 species per plot to 2 species per plot (Fig. 1H). This effect on species richness corresponds to a lower abundance of non-honeybee visitors (Fig. 1E). Manual pest removal had an especially strong effect on fly flower visitors (Fig. S8H), though honeybees were also negatively affected (Fig. 1B). Other bees were not affected by pest removal (Fig. S8E).

Increasing agroecological soil management practices approximately doubled honeybee abundance (Fig. 1C) and visitor richness (Fig. 1I), through benefiting the abundance of non-honeybee visitors (Fig. 1F).

Florivory was unaffected by shrubland cover, manual pest removal, or soil management (Table 1).

Effects of exclosure treatments, landscape and agroecology on pumpkin yield

Hand pollination and florivory exclusion treatments significantly affected early and harvestable fruit set. Flowers that were hand-pollinated and excluded from florivory had the highest early fruit set (mean: 68.80 %), and flowers bagged before opening had no fruit set. From the remaining treatments, flowers with animal pollination had the lowest early fruit set (mean: 40.80 %). Flowers that were hand-pollinated but were still exposed to florivory had an intermediate early fruit set (mean: 61.32 %). There was no significant difference between the two hand-pollinated treatments, but the animal-pollinated treatment had significantly lower fruit set than either hand-pollinated treatment, both during early fruit set (Fig. 2A), as well as at harvestable fruit set (Fig. S9; Table S6). Shrubland cover did not affect early or harvestable fruit set. Treatment had no effect on seed set, fruit weight or fruit size, but shrubland cover had a negative effect on all three fruit quality metrics (Fig. 2). Manual pest removal and agroecological soil practices had no effect on any yield metric (Table 2).

Effects of flower visitors and florivory on pumpkin yield

Visitor density was negatively related to early fruit set across treatments (Fig. 3A), and both early and harvestable fruit set responded to visitor richness in interaction with experimental treatment (Fig. 3B; Table S7). In both non-excluded treatments (exposed to florivory) early fruit set increased with increasing visitor richness. However, early fruit set of hand-pollinated and excluded flowers correlated negatively with visitor richness (Fig. 3B). The florivory proportion had no effect on early or harvestable fruit set. Fruit quality, in terms of seed set, fruit weight and fruit size was unaffected by pollination or florivory (Table S7).

With increasing visitor richness, there was a significant decrease of the relative difference in fruit set between the animal-pollinated treatment, but not of the hand-pollinated treatment, and the positive control (Fig. 3C). Visitation density and florivory did not affect the relative differences between treatments (Table S7).

Discussion

In our tropical smallholder study system, pumpkin fruit set was

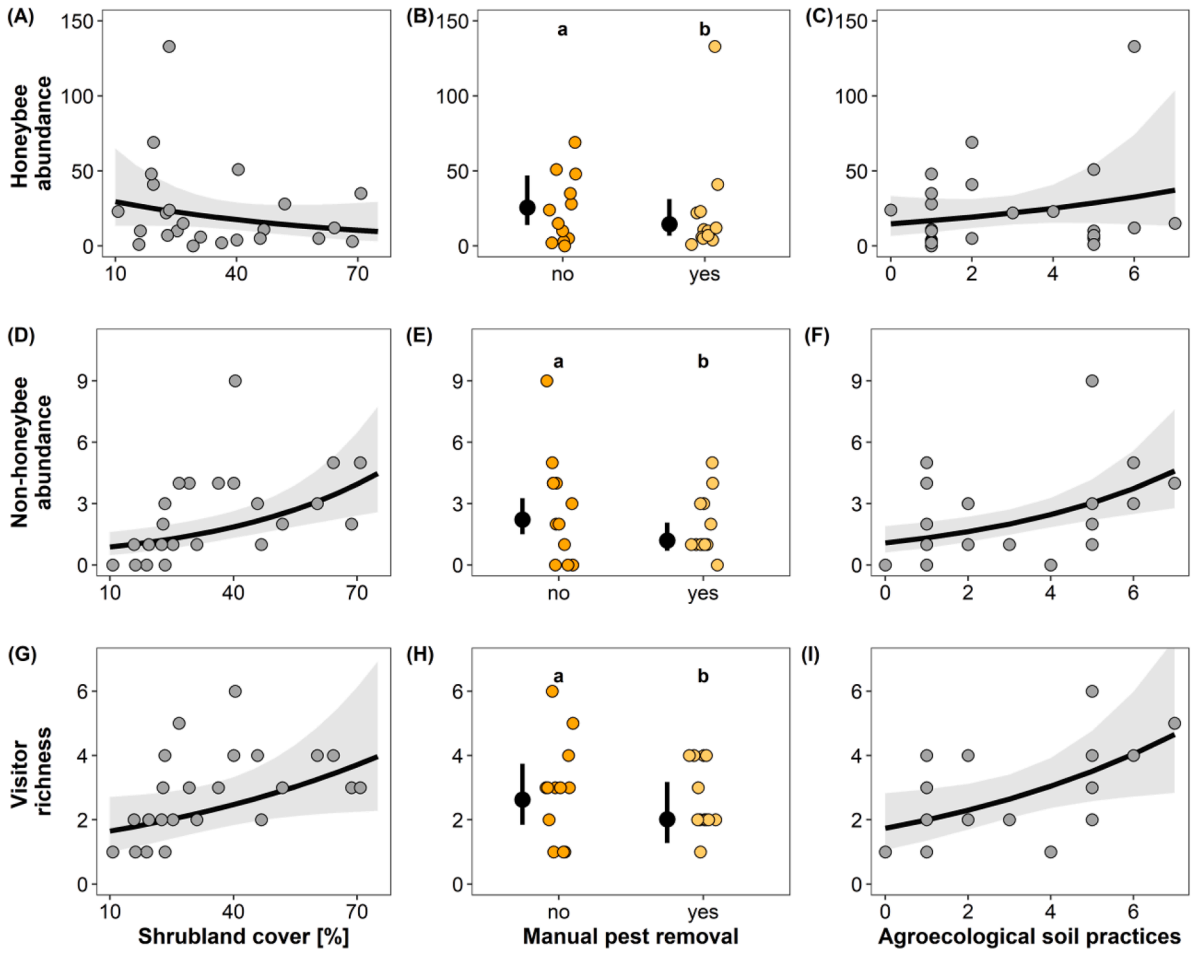

Fig. 1. Response of honeybee abundance (A, B & C), non-honeybee abundance (D, E & F) and flower visitor richness (G, H & I) to shrubland cover, manual pest removal and number of agroecological soil management practices. Abundance is defined as the sum of individuals across the transects, richness is defined as the cumulative species richness across the transects. For shrubland cover and agroecological soil management practices, lines show the direction of the predicted model effect, solid lines indicate a significant effect. Grey areas indicate the 95 % confidence interval of the model prediction. For manual pest removal, the black dot indicates the predicted mean, and vertical lines indicate the range of the 95 % confidence interval of the prediction. Different letters indicate differences between groups. Dots are true datapoints.

constrained by pollinator limitation, rather than by flower-damaging pests. In parallel, we found that flower visitors, but not flower damage, were influenced by surrounding land cover and agroecological practices.

Effects of landscape and agroecology on flower visitors and florivory

Increasing shrubland cover in the landscape had contrasting effects on honeybee abundance and the richness and abundance of other flower visitors. These results align with studies that suggest that agricultural landscapes may favour a few, very adaptable pollinator species (Grab et al., 2019), whilst simultaneously emphasising the dependence of non-managed flower visitors on (semi-)natural habitats in this region (Vogel et al., 2023a). The dominance of honeybees in agricultural landscapes could be due to the wider foraging range of honeybees compared to solitary flower visitors. Additionally, honeybees are generalists and tolerant of habitat disturbance (Steffan-Dewenter et al., 2002), and higher densities of farmers could mean a higher density of honeybee hives, even if in Africa up to 90 % of African honeybees are wild-nesting (Requier et al., 2019). Potential competition effects between honeybees and other flower visitors also cannot be ruled out.

Agroecological pest management is assumed to be more sustainable (Wezel et al., 2020), as killing of non-target organisms such as pollinators is a major disadvantage of conventional pest management involving synthetic pesticides (Ekström & Ekbom, 2011). However, we found that manual pest removal negatively affected flower visitor abundance, specifically honeybees and flies, and richness, but not florivory. Though very low in abundance and richness in general, other bees were not affected by manual pest removal. We hypothesise that the negative effect observed on flies specifically may be because the potential pollinators are not effectively distinguished from other larviform pests in the larval stage by farmers performing manual pest management. Therefore, we suspect that farmers are not only killing the larvae of herbivores, but also the larvae of pollinating flies such as syrphids, which may decrease the presence of the adults later in the season. Research in the study area (Enloe et al., 2021), and in other smallholder communities in Africa (Mkenda et al., 2020) revealed that smallholders cannot always effectively distinguish beneficial insects from pests. Especially in the case of syrphids, which are known to be present on host plants as lavae (Davis et al., 2023), this lack of familiarity would not only negatively affect the pollinating adults, but also the larvae that could act as natural enemies of pests.

Manual pest removal was also negatively correlated with honeybee abundance on our plots. Farmers can identify honeybees and perceive them as beneficial (*personal communication with farmers*), so we do not expect farmers to actively remove honeybees. We hypothesise that the odor of squashed insects might act as a repellent to flower visitors (Abbott, 2006; Dukas, 2001). If this hypothesis turns out to be true, hand

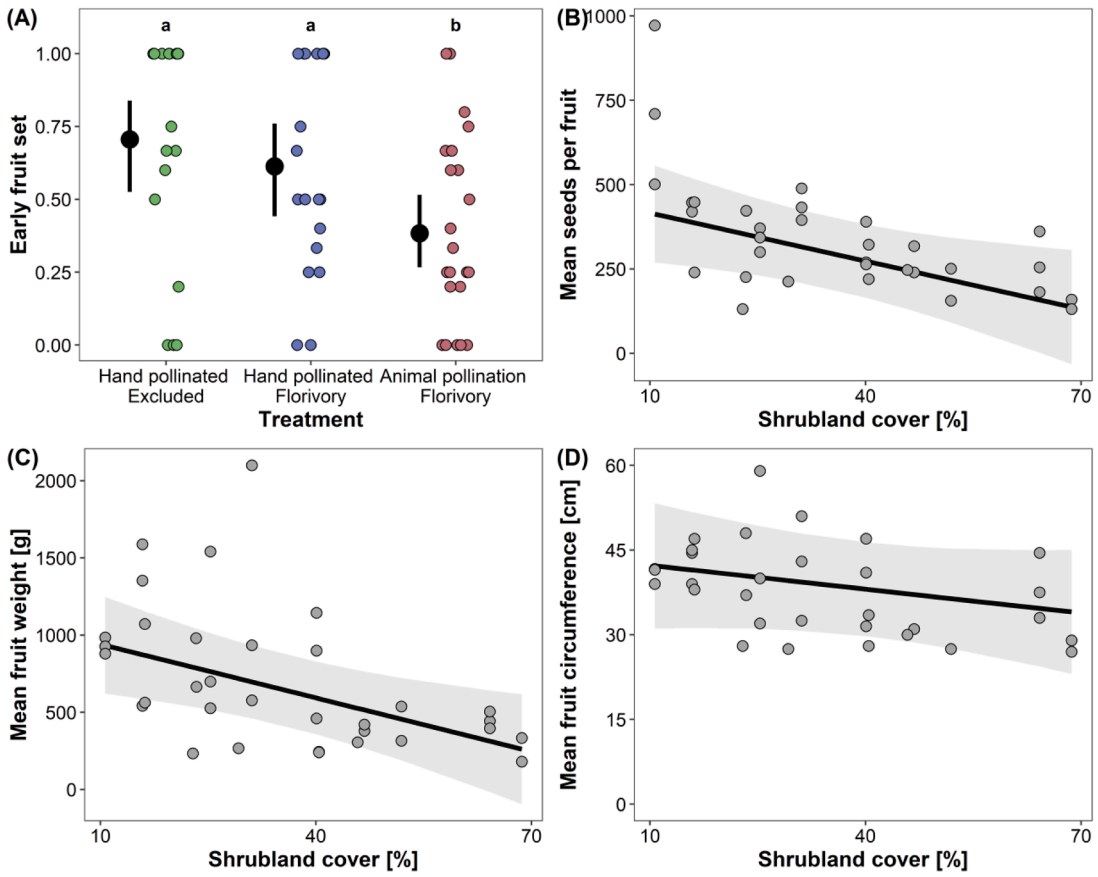

Fig. 2. Response of the proportion of early fruit set by treatment (A), and mean seed set (B), mean fruit weight (C) and mean fruit circumference (D) to shrubland cover. In A, the black dot indicates the predicted mean, and vertical lines indicate the range of the 95 % confidence interval of the prediction, letters indicate group differences. In B, C and D, lines show the direction of the predicted model effect, solid lines indicate a significant effect. Grey areas indicate the 95 % confidence interval of the model prediction.

Table 2
Model results of pumpkin yield responses to treatment, shrubland cover and agroecological practices. Bold p-values indicate a significant response.

Response	Predictors	Chi^2	p-value	DF_{num}/DF_{den}	R^2_m/R^2_c	Model type
Early fruit set	Treatment	12.34	**0.002**	2/37	0.09/0.22	GLMM with a binomial distribution
	Shrubland cover [%]	0.05	0.824	1/20		
	Manual pest removal	0.21	0.647	1/17		
	Number of soil practices	0.01	0.927	1/16		
	Treatment x Shrubland	0.15	0.891	2/38		
Harvestable fruit set	Treatment	13.98	**<0.001**	2/36	0.11/0.25	GLMM with a binomial distribution
	Shrubland cover [%]	0.00	0.997	1/20		
	Manual pest removal	0.85	0.357	1/17		
	Number of soil practices	0.05	0.822	1/17		
	Treatment x Shrubland	0.26	0.876	2/37		
Seed set (seeds/fruit)	Treatment	0.81	0.666	2/16	0.32/0.69	LMM
	Shrubland cover [%]	5.81	**0.015**	1/10		
	Manual pest removal	0.75	0.388	1/11		
	Number of soil practices	0.10	0.748	1/11		
	Treatment x Shrubland	2.73	0.255	2/15		
Fruit girth (cm)	Treatment	3.35	0.187	2/25	0.35/0.35	LMM
	Shrubland cover [%]	6.34	**0.012**	1/25		
	Manual pest removal	1.66	0.197	1/25		
	Number of soil practices	0.94	0.332	1/25		
	Treatment x Shrubland	0.43	0.806	2/25		
Fruit weight (g)	Treatment	0.64	0.727	2/25	0.30/0.30	LMM
	Shrubland cover [%]	7.37	**0.007**	1/25		
	Manual pest removal	2.17	0.141	1/25		
	Number of soil practices	0.00	0.952	1/25		
	Treatment x Shrubland	0.50	0.778	2/25		

DF_{num}: numerator degrees of freedom; DF_{den}: denominator degrees of freedom; R^2_m: marginal R^2; R^2_c: conditional R^2; GLMM: generalised linear mixed effects model; LMM: linear mixed effects model.

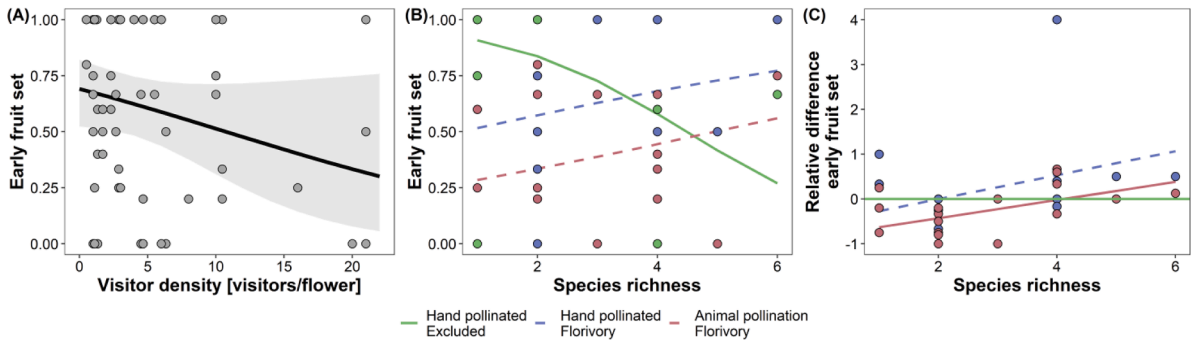

Fig. 3. Responses of early fruit set to visitor density (A), early fruit set to flower visitor richness by exclusion treatment (B), and relative early fruit set difference between the treatments and the positive control (hand-pollinated and excluded) across the visitor richness gradient (C). Lines show the direction of the predicted model effect, solid lines indicate a significant effect, dashed lines indicates a non-significant difference. The grey area in (A) indicate the 95 % confidence interval of the model prediction.

removal of pests would need to be done without leaving dead insects on the plants. Instead, insects should be collected and killed away from the field, at least while the plants are blooming. In our context, pollinator limitation is a bigger constraint to early and harvestable pumpkin fruit set than florivory. This implies that even if manual pest removal is an effective pest management strategy, the negative effects on pollinators could outweigh any benefits achieved with improved pest control. This suggests that outreach about beneficial arthropods to smallholders is essential to avoid off-target effects of manual pest removal.

Diversification of agroecological soil practices positively affected flower visitor abundance and outweighed the negative effects of manual pest removal. Agroecological soil management includes the planting of alternative crops (i.e., intercropping with legumes) that can benefit pollinators by providing alternative floral resources in a landscape heavily dominated by maize agriculture. Additionally, incorporating legume residue, or using manure and compost, creates humid microclimates which could benefit fly larvae (Davis et al., 2023). Sustainable soil management is also key to maintaining habitat for ground-nesting bees such as *Lasioglossum* spp. in agroecosystems (Antoine & Forrest, 2021). A limitation is that we cannot distinguish the relative effects of the individual agroecological soil practices, which should be a focus of future research. Diversified agroecological soil management, however, benefited natural enemies and butterflies in the same study system (Vogel et al., 2023a; Vogel et al., 2023b), and has positive food security outcomes for smallholders (Bezner Kerr et al., 2021). This further emphasises the potential of social and ecological co-benefits of agroecology for smallholder farming.

Effects of landscape and agroecology on pumpkin yield

Though we found no relationship between fruit set and shrubland cover, there were negative effects of shrubland cover on fruit weight, size, and seed set. Productive landscapes tend to be favoured for agriculture, and are more likely to experience high habitat conversion rates (Serneels & Lambin, 2001; Syampungani et al., 2009), potentially explaining why pumpkin may perform better in areas with lower shrubland cover mediated by better soils. In Tanzania, interactive effects of soil quality and pollination have been demonstrated in watermelon (Sawe et al., 2020). Potentially, similar interactive effects between soil quality and pollination occur in Malawi, where increased flower visitor richness in shrubland-rich landscapes compensates for poorer soils, resulting in no net difference in fruit set. Despite trade-offs with fruit quality, conserving shrublands is still important for the conservation of flower visitors, as farmers cite unsuccessful fruit production as a greater concern than seed production in pumpkin (*personal communication with farmers*).

Effects of flower visitors and florivory on pumpkin yield

We demonstrate that pollinator limitation was a larger constraint to fruit set than florivory, but that this constraint can be overcome by increasing flower visitor richness. This is in line with an earlier study on pumpkin pollination in Indonesia (Hoehn et al. 2008), but contrasts with a North American study that did not find pollinator limitation in pumpkins (Reilly et al., 2020), indicating that pollinator limitation is a context-dependent phenomenon in this crop. Pumpkin is native to North America where it has co-evolved with a specialised pollinator, *Eucera pruinosa,* which is absent elsewhere, including in Africa (Pope et al., 2023). In Asia, where pumpkin is also introduced, richer pollinator communities also corresponded to improved yield (Hoehn et al., 2008), but in Kenya, supplementation with a stingless bee did not improve pumpkin yields (Waithaka et al., 2023). Our study does not determine whether richness *per se*, or the increased likelihood of highly effective species being present in richer communities drives the observed positive effect in our study (Martin et al., 2019b). Other studies indicate that some non-specialised visitors, in this case *Bombus* spp. in Central Europe, are more effective pumpkin pollinators than honeybees or halictids (Pfister et al., 2017). Determining which visitors in sub-Saharan Africa areeffective pollinators of pumpkin is a necessary next step to inform more focussed pollinator management recommendations.

Hand-pollinated flowers that were excluded from further visitation had decreased early fruit set with increasing flower visitor richness. Though obviously not a causal relationship, this mirrors the decline in fruit quality with increasing shrubland cover. Flower visitor richness was higher in landscapes with high shrubland cover but could coincide with areas lower in soil quality (Serneels & Lambin, 2001). Furthermore, in plots with high visitor richness, animal-pollinated flowers outperformed hand-pollinated and florivory-excluded flowers, indicating that high pollinator richness potentially compensates poorer soils (Sawe et al., 2020). Moreover, we even found a negative effect of high visitor density on early fruit set. Extremely high honeybee visitation rates can negatively affect fruit set (Rollin & Garibaldi, 2019), and in our context, visitor densities were strongly driven by high honeybee abundances. Honeybees compete with other pollinator species for the same floral resources and have been shown to reduce the occurrence of other bee species (Henry & Rodet, 2018), suggesting that honeybees at high densities could outcompete more effective pumpkin pollinators. However, the positive relationship between richness and fruit set parallels similar results in other crops and agricultural contexts (Garibaldi et al., 2016; Grab et al., 2019) and further emphasises the necessity of maintaining pollinator richness by protecting remaining habitats such as shrublands and implementing pollinator-friendly farming such as soil agroecological practices.

Conclusion

Pumpkin is amongst a diverse range of crops important for smallholder food security and nutrition that depend on pollinators (Chaplin-Kramer et al., 2014; Eilers et al., 2011). Our study underpins the important role that a rich pollinator community, more so than flower-feeding pests, plays for pumpkin productivity in a smallholder agricultural landscape. Therefore, we argue that maintaining and increasing flower visitor richness should be a priority for stakeholders. Despite some trade-offs with fruit quality, surrounding shrubland cover should be protected to conserve potential pollinators. For this, the demand for fuelwood, which is the main driver of deforestation in the Miombo woodland ecoregion, should be addressed (Gumbo et al., 2018) in tandem with outreach to local communities about the importance of these habitats for ecosystem services. Concurrently, the negative relationship of shrubland cover with fruit quality needs further research so that the relative importance of shrublands for pollinators and productivity can be disentangled – we suspect soil quality may be an important component, underpinning the importance of agroecological soil management practices to enhance soil fertility. Farmers would likely benefit from outreach on what constitutes a pest and a beneficial insect to prevent manual removal of pollinators from farms. Finally, agroecological soil management has important benefits for smallholders (Rosset & Alteiri, 2017) and we show diverse practices can co-benefit flower visitors. Diversifying agroecological soil management, therefore, should be actively encouraged to sustainably improve the livelihoods of smallholder farmers in sub-Saharan Africa.

Author contributions

CV, TM, MM, LD, RBK, AI, KP and ISD conceptualized the study. CV collected the flower visitor data and performed the exclusion experiment. TM and MM collected the pumpkin harvest data. LD and RBK conceptualized the pest and soil management survey, LD coordinated the collection of that data. GK performed the landscape cover analysis. CV performed the statistical analyses with input from AI, KP and ISD. CV wrote the first draft of the manuscript. All authors have read, revised and agreed on the final version of this study.

Open research statement

All data included in this manuscript will be made public upon acceptance. The link to the repository (private for peer review) is: https://datadryad.org/stash/share/f9EGjLmPccWzwYFm54l3gTyYnXIDt8DlvDRzj2_v3uM

Declaration of Competing Interest

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

Acknowledgments

We dedicate this paper to the memory of our friend, colleague, and co-author, Tapiwa Mkandawire. He was committed to improving the livelihoods of smallholder farming communities. He was knowledgeable, hard-working, full of humour, and kind. He is missed.

We would like to give our thanks to all participating farmers for their willingness to be interviewed and for allowing us to collect data on their fields. We would also like to thank Innocent Mhoni, Pressings Moyo and Penjani Kanyimbo (sadly also deceased) for their assistance in the field. We also thank the senior staff at Soils, Food and Healthy Communities (SFHC), Lizzie Shumba and Esther Lupafya, for facilitating the research in Malawi. We would also like to thank Adomas Liepa for his support with the GIS landscape classification. Finally, we would like to thank Fabian Bötzl for his advice on the statistical analyses. This research was funded through the 2017-2018 Belmont Forum and BiodivERsA joint call for research proposals, under the BiodivScen ERA-NetCOFUND program, and funded by the Natural Sciences and Engineering Research Council of Canada (NSERC Grant #523660-2018), National Science Foundation (NSF Grant #1852587), German Federal Ministry of Education and Research (BMBF #01LC11804A) and the Research Council of Norway (#295442). Cassandra Vogel was supported by a SCIENTIA postdoctoral scholarship.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2023.10.004.

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