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RESEARCH ARTICLE

The effects of crop type, landscape composition and agroecological practices on biodiversity and ecosystem services in tropical smallholder farms

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Abstract

1. In the tropics, smallholder farming characterizes some of the world's most biodiverse landscapes. Agroecology as a pathway to sustainable agriculture has been proposed and implemented in sub-Saharan Africa, but the effects of agricultural practices in smallholder agriculture on biodiversity and ecosystem services are understudied. Similarly, the contribution of different landscape elements, such as shrubland or grassland cover, on biodiversity and ecosystem services to fields remains unknown.
2. We selected 24 villages situated in landscapes with varying shrubland and grassland cover in Malawi. In each village, we assessed biodiversity of eight taxa and ecosystem services in relation to crop type, shrubland and grassland cover and the number of agroecological pest and soil management practices on smallholder's fields of different crop types (bean monoculture, maize-bean intercrop and maize monoculture).
3. Increasing shrubland cover altered carabid and soil bacteria communities. Carabid abundance increased in maize but decreased in intercrop and bean fields with increasing shrubland cover. Carabid abundance and richness and wasp abundance increased with soil management practices. Carabid, spider and parasitoid abundances were higher in bean monocultures, but this was modulated by surrounding shrubland cover. Natural enemy abundances in beans were especially high in landscapes with little shrubland, possibly leading to lower bean damage in monocultures compared to intercropped fields, whereas maize monocultures had higher damage. In maize, grassland cover and pest management practices

were positively related to damage. Carabid abundance was higher fields with high bean damage, and increased carabid richness in fields with high maize damage. Parasitoid abundance was negatively associated with bean damage.

4. *Synthesis and application*. Our results suggest that maintaining biodiversity and ecosystem services on smallholder farms is not achievable with a 'one size fits all' approach but should instead be adapted to the landscape context and the priorities of smallholders. Shrubland is important to maintain carabid and soil bacterial diversity, but legume cultivation beneficial to natural enemies could complement pest management in landscapes with a low shrubland cover. An increased number of agroecological soil management practices can lead to improved pest control while the effectiveness of agroecological pest management practices needs to be re-evaluated.

KEYWORDS

agroecology, biodiversity, crop diversity, intercropping, landscape change, pest control, pollination, soil health

1 | INTRODUCTION

Smallholder agriculture constitutes the livelihood of over two billion people and contributes a third of the global food supply (Ricciardi et al., 2018; Steward et al., 2014). Simultaneously, smallholder farms are within the world's most biodiverse landscapes (Newbold et al., 2015), but (semi-)natural habitats, defined as habitats with most biodiversity and ecosystem processes intact, are being lost rapidly to make room for agricultural production in these landscapes (IPBES, 2019). To alleviate poverty and food insecurity in rural communities, there has been a push to intensify and specialize agriculture with synthetic input use (Snapp, 2020)—even though the evidence base for benefits is ambiguous (Rasmussen et al., 2018). Both the loss of semi-natural habitats as well as intensification are main drivers of biodiversity decline and loss of ecosystem services (ES) supporting agricultural production (IPBES, 2019). Smallholders, defined by farming an area <2 ha by the FAO, are underrepresented in studies investigating the effects of changing land-use and agricultural practices on biodiversity and ES (Steward et al., 2014). The few studies available from tropical smallholder agricultural systems usually focus on commercially important crops such as coffee and cacao and not on crops directly consumed by smallholders (Sasson, 2012; Vanlauwe et al., 2014).

Biodiversity and associated ES in crop fields are influenced by the composition of the surrounding landscape (Martin et al., 2019). Generally, beneficial biodiversity, such as pollinators and natural enemies react positively to increased landscape level semi-natural habitat cover (Dainese et al., 2019), while crop pests respond inconsistently (Tamburini et al., 2020). Different semi-natural habitat types, such as shrubland or grassland, may differ in their potential as source habitats for beneficial biodiversity (Michalko & Birkhofer, 2021), and may mediate the delivery of ecosystem services, but this is rarely investigated. In addition, the importance of these landscape elements for different taxa may differ across spatial scales (Martin et al., 2019).

At the field level, biodiversity and related ES are directly impacted by the management choices of farmers. For example, intercropping has the potential to counteract landscape simplification, by increasing habitat heterogeneity for beneficial biodiversity at the field level while maintaining productivity (Brandmeier et al., 2021). Increasing plant diversity in managed landscapes decreases pest abundance and crop damage and increases natural pest control (Wan et al., 2020). Not all crops, however, provide the same services; whether intercropping benefits are affected by crop type or can be optimized by a combination of management at the field and the landscape level is largely unknown. In tropical agriculture, agroecology represents a more holistic and sustainable alternative to conventional agriculture and addresses both ecological and social aspects of food systems (Wezel et al., 2020). Agroecology benefits smallholders through, improved food security and nutrition (Bezner Kerr et al., 2021) and climate change adaptation (Snapp et al., 2021). Agroecology aims to reduce synthetic input dependency by including a wide range of agroecological pest management practices, and agroecological soil management practices (Table 1). Cobenefits agroecological practices and ES are assumed, but not often empirically studied.

We aimed to investigate the combined effects of crop type (bean monoculture, maize-bean intercrop and maize monoculture) and landscape shrubland and grassland cover, as well as an increased number of pest and soil management practices across a range of indicators related to biodiversity and ES relevant to crop production in African smallholder agriculture. Our study area in Malawi illustrates many of the challenges faced by smallholder communities in sub-Saharan Africa. Northern Malawi is located in the Miombo woodland ecoregion, a global biodiversity hotspot, which is highly threatened by habitat conversion and overexploitation despite its importance

TABLE 1 All possible agroecological pest management practices and agroecological soil management practices applied in the sampled fields.

Practice group	Practice type
Agroecological pest management	Manual removal/killing of insects
	Spreading ash on affected crops
	Adjusting planting dates
	Using non-synthetic repellent of any kind
	Applying a soup made of small fish (with the aim of attracting ants)
Agroecological soil management	Alternative soil landscaping: box ridges, pit planting, contouring, terracing or low-till practices
	Planting of vetiver grass hedges
	Use of mulching
	Legume intercropping
	Incorporation of legume residues
	Crop rotation with legumes
	Use of compost
	Use of animal manure
	Agroforestry

for ES provision (Ribeiro et al., 2020). Participatory research with farmers identified research questions about pest management and how to foster natural enemies to pest control (Enloe et al., 2021), providing the opportunity to study the effects of these practices on biodiversity and ES. We aimed to test the following hypotheses:

1. We expect that intercropping, more pest and soil management practices, and increased shrubland and grassland cover increase the abundance and diversity of beneficial taxa and affect species assemblages. For mobile taxa, such as birds or bees, we expect the scale of landscape effects to be larger, whereas for less mobile taxa, such as ants, we expect a smaller scale.
2. Crop type and shrubland and grassland cover interactively affect pest control and pollination, with beneficial effects of intercropping and increased shrubland and grassland cover on pest control and pollination. Additionally, a higher number of pest and soil management practices is expected to have positive outcomes for ES on fields.
3. We predict that: (A) fields with a higher abundance and diversity of natural enemies have reduced pest damage on crops, and (B) a higher bee abundance and diversity and soil bacterial diversity improve seed set on beans.

2 | MATERIALS AND METHODS

2.1 | Study area and site selection

We conducted our field experiments from February to May 2019 in 24 villages in Mzimba District, northern Malawi. We were granted a research and arthropod sample export permit by the National Commission of Science and Technology in Malawi. The villages were distributed across independent gradients of shrub- and grassland cover in the surrounding landscape at different scales (Figure 1; Table S1), as well as varying numbers of agroecological pest management and agroecological soil management practiced at the household scale. We use the terms 'pest management practices' and 'soil management practices' to refer to a range of traditional and introduced agroecological practices aimed at reducing pest damage and improving soil health respectively (Table 1). Villages were separated from each other by at least 2 km. There is limited conservation enforcement in shrublands or grasslands in the study region and they are therefore impacted by activities of local communities, such as livestock grazing or extraction of firewood (Gumbo et al., 2018).

In each village we selected a maize monoculture and a maize-bean intercropped field (Figure 1; Figure S2; Table S2). In 14 villages, we additionally selected a bean monoculture field, resulting in a total of 62 fields (mean field size: 0.30 ha; range: 0.08–0.80 ha). Malawi is located in the seasonal tropics and experiences a marked peak in rainfall from December to late March (Mungai et al., 2016). All selected fields were sown between December 2018 and January 2019, at the onset of the first rains. Fields were solely rain-fed throughout the growing season. Field management, including soil preparation and sowing, were done by hand-hoe, as per usual practice. We aimed for consistency between the fields across villages, but since we used smallholder farmers' existing fields, we could not fully control for planting densities and crop varieties (Table S2).

2.2 | Data collection

Biodiversity was assessed through two rounds of data collection between 22 February and 26 April 2019 (Table S2). The first round of observations was performed when crops were still growing vegetatively. During the second round of observations crops were starting to produce cobs (maize) and pods (beans). Because birds are highly mobile, we recorded (i) the abundance and richness of birds at the village level (n = 24) using point counts (Supporting Information 1i). For assessing ecosystem service potentials, birds were split into feeding guilds (carnivorous, nectivorous, insectivorous, granivorous, omnivorous, frugivorous; Table S3). In parallel, on all 62 fields (ii) we collected arthropod taxa using pitfall traps for ground-dwelling arthropods (carabids, spiders and ants) and pan traps for flower visiting taxa (parasitoids, other wasps and bees; Figure S3) for which we analysed richness (carabids, ants and bees) and abundances (carabids, spiders, parasitoids, other wasps and bees). Trap catches resemble activity densities but we refer to them as 'abundances' for the sake of simplicity throughout (Supporting Information 1ii). During the second sampling round, we collected soil samples from the fields and (iii) extracted bacterial DNA from these samples (Supporting Information 1iii). To quantify pest control services, we assessed (iv) pest damage on the leaves of 20 bean and/or maize plants per fields. These assessments were done in parallel to the biodiversity assessment (Supporting Information 1iv). At harvest,

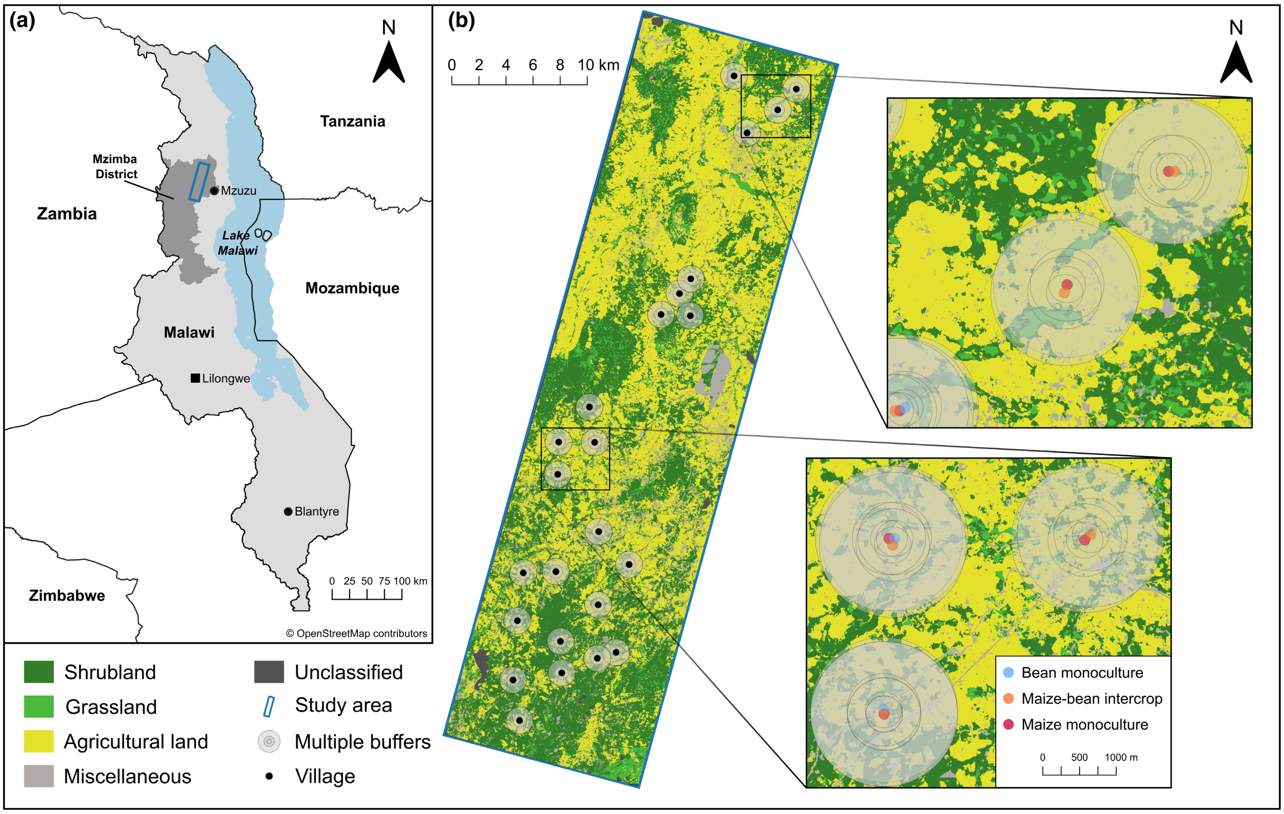

FIGURE 1 Map showing the study region within Malawi (a), and the distribution of study sites within the study region by the location of maize fields (b). Insets show examples of the distribution of fields within the landscapes, with the 250, 500 and 1000 m buffers around each field. As the dot symbol of the villages is bigger than the 250 m buffer in the overview map of (b), only the 500 and 1000 m buffers are visible in this case.

we additionally assessed (v) damage on the cobs of 10 plants on 40 fields, and (vi) bean seed set on 10 plants on 14 fields (Supporting Information 1vi). Detailed information on the methodology and recording of individual taxa and ecosystem services is provided in Supporting Information 1. Although our study included animals, we did not require approval by an ethics committee, as only arthropods were collected.

Additionally, we (vii) quantified shrubland and grassland cover in a 250, 500 and 1000 m radius surrounding all fields using satellite imagery and GIS (Supporting Information 1vii). To quantify the implementation of pest and soil management practices on and around the fields, we surveyed households managing these fields. Surveys were performed from 8 to 25 March 2020. One household declined to participate in the survey. Each household that participated in the survey answered questions, translated into the native language (chiTumbuka) concerning the implementation of various pest and soil management practices on the surveyed fields. Farmers were asked about specific practices (i.e. 'Do you perform X practice on this field?'), but were also asked about any additional practices performed on the fields. Farmers reported five agroecological pest management practices and nine agroecological soil management practices (Table 1). Agroecological practices explicitly excluded synthetic inputs, such as synthetic pesticides and fertilizers. Pest and soil management practices were summed per field for the analyses.

For the pest and soil management survey, the Institutional Review Board of Cornell University for Human Subjects Research reviewed and approved the research study design (protocol 1811008425).

2.3 | Statistical analysis

We tested the effects of crop type, pest and soil management practices, shrubland and grassland cover, as well as the interaction between the latter two and crop type on (i) biodiversity (cumulative across sampling rounds, see above). For the abundance and richness of birds at the village level, we used negative binomial generalized linear models, for the abundance and/or richness of arthropod taxa and the Shannon diversity of soil bacteria we used generalized linear mixed models with Gaussian (soil bacteria), Poisson or negative binomial (arthropods) residual distributions and 'village' as a random intercept (Supporting Information 2iii, Table 2; Figure S4). Additionally, we assessed the effects of crop type, shrubland cover, grassland cover, pest and soil management practices on species assemblages of birds, carabids, ants, bees and soil bacteria using nonmetric multidimensional scaling (NMDS, Table 3). We also tested the effects of crop type, shrubland cover, grassland cover, pest and soil management practices on (ii) ecosystem services (% maize leaf damage, % cob damage, % bean leaf damage and bean

TABLE 2 Results from generalized linear models (GLMs; for birds and bean leaf damage), linear models (LMs; for bean seed set), linear mixed effects models (LMMs; for soil bacteria Shannon's diversity) and generalized linear mixed models (GLMMs; for all other responses) including the fixed effects crop type, shrubland cover, grassland cover, agroecological pest management practices and agroecological soil management practices for different responses related to biodiversity and ecosystem services. Activity densities measured with different trap types are referred to as 'abundance' for matters of simplicity. Separate models were fitted for each response at three different spatial scales (250, 500 and 1000 m), the model with the lowest AICc was chosen and the scale of this model is stated. DF_{num}: numerator degrees of freedom; DF_{den}: denominator degrees of freedom; $R^2 = R^2$ (LMs & GLMs), pseudo R^2 (GLMs with beta distribution) or marginal R^2/conditional R^2 (LMMs and GLMMs). (*) indicates $p < 0.100$, * indicates $p < 0.050$, ** indicates $p < 0.010$. For model specifications, see Supporting Information 2.

Response	Model type	Residual distribution	Scale	Predictors	Chi^2-value	*p*-value	df_{num}, df_{den}	R^2
Bird abundance	GLM	Negative binomial	1000 m	Shrubland cover	0.01	0.909	1, 20	0.11
				Grassland cover	0.01	0.916	1, 21	
				Pest management practices	1.46	0.227	1, 19	
				Soil management practices	0.71	0.401	1, 18	
Bird richness	GLM	Negative binomial	1000 m	Shrubland cover	0.04	0.834	1, 20	0.05
				Grassland cover	0.19	0.66	1, 21	
				Pest management practices	<0.01	0.967	1, 19	
				Soil management practices	<0.01	0.95	1, 18	
Carabid abundance	GLMM	Negative binomial	1000 m	Crop type	0.72	0.697	2, 34	0.09/0.26
				Shrubland cover	0.21	0.643	1, 20	
				Grassland cover	0.65	0.42	1, 46	
				Pest management practices	0.5	0.48	1, 49	
				Soil management practices	5.34	**0.021***	1, 46	
				Crop type × shrubland cover	7.55	**0.023***	2, 30	
				Crop type × grassland cover	2.18	0.336	2, 38	
Carabid richness	GLMM	Poisson	1000 m	Crop type	0.38	0.827	2, 29	0.06/0.12
				Shrubland cover	0.19	0.673	1, 21	
				Grassland cover	1.75	0.186	1, 22	
				Pest management practices	0.23	0.629	1, 40	
				Soil management practices	6.36	**0.012***	1, 40	
				Crop type × shrubland cover	2.96	0.227	2, 31	
				Crop type × grassland cover	2.54	0.281	2, 30	

(Continues)

TABLE 2 (Continued)

Response	Model type	Residual distribution	Scale	Predictors	Chi^2-value	*p*-value	df_{num}, df_{den}	R^2
Spider abundance	GLMM	Negative binomial	1000 m	Crop type	8.68	**0.013***	2, 32	0.13/0.35
				Shrubland cover	2.34	0.126	1, 19	
				Grassland cover	0.23	0.628	1, 20	
				Pest management practices	0.58	0.445	1, 48	
				Soil management practices	0.08	0.778	1, 48	
				Crop type × shrubland cover	1.22	0.543	2, 32	
				Crop type × grassland cover	4.37	0.112	2, 34	
Ant richness	GLMM	Poisson	1000 m	Crop type	0.88	0.645	2, 39	0.02/0.03
				Shrubland cover	2.42	0.120	1, 20	
				Grassland cover	1.10	0.294	1, 39	
				Pest management practices	1.43	0.232	1, 46	
				Soil management practices	0.05	0.830	1, 48	
				Crop type × shrubland cover	0.28	0.870	2, 36	
				Crop type × grassland cover	0.18	0.914	2, 35	
Parasitoid abundance	GLMM	Negative binomial	1000 m	Crop type	7.88	**0.019***	2, 31	0.08/0.15
				Shrubland cover	3.20	**0.074 (*)**	1, 20	
				Grassland cover	0.99	0.319	1, 21	
				Pest management practices	0.55	0.459	1, 46	
				Soil management practices	0.27	0.601	1, 47	
				Crop type × shrubland cover	10.35	**0.006****	2, 31	
				Crop type × grassland cover	3.29	0.193	2, 33	
Wasp abundance	GLMM	Poisson	1000 m	Crop type	4.33	0.115	2, 36	0.05/0.14
				Shrubland cover	0.10	0.358	1, 20	
				Grassland cover	0.85	0.752	1, 42	
				Pest management practices	0.05	0.825	1, 47	
				Soil management practices	9.87	**0.002****	1, 48	
				Crop type × shrubland cover	0.18	0.910	2, 32	
				Crop type × grassland cover	0.68	0.713	2, 41	

TABLE 2 (Continued)

Response	Model type	Residual distribution	Scale	Predictors	Chi^2-value	*p*-value	df_{num}, df_{den}	R^2
Bee abundance	GLMM	Negative binomial	1000 m	Crop type	0.64	0.727	2, 35	0.02/0.03
				Shrubland cover	1.95	0.163	1, 20	
				Grassland cover	0.30	0.587	1, 40	
				Pest management practices	0.03	0.861	1, 45	
				Soil management practices	0.08	0.782	1, 46	
				Crop type × shrubland cover	0.05	0.974	2, 32	
				Crop type × grassland cover	0.46	0.794	2, 41	
Bee richness	GLMM	Poisson	1000 m	Crop type	2.99	0.224	2, 30	0.02/0.03
				Shrubland cover	1.90	0.167	1, 21	
				Grassland cover	0.48	0.535	1, 22	
				Pest management practices	0.17	0.676	1, 45	
				Soil management practices	0.00	0.973	1, 45	
				Crop type × shrubland cover	0.41	0.813	2, 31	
				Crop type × grassland cover	2.28	0.321	2, 32	
Soil bacteria Shannon diversity	LMM	Gaussian	500 m	Crop type	0.68	0.521	2, 28	0.16/0.36
				Shrubland cover	1.04	0.321	1, 20	
				Grassland cover	1.31	0.268	1, 17	
				Soil management practices	0.26	0.615	1, 44	
				Crop type × shrubland cover	0.46	0.639	2, 30	
				Crop type × grassland cover	0.87	0.429	2, 27	
Bean leaf damage (%)	GLM	Beta	250 m	Crop type	9.97	**0.002****	1, 29	0.08
				Shrubland cover	3.51	**0.061 (*)**	1, 29	
				Grassland cover	2.52	0.113	1, 29	
				Pest management practices	3.06	**0.080 (*)**	1, 29	
				Soil management practices	0.18	0.673	1, 29	
				Crop type × shrubland cover	1.33	0.248	1, 29	
				Crop type × grassland cover	3.69	**0.055 (*)**	1, 29	

(Continues)

TABLE 2 (Continued)

Response	Model type	Residual distribution	Scale	Predictors	Chi^2-value	*p*-value	df_{num}, df_{den}	R^2
Bean seed set	LM	Gaussian	1000 m	Crop type	1.32	0.295	1, 13	0.45
				Shrubland cover	2.80	0.146	1, 12	
				Grassland cover	0.13	0.728	1, 11	
				Pest management practices	5.98	**0.050 (*)**	1, 10	
				Soil management practices	3.52	0.110	1, 9	
				Crop type × shrubland cover	3.75	0.101	1, 8	
				Crop type × grassland cover	0.01	0.910	1, 7	
Maize leaf damage (%)	GLMM	Beta	500 m	Crop type	4.13	**0.042*****	1, 41	0.46/0.53
				Shrubland cover	3.40	**0.065 (*)**	1, 41	
				Grassland cover	15.15	**<0.001*****	1, 41	
				Pest management practices	5.83	**0.016***	1, 41	
				Soil management practices	2.23	0.135	1, 41	
				Crop type × shrubland cover	0.13	0.718	1, 41	
				Crop type × grassland cover	1.41	0.235	1, 41	
Maize cob damage (%)	GLMM	Beta	250 m	Crop type	0.29	0.592	1, 30	0.06/0.06
				Shrubland cover	0.01	0.944	1, 30	
				Grassland cover	0.61	0.434	1, 30	
				Pest management practices	0.00	0.995	1, 30	
				Soil management practices	0.17	0.682	1, 30	
				Crop type × shrubland cover	0.65	0.422	1, 30	
				Crop type × grassland cover	0.02	0.877	1, 30	

TABLE 3 Results of the PERMANOVAs assessing responses of species assemblages to shrubland cover, grassland cover and the number of agroecological pest- and soil management practices. Df indicate residual degrees of freedom. (*) indicates $p<0.100$, * indicates $p<0.05$, *** indicates $p<0.001$. For model specifications, see Supporting Information 2.

Response	Distance	Scale	Predictors	F-value	p-value	df	R^2
Birds	Bray–Curtis	1000 m	Shrubland cover	1.13	0.341	18	0.45
			Grassland cover	0.67	0.761		
			Pest management practices	0.69	0.731		
			Soil management practices	0.76	0.677		
Carabids	Bray–Curtis	1000 m	Crop type	0.80	0.773	41	0.85
			Shrubland cover	3.17	**<0.001*****		
			Grassland cover	1.19	0.245		
			Pest management practices	1.00	0.435		
			Soil management practices	0.01	0.965		
Ants	Jaccard	1000 m	Crop type	0.83	0.302	52	0.88
			Shrubland cover	1.54	0.969		
			Grassland cover	2.45	0.690		
			Pest management practices	0.69	0.809		
			Soil management practices	0.95	0.545		
Bees	Bray–Curtis	1000 m	Crop type	0.94	0.392	44	0.86
			Shrubland cover	1.74	0.991		
			Grassland cover	1.61	0.547		
			Pest management practices	1.11	0.928		
			Soil management practices	0.96	0.784		
Soil bacteria	Bray–Curtis	500 m	Crop type	0.86	0.341	45	0.99
			Shrubland cover	1.54	**0.011***		
			Grassland cover	1.08	0.317		
			Soil management practices	1.94	0.130		

seed set) using linear models for bean seed set, generalized linear models and generalized linear mixed models with beta distributions for bean and maize damage respectively. All models stated above were calculated separately for shrubland and grassland covers at 250, 500 and 1000 m scales. Out of these, we selected the model with the lowest AICc as the most suitable landscape scale of effect for each response (Table S4). Finally, we tested (iii) the effect of biodiversity (abundance or richness) on all ecosystem services, using linear models for bean seed set, and generalized linear models and generalized linear mixed models with a beta distribution bean and maize damage respectively (Table 4). All models were checked carefully for under- and overdispersion, collinearity and suitability of the chosen residual distributions using the 'performance' package and fulfilled model assumptions (Lüdecke et al., 2021). Detailed information on the statistical analyses and the packages used is provided in Supporting Information 2. All analyses were performed in R version 4.0.5 (R Core Team, 2020).

3 | RESULTS

We observed 897 birds of 37 species (Table S3) and collected 256 carabids of 71 (morpho-)species (Table S5), 2460 spiders, 58 ant (morpho-)species (Table S6), 928 parasitoids, 560 other wasps and 296 bees of 54 (morpho-)species (Table S7). DNA metabarcoding of the soil bacterial microbiome resulted in over 15,500 OTUs, although after data cleaning and low-abundance filtering, 515 taxa remained (Table S8). Based on AICc, we selected models with the largest scale of 1000 m for the abundance and richness of birds, all arthropod taxa and bean seed set, whereas the 500 m scale was selected for soil bacteria Shannon diversity and maize leaf damage. The smallest scale of 250 m was selected for bean leaf and maize cob damage (Table S4).

3.1 | Effects on biodiversity

Increasing shrubland cover altered carabid (Figure S4B) and soil bacteria assemblages (Figure S4E, Table 3). Shrubland cover was positively related to carabid abundance in maize but negatively in bean or intercrop (Figure 2a). Additionally, crop type and shrubland interactively affected parasitoid abundance, with parasitoids in bean fields negatively related to shrubland cover. In maize and intercropped fields, the abundance of parasitoids was significantly lower than in beans and remained relatively constant across the shrubland gradient (Figure 2g). Across the gradient of shrubland cover, spider

TABLE 4 Results of the linear models (LMs), generalized linear models (GLMs) and generalized linear mixed models (GLMMs) for the effects of the biodiversity measured on different ecosystem service responses. Df_{num}: numerator degrees of freedom; Df_{den}: denominator degrees of freedom; $R^2 = R^2$ (LMs), pseudo R^2 (GLMs with beta distribution) or marginal R^2/conditional R^2 (GLMMs). (*) indicates $p < 0.1$, * indicates $p < 0.05$. For model specifications, see Supporting Information 2.

Response	Model	Residual distribution	Predictors	Chi^2-value	*p*-value	df_{num}, df_{den}	R^2
Bean leaf damage (%)	GLM	Beta	Carabid abundance	4.80	**0.029***	1, 31	0.02
			Spider abundance	1.48	0.224	1, 31	
			Parasitoid abundance	3.87	**0.049***	1, 31	
			Wasp abundance	1.41	0.234	1, 31	
			Insectivorous bird abundance	0.08	0.783	1, 31	
Bean leaf damage (%)	GLM	Beta	Carabid richness	0.49	0.483	1, 33	0.01
			Ant richness	0.03	0.870	1, 33	
			Insectivorous bird richness	0.23	0.633	1, 33	
Bean seed set	LM	Gaussian	Bee activity density	0.34	0.572	1, 14	0.03
			Bee richness	0.05	0.839	1, 13	
			Soil bacterial richness	0.01	0.927	1, 12	
Maize leaf damage (%)	GLMM	Beta	Carabid abundance	2.01	0.157	1, 43	0.09/0.28
			Spider abundance	<0.01	0.946	1, 43	
			Parasitoid abundance	0.60	0.437	1, 43	
			Wasp abundance	2.93	**0.087 (*)**	1, 43	
			Insectivorous bird abundance	0.02	0.900	1, 43	
Maize leaf damage (%)	GLMM	Beta	Carabid richness	4.17	**0.041***	1, 44	0.11/0.28
			Ant richness	0.10	0.755	1, 44	
			Insectivorous bird richness	0.43	0.511	1, 44	
Maize cob damage (%)	GLMM	Beta	Carabid abundance	0.85	0.357	1, 32	0.07/0.09
			Spider abundance	1.54	0.215	1, 32	
			Parasitoid abundance	0.07	0.790	1, 32	
			Wasp abundance	<0.01	0.951	1, 32	
			Insectivorous bird abundance	0.51	0.475	1, 32	
Maize cob damage (%)	GLMM	Beta	Carabid richness	<0.01	0.958	1, 33	0.01/0.09
			Ant richness	0.08	0.772	1, 33	
			Insectivorous bird richness	<0.01	0.965	1, 33	

abundance was highest in beans, lowest in maize and intermediate in intercropped fields (Figure 2e). Shrubland cover did not affect other taxa significantly (Figure 2, Figures S4 and S5). Neither grassland cover nor the number of pest management practices affected any of the investigated taxa significantly (Tables 2 and 3). Carabid abundance and richness (Figure 2b,d) and wasp abundance (Figure 2j; Table 2) were positively related to the number of soil management practices.

3.2 | Effects on ecosystem services

Crop type affected the leaf damage by herbivores in both maize and beans (Table 2). For beans, leaf damage was significantly higher in intercropped beans compared to beans in monoculture (Figure 3a), whereas in maize, intercropped maize experienced less damage than maize in monoculture (Figure 3d). Grassland cover did not affect bean leaf damage significantly (Figure 3c), but increased maize leaf damage both in monoculture and intercrop (Figure 3e). The number of pest management practices was positively related to leaf damage in maize (Figure 3f), but not beans (Figure 3c). Shrubland cover and the number of soil management practices did not affect ecosystem services significantly (Table 2). Bean seed set or maize cob damage were not significantly affected by crop type, shrubland cover, grassland cover or pest or soil management practices (Figure S6; Table 2).

3.3 | Effects of biodiversity on ecosystem services

Carabid abundance was positively related to bean leaf damage (Figure S7A) whereas higher parasitoid abundance was negatively related to bean leaf damage (Figure S7C). Carabid richness was positively related to maize leaf damage (Figure S7E). Abundances and

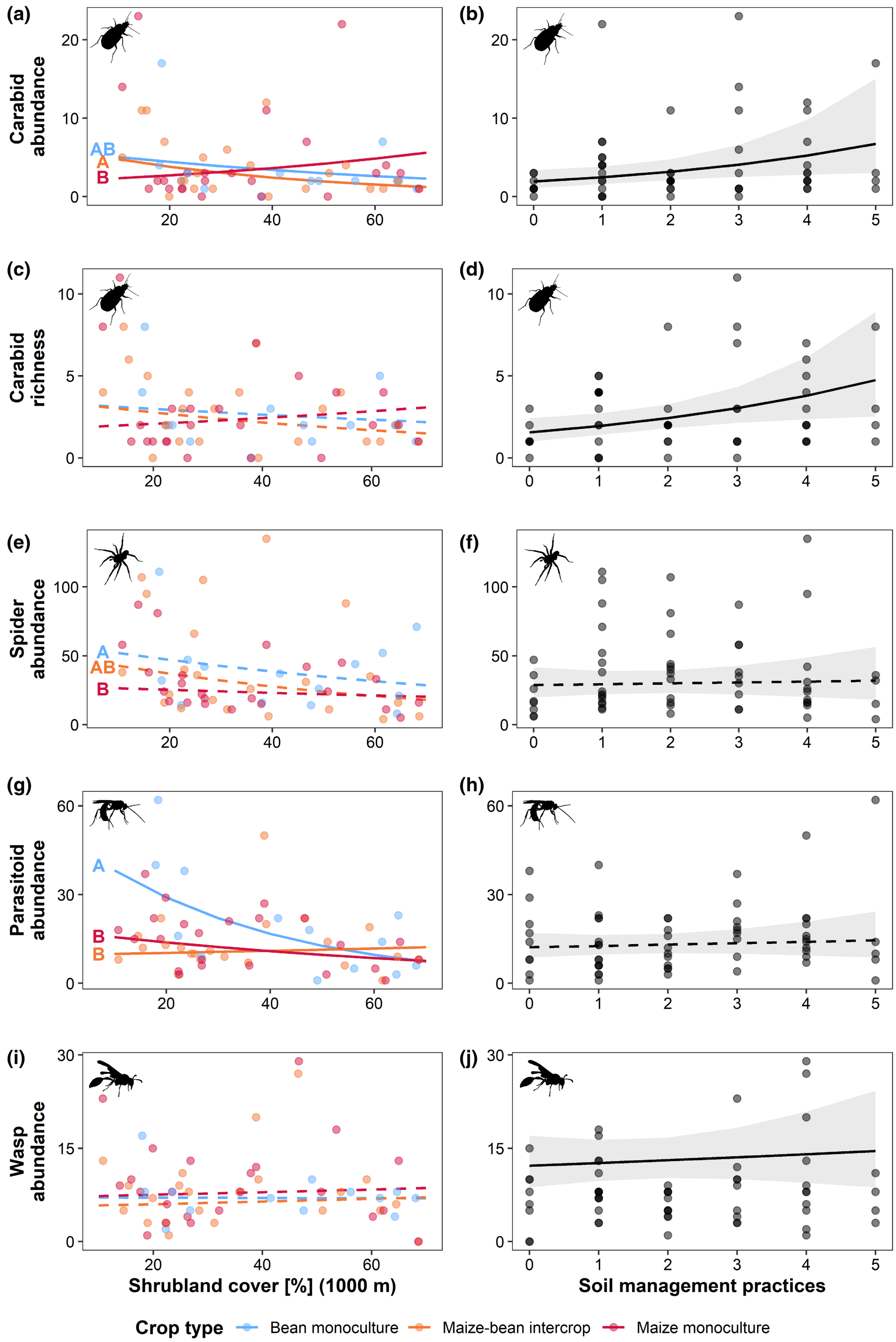

FIGURE 2 Abundance or richness responses (b & c) to shrubland cover by crop type and the number of agroecological soil management practices. The scale of effect of shrubland cover was chosen based on AICc comparison (Table S4). Plotted taxa responded significantly to any one of these effects. Letters on the left-hand side of the panels indicate significant differences between crop types ($p<0.05$), lines represent model predictions (for statistics, see Table 2). Solid coloured lines represent a significant crop type × shrubland cover interaction ($p<0.05$); dashed lines show nonsignificant interactions. Confidence intervals were omitted to increase visibility. A solid black line represents a significant ($p<0.05$) soil management practices effect (with the 95% confidence interval). Dots are true datapoints. Since no taxon responded significantly to grassland cover or the number of agroecological pest management practices, these results are not shown (for statistics, see Table 2). Remaining taxa (that showed no significant responses) are shown in Figure S5.

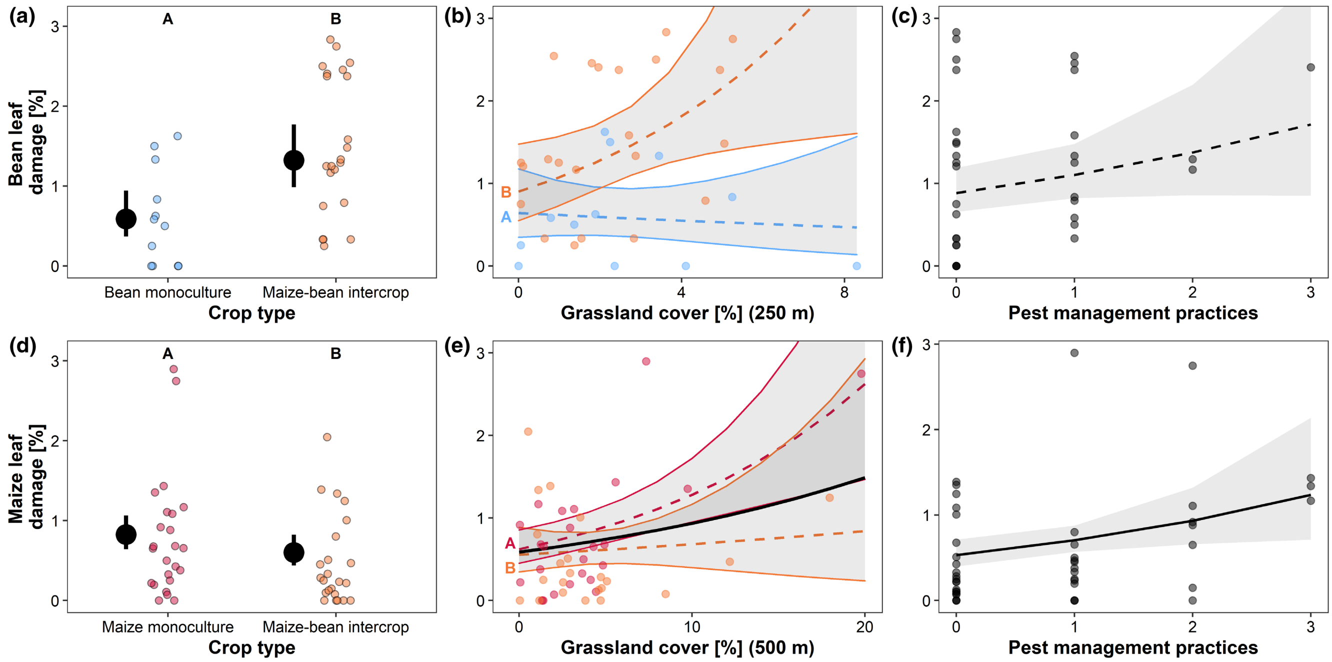

FIGURE 3 Response of bean and maize damages to crop type (a & d), grassland cover (b & e) and the number of agroecological pest management practices (c & f). The scale of grassland cover was chosen based on AICc comparison (Table S4). Black dots (a & d) and lines represent model predictions with 95% confidence interval. Different letters and solid lines indicate significant differences or effects ($p<0.05$) and dots represent true datapoints. Dashed coloured lines represent non-significant crop type × grassland cover interactions ($p>0.05$). Since we found no significant effects of grassland cover or agroecological soil management practices on any ecosystem service, these results are not shown (for statistics, see Table 2). Remaining ES with nonsignificant responses are shown in Figure S6.

richness of other taxa did not significantly affect the damage on maize leaves, maize cobs and bean leaves (Figure S7). We also found no significant effects of bees or soil bacteria Shannon diversity on bean seed set (Table 4).

4 | DISCUSSION

We show that the responses to crop type, landscape composition and agroecological management practices are not consistent across different taxa and ecosystem services (ES). Consequently, maintaining biodiversity and ES on smallholder farms does not have a 'one-size fits all' solution but depends on landscape and crop context. Although more challenging for making broad recommendations, adapting practices to suit a particular agroecosystem and socio-cultural context is central to agroecological approaches, which are guided by adaptive principles rather than recipes for management (Rosset & Altieri, 2017).

4.1 | Effects on biodiversity

Despite a generally positive relation between vegetation diversity and insect predator abundance and richness (Wan et al., 2020) we find that parasitoid, spider and carabid abundances were higher in bean monoculture fields than in maize or intercropped fields. Our results indicate that not monoculture per se, but rather maize cultivation affects natural enemy abundance negatively in our system. Beans may also provide relatively palatable leaves, floral resources and denser ground cover compared to maize. Additionally, maize is an input-intensive crop (Norris et al., 2016), even in our relatively low intensity system (Burke et al., 2022). We also found that the relative benefits for biodiversity of bean cultivation compared to maize were much higher in areas with little surrounding shrublands or grasslands. Since farmers have little individual influence on the habitats surrounding their fields, our results suggest that farmers in landscapes with little shrublands or grasslands could maintain or even increase biodiversity on their fields by growing grain legumes. As cobenefits, legumes are an important addition to the nutrient-poor Malawian diet (Kamanga et al., 2014), and their cultivation improves soil quality (Mhango et al., 2013). Therefore, increased legume cultivation in such landscapes should be encouraged in farmer outreach projects.

In contrast with our expectations, parasitoid abundance in beans was negatively related to increasing shrubland cover. There are several possible reasons for this: first, the presence of flowering beans in a maize-dominated landscape, low in shrublands that contain flowering vegetation, could provide nectar as a food source as well as host pests for reproduction, concentrating parasitoids there. Second, shrublands may provide suitable and attractive alternative habitat for parasitoids, resulting in a parasitoid dilution in shrubland-dominated landscapes. For carabids and spiders, certain species could benefit from specific microhabitats or pest species provided by beans. In addition, increasing shrubland cover altered carabid assemblages, suggesting that as shrublands are converted, species are being filtered out and replaced by others. Assuming this change is unidirectional (i.e. shrublands are converted to agricultural fields, but not the other way around), this means that for maintaining the regional species pool, shrublands should be conserved. Similarly, increasing shrubland cover altered the assemblages of soil bacteria, with potential consequences for crop performance and protection against pests (Badri et al., 2013). With the exception of soil bacteria, which responded on a smaller scale, we find that the 1000 m scale was the scale of effect for the abundance and richness of birds and arthropods, indicating that landscape management on a larger spatial scale is important to maintain the diversity of mobile taxa. We found no evidence that surrounding grasslands affected biodiversity on smallholder fields in our study. In our context, the cover of grasslands was, however, low compared to shrubland cover, potentially limiting the importance of surrounding grassland cover for biodiversity and ES.

Overall, we found little effect of agroecological pest or soil management practices on arthropods, except for carabid abundance and richness and wasp abundance which were positively related to the number of soil management practices used. The number and intensity of soil disturbances can be an important factor modifying carabid assemblages (Pisani Gareau et al., 2020). Increasing carabid richness through agroecological soil management may have the additional benefit of improved pest control, as it is richness, and not only abundance, that is important for the delivery of ecosystems services to crops (Dainese et al., 2019). In addition, increased habitat heterogeneity in fields with a higher number of agroecological soil management practices may promote wasp activity, further indicating that agroecology can have important cobenefits for biodiversity and natural pest control on smallholder farms. The effects of different agroecological pest and soil management practices potentially differ between crop types, but it was not possible to investigate such interactions with our study design. Investigating the efficacy of various agroecological practices in different crops should be prioritized in future studies.

4.2 | Effects on ecosystem services

Maize benefitted from reduced leaf damage in intercropped fields, whereas beans were disadvantaged when they were intercropped with maize. This highlights that trade-offs may occur between partner crops in mixtures—and that not all crops have less herbivory when intercropped compared with cultivation in monocultures (Wan et al., 2020). In some cases, increasing semi-natural or non-crop habitat cover could mitigate pest pressures in crops (Tamburini et al., 2020). However, we found that maize experienced increased pest damage with increasing grassland cover. As maize itself is a grass (family Poaceae), grasslands may harbour herbivores that may also feed on maize. The inconsistent responses of pest damage on the two crops highlight the need to better understand the specific interactions between pests and their natural enemies in different crops to design appropriate pest management strategies and adapt these to the priorities of smallholder farmers (Wezel et al., 2014). Soil properties might mediate relationships between landscape level drivers and ES as land-use is not random and more fertile areas tend to be converted to agriculture first (Serneels & Lambin, 2001). Therefore, understanding the underlying soil properties of agricultural areas may further elucidate the relationships between landscapes and ES.

Agroecological pest management is proposed as a low-cost, culturally appropriate method of managing pests in smallholder farms (Harrison et al., 2019). Surprisingly, the number of pest management practices was positively associated with maize leaf damage, suggesting that agroecological pest management failed in decreasing pest damage. However, it is likely that farmers who observed a lot of pests or pest damage also performed a higher number of pest management practices in reaction on their fields, and we were not able to determine the causal directionality in this study.

4.3 | Effects of biodiversity on ecosystem services

Carabid abundance and richness were positively related to bean and maize leaf damage respectively. We suspect this is because carabids were attracted to fields with high prey availability, as suggested by (Boetzl et al., 2020). In contrast, increasing parasitoid abundance was related to reduced pest damage in beans, emphasizing the importance of this group for biological pest control (Wan et al., 2020). Although it is challenging to clearly disentangle the biodiversity contributions to ES in our study, the indirect relationships shown here (e.g. higher natural enemy abundances in bean monocultures) suggest that maintaining biodiversity is important for ES delivery to smallholder fields.

5 | CONCLUSIONS

5.1 | Synthesis and applications

We found that responses by different taxa and ecosystem services to crop type, landscape composition and agroecological practices vary by context. Adapting and improving practices to suit the landscape setting and the priorities of the smallholder farmer will be important when putting the findings into practice. Our findings also call for a better ecological understanding of pest and natural enemy dynamics in these systems to improve the efficiency of agroecological practices.

First, our study highlights the benefits of legume cultivation, especially in landscapes with low shrubland cover (< ~50%) as a method of increasing natural enemy abundances on crops. We find evidence that increased natural enemy abundance, particularly of parasitoids, decreased bean damage. In practice, this means that bean cultivation in landscapes with low shrubland cover may benefit pest control and foster parasitoid populations. Second, our study highlights the importance of maintaining semi-natural shrublands for the diversity of carabids and soil bacteria. We encourage stakeholders to increase efforts to maintain the quantity and quality of remaining shrublands to conserve biodiversity and the ecosystem services they provide. Sustainable use of the remaining Miombo woodlands should maintain biodiversity as well as resources and ecosystem services essential for the livelihoods of smallholders (Gumbo et al., 2018). Third, we show that agroecological soil management is positively related to important natural enemies of crop pests. As diversification of agroecological soil management practices also provides important benefits to soil health and social outcomes (Bezner Kerr et al., 2021), farmers should be encouraged to implement, diversify and experiment with agroecological soil management on their farms as a low-cost alternative to synthetic fertilizers. Finally, we found that intercropping benefitted maize, but disadvantaged beans and that agroecological pest management had limited damage-reducing success. Farmers thus need to consider trade-offs and to adapt the implementation of intercropping to the crop they prioritize. Informed decisions, based on a better ecological understanding of the complex nature of pest and natural enemy dynamics, and of which (group of) practices should be used in which contexts, can help farmers focus their pest management where it is most important. Teaching farmers how to monitor pests early on before major crop damage is caused may lead to a better timing of agroecological pest management practices and increase its effectivity.

In conclusion, encouraging legume cultivation, increasing agroecological soil management and the conservation of remaining shrubland habitats, are all important factors for maintaining biodiversity and ecosystem services on smallholder farms, and therefore important components for fostering the sustainable development of smallholder agriculture in the tropical agroecosystems of sub-Saharan Africa.

AUTHOR CONTRIBUTIONS

Cassandra Vogel, Katja Poveda, Aaron Iverson, Timothy L. Chunga, Tapiwa Mkandawire, Rachel Bezner Kerr and Ingolf Steffan-Dewenter were all involved in the conceptualization and planning of the study. Cassandra Vogel, Timothy L. Chunga and Tapiwa Mkandawire performed the fieldwork, with Tapiwa Mkandawire specifically identifying the birds, and Timothy Chunga responsible for coordinating various fieldwork activities. Rachel Bezner Kerr designed the farmer survey. Fabian A. Boetzl identified the carabids. Georg Küstner conducted the landscape analysis. Alexander Keller performed the cleaning and preparation of the microbial DNA data. Cassandra Vogel and Fabian A. Boetzl analysed the data. Cassandra Vogel wrote the initial manuscript. All authors contributed significantly to the interpretation of the results and the writing of the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.q573n5tn2 (Vogel et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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