Received: 31 January 2022 | Accepted: 7 May 2023

DOI: 10.1111/1365-2664.14446

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Local and landscape scale woodland cover and diversification of agroecological practices shape butterfly communities in tropical smallholder landscapes

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Funding information
FARMS4Biodiversity Project; German Federal Ministry of Education and Research, Grant/Award Number: BMBF 01LC11804A; Research Council of Norway, Grant/Award Number: 295442; National Science Foundation, Grant/Award Number: 1852587; Natural Sciences and Engineering Research Council of Canada, Grant/Award Number: 523660-2018; SCIENTIA Postdoctoral Scholarship

Handling Editor: Urs Kormann

Abstract

1. The conversion of biodiversity-rich woodland to farmland and subsequent management has strong, often negative, impacts on biodiversity. In tropical smallholder agricultural landscapes, the impacts of agriculture on insect communities, both through habitat change and subsequent farmland management, is understudied. The use of agroecological practices has social and agronomic benefits for smallholders. Although ecological co-benefits of agroecological practices are assumed, systematic empirical assessments of biodiversity effects of agroecological practices are missing, particularly in Africa.
2. In Malawi, we assessed butterfly abundance, species richness, species assemblages and community life-history traits on 24 paired woodland and smallholder-managed farmland sites located across a gradient of woodland cover within a 1 km radius. We tested whether habitat type (woodland vs. farmland) and woodland cover at the landscape scale interactively shaped butterfly communities. Farms varied in the implementation of agroecological pest and soil management practices and flowering plant species richness.
3. Farmland had lower butterfly abundances and approximately half the species richness than woodland. Farmland butterfly communities had, on average, a larger wingspan than woodland site communities. Surprisingly, higher woodland cover in the landscape had no effect on butterfly abundance in both habitats. In contrast, species richness was higher with higher woodland cover. Butterfly species assemblages were distinct between wood- and farmland and shifted across the woodland cover gradient.
4. Farmland butterfly abundance, but not species richness, was higher with higher flowering plant species richness on farms. Farms with a higher number of agroecological pest management practices had a lower abundance of the dominant butterfly species, but not of rarer species. However, a larger number of

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agroecological soil management practices was associated with a higher abundance of rarer species.

5. *Synthesis and applications*: We show that diversified agroecological soil practices and flowering plant richness enhanced butterfly abundance on farms. However, our results suggest that on-farm measures cannot compensate for the negative effects of continued woodland conversion. Therefore, we call for more active protection of remaining African woodlands in tandem with promoting agroecological soil management practices and on-farm flowering plant richness to conserve butterflies while benefiting smallholders.

KEYWORDS

agroecology, butterflies, conservation, landscape change, Miombo woodlands, smallholder agriculture, sub-Saharan Africa

1 | INTRODUCTION

Converting natural habitats to agriculture and subsequently intensifying agricultural landscapes—with monocultures of few genetically similar crops, increased use of synthetic inputs and increased mechanization—are major drivers of biodiversity loss (IPBES, 2019). Recently, alarming decreases in insect abundance and biomass have been reported (van Klink et al., 2020), endangering the ecosystem services they provide. Biodiversity loss is predicted to be especially severe in regions of the world which are biodiversity rich but economically poor, such as vast areas of the tropical South (Newbold et al., 2015). Yet, tropical agricultural landscapes, often managed by smallholders, are under-represented in studies on the response of insect diversity to landscape conversion and subsequent agricultural management (however, see Jew et al., 2015; Tommasi et al., 2021; Schmitt et al., 2021), even though climatic, geographical and management differences may largely influence how insects respond to differences in the landscape (Crossley et al., 2021).

Butterflies (Lepidoptera: Rhopalocera) are indicators of environmental change (Hill et al., 2021) and are among the insect taxa most strongly affected by landscape conversion (Sánchez-Bayo & Wyckhuys, 2019). In Europe, the most serious threat to butterfly abundance and species richness is the degradation and loss of habitat caused by extension and intensification of agriculture over the last century (Warren et al., 2021). In South Africa, habitat degradation has also been identified as a major threat (Edge & Mecenero, 2015). In addition, differences between natural to agricultural habitats can result in butterfly communities with distinct species assemblages and traits (Schmitt et al., 2021), which has implications for butterfly conservation across the wider landscape, as species may be lost even if species richness does not change. Since landscape differences do not affect all butterfly species equally, this results in shifts in community life-history traits. For instance, increasing land-use intensity can favour large-winged butterflies (Börschig et al., 2013). Additionally, species with higher habitat or larval host plant specialization may be especially sensitive to land-use changes (Öckinger et al., 2010), and therefore, the conversion of natural landscapes to agriculture results in the loss of specialized species (Börschig et al., 2013; Gossner et al., 2016; Steffan-Dewenter & Tscharntke, 2000).

The Miombo woodland ecoregion, covering a vast area in southern Africa, illustrates many of the biodiversity conservation challenges in sub-Saharan Africa and more generally in the Global South (Syampungani et al., 2009). The ecoregion is characterized by a high degree of floral endemism and biodiversity (Ribeiro et al., 2020), and it provides essential resources and ecosystem services to the rural poor in the region (Gumbo et al., 2018). Despite this, the woodland is being converted at a rapid rate (Chirambo & Mitembe, 2014), and the remaining woodland remnants are heavily exploited by human activities (Gumbo et al., 2018). An overall characterization and understanding of how entomofauna in this region is interactively affected by local habitat differences, such as woodland versus farmland, and differences in woodland cover across the wider landscape is limited (Ribeiro et al., 2020).

Land clearing for agriculture is a main driver of habitat conversion in sub-Saharan Africa (Gumbo et al., 2018). But once this habitat is converted, what can be done to mitigate the negative effects of habitat conversion for butterflies on farmlands? In the smallholder agricultural context, agroecology is considered a socially just and culturally appropriate way to improve agronomic outcomes for farmers and contrasts with the industrial model of agriculture, which is intensive in its use of synthetic inputs (Rosset & Altieri, 2017). Agroecology is considered a systemic approach, with less focus on individual practices per se, but an appreciation that smallholder farmers should implement a diversity of agroecological practices most appropriate to their needs (Wezel et al., 2020). In particular, agroecological systems that implement a high diversity of agroecological practices are more likely to have positive outcomes for food-insecure smallholders (Bezner Kerr et al., 2021). Agroecological pest management practices include the use of botanical sprays or covering affected crops with ash to smother pests (*Personal communication with farmers*). Although agroecological practices avoid the use of synthetic pesticides, agroecological practices aimed at managing pests may still affect farmland butterflies negatively if the larvae of these butterflies reside on crops. Alternatively, agroecological soil management practices, including compost use, agroforestry and legume intercropping, may positively affect farmland butterfly abundance, in part because they increase crop diversity, which positively affects butterfly communities (Sirami et al., 2019; Table 1). The ecological co-benefits of diversified agroecological practices on insects are assumed, but not often tested. Particularly, studies assessing the impacts of the diversification of agroecological pest or soil practices on butterflies are lacking. In addition to agroecological practices, increasing flowering plant species richness has positive outcomes for butterfly abundance and species richness (Topp & Loos, 2019). Thus, increasing flowering plant species richness, either by allowing flowering weeds to grow in field edges or by planting a higher diversity of flowering crops, may be relatively easy to implement to improve butterfly occurrence on farmlands, also within the context of smallholder agriculture.

Our study region of northern Malawi, located within the Miombo woodland ecoregion, exemplifies many of the aforementioned challenges, such as rapid deforestation (Chirambo & Mitembe, 2014). Furthermore, agroecological practices in the study region are widely promoted by a local organization as a tool to improve the livelihoods of its largely rural population, with considerable uptake of agroecological practices by smallholders (Kansanga et al., 2021). Therefore, the study region provides the opportunity to test the following hypotheses:

1. Local habitat type (wood- or farmland) and the woodland cover in the surrounding landscape interactively affect butterfly abundance, species richness and assemblages mediated by changes in community life-history traits. We expect a higher abundance and species richness in woodland than in farmlands and an increase in abundance and species richness with higher woodland cover in the landscape. Life history traits will shift from specialized smaller-winged species with a narrow range of larval host plants and habitat preferences in woodland to more generalized species with larger wings and less specialized larval host plants and habitat preferences in farmland with less woodland in the landscape.
2. Farmlands with higher implementation of agroecological soil management as well as a higher richness of flowering plants have higher butterfly abundance and species richness. On the other hand, agroecological pest management practices reduce butterfly abundance and species richness on farms.

TABLE 1 Agroecological pest and soil management practices reported by participating smallholder farmers and the number of farms (out of 24) implementing these practices.

Practice group	Practice type	Number of farms
Pest management practices	Botanical extracts	2
	Manual removal/killing of insects	12
	Spreading ash on affected crops	9
Soil management practices	Alternative soil landscaping: box ridges, pit planting, contouring, terracing or low-till practices	8
	Planting of vetiver hedges	3
	Use of mulching	2
	Legume intercropping	12
	Incorporation of legume residues	10
	Crop rotation with legumes	9
	Use of compost	13
	Use of animal manure	13
	Agroforestry	1

2 | MATERIALS AND METHODS

2.1 | Study system

The study was conducted in Mzimba district, northern Malawi, during the rainy season between November 2019 and February 2020. Since Malawi is in the seasonal tropics, the rainy season is both the main crop growing season and the season in which natural vegetation primarily grows and flowers. Due to the availability of vegetation during this period, the rainy season coincides with the main period of insect activity and richness (Kishimoto-Yamada & Itioka, 2015; Schmitt et al., 2021). To conduct the study, we obtained the relevant insect collection and research permit from the National Commission of Science and Technology.

Within our study region, we chose 24 smallholder farms with nearby woodland patches. Farms were located in villages that were specifically selected because they spanned a gradient of woodland cover in a 1 km radius (15%–75%; Figure 1; Kpienbaareh et al., 2022). Details on how the surrounding landscape cover was quantified is given in Supporting Information 1. All chosen farms were representative of our study region. Maize (the main food staple) and tobacco (the main cash crop) are dominant crops, though a highly variable number of legumes and vegetable crops were also grown, often in mixtures. Crops are sown at the onset of rain (late November through December), and the harvesting of maize occurs in April, though other crops may be harvested earlier. Agroecological practices are used throughout our study period as the early months of growth are when the crops are most sensitive to pests and require good soil conditions for growth and yield. Farms in this region are typically small, ranging from 0.5 to 1.4 hectares (FAO, 2018). We considered these farms as "farmland" and the butterflies there as "farmland butterflies".

In contrast, "woodland", was the grassy, shrubby or forested woodlands that border villages and form a part of the Miombo-Mopane ecoregion (Ribeiro et al., 2020). Woodlands were not always uniform in vegetation structure (Figure 1), we considered this variation as an expected characteristic of unmanaged habitats.

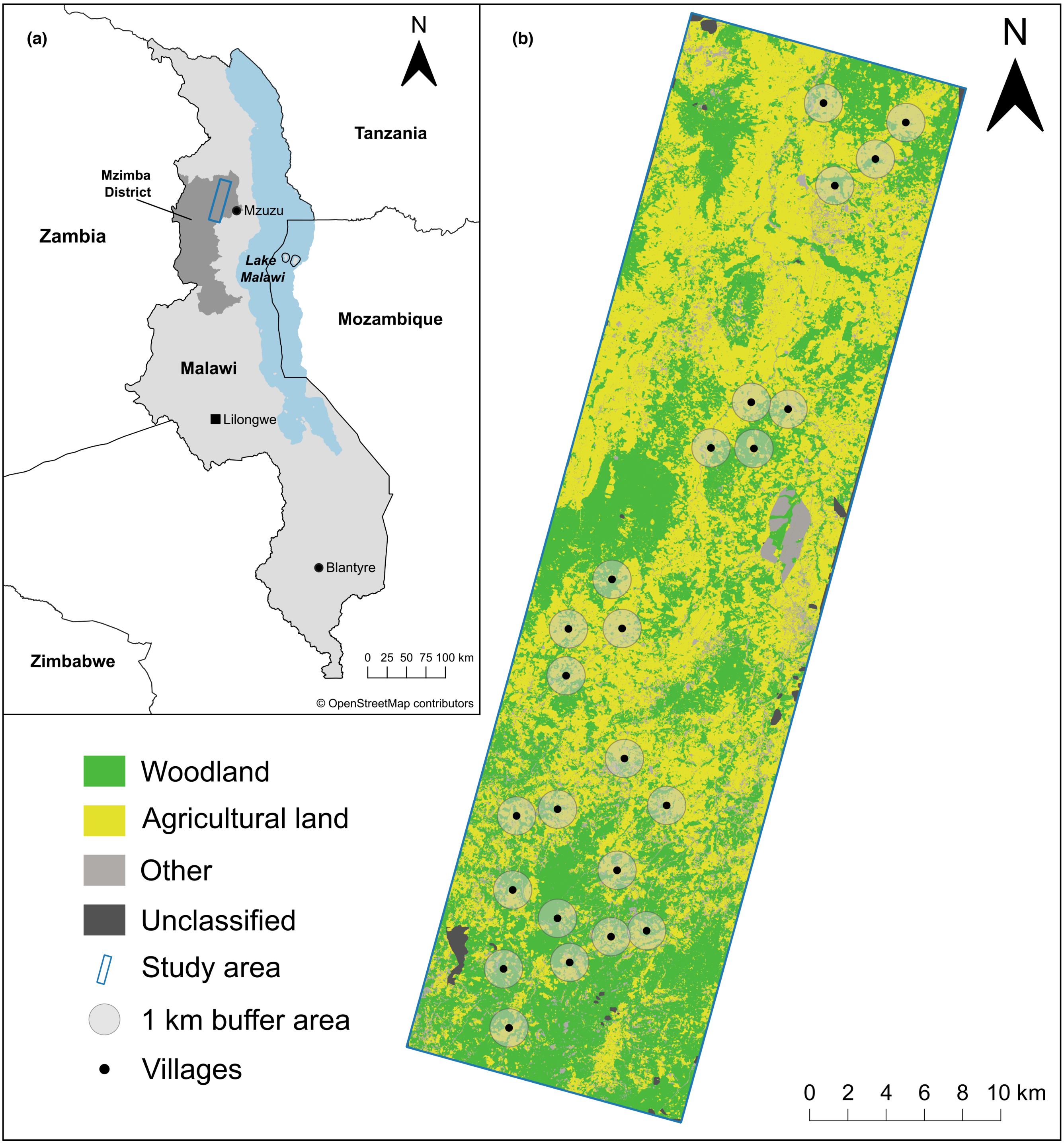

FIGURE 1 Map showing the location of the study area in northern Malawi (a), and the land cover classification map of the study area with all 24 villages (b). Villages are shown using the locations of the starting points of the third subtransects of the first farmland transect walks as the centre of the respective 1 km buffer area.

True savannah is absent in our study region. Though some sections of woodland have official protection status, this is not adequately enforced. Additionally, woodlands are not always effectively managed, but are extensively used by local people for various day-to-day activities important for their livelihoods, such as the grazing of livestock and the collection of firewood (Gumbo et al., 2018). In our study, we use the terms "woodlands" or "woodland sites" to refer to local habitat type differences (as compared to "farms" or "farmland sites") and "woodland cover" to refer to the proportion of woodland cover in the landscape.

2.2 | Transect walks

Five paired transect walks were carried out on all farms and the surrounding woodland (Figure S2). The precise location of the transect within each habitat varied from visit to visit. The distance between the farm- and woodland transect was between 58 and 702 m (mean: 266 m), so that we could consider them part of the same landscape but that they would not be too close to the farms in the study. The order in which transects were sampled in each round was random, also the order of farm- and woodland transects within the study site was random. We were given permission by farmers to access their land for the transect walks.

We performed variable transect walks with a length of ~300 m, divided into 6 subtransects of ~50 m (Pollard, 1977; Westphal et al., 2008). Butterflies were collected 2.5 m left and 2.5 m right from the transect route and sampling time was 3 min per 50 m subtransect adding up to 18 min per transect. While walking, a slow constant pace was kept throughout all transects. Transect walks were only performed between 8 AM and 5 PM, in warm and/or sunny conditions in absence of heavy winds or rains. Butterflies were identified in the field and afterwards released. Occasionally, species were brought to the lab for identification. Butterfly identification followed Collins & Martins, 2016 and Woodhall, 2020. Flowering plant species richness was conducted by counting the number of different flowers present in the transects during each walk. Butterflies are stored at the Soils, Food and Healthy Communities (SFHC) Farmer Research and Training Centre in Ekwendeni, Malawi.

2.3 | Butterfly life-history traits

Life history traits following Woodhall, 2020, were female wingspan size, which is considered a proxy for dispersal ability (Sekar, 2012), larval host-plant specialization and habitat specialization. For the wingspan of each species, we took the mean of the wingspan range reported for female individuals. For larval host-plant specialization, we considered a larva monophagous if it only feeds on one plant species or genus, oligophagous if its host plants are restricted to a single plant family and polyphagous if it feeds on host plants belonging to more than one plant family. Habitat generalists were butterflies with little habitat preference, forest specialists were butterflies that were described as preferring woody or forest edge habitats and savannah specialists were butterflies preferring grassland or savannah habitats (Table 1).

2.4 | Farmer surveys

To assess the implementation of agroecological agricultural practices on the farms on which butterflies were assessed, we performed structured interviews from 8 to 26 of March 2020. Respondents had the study explained to them and gave informed consent prior to answering questions. The Institutional Review Board of Cornell University for Human Subjects Research reviewed and approved the research study design (protocol 1811008425). We asked questions about agroecological practices performed for up to three fields per farm (Table 1). The questions were posed as a yes or no question (did you perform × practice on this field?) as well as any additional practices at the end of the questionnaire. The questions were asked only to the adults of the household managing the farm (men or women), as we assumed that they would be most knowledgeable about the practices applied to the fields and not to other family members who may be living on the property. A list of questions posed to farmers are given in Supporting Information 2. Farmers did not report using synthetic pesticides on their farms. Farmers reported up to three different agroecological practices that aimed to manage pests on fields (hereafter, "pest management practices") and nine practices that aimed to maintain soil quality (hereafter, "soil management practices") (Table 1).

2.5 | Statistical analysis

All data analysis was performed in the R version 4.0.5 (R Core Team, 2020).

To test the relationship between habitat and butterflies we used the following predictors: local habitat type (wood- vs. farmland) and woodland cover in the landscape, with an interaction term between the two. To test for the relationship between farmland management on farmland butterflies, we used the following predictors: number of pest management practices, number of soil management practices and flowering plant species richness. We used the scaled predictors from −1 to 1 in all models as our predictors represented different units of measurement.

For the responses, we summed butterfly abundance and calculated cumulative species richness across the five transect rounds per habitat type (wood- and farmland) and village, resulting in 48 butterfly communities. We used total butterfly abundance, *Catopsilia florella* (the dominant butterfly species) abundance, non–*C. florella* abundance and species richness as response variables. For all models testing abundances, we used negative binomial linear mixed models using the function 'glmer.nb' and for species richness models with a Poisson distribution using the function 'glmer' from the LME4 package to test these response variables against the landscape predictors. We used village as a random effect to account for the nestedness of the paired transects (Bates et al., 2019).

To assess the effect of habitat type and woodland cover on butterfly community (including *C. florella*) life history traits, we calculated community weighted means of female wingspan for each site. This was tested against the landscape predictors using linear mixed models, again with village as a random effect. To test the response of the proportion of the three different larval host plant specializations or habitat specializations, we used a binomial generalized mixed model. In these models, the number of individuals representing the trait versus the number of individuals that did not represent the trait was tested.

To test if farm- and shrubland species communities became more similar or different along the woodland cover gradient, we calculated the proportion each species represented in the community at each site and habitat type. We used the function 'vegdist' from the VEGAN package to calculate Bray-Curtis distances between paired farm- and shrubland communities and used a linear model to assess changes in community difference across the woodland cover gradient (Oksanen et al., 2020). To test whether species assemblage differed with habitat types and or changed with increasing woodland cover in the landscape, we calculated a PERMANOVA using Bray-Curtis distances from the 'adonis' function, again from the VEGAN package. The PERMANOVA had 999 permutations and included 'strata = village' to correct for nestedness. Visualization of the species assemblages is done through an non-metric multidimensional scaling (NMDS).

For farmland butterflies, we used the same response variables (total butterfly abundance, *C. florella* abundance, non–*C.florella* abundance and total species richness). For abundance responses, we used a generalized linear model with a negative binomial distribution and for richness we used generalized linear model with Poisson distribution to test the effects of the number of agroecological pest- or soil management practices and flowering plant species richness on farms.

All models were tested for the assumptions of normality, over- and underdispersion, distributions (of residuals) and heteroscedasticity. Assumptions of co-linearity were checked using the PERFORMANCE package (Lüdecke et al., 2021). For visualization, we plotted predicted values from the model with unscaled predictors using the 'ggeffect' function from the GGEFFECTS package (Lüdecke, 2018).

3 | RESULTS

In total, we counted 5242 individual butterflies, belonging to 70 different taxa (Table 1), with 34 taxa represented on farmland habitats and 66 taxa found in woodland habitats. The most common butterfly was *Catopsilia florella* (Pieridae) with 3457 individuals, accounting for 66% of all recorded butterflies in our study.

3.1 | Butterfly community and life history trait responses to habitat type and landscape woodland cover

On a local scale, woodland habitats supported higher butterfly abundance than farmland habitats (Figure 2a), both the dominant species *C. florella* (Figure 2c) and non-dominant butterflies (Figure 2d) but abundance was unrelated to woodland cover in the surrounding landscape (Table 2). Species richness was also almost twice as

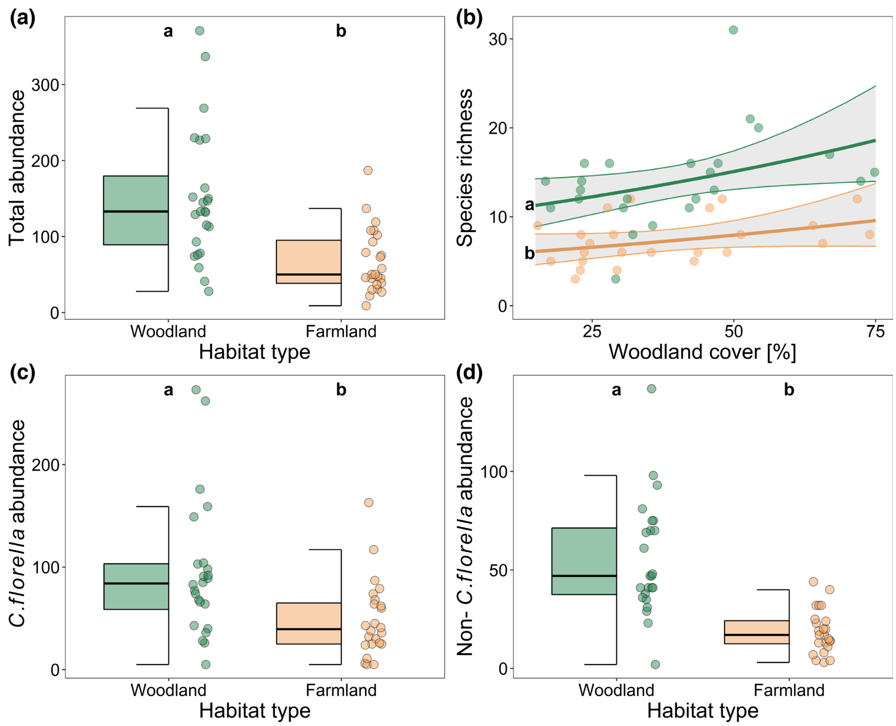

FIGURE 2 Total butterfly abundance (a), cumulative species richness (b), *Catopsilia florella* abundance (c) and non–*C. florella* abundance (d) in response to habitat type (woodland in green, farmland in orange) and the cover of woodland within a 1 km radius. Boxplots (a, c and d) indicate a significant effect of habitat type only, with the median and the first and third interquartile is indicated by the boxplot, and the minimum and maximum by the whiskers. Datapoints on the right indicate the spread of the data and may show outliers. (b) shows a significant response to landscape-scale woodland cover. Significant differences between wood- and farmland are indicated with letters, significant changes across the woodland cover in the landscape are indicated with a solid line. Lines show the direction of the prediction, grey areas around the lines show the 95% confidence interval.

TABLE 2 The results of the models assessing the responses of the butterfly community and life-history traits to habitat type, the cover of woodland in the landscape and their interaction. df_{num}, numerator degrees of freedom; df_{den}, denominator degrees of freedom; R^2_m, marginal R^2; R^2_c, conditional R^2. Bold *p*- values indicates $p<0.100$, * indicates $p<0.050$, ** indicates $p<0.010$ and *** indicates $p<0.001$.

Response	Model type	Predictors	Chi^2	*p*-value	df_{num}/df_{den}	R^2_m/R^2_C
Total butterfly abundance	GLMM with negative binomial distribution	Woodland cover	0.06	0.803	1/40	0.33/0.73
		Habitat type	48.89	**<0.001*** **	1/22	
		Type × woodland cover	0.02	0.882	1/22	
Butterfly richness	GLMM with Poisson distribution	Woodland cover	6.01	**0.014***	1/43	0.51/0.63
		Habitat type	47.10	**<0.001*** **	1/22	
		Type × woodland cover	0.02	0.88	1/23	
C. florella abundance	GLMM with negative binomial distribution	Woodland cover	0.71	0.40	1/39	0.19/0.75
		Habitat type	27.70	**<0.001*** **	1/22	
		Type × woodland cover	0.20	0.654	1/22	
Non-*C.florella* abundance	GLMM with negative binomial distribution	Woodland cover	2.58	0.108	1/43	0.51/0.75
		Habitat type	70.41	**<0.001*** **	1/22	
		Type × woodland cover	1.28	0.247	1/23	
Wingspan (community weighted means)	LMM	Woodland cover	1.17	0.291	1/23	0.33/0.35
		Habitat type	22.35	**<0.001*** **	1/22	
		Type × woodland cover	0.69	0.416	1/23	
Proportion monophagy	GLMM with binomial distribution	Woodland cover	0.71	0.399	1/44	0.18/0.47
		Habitat type	8.85	**0.003** **	1/22	
		Type × woodland cover	2.79	**0.095**	1/23	
Proportion oligophagy	GLMM with binomial distribution	Woodland cover	1.07	0.302	1/39	0.02/0.08
		Habitat type	10.70	**0.001** **	1/22	
		Type × woodland cover	12.25	**<0.001*** **	1/22	
Proportion polyphagy	GLMM with binomial distribution	Woodland cover	0.41	0.520	1/42	0.01/0.06
		Habitat type	5.55	**0.018***	1/22	
		Type × woodland cover	11.05	**<0.001*** **	1/23	
Proportion habitat generalists	GLMM with binomial distribution	Woodland cover	2.71	**0.100**	1/43	0.04/0.11
		Habitat type	41.97	**<0.001*** **	1/22	
		Type × woodland cover	12.37	**<0.001*** **	1/23	
Proportion forest specialists	GLMM with binomial distribution	Woodland cover	3.88	**0.049***	1/43	0.04/0.18
		Habitat type	14.18	**<0.001*** **	1/22	
		Type × woodland cover	1.04	0.308	1/23	
Proportion savannah specialists	GLMM with binomial distribution	Woodland cover	5.86	**0.016***	1/49	0.03/0.12
		Habitat type	17.90	**<0.001*** **	1/22	
		Type × woodland cover	10.42	**0.001** **	1/22	

high in woodland habitats compared to paired farmland habitats and was higher with increasing woodland cover in both habitats (Figure 2b; Table 2). Even though differences between farmland and woodland butterfly communities did not significantly change across the woodland cover gradient ($F_{1/22}=0.33$, $p=0.574$), species assemblages were distinctly different between wood- and farmland habitats and were modified by higher woodland cover in the landscape (Figure S3; Table S2).

The community weighted means of female wingspan showed no differences with increasing woodland cover (Table 2), but overall, butterflies in farmlands were significantly larger than woodland butterflies (Figure S4a). The proportion of individuals whose larvae are monophagous (0%–12.5% per site), was higher in woodland habitats, as they were almost absent from farmland habitats (Figure S4b). The proportion of oligo- (19.4%–96.4% per site; Figure S4c) and polyphagous (3.6%–80.6% per site; Figure S4d) butterflies remained almost constant across the woodland cover gradient in woodland habitats (~70% per site for oligo- and ~25% per site for polyphagous butterflies), but the proportion of oligophagous butterflies was lower whereas the proportion of polyphagous butterflies was higher with increasing woodland cover in the landscape (Table 2).

Habitat generalists, representing 3%–74% of individuals per site, were better represented in woodland than in farmland habitats. In woodlands, the proportion of generalists remained relatively stable with higher woodland cover, whereas in farmlands the proportion of generalists positively related to woodland cover (Figure S4e). Forest habitat specialists were the least represented (0%–28% per site) but were more common in farmlands compared to woodlands and higher on sites with higher woodland cover in the landscape (Figure S4f). Savannah specialists were better represented in the community (19%–96% per site) than forest specialists. There was a higher proportion of savannah specialists in farmlands than woodlands, but this proportion in farmland habitats was lower with higher woodland cover in the landscape. The proportion of savannah specialists in woodlands (~75%), however, remained relatively constant across the woodland cover gradient (Figure S4g; Table 2).

3.2 | Farmland butterfly community responses to agroecological practices and flowering plant species richness

Farms with a higher number of agroecological pest management practices had a lower total butterfly abundance (Figure 3a), due to a lower abundance of *C. florella* (Figure S5d), but not of the other butterfly species (Figure 3d). In contrast, more agroecological soil management practices were related to a higher abundance of non–*C. florella* butterflies (Figure 3e) but not the abundance of *C. florella* (Figure S5e). Higher flowering plant species richness on farms was positively related to total butterfly abundance (Figure 3c) due to increased non–*C. florella* abundance (Figure 3f), but not *C. florella* abundance (Figure S5f). Species richness showed no relationship with pest or soil management practices nor with higher flowering plant species richness (Figure S4a–c; Table 3).

4 | DISCUSSION

Our study shows that the presence of woodlands on a local and landscape scale have positive effects on butterfly communities in a biodiversity-rich ecoregion in sub-Saharan Africa. Agroecological soil management practices and maintaining flowering plant species richness on farmlands have the potential to mitigate some of the negative effects of landscape transformation, but only if woodland areas in the region are simultaneously protected.

4.1 | Butterfly community and life-history trait responses to habitat type and landscape woodland cover

In contrast to studies that examine local habitat differences or rely on a surrounding landscape gradient only, to our knowledge,

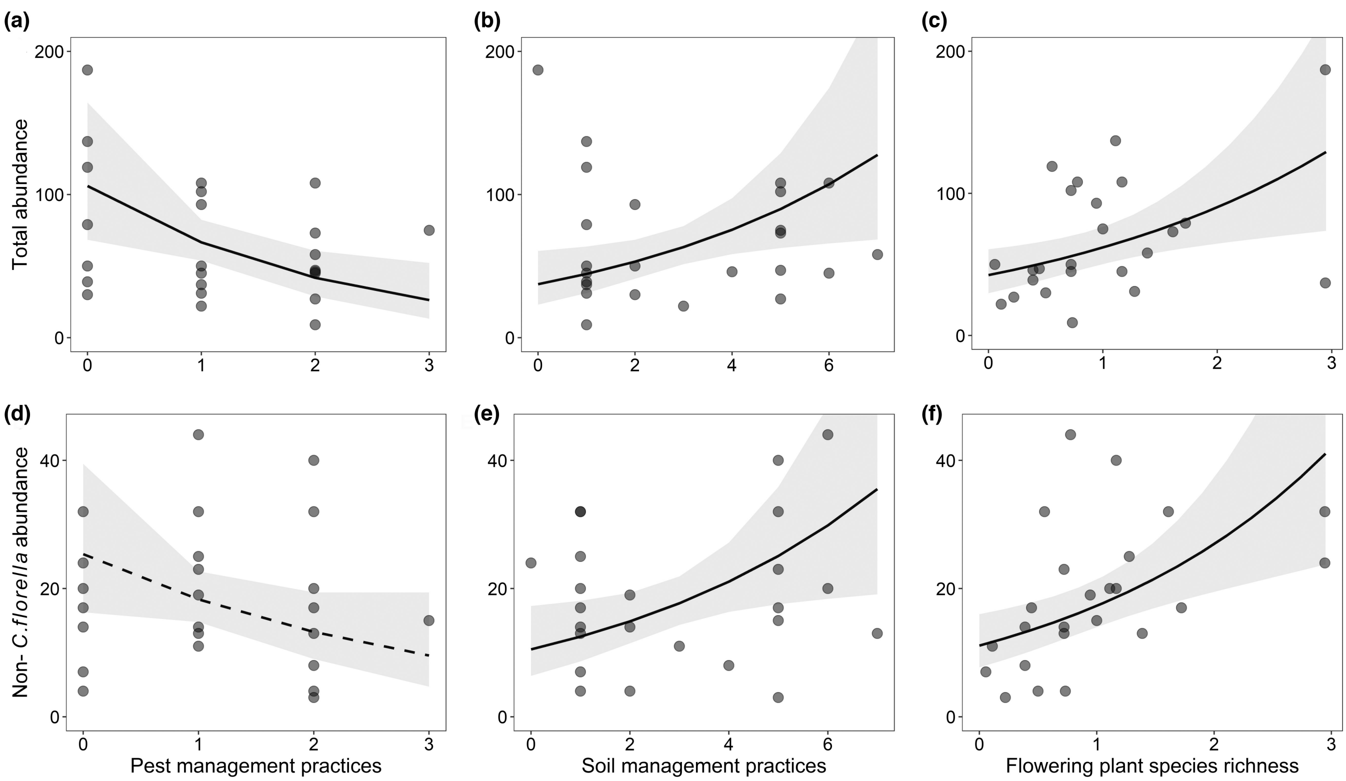

FIGURE 3 Responses of total farmland butterfly abundance and non–*Catopsilia florella* butterfly abundance to the number of agroecological pest management practices (a, d), number of soil management practices (b, e) and flowering plant species richness along the transects on farms (c, f). Significant effects are indicated with solid lines, and dashed lines indicate a non-significant relationship. Lines indicate predicted effects. Grey areas show the predicted 95% confidence interval.

TABLE 3 Results of the generalized linear models (GLMs) with Poisson distribution assessing the responses of farmland butterfly communities to the number of traditional pest and soil management practices per hectare and the flowering plant species richness on the farms. df_{num}, numerator degrees of freedom; df_{den}, denominator degrees of freedom; $R^2{}_m$. Bold p-values indicates $p < 0.100$, * indicates $p < 0.050$, **, and indicates $p < 0.010$.

Response	Model type	Response/predictors	Chi²	p-value	df_{num}/df_{den}	R^2
Total butterfly abundance	GLM with negative binomial distribution	Number of agroecological **pest** management practices	7.46	**0.006****	1/22	0.55
		Number of agroecological **soil** management practices	5.30	**0.021***	1/21	
		Flowering plant species richness	7.62	**0.006****	1/20	
Butterfly species richness	GLM with Poisson distribution	Number of agroecological **pest** management practices	0.09	0.761	1/22	0.24
		Number of agroecological **soil** management practices	0.78	0.377	1/21	
		Flowering plant species richness	3.47	**0.062**	1/20	
C. florella abundance	GLM with negative binomial distribution	Number of agroecological **pest** management practices	4.57	**0.033***	1/22	0.37
		Number of agroecological **soil** management practices	2.53	0.112	1/21	
		Flowering plant species richness	3.14	**0.076**	1/20	
Non-*C. florella* abundance	GLM with negative binomial distribution	Number of ecological **pest** management practices	3.50	**0.061**	1/22	0.82
		Number of agroecological **soil** management practices	6.11	**0.013***	1/21	
		Flowering plant species richness	10.60	**0.001****	1/20	

this study is the first to investigate the interactive effects of the two landscape types with a surrounding landscape gradient in sub-Saharan Africa. Contrary to our expectations, we find no evidence that landscape and local scale woodland cover interactively affected butterfly abundance or richness. Rather, we find that habitat type differences drove abundance patterns whereas landscape-scale woodland cover explained differences in butterfly richness between sites.

On a local scale (~300 m), we find that farmlands support a lower butterfly abundance, even of the most abundant species, and a lower species richness compared to woodlands, while also altering butterfly community life-history traits. These results are consistent with findings elsewhere in Africa (Jew et al., 2015) and add to the understanding that maintaining suitable habitat on a local scale of less than 1 km radius is essential to maintain butterfly abundance and species richness. The importance of woodlands is clearly reflected in the fact that only half of the species of the total butterfly species pool was found on farmlands in this study. In addition, species assemblages between farm- and woodland habitats differed, with some species, for example *Acada biseriata* (Hesperiidae) and *Ypthima asterope* (Nymphalidae) being completely absent in farmland habitats. Similar assemblage differences have been found elsewhere in Africa (Schmitt et al., 2021). African smallholder agriculture is characterized by relatively high diversity of crops within a smaller farm area compared to temperate agriculture (FAO, 2018). Often, the assumption is that these systems can support a higher biodiversity, but our findings suggest that even smallholder farmlands are unsuitable habitats for certain butterfly species.

We observed a shift from smaller butterflies in woodland, which might be poorer dispersers (Sekar, 2012), to larger butterflies in farmland. Similar results have been found in Europe, where intensively used landscapes favoured strong dispersers (Börschig et al., 2013). We suspect that in our context, this might be because the poorer dispersing butterflies remain within their source woodland habitat, whereas the better dispersers are able to disperse through larger patches of relatively unsuitable farmland habitat. This also means that small butterflies, such as *Zyntha hintza* (Lycaenidae) might be particularly at risk from disappearing from the landscape if more woodland is converted to farmland. Additionally, butterflies with monophagous larvae and those that are considered habitat generalists were also highly dependent on local woodland habitats. The high dominance of *C. florella*, an oligophagous savannah specialist, also makes the interpretation of the proportional data challenging. Though we expected a higher proportion of generalists in farmland than in woodlands, we suspect that the higher variation within woodland habitats compared to farmland habitats catered to habitat generalists.

On a landscape scale, butterflies have been shown to be negatively affected by the fragmentation of their habitats (Krauss et al., 2003). Smaller woodland patches are often more heavily exploited due to increased resource use per available area (Gumbo et al., 2018), degrading the biodiversity. Miombo woodlands are particularly rich in plant species and often have high rates of endemism but constitute also one of the most at-risk biomes globally (Laurance et al., 2014). Therefore, we expected an increase in butterfly abundance and species richness with higher woodland cover in the landscape. In line with our expectations, we observed higher species richness and changes in species assemblage with increasing woodland cover, but no differences in abundance. This seems counter-intuitive since species richness is often correlated with abundance. However, local effects are often more important for abundance, whereas landscape effects on larger scales drive species richness patterns (Brückmann et al., 2010). Woodland habitats with lower woodland cover in the surrounding landscape had lower butterfly species richness, with a reduction of approximately 30% in the woodland with the least amount of surrounding woodland cover compared to the woodland sites surrounded by the highest woodland cover. This lower species richness could be explained by a decline in habitat quality and negative effects of lower connectivity in these fragmented habitats (Brückmann et al., 2010). Additionally, high woodland cover in the landscape was important to maintain higher forest specialist butterflies in both wood- and farmland habitats. These relationships with woodland cover in the landscape have implications for butterfly conservation, as both local woodland sites as well as landscape-scale woodland cover is important for maintaining butterfly diversity.

Butterflies and their larvae are important food sources for other animals, such as birds, and might act as pollinators in the tropics contributing to floral diversity in the region (Butler & Johnson, 2020; Goldblatt & Manning, 2006; Johnson, 2004). Pollinators have been shown to be drivers of plant species richness (Wei et al., 2021), and therefore reductions in butterfly species richness might have unforeseen implications elsewhere in the ecosystem. In southern Africa, some butterfly species are at risk of disappearing (Edge & Mecenero, 2015), and our results indicate that, at least on a local scale, the same could occur in Malawian landscapes. Overall, we found only a subset of 70 species known in Malawi, where 488 butterfly species have been reported (African Butterfly Database, n.d.). Further studies in the region, such as comparing butterfly species richness in these agriculture-dominated landscapes with legally protected areas might be a next step to further elucidate the species losses that has occurred thus far. Additionally, understanding plant-butterfly networks in the Miombo woodland ecoregion will be an important area for future study, to better understand the possible consequences of disappearing butterfly diversity, both as pollination partners as well as larvae-host plant relationships. Overall, the results emphasize that remaining Miombo woodlands in Malawi need more active protection to prevent further habitat and biodiversity loss. Additionally, engaging local communities will be essential so that resources in the remaining woodlands can be utilized in an ecologically and socially sustainable way for both rural communities and biodiversity (Gumbo et al., 2018).

4.2 | Farmland butterfly community responses to agroecological practices and flowering plant species richness

Agroecological practices are a low-cost and culturally appropriate method of developing smallholder agriculture, with numerous agronomic benefits for smallholder farmers (Bezner Kerr et al., 2021) whereas co-benefits for butterfly diversity are assumed but lacked evidence in Africa so far. We found that, overall, diversifying pest or soil agroecological practices did not benefit nor harm species richness of butterflies on farms. However, increasing agroecological pest management practices, such as killing insects by hand or using botanical sprays, reduced *C. florella* abundance, and therefore also total abundance, on farms. *C. florella*, a migratory species with a wide host-plant breadth, may be a pest for certain crops (Woodhall, 2020). A limitation of our study is that we cannot disentangle the effects of the individual pest management practices, as sample size for each individual practice was limited. However, since *C. florella* is a generalist species which can feed on a wide range of host plants (Woodhall, 2020), we suspect that farmers may consider *C. florella* caterpillars a pest and manually remove them from crop plants. Additionally, adult butterflies may be deterred from visitation by repellents. However, non–*C. florella* butterfly abundance was unaffected by increased agroecological pest management, indicating a limited negative effect on butterfly communities overall.

In contrast, diversifying soil agroecological practices did not affect *C. florella* abundance but improved non–*C.florella* butterfly abundance. Many soil agroecological practices, such as intercropping (with legumes), increase diversification of crop plants grown on farms, which benefits pollinators (Norris et al., 2018). In addition, healthy soils could promote crop health, which mediates plant-butterfly interactions by increasing the quality of farmland plants for butterflies as a food source (Grundel et al., 1998). Non–*C. florella* butterflies, as the rarer, non-dominant butterflies, have a higher risk of disappearing from the landscape if they are not adequately protected. Therefore, we suggest promoting diversified soil agroecological practices as a method for developing smallholder agriculture and preserving butterfly biodiversity. Further studies into the effects of individual agroecological soil and pest management practices on butterflies could be important to understand which specific agroecological pest and soil management practices have positive or negative effects on butterfly abundance and how to further advise smallholders on the application of these practices to benefit both themselves and the butterfly community.

Higher flowering plant species richness on farms strongly benefitted butterfly abundance of both the dominant and non-dominant species. The significance of flowering plants on species richness corresponds with previous studies in natural ecosystems in Africa (Topp & Loos, 2019). Though flowering plant species richness on our transects was generally low, our results indicate similar effects in agroecosystems in our study region. We assume that a higher number of flowering crop species ensure more continuous resources through time (Lasway et al., 2022). In temperate systems, set-aside habitats such as flower strips show promising benefits for butterfly abundance and richness, mediated by an increase in flowering plant species richness (Boetzl et al., 2021; Wix et al., 2019). Given the financial and temporal constraints on smallholder farmers in our study region, we do not necessarily suggest set-aside habitats in our context, although they promote bee diversity in East Africa (Lasway et al., 2022). Our results, however, reveal a large benefit in butterfly abundance for a relatively small increase in flowering plant species richness. In a practical sense, this means encouraging farmers to grow a variety of flowering crops and tolerating flowering weeds on field edges. Further research addressing a wider range of flowering plant richness, and including plant identity, is needed to assess the robustness of our result and to what extent it can truly benefit butterflies on farmland habitats. However, we think that this practice could be a relatively simple, cost- and labour-effective measure and would contribute to the preservation of butterfly abundance on smallholder farms and might also promote other ecosystem services such as natural pest control.

5 | CONCLUSIONS

To maintain butterfly communities with a diversity of life-history traits in the proximity of farmlands, smallholder farmers should be encouraged to maintain woodland habitats in proximity to their communities as well as across the wider landscape. Additionally, we show the potential for agroecology compared to input-intensive agriculture as a tool for mitigating negative effects of agriculture on butterfly abundance in Africa, as increasing the number of agroecological soil practices, as well as increasing flowering plant species richness on farms, was associated with higher butterfly abundance on farms.

On a landscape level, we found that lower woodland cover decreased species richness both in wood- and farmland habitats. The reduced farmland species richness indicates that on-farm measures aimed at conserving butterflies will have limited success if at least ~50% woodland cover within 1 km radius in the landscape is not conserved. Therefore, we call upon stakeholders in our study region and in the wider Miombo woodland ecoregion to increase efforts to conserve the quantity and quality of remaining woodlands throughout the landscape so that butterflies and other biodiversity can be conserved in the region, and their ecosystem services can be maintained. In tandem, increasing agroecological soil management practices and flower plant species richness, if even by a single additional species, on farms could be a practical solution to mitigate the negative effects of agriculture on butterfly communities, while also benefiting the livelihoods of rural smallholders.

AUTHOR CONTRIBUTIONS

Ingolf Steffan-Dewenter conceived the study and designed it together with Jochen Krauss, Cassandra Vogel and Vera Mayer. Vera Mayer and Mwapi Mkandawire selected the sites and collected the butterfly and vegetation data. Vera Mayer identified the butterflies. Georg Küstner conducted the landscape analysis. Rachel Bezner Kerr designed and coordinated the farmer survey. Cassandra Vogel performed data analysis and led the writing of the manuscript with significant contribution of Vera Mayer. All authors contributed to the writing process of the manuscript and gave their final approval.

ACKNOWLEDGEMENTS

First and foremost, we thank all the smallholder farmers who gave us permission to collect data on their farms. Second, we thank Petros Munthali and Timothy Chunga for their help during data collection and Katja Poveda for her input into the methods. We also thank Ray Murphy for his assistance with identifying the butterflies, Adomas Liepa and Daniel Kpienbaareh for their support concerning the GIS landscape classification, and the senior management of SFHC, Esther Lupafya, Laifolo Dakishoni, and Lizzie Shumba in facilitating the fieldwork. We thank Fabian Boetzl for his input in the statistical analysis. We thank the paper club at the Zoology 3 department in Würzburg for their helpful input on the manuscript and Planet Labs Inc. for making the PlanetScope data freely available via its Education and Research Program. We thank the National Commission of Science and Technology in Malawi for issuing the collection and research permit that made this study possible. We thank David Banda for translating the abstract. This research was funded as part of the FARMS4Biodiversity Project through the 2017-2018 Belmont Forum and BiodivERsA joint call for research proposals, under the BiodivScen ERA-Net COFUND program, and with the funding organizations German Federal Ministry of Education and Research (BMBF 01LC11804A), Research Council of Norway (295442), National Science Foundation (NSF 1852587) and the Natural Sciences and Engineering Research Council of Canada (NSERC 523660-2018). CV is supported by a SCIENTIA Postdoctoral Scholarship. Open Access funding enabled and organized by Projekt DEAL.

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.5qfttdz9p (Vogel et al., 2023).

STATEMENT OF INCLUSION

Our study brings together authors from three different countries, including an author from the country where the data were collected—Malawi. The study is part of a larger participatory research project (FARMS4Biodiversity) bringing together local and international institutions aimed at exploring social and ecological consequences of landscape change and agroecological practices in northern Malawi. Throughout this study and the project, the priorities and interests of smallholder communities was always considered, and a team of trained farmer-researchers (including our co-author, Mwapi Mkandawire), co-designed and were fundamental to the project. A local Malawian non-profit organization, SFHC, is a research partner of this study and works to ensure that research results are shared and benefit the local communities. As part of this study and the FARMS4biodiversity project, we have disseminated the information gathered in this and other studies to participating farmers and their communities in the local language (chiTumbuka) and in an accessible way, including written pamphlets and an in-person workshop with all participating farmers in January 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.

Supporting Information 1. Landscape analysis.

Supporting Information 2. Farmer questionnaire.

Figure S1. Photographs of woodland habitats surrounding villages in our study region of Mzimba district, Malawi. Woodlands can show some variation in vegetation structure, on the left there is a denser woodland habitat, whereas on the right the woodland is less dense, and trees are interspersed by grassy patches. Photographs were taken in February 2020.

Figure S2. Scheme of the transect method (A) and a transect walk at a particular site on a satellite picture (B). Transect walks were each conducted in the wood- and the farmland. Every transect had a width of 5 m and a total length of about 300 m (divided into 6 subtransects of 50 m each). Every village was sampled 5 times. The white line shows the transect route. The beginning and the end of a subtransect are indicated by yellow dots.

Figure S3. NMDS plot visualising the results of the PERMANOVA testing the response butterfly species assemblages in farmland (orange) and woodland (green) and along the woodland cover gradient. The clustering of the two habitat types is indicated by the ellipses. The direction of change with increasing woodland cover in a 1 km radius is indicated with a vector.

Figure S4. Life-history trait responses to habitat type (woodland in green, farmland in orange) and the woodland cover within a 1 km radius. CWM = community weighted means of female wingspan (A). Boxplots (A and B) indicate a significant effect of habitat type only, with the median and the first and third interquartile is indicated by the boxplot, and the minimum and maximum by the whiskers. Datapoints on the right indicate the spread of the data and may show outliers. Scatterplots (C–G) show a significant response to landscape-scale woodland cover. Significant differences between habitat types are indicated with letters, significant changes across woodland cover in the landscape are indicated with a solid line. Lines show the direction of the prediction, grey areas around the lines show the 95% confidence interval.

Figure S5. Responses of total farmland butterfly species richness (A–C) and *C. florella* butterfly abundance (D–F) to the number of agroecological pest management practices (A and D), number of soil management practices (B and E) and flowering plant species richness along the transects on farms (C and F). Significant effects are indicated with solid lines, dashed lines indicate a non-significant relationship. Lines indicate predicted effects. Grey areas show the 95% confidence interval.

Table S1. Butterfly species found during the study period. Butterfly life-history traits are from Woodhall's "Butterflies of South Africa: a field guide" (2020).

Table S2. Results of the Bray-Curtis distances PERMANOVA testing the effect of habitat type and woodland cover in a 1 km radius on butterfly species assemblages.

How to cite this article: Vogel, C., Mayer, V., Mkandawire, M., Küstner, G., Kerr, R. B., Krauss, J., & Steffan-Dewenter, I. (2023). Local and landscape scale woodland cover and diversification of agroecological practices shape butterfly communities in tropical smallholder landscapes. *Journal of Applied Ecology*, *00*, 1–14. https://doi.org/10.1111/1365-2664.14446