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Smallholder agriculture in African dryland agroecosystems has limited impact on trophic group composition, but affects arthropod provision of ecosystem services

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ABSTRACT

Agricultural intensification is a major driver of biodiversity loss, but the majority of studies highlighting these threats come from industrialised agriculture in temperate countries of the global North. However, more than 30% of global food production is produced by smallholder farmers, particularly in Africa. We know very little about the impact of these farming practices on arthropod communities and associated ecosystems in dryland agroecosystems. We investigated the trophic group composition of arthropod communities (detritivorous, herbivorous, predatory & mixed feeders) and levels of associated ecosystem functions in replicated maize fields, paired adjacent natural bushveld habitats and the edge habitats between them in north-eastern Namibia and central-eastern Botswana during the dry and wet seasons. Predator activity densities differed significantly between habitats depending on the season, with higher numbers in natural habitats in the wet season but lower numbers in the dry season compared to maize fields. In general, edge habitats had higher numbers of predators than the other habitats. Predator attack rates on artificial caterpillars in both seasons and dung removal in the wet season were higher in habitats with natural vegetation (natural and edge). However, dung removal in the dry season and herbivory in the wet season were highest in the maize fields, the latter due to high level of fall armyworm infestation. Wet season multifunctionality was higher in natural habitats in Botswana, and to a lesser extent in Namibia, than in maize fields. Smallholder agriculture is not detrimental to decomposers, herbivores and mixed feeders compared to adjacent natural habitats, but may be detrimental to the provision of some ecosystem services. These results highlight the challenge of sustainably managing dryland agricultural land that is marginal for crop production, while providing smallholders with an optimal environment to benefit from the ecosystem services associated with arthropod communities. New conservation agriculture practices need to support the production of higher and more stable yields over time, while maintaining the limited impact of smallholder agriculture on biotic communities.

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1. Introduction

Agriculture is the most dominant form of land use worldwide and agro-ecosystems occupy ~40% of the Earth's terrestrial surface (FAO, 2009). Given the projected increase in human population by 2050, the expansion and intensification of agriculture has been proposed as a necessity to maintain food production, where intensive agriculture includes improved crop varieties and synthetic agrochemical inputs (Tscharntke et al., 2012). However, this agricultural intensification is a major driver of biodiversity loss in tropical (Oakley and Bicknell, 2022) and dryland (Darkoh, 2003) regions of Africa with potentially severe consequences for arthropods, such as insects (Cardoso et al., 2020) and the overall health and profitability of natural and agroecosystems (de la Riva et al., 2023).

The majority of studies comparing arthropod diversity between agricultural and natural or semi-natural habitats are from countries in temperate regions of the global north (e.g. Henle et al., 2008, Reganold et al., 2011; Tsiafouli et al., 2015). While the impacts of industrialised agriculture on arthropod biodiversity are more commonly studied in tropical agroecosystems in Asia (e.g. Azhar et al., 2022) and East Africa (e.g. Vogel et al., 2021; Lasway et al., 2022; Vogel et al., 2023), little is known about such threats and their impacts in drier regions of southern Africa (Köppen-Geiger classification as semi-arid), where the climate vulnerability of agriculture is generally high. Seasonal rainfall dynamics have pronounced effects on arthropod communities in dryland ecosystems (Fischer et al., 2022), as they influence microclimatic conditions (Pincebourde et al., 2016) and resource availability (Schmitt et al., 2021). Ecosystem functions provided by arthropods in dryland agriculture are important even when there is no standing crop (dry season), as dung removal, for example, still contributes to nutrient cycling, and predation functions may still reduce population sizes of pests in the wet season. Growing human populations, recurrent floods and droughts with associated crop failures and government programmes to promote industrialised agriculture are all contributing to increasing demand for land in this sub-region, potentially threatening biodiversity (Darkoh, 2003, Biggs et al., 2008).

These dynamics and the existing knowledge gap are alarming, as biodiversity loss due to agricultural intensification or cropland expansion often associated with a decline in important ecosystem functions (Soliveres et al., 2016) and services (Birkhofer et al., 2018). This is not only true for dryland agriculture in general, but also for dynamics and relationships in agroecosystems under different semi-arid conditions. Arthropods, such as insects or arachnids, are important providers of ecosystem services such as biological control of crop pests (Diehl et al., 2013), nutrient cycling (Frank et al., 2017), and others (Birkhofer et al. in print). Ecosystem disservices, such as insect and acarine herbivory on crop plants or crop seeds, are often lower in more diverse ecosystems (Barnes et al., 2020), in part due to potentially more diverse and effective biotic antagonists, and may be highest in areas with high host plant densities (”resource concentration hypothesis”, Grez and González 1995). Alternative farming approaches, such as organic or conservation agriculture, which rely on natural regulatory services, have been proposed to simultaneously protect biodiversity, maintain crop production and reduce environmental damage (Birkhofer et al., 2016; Rundlöf et al., 2016; Wittwer et al., 2021). However, the decline in taxonomic diversity is only one dimension of biodiversity loss, as a high functional diversity (e.g. a wide range of trophic groups) may be equally important for the provision of ecosystem functions or services (De la Riva et al., 2023), such as pollination (Woodcock et al., 2016) or pest control (Greenop et al., 2018).

Our current understanding of the effects of semi-natural or natural habitats in agricultural landscapes on the taxonomic and functional diversity of arthropod communities and associated ecosystem functions is almost exclusively based on industrialised agricultural systems (Lichtenberg et al., 2017). In these landscapes, semi-natural habitats such as flower fields (Mader et al., 2017) and fallows (Feng et al., 2021) may contribute to a higher arthropod diversity with high activity levels in ecotone habitats between semi-natural and agricultural habitats (Birkhofer et al., 2014). However, more than 30% of the global food production is produced by smallholder farmers (<2 ha arable land), and this is particularly true for agriculture in Africa (Ricciardi et al., 2018). According to the International Fund for Agricultural Development, Africa has more than 33 million smallholder farms and these producers contribute up to 70% of the continent's food supply (IFAD 2013). However, even in iconic regions and biodiversity hotspots such as the Amazon, the impact of smallholder agriculture on biodiversity is understudied (Socolar et al., 2019). This highlights the need to study the impact of smallholder agriculture on arthropods and associated ecosystem functions and services. Ultimately, the effects of smallholder agriculture on arthropod diversity are expected to be weaker than those of industrialised agriculture compared to natural habitats. Given this assumption, it remains unknown to what extent ecosystem functions and multifunctionality are weakened by smallholder agriculture compared to natural ecosystems, and how smallholder agriculture affects the relationships between ecosystem function trade-offs and synergies (Birkhofer et al., 2015).

Here we compare the functional composition of ground-dwelling arthropod communities in smallholder maize fields with adjacent natural and ecotone habitats together and associated ecosystem functions (proxies for ecosystem services & disservices) in two semi-arid to arid regions that differ in long-term wet season precipitation: north-eastern Namibia (long-term average precipitation February = 135.7 mm) and central-eastern Botswana (72.4 mm). We hypothesise that 1.) all trophic groups will be most numerous in the ecotone habitat, but 2.) least numerous in the maize fields with the exception of herbivores, which will be most numerous in the maize fields during the wet season. We further hypothesise that 3.) differences in numbers of individuals in trophic groups will result in corresponding differences in the levels of associated ecosystem functions, namely high levels of attack on artificial caterpillars and maize seeds under high predator numbers, high levels of dung removal under high detritivore numbers, and high levels of herbivory under high herbivore numbers. Finally, we hypothesize that 4.) we will observe synergies between ecosystem functions, as for example high levels of dung removal will be associated to high levels of soil organic carbon.

2. Materials and methods

2.1. Study sites

Eight arable fields with adjacent natural habitats and edge habitats between them were selected in two countries (N=48 subplots), the Zambezi region of Namibia (south of Kongola; Köppen-Geiger climate classification 1991–2020: BSh, hot semi-arid climate) and the Central region of Botswana (around Tsetsebjwe; Köppen-Geiger climate classification 1991–2020: BWh, hot desert climate) (Figure S1). The eight arable fields in Namibia and Botswana, respectively, were selected to be dominated by maize, but were intercropped irregularly with cowpeas, beans, millet, peas, watermelons or groundnuts (Figure S2a&b). Maize plants ranged from seven-leaf to tussock stage, with considerable variation in growth stage between and within fields during our wet season sampling. Smallholder subsistence farming (on communal land in Namibia) is based on traditional cultivation practices such as growing the same crops in the same fields over time (no crop rotation), and using minimal or no fertilizer (mainly manure) and hand ploughing. The adjacent natural habitats were mainly dominated by the shrub and tree species *Baphia massaiensis*, *Combretum collinum*, *Combretum mossambicense* and *Terminalia sericea* in Namibia and by *Combretum apiculatum*, *Colophospermum mopane* and *Grewia bicolor* in Botswana (figure S2c&d). Natural habitats are often used by local farming communities for grazing by small livestock and for collecting firewood. In the natural habitat during the wet season, grass and herb cover and mean maximum height of non-woody vegetation were higher in Botswana than in Namibia (Table S1). In the dry season, there was no standing crop in the arable fields and no non-woody vegetation such as grass or herbs in the natural habitat. The soils in Namibia had a sand to loamy sand texture, while the soils in Botswana had a loamy sand to sandy loam texture. Arable soils in Namibia had higher electrical conductivity and lower clay and potassium contents than those in Botswana (Table S1 for soil properties, Table S2 for the respective methods). Natural habitat soils in Namibia had higher sand content and lower soil organic carbon content than natural habitat soils in Botswana.

2.2. Arthropod sampling and identification

Ground-dwelling arthropods were sampled using pitfall traps during the wet (Botswana: 21–25 Feb 2020, Namibia: 10–14 Feb 2020) and dry (Botswana: 29 Sept–03 Oct 2022, Namibia: 19–23 Sept 2022) seasons for 72 hours each. Due to the global pandemic it was not possible to sample in consecutive wet and dry seasons. The monthly average minimum and maximum temperature and the average monthly precipitation of our sample dates were within the long-term averages (1991–2020), with the exception that precipitation was slightly higher than the averages in the wet season in Namibia (long-term: 135.7 mm, February 2020: 187.3 mm) and Botswana (long-term: 72.4 mm, February 2020: 103.3 mm) and that maximum temperatures were slightly above the average maximum in Botswana in the wet (long-term: 31.9°C, February 2020: 33.0°C) and dry season (long-term: 31.2°C, September 2022: 32.0°C) (World Bank Group Climate Change Knowledge Portal 2023 & World Weather Online 2023).

Five pitfall traps were placed on a line transect 30 m into each maize field, parallel to five traps along the edge of the natural habitat and another five traps 30 m into the natural habitat with 5 m between traps within a trapline (Figure S3). This resulted in a minimum distance of 30 m distance between each trapline. Pitfall traps do not provide an absolute area-based measures of abundance, but rather reflects both the local abundance and the activity of species (Woodcock, 2005). Pitfall traps consisted of 0.5 litre plastic beakers placed at ground level and fitted with a wire mesh (mesh size 20 mm) to prevent by-catch of vertebrates and a roof to reduce flooding from precipitation or evaporation. Propylene glycol was mixed with water in a 3:1 ratio and an odourless detergent was added to this trapping fluid to reduce surface tension. It was not possible to leave the traps for more than 72 hours as trampling by animals (goats, donkeys and wildlife) and evaporation would have damaged a significant number of traps or samples. In one natural habitat in Namibia, all five pitfall traps were lost due to destruction during the dry season. A total of 475 traps were analysed in this study. All arthropods were collected from the traps using a commercial tea strainer and transferred to 70% ethanol in the field. Arthropod samples from the traps were then sorted and identified to order and suborder level. As Coleoptera were quite abundant and to be able to assign them to major trophic groups, all individuals of this order were identified to family level.

We grouped taxonomic groups into trophic groups (detritivores, herbivores, predators and mixed feeders) as a common approach to linking aspects of functional composition to ecosystem functions and services (e.g. Blaum et al., 2009; Fischer et al., 2022; see Table S3 for details). Taxonomic groups that are not adequately sampled with pitfall traps to reflect local activity density were not included in the analyses (e.g. primarily flying taxonomic groups such as Lepidoptera and Diptera, or soil mesofauna such as Acari and Collembola).

2.3. Ecosystem functions

We measured ecosystem functions as proxies for ecosystem services and disservices, including animal predation (artificial caterpillars), herbivory (fall armyworm infestation and leaf consumption), seed predation (maize seed consumption and decomposition (dung removal).

To estimate the potential efficacy of predator biological control in smallholder maize fields, adjacent natural and ecotone habitats, we used artificial caterpillars made from commercially available green plasticine (Becks Plastilin green), with 4 mm in diameter and 40 mm in length, to determine the attack rates of arthropod predators on these caterpillar host proxies (Howe et al., 2009). The size and colour were chosen to mimic a severe, invasive maize pest, the fall armyworm *Spodoptera frugiperda* (Smith, 1797), which causes estimated yield losses of up to 57% for smallholder maize farmers in the study regions (Yigezu et al., 2020; Kenis et al., 2022; Makale et al., 2022). At each pitfall trap site, four (wet season 2020), or five (dry season 2022) artificial caterpillars were attached to the branches and leaves of a single plant using odourless superglue (Henkel Pattex Sekundenkleber). Maize plants were used to place artificial caterpillars in arable fields during the wet season, but no artificial caterpillars were placed in arable fields during the dry season due to the complete absence of vegetation (total N=1760 artificial caterpillars). Non-crop plants were used to place artificial caterpillars in the edge and in the natural habitat during the wet and dry seasons. All artificial caterpillars were placed between 10 and 30 cm above the ground. Bite marks of vertebrates (mammals, birds or reptiles) were not counted, as this study focused solely on arthropods only. A more refined identification of attack marks (e.g. to family level) was not reliable, as no previous studies have collected information on the specific marks of arthropods in the study regions (our classification thus reflects the coarse level in the best-practice guidelines, (Low et al., 2014). It was not possible to keep artificial caterpillars in the field for more than 72 hours due to the detrimental effects of high ambient temperatures and high attack rates. Therefore, artificial caterpillars were examined for arthropod attack marks after 72 hours. The number of caterpillars with arthropod attack marks at each site and in each habitat per sampling season was used for statistical analyses (see also Tvardikova and Novotny, 2012) as a percentage of retrieved caterpillars with arthropod attack marks. Predation on artificial caterpillars in maize fields, but not in edge or natural habitats, is considered as proxy of an ecosystem service in the context of our study.

Leaf herbivory was assessed on maize plants in the arable fields and on the dominant shrub species in the adjacent natural habitat during the wet season only (Table S1). A sample of ten randomly selected leaves from five randomly selected individual plants per sample site was analysed for herbivory using the BioLeaf smartphone app (Machado et al., 2016). BioLeaf is based on image analysis and calculation of the percentage of missing leaf tissue from photographs. In the context of our study, herbivory on maize plants is considered to be a proxy of an ecosystem disservice.

Seed predation was assessed using seed cards made from medium grain sandpaper, each seed card containing nine maize (*Zea mays*) seeds, glued with odourless superglue with 20 mm between each seed in a three by three grid. One seed card was placed 60–70 cm from each pitfall trap in all three habitats. A wire cage (mesh size 20 mm) was placed over each seed card to exclude vertebrate seed predators such as birds and rodents (e.g. Tschumi et al., 2018). The 480 seed cards contained a total of 4320 maize seeds. Seed predation was recorded for each seed in the 3×3 grid after 72 h seed card deployment and as a percentage of seeds removed. In the context of our study, predation recorded on maize seeds in the maize fields is considered to be a proxy of an ecosystem disservice.

In both sampling sites (Namibia and Botswana), the maize plants sampled were all young (~2–4 weeks old) as the fall armyworm, *S. frugiperda* has a high preference for maize (Kenis et al., 2022) and is more economically damaging to young plants (mostly feeding on the whorl of young plants up to ~4–6 weeks). We used the symptoms of fall armyworm larval damage (leaf skeletonisation, whorl damage, frass and small to medium leaf holes and windows) to assess the extent of the pest's infestation between the two sampling sites (Namibia and Botswana). In each field, we started sampling from the fifth row of maize to avoid field edge effects. For each row, ten plants were randomly selected every 10 m along the row and this was repeated for six random rows (total of 100 plants/field). For each plant, we scored the presence (score 1) or absence (score 0) of fall armyworm using symptomatic plant damage as a proxy for pest presence, or the positive presence of the pest insect itself (see Kenis et al., 2022). Fall armyworm damage was expressed as an average percentage of presence for the rows sampled across the different fields and sites. In the context of our study, fall armyworm infestation in the maize fields is considered to be a proxy of an ecosystem disservice.

Cattle dung was collected from three randomly selected paddocks and homogenised by hand in a 10 L container, following the methods of Gotcha et al. (2022). This dung was used as a bait for dung beetles, which use it as a biomass resource. Three replicates of pitfall traps were deployed in both the natural and the maize fields (Fig. S1). Following the pitfall trap design, traps were placed in lines 1.) 25 m from the field edge to the inside of the maize crop and, 2.) 25 m into the natural habitat (see Fig. S1). A distance of approximately 10 m was maintained between trap intervals within a transect. A 2 L container (115 mm height × 160 mm diameter) was buried level with the ground surface, and a square (200 mm × 200 mm) wire mesh (hexagonal pore size; 10 × 10 × 15 × 15 × 10 × 10 mm) was placed over the trap to support an initial 175 g ball of cattle dung (see methods of Gotcha et al., 2021). Dung baited traps were deployed between 17:00 and18:00 and checked each morning between 07:00 and 08:00 for three days. For each of these three days, a fresh homogenised dung pat was used each evening. The dung that remained on the wire mesh each morning was weighed (final mass) after accounting for water loss, and the difference in weight was used as proxy of dung removal. A control 2 L container (similar to treatment containers) was deployed for each of the study sites and across the three sites to account for water loss. These control containers were buried level with the ground surface, consistent with treatments and a 175 g dung was placed on top of wire mesh similar to treatments, albeit covered with fine wire mesh on top to exclude dung beetles. The moisture content of cattle dung was determined by exposing similar dung pats (175 g) to a similar overnight treatment in medium insect cages (Mad Hornet Entomological Supplies, Betty's Bay, South Africa) with vinyl windows (34 × 34 × 61 cm), but without access to arthropods. The difference between the initial mass and the final mass (after ~14 h) was considered as water loss from the dung. The sampling time was sufficient to allow for the activity of crepuscular and nocturnal dung-feeding arthropods (Gotcha et al., 2022). The difference between the initial dung mass and the final mass was considered to be the dung resource used by dung removing arthropods and as a proxy for an ecosystem service.

2.4. *Statistical analyses*

The multivariate dataset on the composition of arthropod trophic groups (average activity density per pitfall trap) with the dependent variables predator, herbivore, detritivore and mixed feeder activity density was tested using permutational analysis of variance (PERMANOVA, Anderson, 2014). The model was based on the fixed factors country (2 levels: Namibia or Botswana), season (2 levels: wet or dry) and habitat (3 levels: maize fields or edge habitats or natural habitats) and the random factor site (16 levels: 8 sites in each country) nested within country to account for the paired design. All two- and three-way interactions were included with the exception of the three-way interaction site × season × habitat. The similarity matrix for the multivariate PERMANOVA model was based on Gower similarities and PERMANOVA was run with 9999 permutations of residuals under a reduced model (Anderson et al., 2008). Gower similarities were chosen for the multivariate analysis of trophic group composition because this measure of similarity gives equal weight to all trophic groups, regardless of their relative differences in activity densities. After obtaining a significant result for individual fixed factors and interactions between fixed factors, the significant model terms were tested for homogeneity of multivariate dispersion using a distance-based test for homogeneity of multivariate dispersions.

The significant fixed factors and interactions between fixed factors from the multivariate model were then tested with PERMANOVA models for the four individual trophic groups with resemblance matrices based on Euclidean distances to identify individual trophic groups that responded to the factors. All significant fixed factors and interactions between fixed factors are reported with the square root transformed estimates of the components of variation as a measure of effect strength to compare the importance of different significant terms within a model (Anderson, 2014). Significant model terms that include the factor country are reported as mean differences between factor levels, and significant terms that do not include the factor country are always reported as paired mean differences in Gardner-Altman plots (Ho et al., 2019) to reflect the paired nature of the study design in space (three habitats per sample site) and time (repeated sampling of the same sites in the wet and dry seasons). We then tested relationships between preselected trophic groups and potentially associated ecosystem service and disservice proxies for the relationships between 1.) detritivore activity density and dung removal, 2.) herbivore activity density and herbivory, and between predator activity density and 3.) herbivory, 4.) seed predation, and 5.) caterpillar attacks using Spearman rank order correlations.

Multifunctionality was calculated as the sum of the values of each of the five proxies, after standardizing each function to its maximum value (100%) and using the reciprocal values for the proxies for the disservices herbivory and crop seed predation (highest value was transformed to lowest value). Higher multifunctionality scores reflect high dung removal, attacks on artificial caterpillars, soil organic carbon and low herbivory and crop seed predation. The multifunctionality score was analysed with the same PERMANOVA model as described above, excluding the factor season and using Euclidean distances.

3. Results

3.1. *Trophic groups*

The 475 pitfall traps collected 17008 arthropods belonging to 23 orders and suborders (excluding beetles) and 15 beetle families during the wet and dry seasons in Botswana and Namibia across the three habitats (arable, edge and natural; Table S4) with (in order of dominance) Formicidae, Coleoptera, Araneae, Isoptera and Grylloidea contributing more than 90% of all individuals. The composition of trophic groups was significantly affected by differences between habitats (Table 1a, $\sqrt{}$component of variation as effect size=2.95) and by the interactions between habitat and season ($\sqrt{}$comp. var.=5.40) and between habitat and country ($\sqrt{}$comp. var.=4.07), but not by the interaction between country and season. Season and country alone, as well as the three-way interaction between habitat, season and country, did not significantly affect the trophic group composition (all P>0.050). The multivariate dispersion of trophic group composition did not deviate significantly from homogeneity for any of the significant factors or interactions (PERMDISP, all P>0.050).

Predator activity density differed significantly between habitats ($F_{2,88}$=3.54, P=0.033, $\sqrt{}$comp. var.=0.61), with paired mean differences between maize and edge (edge>maize: 1.25 individuals), and between natural and edge (edge>natural: 1.28 individuals) habitats across seasons being greater than between maize and natural habitats (0.08 individuals). Predator activity density also differed significantly between habitats depending on season ($F_{2,88}$=4.30, P=0.017, $\sqrt{}$comp. var.=0.99), but not between habitats depending on the country ($F_{2,88}$=2.57, P=0.084). While paired mean differences in predator activity density were higher in natural habitats than in maize fields in the wet season, the opposite pattern was observed in the dry season (Fig. 1a&b). Paired mean differences in predator activity density were higher in edge habitats than in natural habitats only in the dry season (Fig. 1d), but not in the wet season (Fig. 1c). Paired mean differences in

Table 1
Effects of the fixed factors country (levels: Botswana vs. Namibia), season (levels: wet vs. dry), habitat (levels: maize vs. edge vs. natural) and the random factor site on the a) composition of arthropod trophic groups, b) proportion of arthropod attack marks on artificial caterpillars, c) arthropod predation on maize seeds and d) dung removal based on permutational analysis of variance with degrees of freedom (df), pseudo-F and P values for each model. Bold indicates significant fixed factors or interaction terms with fixed factors.

	a) Trophic groups			b) Attack marks		
Source	df	Pseudo-F	P	df	Pseudo-F	P
Country (Co)	1	0.43	0.749	**1**	**5.13**	**0.033**
Season (Se)	1	1.83	0.175	**1**	**51.33**	**0.001**
Habitat (Ha)	**2**	**3.26**	**0.008**	**2**	**5.89**	**0.009**
Site (Co)	14	3.12	<0.001	14	1.22	0.346
Co×Se	1	0.45	0.686	1	1.40	0.247
Co×Ha	**2**	**3.15**	**0.009**	2	0.04	0.968
Se×Ha	**2**	**4.73**	**0.001**	1	0.50	0.484
Si(Co)×Se	14	2.67	<0.001	14	1.26	0.321
Si(Co)×Ha	28	0.99	0.517	28	0.84	0.647
Co×Se×Ha	2	0.66	0.650	1	0.47	0.468
Res	27			14		
Total	94			79		
	c) Seed predation			d) Dung removal		
Source	df	Pseudo-F	P	df	Pseudo-F	P
Country (Co)	**1**	**13.14**	**0.005**	**1**	**194.02**	**<0.001**
Season (Se)	**1**	**20.73**	**0.001**	**1**	**787.50**	**<0.001**
Habitat (Ha)	2	2.05	0.151	1	2.27	0.157
Site (Co)	14	0.97	0.507	14	12.98	<0.001
Co×Se	**1**	**13.78**	**0.003**	**1**	**249.12**	**<0.001**
Co×Ha	2	1.20	0.323	1	0.46	0.500
Se×Ha	2	3.15	0.068	**1**	**38.25**	**<0.001**
Si(Co)×Se	14	1.00	0.476	14	10.89	<0.001
Si(Co)×Ha	28	1.14	0.368	14	0.92	0.556
Co×Se×Ha	2	0.88	0.431	1	1.33	0.265
Res	28			14		
Total	95			63		

predator activity density did not differ between maize and edge habitats in the wet (1.24 individuals) and dry (1.27 individuals) seasons. The activity density of herbivores, detritivores and mixed feeders did not differ significantly between countries, seasons or habitats or their interactions (all P>0.050).

3.2. Ecosystem functions

The percentage of artificial caterpillars with arthropod attack marks differed significantly between countries ($\sqrt{\text{comp. var.}}=5.55$), seasons ($\sqrt{\text{comp. var.}}=19.69$) and habitats ($\sqrt{\text{comp. var.}}=5.79$), with no significant interactions between these factors (Table 1b). The percentage of artificial caterpillars with arthropod attack marks was on average 1.3 times higher in Namibia (mean and SD: 37.2±20.4%) than in Botswana (28.1±18.7%). Based on the paired mean difference, 30.6% more artificial caterpillars had attack marks in the wet season than in the dry season. Overall, 15.7% more caterpillars in natural habitats (Figs. 2a) and 7.5% more caterpillars in edge habitats had attack marks compared to the maize fields (Fig. 2b). In the natural habitats 5.5% more caterpillars had attack marks compared to the edge habitats (Fig. 2c).

Herbivory was estimated only in the wet season and only in the maize fields and natural habitats, but not in the edge habitats. Herbivory did not differ significantly between countries, but differed between habitats ($F_{1,14}=29.57$, $P<0.001$, $\sqrt{\text{comp. var.}}=21.24$) and between habitats depending on the country ($F_{1,14}=6.24$, $P=0.027$, $\sqrt{\text{comp. var.}}=12.86$). Based on the paired mean difference, 2.4% more leaf area per leaf was consumed in maize fields compared to natural habitats across countries. Overall, 3.4% more leaf area was consumed in maize fields compared to the natural habitats in Botswana (Fig. 3a), but this difference was only 1.4% between natural habitats and maize fields in Namibia (Fig. 3b).

Predation of maize seeds by arthropods differed significantly between countries ($\sqrt{\text{comp. var.}}=9.37$) and seasons ($\sqrt{\text{comp. var.}}=12.16$) and between countries depending on season (Table 1c, $\sqrt{\text{comp. var.}}=13.84$), but not between habitats or depending on habitat (all P>0.050). The percentage of maize seeds consumed by arthropods was on average 5.5 times higher in Botswana (17.9±31.8%) than in Namibia (3.3±6.2%). Based on the paired mean difference 17.2% more maize seeds were consumed in the dry season than in the wet season in both countries. In Botswana, 32.1% more maize seeds were consumed in the dry season than in the wet season, but in Namibia this difference was only 1.6% between the dry and wet seasons.

Fall armyworm infestation of maize plants did not differ significantly between countries and the pest species was present on more than half of the plants surveyed in both countries (Namibia: 52.3%±18.7%; Botswana: 61.3%±26.4%).

Dung removal differed significantly between countries ($\sqrt{\text{comp. var.}}=57.05$) and seasons ($\sqrt{\text{comp. var.}}=105.48$) and between seasons depending on country ($\sqrt{\text{comp. var.}}=83.78$) and depending on habitat (Table 1d; $\sqrt{\text{comp. var.}}=9.84$). The mass of dung removed was on average 2.8 times higher in Namibia (125.7±44.8 g) than in Botswana (44.8±37.4 g). Based on the paired mean difference, 107.0 g more dung was removed in the wet season than in the dry season in both countries. Overall, 228.0 g more dung was removed in the wet season than in the dry season in Namibia, but this difference was only 61.1 g between the wet and dry seasons in Botswana. On average, 12.3 g more dung was removed in the natural habitat than in the maize fields in the wet season (Fig. 4a), but 7.6 g less dung was removed in the natural habitat compared to the maize fields in the dry season (Fig. 4b).

3.3. Multifunctionality and relationships between trophic groups and ecosystem functions

Predator activity density (including seed predators) and seed predation were significantly related in all samples, with higher predator numbers being associated with higher percentages of seeds removed ($N=95$, $R_S=0.26$, $P=0.010$). When analysed within individual levels of fixed factors these relationships were significant in Botswana ($N=48$, $R_S=0.41$, $P=0.004$), in edge ($N=31$, $R_S=0.43$, $P=0.015$) and maize ($N=32$, $R_S=0.36$, $P=0.044$) habitats and in the dry season ($N=47$, $R_S=0.31$, $P=0.037$). Dung removal and detritivore activity density, herbivory and herbivore activity density, and fall armyworm infestation, herbivory and caterpillar attack marks and predator activity density were not significantly related to each other (P>0.050). Out of the ten pairwise correlations between individual ecosystem functions, only two were significantly correlated. Dung removal and caterpillar attack marks were positively ($N=48$, $R_S=0.64$, $P<0.001$) correlated and seed predation and caterpillar attack marks were negatively correlated ($N=79$, $R_S=-0.27$, $P=0.017$).

Multifunctionality differed significantly between countries ($F_{1,14}=18.82$, $P=0.001$, $\sqrt{\text{comp. var.}}=46.47$) and habitats ($F_{1,14}=22.39$, $P<0.001$, $\sqrt{\text{comp. var.}}=37.38$), and the effects of both factors depended on each other ($F_{1,14}=9.59$, $P=0.008$, $\sqrt{\text{comp. var.}}=33.50$). Multifunctionality was 89.5 percentage points (out of a possible 500) higher in natural than in maize habitats in Botswana (Fig. 5a), but only 18.7 percentage points higher in natural than in maize habitats in Namibia (Fig. 5b).

4. Discussion

Our results show that traditional smallholder agriculture is not detrimental to decomposers, herbivores and mixed feeders compared to adjacent natural habitats. Only predators had lower activity densities in maize fields and only in the wet season, while predator activity densities were even higher in arable fields in the dry season. This result differs from the known pronounced negative effects of agriculture on arthropods in industrial agriculture compared to semi-natural or natural habitats. However, smallholder agriculture affected the provision of

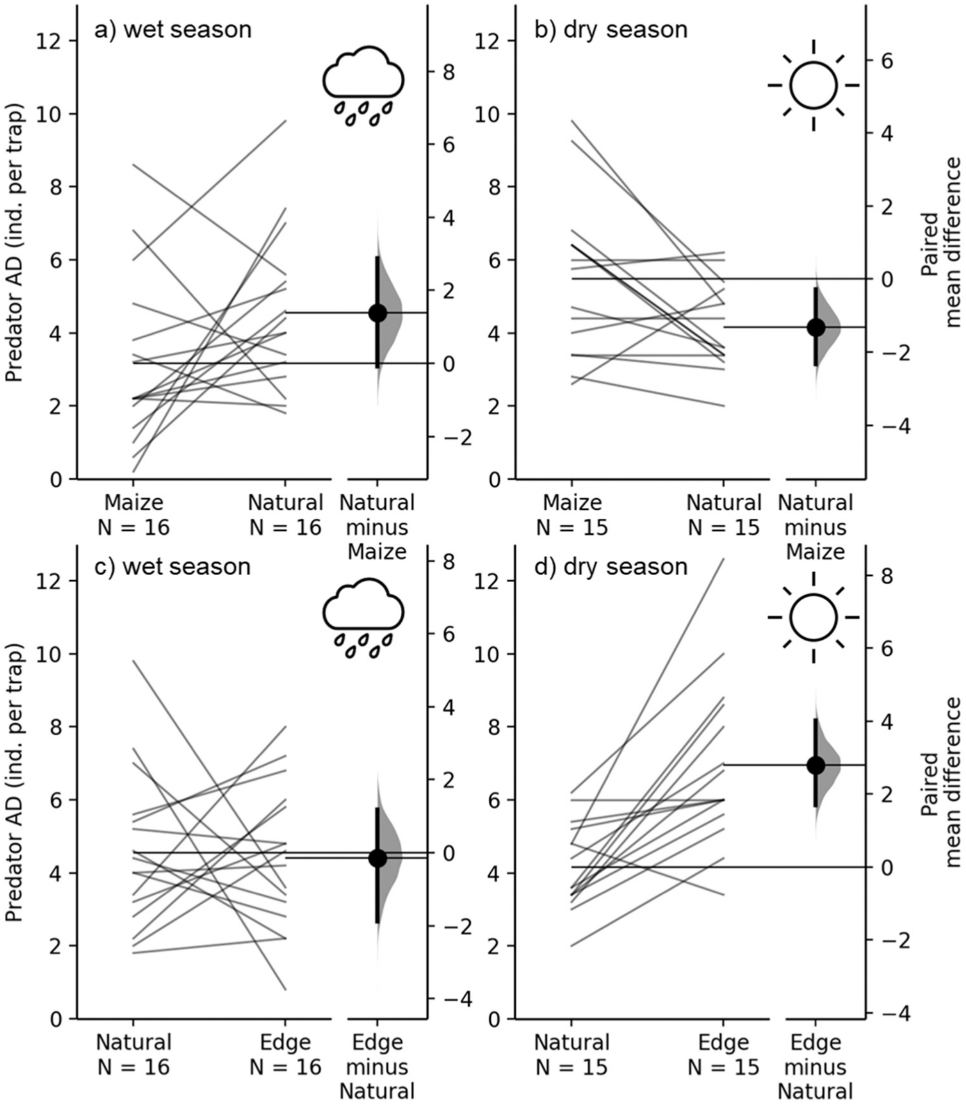

Fig. 1. The paired mean difference in predator activity density (AD) between maize and natural habitats in the a) wet and b) dry seasons and between natural and edge habitats in the c) wet and d) dry seasons. Predator activity density for pairwise habitat comparisons is plotted on the left axis as a slopegraph: each paired set of habitats at the same field site is connected by a line. The paired mean difference is plotted on the right axis as a bootstrap sampling distribution. The mean difference is shown as a point; the 95% confidence interval is indicated by the ends of the vertical error bars. Note that all five pitfall traps from one natural habitat (Namibia dry season site 4) were lost due to destruction (N only 15).

ecosystem services in our study and at least in Botswana reduced multifunctionality compared to adjacent natural habitats in the wet season.

4.1. Trophic groups

The composition of arthropod trophic groups did not differ significantly between maize fields and natural habitats (rejecting our 2nd and 3rd hypotheses), but the ecotones between these two habitats were areas of highest predator activity densities (partially confirming our 1st hypothesis). Of the four trophic groups, only predator activity density responded to habitat alone and to habitat depending on season. In the wet season, more predators were observed in the natural habitat than in the maize fields, and the opposite pattern was observed in the dry season. The natural habitats had very little to no vegetation cover on the ground and were therefore comparable to the maize fields in the dry season with the exception of the presence of shrubs. Shrubs and trees are utilized by insectivorous birds and higher predation by birds may have been a reason for the lower predator numbers in natural habitats. These pronounced seasonal differences between the wet and dry seasons are known for arthropods from other dryland ecosystems (Lingbeek et al., 2017). In particular, seasonal rainfall dynamics and the resulting patterns of plant cover influence the composition of arthropod communities in dryland ecosystems (Fischer et al., 2022), as well as the availability of microclimate refugia (Pincebourde et al., 2016).

In other afrotropical sub-regions, such as the semi-deciduous forest zone (Damptey et al., 2023) or mountainous urban green spaces (Damptey et al., 2022) in Ghana, natural habitats (such as primary forests or woodlands) generally have higher predator activity densities than disturbed habitats (such as agroforestry plantations or urban built-up areas). Local vegetation characteristics and plant community composition are important drivers of the observed preferences for natural habitats in these regions (Damptey et al., 2022). Local management to promote habitat heterogeneity and vegetation structure, such as the use of removed woody branches to cover the soil surface in shrublands (brush packing), are appropriate approaches to promote insect abundance in South African savanna ecosystems (Marquart et al., 2022). In Namibia, ground-dwelling beetles showed a strong preference for low to medium levels of shrub cover compared to higher levels (Hering et al.,

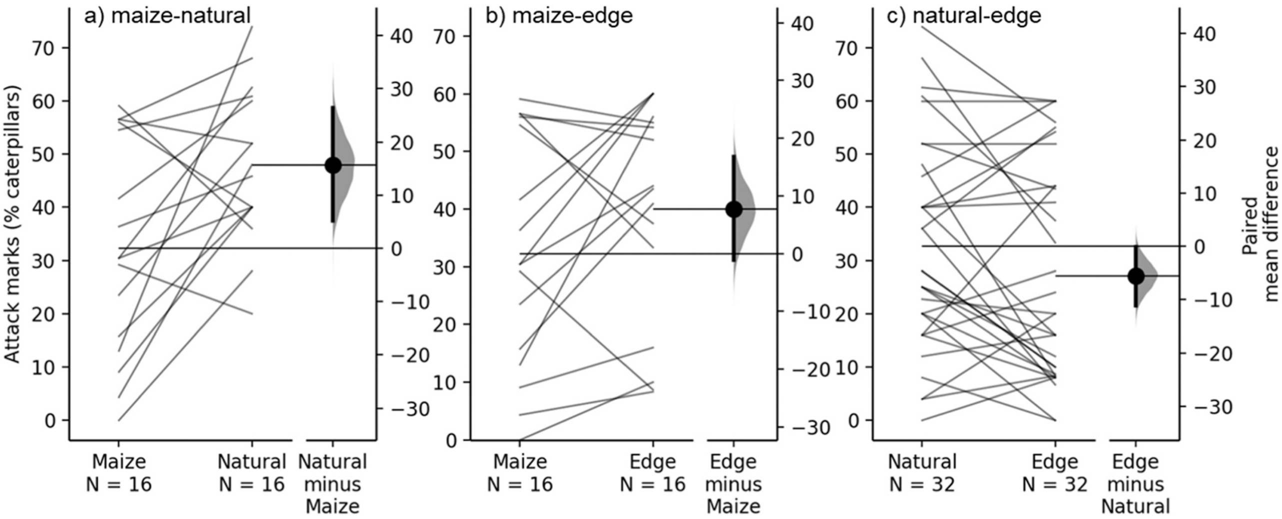

Fig. 2. The paired mean difference for the percentage of artificial caterpillars with attack marks between a) maize and natural habitats, b) maize and edge habitats and c) natural and edge habitats. The percentage of artificial caterpillars with attack marks for pairwise habitat comparisons is plotted on the left axis as a slopegraph: each paired set of habitats at the same field site is connected by a line. The paired mean difference is plotted on the right axis as a bootstrap sampling distribution. The mean difference is shown as a point; the 95% confidence interval is indicated by the ends of the vertical error bars.

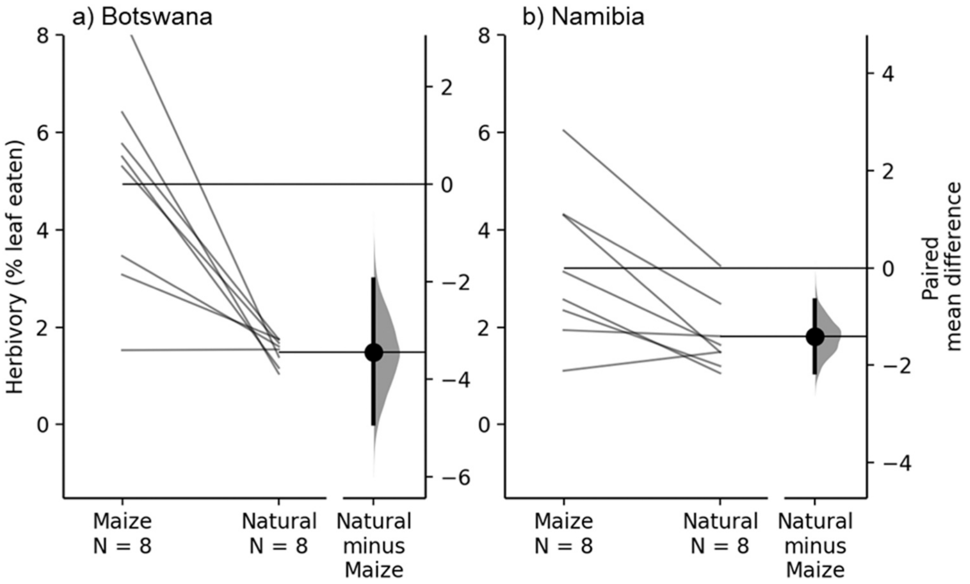

Fig. 3. The paired mean difference in herbivory between maize and natural habitats in the a) Botswana and b) Namibia in the wet season. Herbivory for pairwise habitat comparisons is plotted on the left axis as a slopegraph: each paired set of habitats at the same field site is connected by a line. The paired mean difference is plotted on the right axis as a bootstrap sampling distribution. The mean difference is shown as a point; the 95% confidence interval is indicated by the ends of the vertical error bars.

2019). Ground beetles (Carabidae, Coleoptera), as an important predator group of plant seeds and insect prey, showed a hump-shaped response to shrub biomass in European dry grasslands (Schirmel et al., 2015). Results from semi-arid and arid regions show the range of preferences amongst ground-dwelling arthropods. Indeed, Blaum et al. (2009) showed that the predaceous arachnid taxa along a shrub encroachment gradient in Namibia showed either increasing (scorpions), decreasing (solifuges) or hump-shaped (spiders) responses in activity density to shrub cover levels.

The major characteristics of herbaceous vegetation (such as cover or height) of maize fields and natural habitats in our study were comparable within seasons, as both were covered by herbaceous vegetation in the wet season, but had almost no herbaceous vegetation in the dry season. This similarity may explain why activity densities of most trophic groups were generally not significantly different between habitats. It is also unlikely that characteristics of herbaceous vegetation contributed significantly to the contrasting pattern of predator activity density between the wet and dry seasons. Predatory arthropods show a preference for areas that are rich in food resources (Birkhofer et al., 2011), and the activity density of granivorous ground beetles is at least partly dependent on the availability of food resources in South African savanna ecosystems (Foord et al., 2018). Natural habitats in our study had a relatively higher total arthropod activity density per trap compared to maize fields in the wet season (45.3±35.9 vs. 27.3±9.9), while the availability of potential prey in the dry season showed the opposite pattern (27.4±20.8 vs. 39.3±23.6). The predator activity density resembles this pattern for overall arthropod numbers between habitats and seasons, suggesting that the response of this trophic group

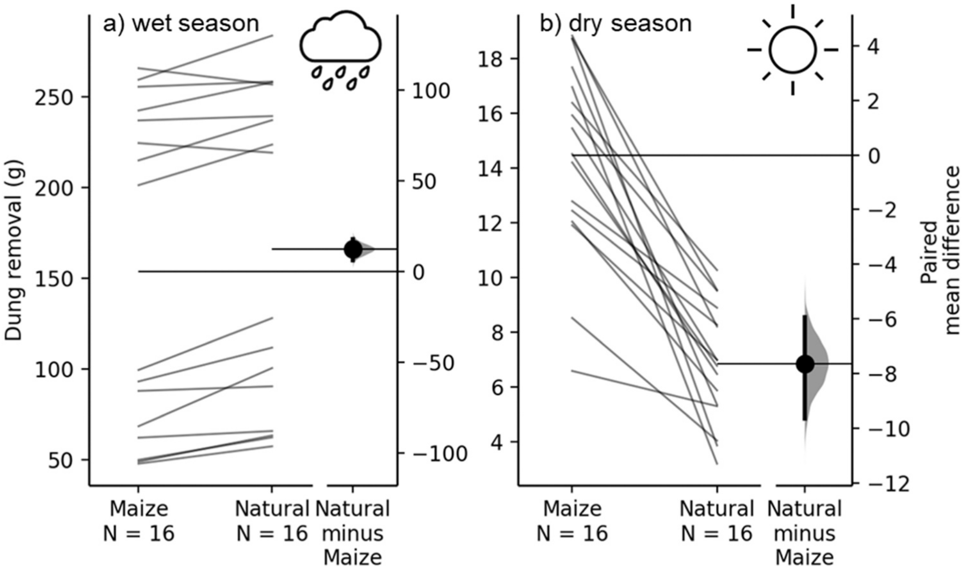

Fig. 4. The paired mean difference in dung removal between maize and natural habitats in the a) wet (upper 8 pairs are Namibia) and b) dry season. Dung removal for pairwise habitat comparisons is plotted on the left axis as a slopegraph: each paired set of habitats at the same field site is connected by a line. The paired mean difference is plotted on the right axis as a bootstrap sampling distribution. The mean difference is shown as a point; the 95% confidence interval is indicated by the ends of the vertical error bars.

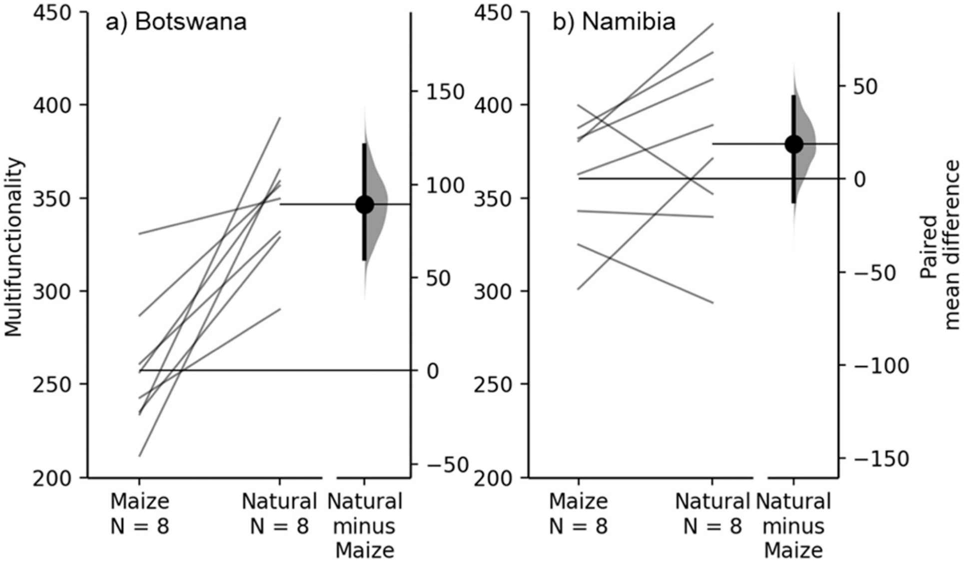

Fig. 5. The paired mean difference in multifunctionality with high values indicating higher levels of ecosystem service proxies (dung removal, artificial caterpillar attacks and total soil organic carbon content) and lower levels of ecosystem disservice proxies (maize seed predation and maize leaf herbivory) wet season maize fields in a) Botswana and b) Namibia. Multifunctionality scores for pairwise habitat comparisons are plotted on the left axis as a slopegraph: each paired set of maize and natural habitats at the same field site is connected by a line. The paired mean difference is plotted on the right axis as a bootstrap sampling distribution. The mean difference is shown as a point; the 95% confidence interval is indicated by the ends of the vertical error bars.

is rather related to food availability rather than differences in herbaceous vegetation structure.

The history of arable fields could influence the composition of arthropod communities (e.g., De Heij et al., 2022), with our study sites having different histories in terms of fire events, crop sequences or changes in cultivation. This heterogeneity could explain some of the deviations from the more general patterns in our data and deserves more attention in future studies.

4.2. Ecosystem functions

To link changes in arthropod diversity to ecosystem processes it is important to consider functional aspects of biodiversity (Dippenaar--Schoeman et al., 2015, de la Riva et al., 2023). Proxies for ecosystem services, such as artificial caterpillar attacks for biological control services or dung removal for nutrient cycling and sanitation services, were higher in the wet season, while proxies for disservices, such as predation on crop seeds, were lower in the wet season, regardless of habitat type. This is an important result for smallholder farmers, as the ecosystem services are more relevant in the wet season with a standing crop. Decomposers and predators are known to suffer from drought conditions in agricultural fields in Europe (Frampton et al., 2000, Birkhofer et al., 2021), and in dry savanna ecosystems in Namibia (Fischer et al., 2022), while abundances and activities peak during rainy periods, similar to soil arthropods in South Africa (Janion-Scheepers et al., 2016 and references therein), and dung beetles in Australia (Davis, 1996) and Botswana (Sands et al., 2022). However, in our study, only maize seed predation was statistically related to the activity density of a trophic group (partially confirming our 4th hypothesis). Therefore, differences in the levels of ecosystem service proxies between seasons in this study are likely to be related, at least in part, to differences in activity rather than to differences in abundance. For example, decomposers become less active under drought conditions or move down to deeper soil layers in arable fields (Meyer et al., 2021). Maize seed predation, on the other hand, was higher in the dry season, probably reflecting a general limitation of plant resources for seed predators in this period and an exploitation of the introduced resource.

Attacks on artificial caterpillars (wet & dry) and dung removal (wet) were lowest in maize fields, and maize fields had higher levels of herbivory than natural habitats as a result of a severe fall armyworm infestation that occurred exclusively on maize plants. While seed predation by vertebrate herbivores has been relatively well studied in southern African ecosystems (e.g. Midgley and Bond, 2001), invertebrate seed predation has not been well studied in the region (Joubert et al., 2013). The presence of semi-natural grasslands promotes crop seed predation by invertebrates in Swedish cereal fields (Tschumi et al., 2018), suggesting that generally high seed predation in non-crop habitats benefits seed predation in adjacent crop fields (Sarabi, 2019). This pattern was not evident in our dryland agroecosystem, where crop seed predation was positively correlated with predator activity densities (including seed predators).

In a study of Indonesian oil palm plantations, attacks on artificial caterpillars decreased with distance from the border into the plantation (Nurdiansyah et al., 2016). Attacks were also lower in cotton fields than in adjacent non-crop habitats in Uganda (Howe et al., 2015), in old-growth forest and forest fragments than in rice paddies in Madagascar (Schwab et al., 2021), and in forest fragments than in surrounding maize fields in Argentina (Ferrante et al.2017). However, a review of results from sentinel prey methods did not find generally higher attack rates on artificial prey in uncultivated compared to cultivated areas (Lövei and Ferrante, 2017). In our study, the percentage of attacked artificial caterpillars gradually decreased from the natural habitat to the edge and into the maize habitat. This suggests a relatively higher predation pressure on caterpillars that visually resemble fall armyworm larvae to some extent, but artificial caterpillars are a very simple method of estimating these interactions, ignoring chemical and/or behavioural cues and responses. A high attack percentage in natural habitats does not support biological control of pests such as the fall armyworm because it does not find host plants in natural habitats. It does, however, support the notion that predator abundance and efficacy are higher in more heterogeneous habitats, such as our natural habitats. Previous studies have identified ants or cricket species as important predators causing attack marks on artificial caterpillars in the tropics (Tvardikova and Novotny, 2012, Nurdiansyah et al., 2016). In Europe, ground beetles are important attackers of artificial caterpillars while ants and other insects are less important in forest ecosystems (Ferrante et al., 2014). The percentage of artificial caterpillars that were attacked by arthropods in our study was not significantly related to the local ant or predator activity density.

Dung removal is related to temperature, dung mass and dung beetle density (Gotcha et al., 2022). Our results showed that dung removal was higher in Namibia than in Botswana, and that more dung was removed in the wet season than in the dry season between countries. Higher ambient temperatures at our Namibian site compared to Botswana may account for the higher dung removal in Namibia due to higher activity of dung removing arthropods such as dung beetles (see Gotcha et al., 2022). In addition, dung beetle densities peak in summer, when mammal and dung resources are abundant. This may help to explain the higher use of dung resources in summer compared to the dry season. As dung removal efficiency is a function of beetle density, resource availability and beetle species, species diversity, densities and per capita efficiency between the two sites require further investigation.

The observed higher percentages of herbivory due to armyworm infestation in maize compared to natural habitats in the wet season are accompanied by lower rates of crop seed predation. Together with the simultaneously higher levels of dung removal and caterpillar attack percentages in Namibia and Botswana, these trade-offs and synergies show how important it is to jointly consider multiple ecosystem service proxies in studies that aim to address the effects of agricultural management on arthropod communities and their role in local food webs (Birkhofer et al., 2018, Birkhofer et al., 2021). When considering together, maize fields had significantly lower multifunctionality than natural habitats in Botswana, but not in Namibia. Regional differences in the response of multifunctionality to land use (Allan et al., 2014) or specific geographical distributions of bundles of ecosystem services are well known (Mouchet et al., 2017) and the higher long-term and study period precipitation in the wet season in Namibia may have resulted in the observed higher multifunctionality. In our study, the more pronounced differences in multifunctionality between maize and natural habitats are most likely due to the access of farmers in Botswana to machinery for pre-sowing ploughing, as this practice may have negatively affected the provision of ecosystem services by arthropod communities. It is noteworthy that multifunctionality in Namibian smallholder maize fields was generally high and comparable to the levels of multifunctionality in natural habitats in Botswana and Namibia. This finding highlights opportunities for smallholder farmers to cultivate crops without reducing arthropod numbers and associated ecosystem functions.

4.3. *Conclusions*

Our results highlight the challenge of sustainably managing dryland agricultural fields that are marginal for crop production, while simultaneously providing smallholder farmers with an optimal environment to benefit from the ecosystem services associated with arthropod communities. It is important to better understand the impact of current traditional smallholder agriculture on biodiversity in order to understand how the adoption of new practices (e.g. in conservation agriculture, Siyambango et al., 2022) will not only improve yields but also affect environmental conditions. The limited impact of traditional smallholder agriculture on the composition of trophic groups in arthropod communities compared to adjacent natural habitats in our study contrasts strongly with the severe impact of industrialised agriculture in Europe (Outhwaite et al., 2022) and its impact on arthropods compared to adjacent semi-natural habitats (Birkhofer et al., 2014, Feng et al., 2021). The size of arable fields (Batáry et al., 2017), the amount and frequency of pesticide use (Geiger et al., 2010), and the high degree of mechanisation (Müller et al., 2022) in conventional agricultural production systems in Europe are all major causes of mortality in arthropod communities. Smallholder farmers in Namibia and Botswana manage relatively small fields, rarely use pesticides or use machinery, and rely more on traditional agricultural practices such as physical pest control for subsistence farming. Ideally, new conservation agriculture practices will help to produce higher and more stable yields over time, while maintaining the limited impact of smallholder farming on biotic communities and generally high levels of multifunctionality (in Namibia) as shown in our study. Adjacent natural habitats can play an important role in contributing to these goals in the future, but we need to understand how they contribute to the activity of beneficial and pest organisms and associated ecosystem services and disservices.

CRediT authorship contribution statement

Machekano Honest: Data curation, Investigation, Methodology, Writing – review & editing. **Fabiano Ezequiel:** Conceptualization, Funding acquisition, Investigation, Project administration, Supervision,

Writing – review & editing. **Kasinda Eva:** Investigation, Methodology, Writing – review & editing. **Buxton Mmabaledi:** Data curation, Investigation, Methodology, Writing – review & editing. **Djoudi El Aziz:** Data curation, Investigation, Methodology, Writing – review & editing. **Alfeus Martha:** Data curation, Investigation, Methodology, Writing – review & editing. **Arvidsson Fredrik:** Data curation, Investigation, Methodology, Writing – review & editing. **Segaiso Bame Alice:** Data curation, Investigation, Methodology, Writing – review & editing. **Birkhofer Klaus:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Nyamukondiwa Casper:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing – review & editing. **Bird Tharina:** Conceptualization, Data curation, Investigation, Methodology, Supervision, Validation, Visualization, Writing – review & editing. **Mpofu Precious:** Data curation, Investigation, Methodology, Writing – review & editing. **Nghipunya Esther Ndapanda:** Data curation, Investigation, Methodology, Writing – review & editing.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2023.108860.

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