The effects of land-use and agroecological practices on biodiversity and ecosystem services in tropical smallholder farms

Die Effekte von Landnutzung und Agroökologie auf Biodiversität und Ökosystemdienstleistungen in der tropischen Subsistenzlandwirtschaft

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“Als iemand echt van de natuur houdt, vindt men overal schoonheid”

“If one truly loves nature, they will find beauty everywhere”

Vincent van Gogh

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Affidavit

I hereby declare that my thesis entitled "**The effects of land-use and agroecological practices on biodiversity and ecosystem services on tropical smallholder farms**" is the result of my own work. I did not receive any help or support from commercial consultants. All sources and/or materials applied are listed and specified in the thesis.

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Summary

Chapter 1 – General introduction

Biodiversity is in rapid decline worldwide. These declines are more pronounced in areas that are currently biodiversity rich, but economically poor – essentially describing many tropical regions in the Global South where landscapes are dominated by smallholder agriculture. Agriculture is an important driver of biodiversity decline, through habitat destruction and unsustainable practices. Ironically, agriculture itself is dependent on a range of ecosystem services, such as pollination and pest control, provided by biodiversity. Biodiversity on fields and the delivery of ecosystem services to crops is often closely tied to the composition of the surrounding landscape – complex landscapes with a higher proportion of (semi-)natural habitats tend to support a high abundances and biodiversity of pollinators and natural enemies that are beneficial to crop production. However, past landscape scale studies have focused primarily on industrialized agricultural landscapes in the Global North, and context dependent differences between regions and agricultural systems are understudied. Smallholder agriculture supports 2 billion people worldwide and contributes to over half the world's food supply. Yet smallholders, particularly in sub-Saharan Africa, are underrepresented in research investigating the consequences of landscape change and agricultural practices. Where research in smallholder agriculture is conducted, the focus is often on commodity crops, such as cacao, and less on crops that are directly consumed by smallholder households, though the loss of services to these crops could potentially impact the most vulnerable farmers the hardest. Agroecology – a holistic and nature-based approach to agriculture, provides an alternative to unsustainable input-intensive agriculture. Agroecology has been found to benefit smallholders through improved agronomical and food-security outcomes. Co-benefits of agroecological practices with biodiversity and ecosystem services are assumed, but not often empirically tested. In addition, the local and landscape effects on biodiversity and ecosystem services are more commonly studied in isolation, but their potentially interactive effects are so far little explored. Our study region in northern Malawi exemplifies many challenges experienced by smallholder farmers throughout sub-Saharan Africa and more generally in the Global South. Malawi is located in a global biodiversity hotspot, but biodiversity is threatened by rapid habitat loss and a push for input-intensive agriculture by government and other stakeholders. In contrast, agroecology has been effectively promoted and implemented in the study region. We investigated how land-use differences and the agroecological practices affects biodiversity and ecosystem services of multiple taxa in a maize-bean intercropping system (Chapter 2), and pollination of pumpkin (Chapter 3) and pigeon pea (Chapter 4). Additionally, the effects of local and landscape scale shrub- to farmland habitat conversion was investigated on butterfly communities, as well as the potential for agroecology to mitigate these effects (Chapter 5).

Chapter 2 – The effects of crop type, landscape composition and agroecological practices on biodiversity and ecosystem services in tropical smallholder farms

Intercropping, a common practice in smallholder agriculture throughout sub-Saharan Africa, is thought to enhance biodiversity and ecosystem services by increasing habitat complexity within fields. However, whether the effects of crop type are mediated by the surrounding landscape is so far unknown. On 62 fields, we investigated the effects of crop type (maize, bean, or maize-bean intercrop), semi-natural habitat cover in the surrounding landscape, and the diversification of agroecological pest- and soil management practices on 7 taxa of functional biodiversity (birds, carabids, spiders, ants, parasitoids, bees, and soil bacteria) and two ecosystem services (pest control and pollination). Densities of spiders and parasitoids, carabid richness and Shannon diversity of soil bacteria were highest in bean monocultures, especially in landscapes with low semi-natural habitat cover. Increasing semi-natural habitat was important to maintain bee and carabid diversity. Diversification of agroecological soil management practices increased Shannon diversity of soil bacteria and altered carabid assemblage composition. Bean monocultures had lower pest damage than intercropped beans, possibly due to increased activity densities of natural enemies – indicating that legume cultivation could complement pest management in landscapes low in semi-natural habitat. Diversified agroecological pest management practices were negatively related to bean seed set. In maize, agroecological pest management was positively related to pest damage during growth, but not at harvest, indicating that the effectiveness of agroecological pest management practices needs re-evaluation. The cultivation of legumes, conservation of semi-natural habitat on the landscape scale and the diversification of soil agroecological practices were important for maintaining on-field biodiversity of different taxa. The interactive effects of crop-type and surrounding landcover reveals that the efficacy of agroecological practices were context dependent and should be adapted to needs and priorities of smallholder farmers.

Chapter 3 - Pumpkin fruit set is limited by herbivory and low pollinator richness in a smallholder agricultural landscape

Pollinators and pests are affected by land-use and agricultural practices, which in turn affects pollination and pest pressure on crops. Pollinator limitation occurs when insufficient

pollination lowers the productivity of crops below potential yields under sufficient pollination. Pollination limitation has been reported on crops throughout the world, but to my knowledge, never in sub-Saharan Africa. On 24 fields of pumpkin, a fully pollinator dependent crop, we used a full factorial hand-pollination and flower exclusion experiment to investigate the relative importance of flower pests and pollinators for pumpkin yields. I investigated the effects of landscape level semi-natural habitat cover and farm-level implementation of manual pest management and the number of soil management practices on pollinators, pest damage and yield. Increased semi-natural habitat cover negatively affected pollinator abundance, but positively affected pollinator richness. This pattern was driven primarily through the high abundance of honeybees on fields in low semi-natural habitat landscapes, despite an increase in other bees and fly pollinators with increasing semi-natural habitat cover. Manual pest management reduced the abundance and richness of pollinators through decreases in honeybees and flies but did not affect non-honeybees. Increasing the number of agroecological soil practices increased both the abundance and richness of pollinators. Pest damage was unaffected by semi-natural habitat and agroecological practices. The flower exclusion experiment showed that pumpkin fruit set was limited both by insufficient pollinators and pests across all landscapes. However, fruit quality (size, weight, and seed set) was negatively correlated with the amount of semi-natural habitat, possibly due to poorer soils in these areas where agriculture is less dominant. However, though we found that fruit set of excluded flowers decreased across the semi-natural habitat gradient, that of animal pollinated flowers increased. This is due increased pollinator richness increasing pumpkin fruit set – showing a direct benefit of biodiversity to smallholder farmers. Therefore, increasing pollinator richness compensated for poorer soils in areas low in semi-natural habitat. In addition, implementing practices that increase pollinator richness, such as increasing the number of agroecological soil practices, would be important to improve fruit set success in Malawi.

Chapter 4 – Higher bee abundance, but not pest abundance, in landscapes with more agriculture on a late flowering legume crop in tropical smallholder farms

Legume crops such as pigeon pea provides important agronomic and nutritional benefits to vulnerable smallholders, but it is understudied how these important crops can be grown to avoid pest. In the seasonal tropics, the peak of insect abundance coincides with the rainy season, but pigeon pea in Malawi flowers in the dry season-indicating that it could be a potentially important resource for bees at this time. We studied the effects of landscape composition (semi-natural habitat cover and agricultural land cover) on the abundance and

richness of bees, and the abundance of blister beetles, the main pigeon pea pests in our study region. We found that bee abundance, but not bee richness, nor the abundance of pests, increased with increasing agricultural area in the landscape. Possibly, the flowering pigeon pea provided a flowering resource in an otherwise resource-scarce environment in the dry season, concentrating bees there. As such, the planting of late-flowering legume crops, such as pigeon pea, could benefit pollinators by bridging periods of low resources in these landscapes.

Chapter 5 – Local and landscape scale conversion of woodland to farmland and agroecological practices shape butterfly communities in tropical smallholder farms

The potentially interactive effects of local and landscape scale habitat conversion on insect communities in tropical agricultural landscapes are understudied, particularly in Africa. Furthermore, the potential for agroecological management to mitigate possible negative effects of semi-natural habitat conversion on insects is also unknown. Therefore, we assessed butterfly abundance, species richness, species assemblages and community life-history traits on 24 paired shrub-and farmland sites along a gradient of semi-natural habitat cover. On farmland sites, we additionally assessed the effects of diversification of pest- and soil management practices and on-farm flowering plant diversity on butterflies. Locally, farmlands had lower abundances and approximately half the species richness than paired semi-natural habitats. Farmland butterfly communities had larger wingspan than farmland communities. Increasing semi-natural habitat cover decreased the abundance of butterflies in both habitats, driven by a decrease of the most dominant butterfly species. In contrast, species richness increased with increasing semi-natural habitat cover. Butterfly species assemblages were distinct between shrub- and farmland and shifted across the semi-natural habitat gradient. Farmland butterfly abundance, but not species richness, increased with increasing flowering plant species richness on farms. Increasing the number of agroecological pest management per hectare decreased the abundance of the dominant species, but not of rarer species. However, increasing agroecological soil management increased the abundance of these rarer species. However, the negative impacts of woodland conversion to farmland, both at landscape and local scales on butterflies suggest that on-farm measures will have limited effects if remaining semi-natural habitats continue to decline.

Chapter 6 – General discussion

Tropical agricultural landscapes are often home to unique and threatened biodiversity as well as to vulnerable smallholder communities. My work in northern Malawi underscores the importance of semi-natural habitats at landscape and local scales for functional biodiversity on farms and provides evidence that increased biodiversity benefits smallholders through pest control and pollination services. Additionally, we found that agroecology can benefit on-farm biodiversity and ecosystem services, but these effects are context-dependent and do not always mitigate the negative effects of habitat loss. Overall, my work identified 5 recommendations for sustainable agricultural development in smallholder landscapes: (i) increasing protection and recovery of semi-natural habitats both at a local and landscape scale, (ii) encouraging the growing of legumes to benefit natural enemies and pollinators, especially in areas surrounded by low proportions of semi-natural habitats, (iii) educating farmers on the differences between pests and beneficial insects(iv) encouraging the diversification of agroecological soil management practices to improve above- and below-ground biodiversity and finally (v) increase on-farm flowering plant species richness for butterfly communities. My results show the potential for agroecology to contribute to sustainable use of tropical agricultural landscapes and reveals that sustainable agroecological intensification can support both biodiversity and the livelihoods of smallholder communities.

Zusammenfassung

Kapitel 1 – Allgemeine Einleitung

Die globale Biodiversität nimmt rapide ab. Dieser Biodiversitätsverlust ist in Regionen die reich an Biodiversität aber wirtschaftlich arm sind besonders stark ausgeprägt, insbesondere in vielen tropischen Regionen, die durch Subsistenzlandwirtschaft geprägt sind. Durch die Zerstörung natürlicher Lebensräume und nicht nachhaltige Land Nutzung ist Landwirtschaft eine der Hauptursachen dieses Biodiversitätsrückgangs. Dabei ist gerade landwirtschaftliche Produktion abhängig von Biodiversität, da Biodiversität Ökosystemdienstleistungen wie Bestäubung und natürliche Schädlingskontrolle bereitstellt. Biodiversität und Ökosystemdienstleistungen auf Feldern werden stark durch die umliegende Landschaft beeinflusst - komplexe Landschaften mit einen großen Anteil (halb-)natürlicher haben in der Regel höhere Abudanzen und eine größere Biodiversität von Bestäubern und natürlichen Feinden die vorteilhaft für die landwirtschaftliche Produktion sind. Forschung auf Landschaftebene hat bisher jedoch vorrangig auf die industrialisierte Landwirtschaft in z.B. Europa oder die USA fokussiert und kontextabhängige Unterschiede zwischen Regionen und landwirtschaftlichen Systemen sind nicht ausreichend studiert..Weltweit sind etwa 2 Milliarden Menschen von Subsistenzlandwirtschaft abhängig. Jedoch sind diese Kleinbauern, in der Forschung über die Konsequenzen von Landnutzung und landwirtschaftlichen Managements auf Biodiversität und Ökosystemdienstleistungen unterrepräsentiert, insbesondere Kleinbauern aus Subsahara-Afrika. Die wenigen verfügbaren Studien legend den Fokus oft auf wirtschaftlich wichtige Kulturpflanzen, wie etwa Kakao, und selten auf Kulturpflanzen, die für Ernährungssicherheit der Kleinbauern wichtig sind, obwohl der Verlust der Ökosystemdienstleistungen diese möglicherweise am härtesten trifft. Agroökologie ist eine nachhaltigere Form des landwirtschaftlichen Managements als die konventionelle Landwirtschaft, und will den Einsatz von Agrochemie zu reduzieren und eine holistische Landwirtschaft fördern. Agroökologie steigert die Ernährungssicherheit von Kleinbauern, insbesondere wenn die Bauern viele verschiedene agroökologische Verfahren nutzen. Vorteile der Agroökologie für Biodiversität und Ökosystemdienstleistungen werden oft vermutet, wurden bislang jedoch selten empirisch getestet. Zusätzlich wurden Effekte auf Biodiversität und Ökosystemdienstleistungen vorrangig getrennt zwischen der lokalen und der Landschaftsebene betrachtet, was das Erkennen potentieller Interaktionen erschwert. Unsere Studienregion in Nord Malawi spiegelt die viele Herausforderungen der afrikanischen

Subsistenzlandwirtschaft wider. Malawi liegt in einem Biodiversitäts-Hotspot, jedoch ist diese Biodiversität durch einen schnellen Rückgang natürlicher Lebensräume und durch die Intensivierung der Landwirtschaft stark gefährdet. Dem gegenüber stehen erfolgreicher Ausbau und Umsetzung von Agroökologie in der Region. Das gab mir die Möglichkeit, die Effekte von Landnutzung und Agroökologie auf Biodiversität und Ökosystemdienstleistungen in Malawi zu untersuchen. Dafür habe ich in Mais und Bohnen in Einzel- und Mischkultur 7 taxonomische Gruppen die verschiedene Ökosystemdienstleistungen erbringen erfasst (Kapitel 2) sowie Bestäuber und Bestäubung auf Kürbis (Kapitel 3) und Straucherbsen studiert (Kapitel 4). Zusätzlich habe ich an Schmetterlingen die Effekte von Lebensraumverlust auf der lokalen und auf Landschaftsebene studiert, und untersucht, ob Agroökologie potenziell negative Effekte mindern kann (Kapitel 5).

Kapitel 2 – Die Effekte von Nutzpflanzenart, Landnutzung und Agroökologie auf Biodiversität und Ökosystemdienstleistungen in der tropischen Subsistenzlandwirtschaft

Mischkultur, wie sie häufig in der afrikanischen Subsistenzlandwirtschaft von Kleinbauern praktiziert wird, wird als vorteilhaft für Biodiversität und Ökosystemdienstleistungen angesehen durch die vergleichsweise erhöhte Habitatkomplexität innerhalb der Felder. Ob jedoch die Effekte von Nutzpflanzenkultur von der umliegenden Landschaft abhängen, ist bislang unklar.Auf 62 Feldern habe ich die Effekte von Nutzpflanzenart (Mais, Bohnen oder Mais-Bohnen-Mischkultur), dem Anteil halb-natürlicher Habitate in der umgebenden Landschaft und der Diversifizierung von agroökologischem Schädlings- und Bodenmanagement auf 7 funktionelle Taxa (Vögel, Laufkäfer, Spinnen, Ameisen, Parasitoide, Bienen und Bodenbakterien) und zwei Ökosystemdienstleistungen (natürliche Schädlingskontrolle und Bestäubung) untersucht. Die Aktivität von Spinnen und Parasitoiden, der Artenreichtum von Laufkäfern und die Diversität von Bodenbakterien waren in Bohnenfeldern am höchsten, insbesondere in Landschaften mit wenig halb-natürlichen Habitaten. Mehr halb-natürliche Habitate in der Landschaft hatte positive Effekte auf die Artenvielfalt von Bienen und Laufkäfern. Diversifizierung von agroökologischem Bodenmanagement steigerte die Bodenbakteriendiversität und veränderte die Zusammensetzung von Laufkäferartengesellschaften. Bohnen in Einzelkultur hatten weniger Schaden durch Schädlinge als Bohnen in Mischkultur, möglicherweise durch die erhöhte Aktivität der natürlichen Feinde. Das weist darauf hin, dass der Anbau von Leguminosen wie Bohnen die Schädlingskontrolle im Gebieten mit wenig halb-natürlichen Habitaten komplementieren kann. Mehr agroökologisches Schädlingsmanagement war negativ korreliert mit der Anzahl der Bohnen pro Hülse. Im Mais war des agroökologische Schädlingsmanagement positiv korreliert mit dem Schaden durch Schädlinge beim Wachstum der Pflanze, jedoch nicht bei der Ernte. Ein Neubewertung der Effektivität des agroökologischen Schädlingsmanagements in der Subsistenzlandwirtschaft ist daher notwendig. Meine Ergebnisse zeigen dass der Anbau von Leguminosen, der Erhalt von halbnatürlichen Habitaten auf der Landschaftsebene sowie die Diversifizierung von agrarökologischen Bodenmanagement für die lokale Biodiversität in den Feldern ausschlaggebend waren. Die interaktiven Effekte von Nutzpflanzenart und Landnutzung in der umliegenden Landschaft zeigen dass der Nutzen von agrarökologischen Maßnahmen Kontextabhängig ist und an die Prioritäten der Kleinbauern angepasst werden muss.

Kapitel 3 – Kürbisfruchtansatz in einer tropischen Agrarlandschaft ist limitiert durch Schädlingsdruck und den geringen Artenreichtum von Bestäubern

Bestäuber und Schädlinge, sowie Bestäubung und Fraßschäden, werden durch Landnutzung beeinflusst. Bestäubungslimitierung liegt vor, wenn Blüten nicht ausreichend von Bestäuber besucht werden und der Ertrag dadurch gemindert wird. Bestäubungslimitierung von Kulturpflanzen wurde in verschiedenen Regionen der Welt gezeigt, bislang jedoch noch nicht in Afrika. Kürbis eignet sich gut, um den Zusammenhang zwischen Bestäubung und Schädlingsdruck zu untersuchen, da Kürbisse vollständig von Bestäubern abhängig sind. Deswegen habe ich auf 24 Kürbisfeldern in einem voll faktoriellen Experiment die relativen Effekte von Schädlingen und Bestäubern auf Kürbiserträge erfasst. Zusätzlich habe ich die Effekte des Anteils halb-natürlicher Habitate auf der Landschaftsebene, der Implementierung von manueller Schädlingsbekämpfung und der Diversifizierung von agroökologischem Bodenmanagement auf Farm Level auf Bestäuber, Schädlinge und Erträge untersucht. Ein steigender Anteil halb-natürlicher Habitate verringerte die Abundanz von Bestäubern, erhöhte jedoch ihren Artenreichtum. Dieses Ergebnis wurde vor allem durch die hohe Abundanz von Honigbienen im Felder in Landschaften mit wenig halb-natürlichen Habitaten getrieben, allerdings stiegen die Abundanzen von anderen Bienen und Fliegen mit steigendem Anteil halb-natürlicher Habitate. Manuelle Schädlingsbekämpfung reduzierte die Abundanzen und den Artenreichtum von Bestäubern durch eine Abnahme von Honigbienen und Fliegen aber nicht von anderen Bienen. Eine Diversifizierung des agroökologischen Bodenmanagements hatte einen positives Effekt auf die Abundanzen und den Artenreichtum von Bestäuber. Der Anteil halb-natürlicher Habitate hatte keinen Einfluss auf durch Schädling verursachte Schäden. Das Experiment zeigt, dass sowohl Schädlinge als auch zu geringer

Bestäuberreichtum zu einem suboptimalen Kürbisfruchtansatz führen. Fruchtqualität (Größe, Gewicht und Samenanzahl) war jedoch negativ mit dem Anteil halb-natürlicher Habitate korreliert, möglicherweise auf Grund von geringerer Bodenqualität. Der Fruchtansatz stieg mit dem Artenreichtum der Bestäuber was einen direkten positiven Effekt der Biodiversität für Kleinbauern zeigt. Schlechte Bodenqualität in Regionen mit wenig verbliebenen halbnatürlichen Habitaten wurden durch eine höhere Artenvielfalt an Bestäubern kompensiert. Zusätzlich könnten Maßnahmen die die Artenvielfalt von Bestäubern erhöhen, wie etwa eine Diversifizierung des agroökologischen Bodenmanagements, dazu beitragen den Fruchtansatz in Malawi zu erhöhen.

Kapitel 4 – Höhere Bienenabundanz aber nicht höheren Schädlingsabundanz in Landschaften mit größerem Anteil von Landwirtschaft an einer spät blühenden Leguminose in der tropischen Subsistenzlandwirtschaft

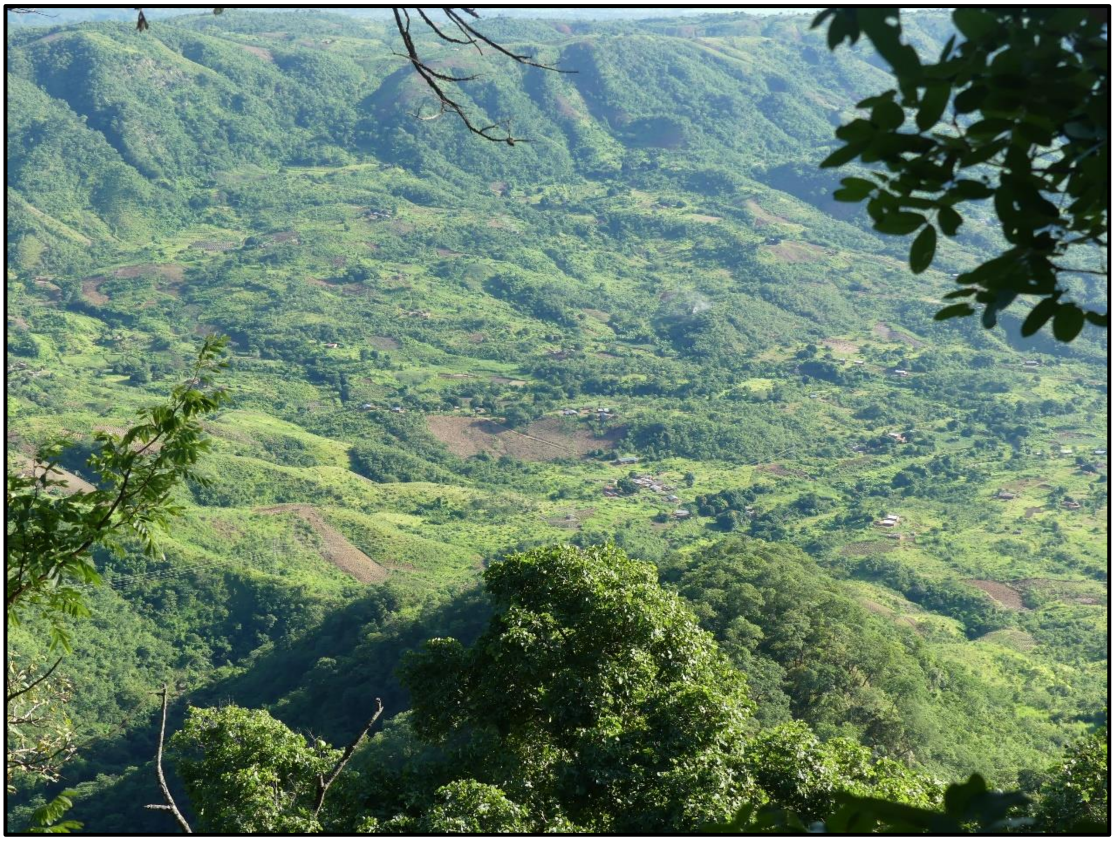
Leguminose Kulturpflanzen haben für Kleinbauern wichtige Vorteile bezogen auf Bodenverbesserung und Ernährungssicherheit. Trotzdem sind die Effekte von Landnutzung auf die Bestäuber und Schädlinge von Leguminosen in der tropischen Subsistenzlandwirtschaft wenig untersucht. In Ländern der saisonalen Tropen wie etwa Malawi ist die Abundanz von Insekten stark an die Regenzeit gebunden. Straucherbsen blühen in Malawi jedoch in der Trockenzeit. In der Blütezeit der Straucherbsen, habe ich die Effekte des Anteils halb-natürlicher Habitate und des Anteils landwirtschaftlicher Nutzfläche auf Bienen und Schädlinge untersucht. An Straucherbsen war die Bienenabundanz, aber nicht deren Artenreichtum oder die Abundanz von Schädlingen höher auf Feldern in Landschaften mit größerem Anteil an landwirtschaftlicher Nutzfläche. In diesen Landschaften in denen Nahrungsressourcen in der Trockenzeit knapp sind wurden Bienen mutmaßlich durch das größere Nahrungsangebot der Straucherbsen angelockt.

Kapitel 5 – Effekte von Landnutzung auf Schmetterlingsgesellschaften auf lokaler und auf Landschaftsebene

Die potentielle interaktiven Effekte von Habitatverlust auf der lokalen wie auch auf der Landschaftsebene auf Insektengesellschaften in tropischen Agrarlandschaften sind nicht ausreichend erforscht, insbesondere in Afrika. Das Potential der Agroökologie mögliche negative Effekte des Habitatverlusts zu mindern, ist zudem unbekannt. Daher habe ich Schmetterlingsgesellschaften auf 24 gepaarten Flächen (Buschland- und Ackerlandflächen) entlang eines Gradienten an halb-natürlichen Habitaten erfasst. Auf Ackerlandflächen wurden zusätzlich die Effekte von agroökologischem Schädlings- und Bodenmanagement und des Artenreichtums blühender Pflanzen auf Schmetterlinge untersucht. Auf Ackerland gab es deutlich weniger Schmetterlinge als im Buschland. Auch war der Artenreichtum auf Ackerland nur halb so hoch wie im Buschland, und Ackerlandschmetterlinge waren im Durchschnitt größer als Buschlandschmetterlinge. Der Anteil halb-natürlicher Habitate auf Landschaftsebene hatte durch die Abnahme der dominanten Schmetterlingsart einerseits einen negativen Effekt auf die Schmetterlingsabundanz. Andererseits hatte der Anteil halb-natürlicher Habitate einen positiven Effekt auf den Artenreichtum. Die Schmetterlingsgesellschaften von Busch- und Ackerland waren verschieden änderten sich jedoch auch entlang des Habitatgradienten. Eine höhere Diversifizierung von agroökologischer Schädlingskontrolle hatte reduzierte die dominante Schmetterlingsart, jedoch nicht andere Arten. Mehr Diversifizierung von agroökologischem Bodenmanagement erhöhte die Abundanz seltener Arten. Auch war ein höhere Pflanzendiversität auf Ackerland positiv mit der Schmetterlingsabudanz korreliert. Das zeigt, dass obwohl Agroökologie positive Effekte auf Schmetterlinge hat, halb-natürliche Habitate besser geschützt werden sollten, um Insektengesellschaften zu unterstutzen.

Kapitel 6 – Allgemeine Diskussion

Ökosysteme in tropischen Agrarlandschaften sind geprägt von einer einzigartigen Biodiversität wie auch von armen Kleinbauern. Meine Arbeit in Nordmalawi zeigt die Wichtigkeit von halb-natürlichen Habitaten für Biodiversität auf dem lokalen und auf Landschaftniveau. Zusätzlich konnte ich zeigen, dass Agroökologie Biodiversität und Ökosystemdienstleistungen unterstutzen kann, positive Effekte jedoch Kontext abhängig sind und nicht immer die negativen Effekte von Habitatverlust mitigieren können. Besonders Schädlingsdynamiken und Schädlingskontrolle bedarf weiterer Forschung. Meine Ergebnisse leiten zu 5 wichtigen Empfehlungen für nachhaltige agroökologische Intensivierung von tropischer Subsistenzlandwirtschaft: (i) verbleibende halb-natürliche Lebensräume, auf lokalem und auf Landschaftsniveau, müssen besser geschützt werden, (ii) der Anbau von Leguminosen sollte gefördert werden, um natürliche Schädlingskontrolle und Bestäuber zu unterstutzen, (iii) Kleinbauern über die Unterschiede zwischen Schädlingen und nutzlichen Insekten aufklären, (iv) die Diversifizierung des agroökologischen Bodenmanagements sollte gefördert worden, und (v) die Diversität blühender Pflanzen auf Ackerland sollte erhöht worden, um Bestäuber zu fördern. Obwohl das Schützen von halb-natürlichen Habitaten von größer Bedeutung ist, zeigen meine Ergebnisse, dass Agroökologie das Potential besitzt, ein wichtiger Teil der nachhaltigen Landnutzung in tropischen Agrarlandschaften zu sein und damit den Lebensunterhalt von Kleinbauern sowie auch die Biodiversität unterstützen kann.



The Malawian landscape: the rural landscape in Malawi is characterised by a mosaic of small fields belonging to smallholder farmers living in loosely organised villages. Interspersed between the villages, particularly on hillsides, are remnants of semi-natural Miombo woodlands and shrublands. Though important habitats for biodiversity, Malawi's remaining semi-natural habitats are disappearing at an alarming rate.

Chapter 1

General Introduction

Biodiversity describes the staggering variety of life on earth – we share our planet with an estimated 8.7 million eukaryotic species, of which over 80% remain undescribed (Mora et al., 2011). Currently, we are losing Earth's biodiversity at 1000 times the background extinction rate (Pimm et al., 2014), a phenomenon termed the "biodiversity crisis". Agriculture is one of the major drivers of biodiversity loss through the conversion of natural habitats and environmentally unsustainable management (IPBES, 2019). Ironically, biodiversity is responsible for a range of natural processes, known as ecosystem services, on which that same agriculture depends (Dainese et al., 2019). The rate of biodiversity loss is predicted to be especially high in regions that are biodiversity rich but economically poor (Newbold et al., 2015): essentially describing vast regions in the tropical Global South dominated by smallholder agriculture. But compared to large-scale temperate farming systems, smallholders are underrepresented in research on the effects of landscape change and management for biodiversity and ecosystem services provided to crops – especially in the context of sub-Saharan Africa. Within the framework of the FARMS4biodiversity project, which aims to study the ecological, geographical, social, and institutional processes and consequences of land-use change and agroecological practices in smallholder farming communities in Malawi (Kpienbaareh et al., 2022a), we investigated the effects of landscape composition and agroecological practices on various groups of functional biodiversity and ecosystem services on crops important for smallholder food security. Specifically, we studied multiple functional taxa on bean-maize cropping systems (Chapter 2) and the pollination and herbivory on pumpkin (Chapter 3) and pigeon pea (Chapter 4), all which are important food crops in the region. Finally, we investigated how local- and landscape-scale habitat conversion from semi-natural habitat to farmland and on-farm agroecological practices shape butterfly communities (Chapter 5).

1.1 Landscape and local effects on biodiversity and ecosystem services

Agriculture feeds the world and is essential to human civilization as we know it. In 2000, over 40% of the terrestrial land surface was already dedicated to agriculture (Ramankutty et al., 2008). The impacts of agriculture on biodiversity can be indirect, such as through the emission of greenhouse gases contributing to climate change, or direct, through loss of natural habitats with increasing cropland expansion, and the subsequent unsustainable management of cropland through agricultural intensification (IPBES, 2019). The loss of natural habitat is the most visible and directly obvious cause of biodiversity loss: cropland expanded by 2.19% globally between 2000-2010 (Hu et al., 2020), and is predicted to increase further in all scenarios by 2050 (Schmitz et al., 2014). Yet it is agricultural intensification – increasing field size and mechanization, increased application of agrochemicals, the growing of a few selected varieties of genetically similar crops and habitat homogenization, that may have contributed more to increases in crop production than agricultural expansion (Hu et al., 2020). Intensification of agriculture threatens human health (Wilson & Tisdell, 2001) and degrades biodiversity, even harming species that were formerly abundant in agricultural landscapes (for example, farmland birds in Europe: Donald et al., 2006). The costs of these gains in production for biodiversity are expected to be especially severe in developing regions in the tropics (Zabel et al., 2019), yet compared to temperate regions, the relationships between land-use change, local management, biodiversity and ecosystem services are much less investigated.

By eroding biodiversity, agriculture could be trading long-term productivity for short-term yield increases, rendering the current developments unsustainable. In fact, up to 40% of global croplands may already be degraded, and in 4 decades there has been an astonishing 700% increase in global fertilizer use, whereas global grain production has only doubled during that same period (Foley et al., 2005). As a nature-based process, agriculture itself is dependent on biodiversity, because biodiversity provides agriculture with ecosystem services: without healthy soils in which to germinate and grow, natural enemies to protect crops from herbivores and pollinators to contribute to fruit and seed set of pollinator-dependent crops, crops would not produce the food and feed on which we all depend.

The presence of biodiversity and ecosystem services on crop fields is affected by the surrounding landscape. Complex landscapes with higher (semi-)natural habitat cover are often observed to support higher biodiversity and ecosystem services than more simple landscapes with less semi-natural habitat (Landis, 2017; Martin et al., 2019). The presence of high biodiversity in agricultural landscapes is important because biodiversity drives ecosystem service delivery to crops and ultimately crop yields (Dainese et al., 2019). Despite huge differences in climate, landscape composition, biodiversity and agronomic practices between regions across the world, most of our current understanding of landscape-scale drivers of pollination and pest control comes from research performed within large-scale temperate agriculture, and not from tropical landscapes dominated by smallholders (Steward et al., 2014). Particularly, applied ecological research from sub-Saharan Africa is limited (Nuñez et al., 2019; Otieno et al., 2020a). This is worrying, as smallholder agricultural landscapes, such as those in sub-Saharan Africa, are high in biodiversity (Mannion et al., 2014), but are rapidly losing semi-natural habitats at a landscape scale (Newbold et al., 2015), with unknown consequences for biodiversity and ecosystem services important for smallholder agriculture.

Pollination, predominantly by insects such as bees or butterflies, is one of the most important ecosystem services in agriculture (Garibaldi et al., 2013). Though many grain staples such as maize and wheat are wind pollinated, up to 70% of our crop species are pollinator dependent, including many high-value crops, such as coffee or oilseeds (Roubik, 1995), and crops important for nutrition in human diets such as legumes and squashes (Eilers et al., 2011). Though the Western Honeybee (Apidae*: Apis mellifera*) is arguably the most well-known pollinator, and apiculture is an important economic activity, honeybees are not necessarily the most efficient pollinator across crops (Garibaldi et al., 2013). Additionally, though the number of honeybee hives has been increasing over the last decades, the rate of increase of honeybee stocks has not kept up with the demand for pollination (Aizen & Harder, 2009). Stochastic declines in colony numbers, caused for example by Colony Collapse Disorder (Oldroyd, 2007), warns us that it is perhaps unwise to put all our eggs in the same basket and rely on a single species for all our pollination needs. Importantly, data suggests that not only the abundance, but the species richness of pollinators is an important driver of pollination services to crops (Dainese et al., 2019). Unfortunately, both the abundance (Koh et al., 2016; Powney et al., 2019) and species richness (Carrasco et al., 2021) of some pollinators has been declining, as is the case with terrestrial insects more generally (van Klink et al., 2020). The use of systemic insecticides known as neonicotinoids has been blamed for declines in wild bees in particular (Rundlöf et al., 2015), but as with most agricultural biodiversity, pollinators are impacted by habitat decline, as well as by a multitude of additional stressors, such as diseases (Dicks et al., 2021). This is problematic, as in some crops, pollination has been found to be the most important factor determining productivity (Fijen et al., 2020). In other cases, crops can even be "pollinator limited" – when sub-optimal yield is caused by insufficient visitation by compatible pollinators. Evidence for pollinator limitation has been reported for crops in the

USA (Reilly et al., 2020), Europe (Holland et al., 2020), and India (Basu, Bhattacharya & Ianetta, 2011), but to our knowledge, never in sub-Saharan Africa. In these cases, improving landscapes for pollinators may be a sustainable pathway for increasing productivity of pollinator dependent crops.

Globally, up to 10% of crop losses are due to pests (Oerke, 2006; Savary et al., 2019). These losses are a major driver of pesticide use, despite the costs for human health and the environment (Wilson & Tisdell, 2001), such as the killing of non-target organisms, including bees (Rundlöf et al., 2015) and natural enemies of pests. The importance of natural pest control and the unsustainability of pesticides is highlighted by explosive outbreaks in rice planthoppers in Asia – which manifested due to destruction of natural control mechanisms caused by rampant pesticide use (Heong, Wong & Delos Reyes, 2015). In addition, pests can develop resistance to pesticides over time, rendering pesticides ineffective for control (Gould, Brown & Kuzma, 2018). Natural enemies, similarly to pollinators, are often more abundant in complex landscapes (Martin et al., 2019), yet pests respond inconsistently to landscape differences (Tamburini et al., 2020). Therefore, it is difficult to unravel the relationships between natural enemies and pest damage outcomes in agricultural landscapes and planning landscapes accordingly is a major challenge for agricultural ecologists and farmers.

In agriculture, biodiversity benefits human beings through ecosystem services, and many scientists use this to justify conservation efforts. Though undeniably important, it is also a deeply anthropogenic, utilitarian view of the natural world. Not all bee species are effective crop pollinators, and therefore do not directly contribute to human well-being. But does that also mean that these species are not inherently valuable and worthy of conservation? As others have also argued (e.g. Kleijn et al., 2015), conservation of biodiversity as a justification for sustainable agriculture should be a goal in and of itself, along with its benefits to agriculture through improved ecosystem services.

1.2 Smallholder farming

Though the connections between landscape, biodiversity and ecosystem services are relatively well studied in large-scale agricultural systems in temperate regions, smallholder agricultural landscapes in the Global South are under-represented in this field of research. This is unjust, not only because smallholder agriculture is the main livelihood of over two billion people (Steward et al., 2014), but smallholders also contribute to over half the global food supply (Herrero et al., 2017) and are therefore important far beyond their own communities. Managing up to 16% of global agricultural area (Samberg et al., 2016), smallholders supply the world with commodities that many people in the Global North consume every day, such as coffee, tea and cacao (Vanlauwe et al., 2014).

Being primarily based in the (sub-)tropics in the Global South (Figure 1.1), smallholders share landscapes with some of the world's most species rich and most threatened biodiversity (Newbold et al., 2015). Therefore, smallholders are inadvertently stewards of much of the world's remaining biodiversity. At the same time, rural smallholders are also some of the most vulnerable communities globally, affected by hunger, poverty and lacking access to basic needs such as quality healthcare and education. This presents a huge challenge: how does one develop smallholder agriculture, and improve rural livelihoods without impacting biodiversity negatively? Overall, the strongest push has been to develop smallholder agriculture through intensification and specialization of input use (Snapp, 2020), with the aim to alleviate poverty and food insecurity in these communities (Poppy et al., 2014). However, the results of this push towards intensification are ambiguous at best, especially when ecosystem service outcomes are considered (Rasmussen et al., 2018), and can exacerbate existing inequalities within smallholder communities (Dawson, Martin & Sikor, 2016). Additionally, increasing dependencies of smallholders on external inputs such as hybrid seeds and synthetic fertilizers produced primarily by for-profit multinational agribusinesses, decreases farmers' autonomy and can fuel a dangerous cycle of debt and socio-economic vulnerability (Mcmichael, 2013). As intensification continuous to drive biodiversity loss, this has the potential to do harm especially to the poorest of low-income farmers who lack the means to compensate the loss of important ecosystem services through conventional agricultural inputs (Poppy et al., 2014). Therefore, we argue that the challenges of smallholder agricultural development and biodiversity loss cannot and should not be viewed as two distinct issues, but rather as two highly interconnected problems (Chappell & LaValle, 2011).

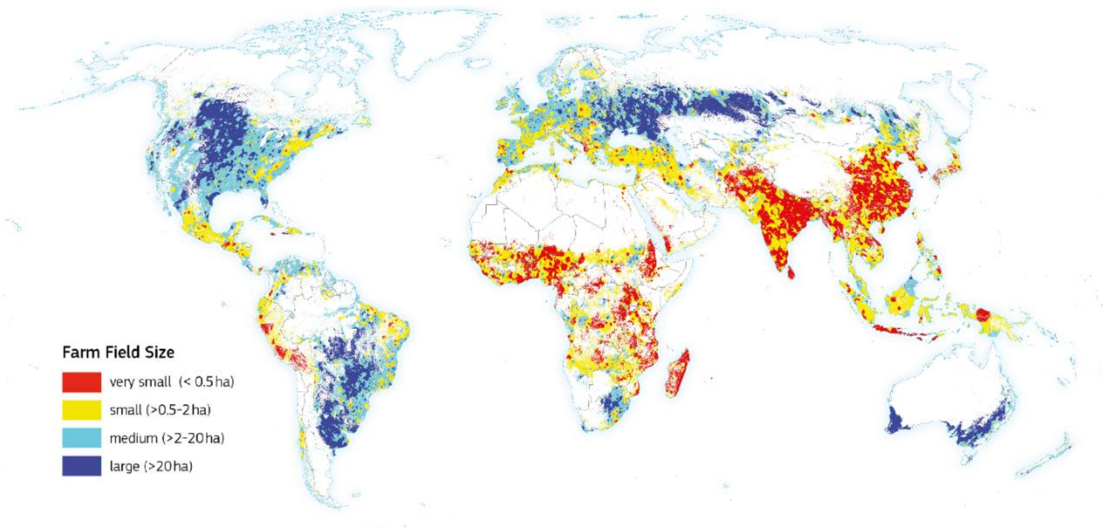


Figure 1.1: global distribution of farm field size. Note the small (yellow) and very small (red) farm fields primarily situated in (sub-)tropical regions in the Global South, such as central America, sub-Saharan Africa, and south and south-east Asia. Image adapted from Fritz et al. (Fritz et al., 2015).

Smallholders in sub-Saharan Africa, face historical, institutional, and biogeographical challenges unique to the region. Even compared to other smallholders throughout the Global South, such as those in Latin America and south-east Asia, food insecurity and poverty in sub-Saharan Africa is particularly pervasive (Fosu, 2015). The reasons for this are multifaceted and complex, and go far beyond simply improving agronomic practices and increasing yield (Snapp, 2020), and many of them are outside the scope of this thesis. Smallholder agricultural practices in contemporary Africa are strongly influenced by the extractive nature of cash crop cultivation in colonial and post-colonial regimes, which fuels inequalities even within countries and communities (Roessler et al., 2020), and push a "Western" industrialised view of agriculture. With Africa's population of 1.25 billion likely to double by 2050, demographic changes could fuel high rates of unregulated land-use change which leads to loss of biodiversity and livelihoods (IPBES, 2018). In contrast with the temperate regions, sub-Saharan Africa never experienced glaciation during the last ice age, which resulted in much older soils which may be more nutrient poor by nature (Hengl et al., 2017). In croplands, continued soil degradation may be particularly severe (Borrelli et al., 2017). However, though the general trend does seem to be a decline in soil quality, there are some caveats to this assumption: there is limited long-term soil data from sub-Saharan Africa, and with correct management, soils can and are managed sustainably by smallholders over extended periods of time (Tully et al., 2015). Another challenge facing smallholders in Africa is the introduction of invasive crop pests. A prominent example of this is the arrival of the Fall Armyworm

(Noctuidae: *Spodoptera frugiperda*) in 2016, a pest of several major African crops including maize, an important staple (Stokstad, 2017). Finally, despite only contributing 7% of global greenhouse gas emissions (Ntinyari & Gweyi-Onyango, 2021), sub-Saharan Africa is bearing the largest burden in terms of impacts. In sub-Saharan Africa, where smallholder farming is mostly rainfed and not irrigated, changes in precipitation could potentially be devastating to both smallholder livelihoods and biodiversity (Serdeczny et al., 2017).

1.3 Agroecology - a pathway to sustainable agricultural development

To meet the challenges of persistent socio-economic problems in farming communities and degradation of biodiversity in agricultural landscapes, agroecology has gained prominence in the last years as a potential pathway to fair and sustainable agricultural development. The definition of agroecology is pluralistic, and can refer to a scientific discipline, a set of agricultural practices and a social movement (Wezel et al., 2020). Firstly, the scientific discipline of agroecology aims to gather evidence and understand the ecological relationship between agriculture and the natural environment, including species that provide ecosystem services. This thesis is one example of such work. Secondly, agroecological practices aim to develop innovative and effective farming methods that implement the local needs and indigenous knowledge of farmers whilst meeting food demands sustainably. This thesis aims to test the effects of such practices on biodiversity and ecosystem service outcomes within a tropical smallholder agricultural context. Thirdly, as a social movement, agroecology aims to advocate for changes in the social and economic roles that producers, industries, and consumers have within global food systems that lead to current inequalities (Gliessman, 2018). Though the three definitions of agroecology are integrated and necessary for transforming current food systems towards a more sustainable future, the latter definition is beyond the scope of this thesis.

The second definition of agroecology – agroecology as practice, has been implemented in a variety of ways. Since agroecology is by design intended to be adapted to context in which it is applied, specific agroecological practices vary from region to region depending on local contexts. There are, however, a few general principles that characterise agroecological practices (Rosset & Altieri, 2017). For example, agroecological practices aim to reduce the inputs of expensive and environmentally damaging synthetic inputs, and instead aim to optimise natural processes. In Malawi, for example, some farmers spread fish stock on crops affected by caterpillar pests with the goal of attracting ants that should eat said pest (Figure 1.2). Such a practice illustrates several important principles in agroecology: *recycling* by re-using leftover fish parts to make stock, *input reduction* by avoiding the use of synthetic pesticides, *biodiversity* by encouraging ants on the crops, *synergies* by enhancing the positive ecological interactions between the natural enemies (ants) and the pests, and *co-creation of knowledge* where the farmer has knowledge about the relevant ecological interaction (ants eat pests) and can teach the practice to others in their household or community (Wezel et al., 2020). Other examples of agroecological pest management practices include the use of botanical extracts, manual removal or killing of pests, or the spreading of ash on pest-affected crops. A major priority of agroecology is the maintenance of healthy agriculture soils. Therefore, there are a wide variety of agroecological soil management practices such as the planting of vetiver hedges, conservation landscaping (such as pit planting or terracing to prevent soil runoff), mulching, the use of manure or compost and the implementation of intercropping, residues, or crop rotation, particularly with legumes (Table 2.S1).

Figure 1.2: worker ants from the genus *Myrmicaria* hunting a pest of maize plants: fall armyworm (*Spodoptera frugiperda*). A form of natural pest control encouraged by farmers through the spreading of fish stock on affected plants to attract ants, an example of an agroecological pest management practice. Mzimba district, Malawi. (Photo: ©Georg Küstner).

Since agroecological practices reduce external inputs, they can be cost-effective and accessible, which is important in the smallholder context where financial resources and access to inputs are often very limited. However, they may also be more knowledge and labour intensive, and therefore specifically burden marginalized groups such as women (Bezner Kerr et al., 2019a). Despite this, agroecology has been shown to improve food sovereignty, food security and nutrition (Bezner Kerr et al., 2021), and resilience to climate change (Snapp et al.

2021). Importantly, Bezner Kerr et al., (2021) showed that if agroecological systems included multiple components, in other words *diversified* agroecological practices, agroecology was more likely to contribute to improved food security and nutrition. Co-benefits of agroecology with biodiversity and ecosystem services are assumed, but rarely empirically tested.

Though the effects of local management and landscape-scale semi-natural habitat cover are more commonly studied in isolation, there is an increasing appreciation these can interactively affect biodiversity and ecosystem services in agriculture (Landis, 2017). Local practices that aim to enhance biodiversity have larger effects within landscapes with less semi-natural habitat cover compared to landscapes high in semi-natural habitat cover (Batáry et al., 2011). However, studies that investigate both landscape and local-scale effects on biodiversity and ecosystem services in smallholder agricultural landscapes are quite rare (though see: (Otieno et al., 2015; Hipólito, Boscolo & Viana, 2018), as notable exceptions). In fact, to our knowledge, no studies that concurrently investigate the effects of local agroecological practices and landscape-scale semi-natural habitat cover, and possible interactions between them, on biodiversity and ecosystem services in smallholder agricultural landscapes. Our work aimed to address this knowledge gap.

1.4 Malawi – a case in point

Malawi, a landlocked country in south-eastern Africa, illustrates many of the challenges for smallholder communities in sub-Saharan Africa and more generally the Global South. Approximately 80% of Malawi’s population is rural. Malawi is amongst the least developed countries in the world, more than 59% of smallholders live below the national poverty line: poverty reduction is a major goal of government and NGO’s active in the country, yet in rural areas poverty and inequality have rather increased in recent years (FAO, 2018). These socio-economic circumstances drive high rates of deforestation in the landscapes in which rural communities live and farm (Chirambo & Mitembe, 2014). Agricultural extension projects by the government are often input focused, such as the Farm Input Subsidy Program that subsidised chemical fertilizer and hybrid seed. Though widely implemented, these programmes have not achieved the desired benefits for smallholder communities (Messina, Peter & Snapp, 2017; Mkindi et al., 2020), and further contribute to biodiversity loss in agricultural landscapes.

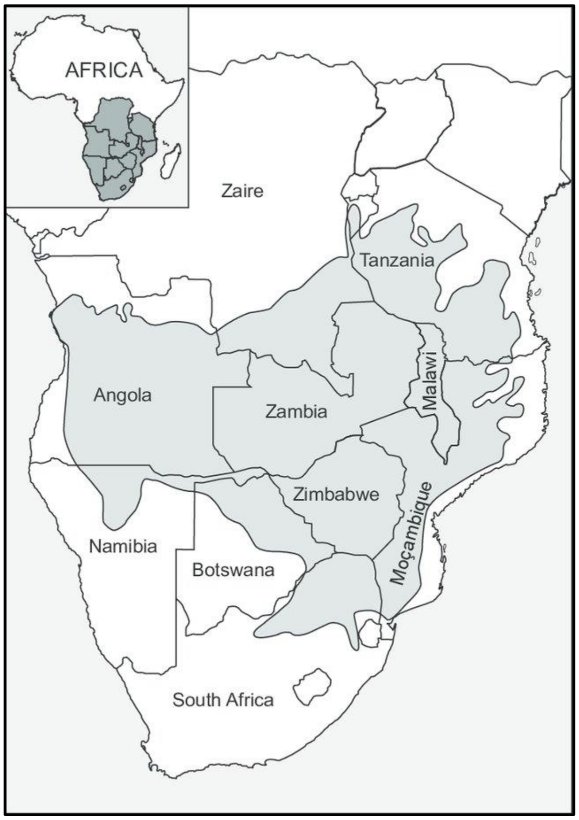


Figure 1.3: The expanse of Miombo woodlands across southern Africa, including Malawi (Chirwa, Syampungani & Geldenhuys, 2008).

The threat to biodiversity is particularly serious because Malawi lies in the Miombo woodland ecoregion (Figure 1.3). This ecoregion is the largest expanse of tropical seasonal woodlands in Africa (and perhaps even globally) and is a biodiversity hotspot (Chirwa, Syampungani & Geldenhuys, 2008). Miombo woodlands, dominated by leguminous trees such as *Brachystegia* spp., support around 8500 plant species, of which over half (54%) are endemic (Ribeiro et al., 2020). In addition, Miombo woodlands are home to the largest remaining assemblages of mammalian megafauna (though mostly restricted to protected habitats in national parks). Despite the importance of insects to ecosystem services, the invertebrate biodiversity of Miombo woodlands is poorly characterised and understood compared to vertebrate biodiversity. However, in Tanzania a study has identified butterfly species that could be considered Miombo woodland specialists (Jew et al., 2015). In addition, unlike elsewhere, most honeybees in Africa are still wild nesting (Requier et al., 2019) and, as they are cavity nesters, trees would be necessary to maintain honeybee colonies. In Malawi, farmers may provide honeybees with nesting opportunities by constructing traditional beehives (Figure 1.4), but these are passively colonised by nest-seeking colonies, not actively inoculated. As well as providing source habitats for biodiversity, the Miombo woodlands themselves are important resources for the rural poor. Direct harvesting or use of biological products, such as fuel wood, wild fruits and mushrooms, bushmeat, honey, grazing of livestock, and medicinal plants, are all important supplements to the livelihoods and food security of rural peoples, particularly in times of hardship (Gumbo et al., 2018). However, this also leads to over-exploitation of these resources (Syampungani et al., 2009), threatening the biodiversity of Miombo woodlands as well as their ability to sustain these resources in the long term.

Figure 1.4: Typical traditionally manufactured beehive on a smallholder farm in Mzimba district, Malawi.

In contrast to input-focussed agricultural extension programmes, various NGOs, including partner NGO Soils, Food and Healthy Communities (SFHC) have successfully promoted and implemented agroecological practices in smallholder communities across Malawi. Agroecological practices such as crop diversification and legume residue management have shown to be successful in improving food security in Malawian households (Madsen et al., 2021). Additionally, previous participatory research with Malawian farmers in our study region also identified research questions on insect pests and how to encourage natural enemies to manage them (Enloe et al., 2021), demonstrating an interest in agroecology by farmers. Therefore, our study region in northern Malawi provides the opportunity to study both the effects of landscape-scale semi-natural habitat cover and agroecology on biodiversity and ecosystem services in smallholder communities.

1.5 The FARMS4Biodiversity project

Building on the work of previous projects investigating the socio-economic outcomes of agroecological practices on Malawian households, the FARMS4biodiversity (Farmer-led Agroecological Research in Malawi using Scenarios for Biodiversity and Ecosystem Services) project aimed to understand the outcomes of land-use change and agroecological practices on biodiversity and ecosystem services. The project had four major work packages. This thesis is part of work package 1, that aimed to investigate scenarios of biodiversity and ecosystem services. The second work package aimed to investigate the community social dynamics that influence farmer practices. The third work package aimed to test how participatory scenario planning can enhance community resilience and biodiversity under different land-use change scenarios. Finally, work package 4 aimed to engage various stakeholders from government, NGOs, local farmers, and traditional leaders in Multi-Actor Platform (MAP) meetings to discuss and build dialogue and solutions. Essential to the project was the inclusion of trained farmer-researchers from the local communities who co-designed the research, assisted in the collection of data, and co-authored the publications generated within the project (Kpienbaareh et al., 2022a).

1.6 Study system and research question

This thesis aimed to characterise the effects of landscape-scale habitat conversion (all chapters), local habitat type (chapter 5), agroecological practices (chapters 2, 3 and 5) and crop-type (chapter 2) on functional biodiversity and associated ecosystem services on crops important to household food security in Malawi. Though chapter 2 also investigated pest control taxa and soil bacterial diversity, and chapters 3 and 4 also investigated the effects of pest pressure, the thesis has a special focus on pollinators (all chapters) and pollination services (chapters 2, 3 and 4).

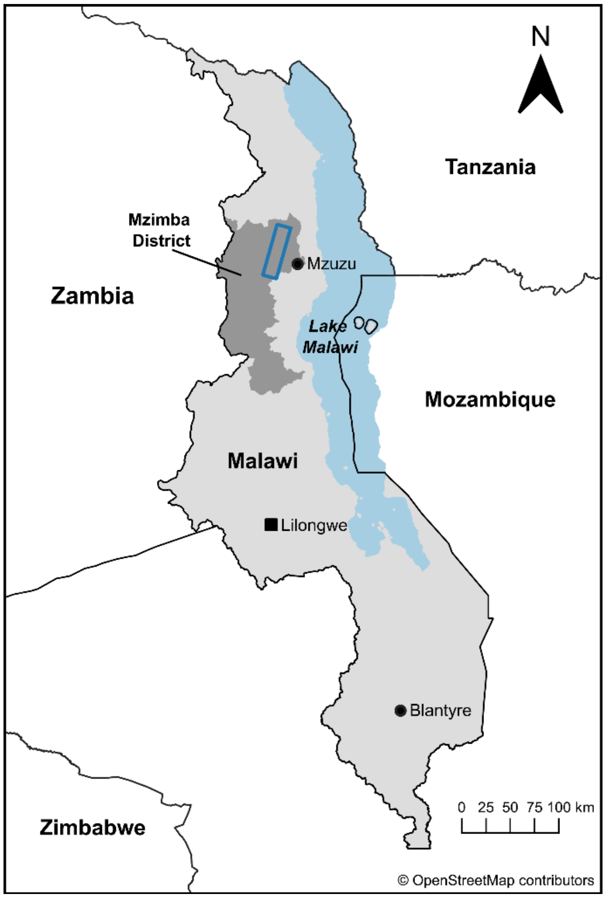
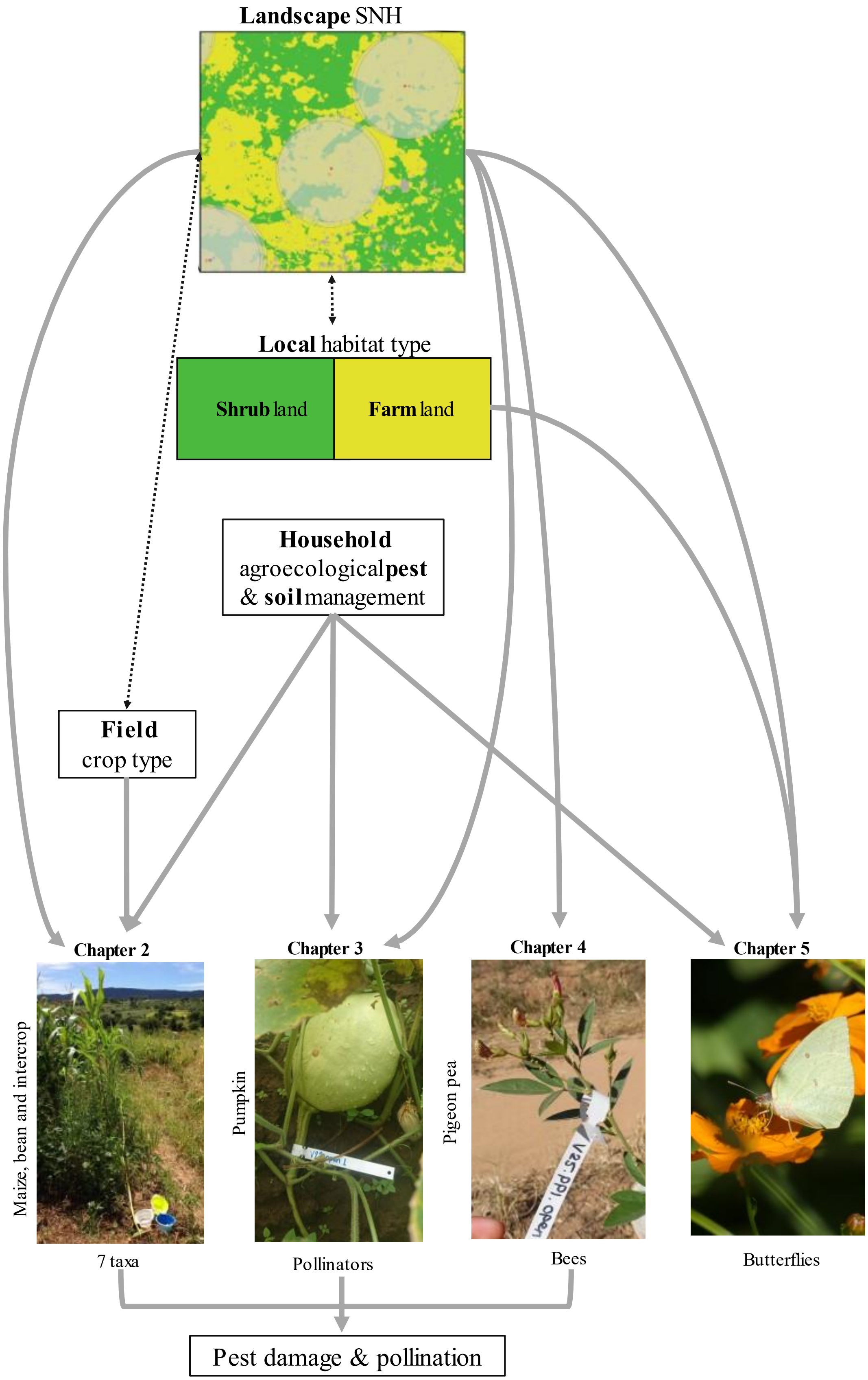


Figure 1.5: Map of Malawi. The study location is indicated by the blue rectangle.

Within our study area in Mzimba district, northern Malawi (Figure 1.5), we selected up to 24 rural villages per chapter/study in which to perform our data collection, which varied in the proportion of semi-natural habitat in the surrounding landscape. In our context, we defined semi-natural habitat as unmanaged (though generally unprotected), naturally occurring grasslands, shrublands and forests. This habitat in our study region contained vegetation typical for the Miombo woodland ecoregion described earlier (Ribeiro et al., 2020), though heavily impacted by the day-to-day activities of local communities.


Landscape SNH
Local habitat type
Shrub land
Farm land
Household
agroecological **pest**
& **soil** management
Field
crop type
Chapter 2
Chapter 3
Chapter 4
Chapter 5
Maize, bean and intercrop
Pumpkin
Pigeon pea
7 taxa
Pollinators
Bees
Butterflies
Pest damage & pollination

(Previous page) Figure 1.6: Conceptual overview showing the main research questions. Drivers decrease in scale from the top of the page downward. Bold arrows indicate direct effects, dashed arrows indicate potential interactions between landscape and local drivers.

The study region is located within the seasonal tropics, with a distinct rainy season from December to April, which coincides with the main growing season and is also the peak of seasonal abundance of insects (Schmitt et al., 2021). The bulk of data collection, therefore, occurred between February and June of 2019 and between December 2019 and April 2020. Major crops grown in the study region are tobacco (the main cash crop) and maize (the main staple), though legumes such as soy and field beans, and vegetable crops such as pumpkin are also commonly grown. Households participating in the studies varied in the implementation of agroecological pest- and soil management practices, which allowed us to investigate the effect of these two groups of practices on biodiversity (chapters 2, 3, and 5) and ecosystem services (chapters 2 and 3). In chapter 3, we investigated the effect of an individual agroecological pest management practice and the number of agroecological soil management practices. We collected data on a variety of crops important for household food security in our region, such as maize and beans (chapter 2), pumpkin (chapter 3) and pigeon pea (chapter 4). To collect biodiversity data, we used a variety of methods, such as direct observations (of birds, chapter 2), pitfall and pan traps (chapter 2), DNA extraction (of soil bacteria, chapter 2) and transect walks for pollinators (chapters 3, 4 and 5) (Figure 1.6). With this information, we attempted to answer the central research question of my thesis:

How does land-use change (semi-natural habitat cover in the landscape) and local agroecological practices affect biodiversity and ecosystem services on smallholder farms?

Agricultural biodiversity: smallholder farms can support a wide range of biodiversity, many who perform ecosystem services to crops. Pictured here are all animals observed by the author on smallholder farms in Malawi. Clockwise, starting at the top left: a variable sunbird (*Cynnyris venustus*) perched on top of sorghum. A carabid (*Orthotrichus* sp.) hunting at night in a casava field. Microscope photograph of a worker ant (*Tetramorium weitzeckeri*) collected in a pitfall trap from a bean field. A large carpenter bee (*Xylocopa* sp.) robbing nectar from an herb. Wasp from the *Thynnidae* family, a parasitoid of beetle larvae. A venomous nocturnal hunter, this spider from the *Ctenidae* family was observed hunting on a path between smallholder fields.

Chapter 2

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

Abstract

1. In the tropical Global South, smallholder farming characterizes some of the world's most biodiverse landscapes. These landscapes are changing rapidly with unknown effects on functional biodiversity and ecosystem services. Agroecology as a pathway to sustainable agriculture has been proposed and implemented in sub-Saharan Africa, but the effects of agricultural practices in smallholder agriculture on functional biodiversity and ecosystem services are understudied.

2. We selected 24 villages situated in landscapes with varying semi-natural habitat (SNH) cover in Malawi. In each village, we assessed functional biodiversity and ecosystem services in relation to crop type, SNH cover and the diversification of agroecological pest management (APM) and agroecological soil management (ASM) on three smallholder farm fields (maize monoculture, maize-bean intercrop, and bean monoculture) located along gradients APM and ASM.

3. Densities of spiders and parasitoids, carabid richness and Shannon diversity of soil bacteria were higher in bean monocultures compared to maize monocultures, especially in landscapes with low SNH. Increasing SNH increased bee richness and altered carabid assemblages. Diversification of ASM increased Shannon diversity of soil bacteria and altered carabid assemblage composition. Bean monocultures had lower pest damage than intercropped beans, possibly due to increased activity densities of natural enemies. APM was negatively related to bean seed set. In maize, APM was positively related to pest damage during growth, but not at harvest.

4. *Synthesis and application:* Our results suggest that maintaining biodiversity and ecosystem services on smallholder farms is not achievable with a "one size fits all" approach but should instead be adapted to the landscape context and the priorities of smallholders. SNH is important to maintain bee and carabid diversity, but legume cultivation beneficial to natural enemies could complement APM in landscapes with a lower cover of SNH. A diversification of ASM could lead to improved soil health and pest control whilst the effectiveness of APM needs to be re-evaluated.

2.1 Introduction

Smallholder agriculture supports many of the world's most food-insecure communities and contributes to over half of the global food supply (Steward et al., 2014; Herrero et al., 2017). Simultaneously, smallholder farms are within the world's most biodiverse landscapes (Newbold et al., 2015). To alleviate poverty and food insecurity in rural communities, there has been a push to intensify and specialize agriculture with input use (Snapp, 2020) - even though the evidence base for benefits is ambiguous (Rasmussen et al., 2018). Additionally, agricultural intensification and the conversion of (semi-)natural habitats (SNH) to agricultural habitats are main drivers of declines in biodiversity and ecosystem services (ES) supporting agricultural production (Rasmussen et al., 2018; IPBES, 2019). In temperate, large-scale agriculture, the effects of changing land-use and agricultural practices on biodiversity and ES are relatively well studied compared to tropical smallholder agriculture (Steward et al., 2014). The few studies available from tropical smallholder agricultural systems usually focus on commercially important crops such as coffee, vanilla, or cacao and not on crops important for household food security (Sasson, 2012; Vanlauwe et al., 2014). Additionally, declines in ES are burdening especially low-income farmers, since they lack the means to compensate lowered productivity through conventional agricultural inputs (Poppy et al., 2014). Therefore, food insecurity and biodiversity loss are highly interconnected problems (Chappell & LaValle, 2011).

Biodiversity and associated ES in crop fields are influenced by the composition of the surrounding landscape (Martin et al., 2019). Generally, beneficial biodiversity, such as pollinators and natural enemies react positively to increased landscape level SNH cover (Dainese et al., 2019), while crop pests respond inconsistently (Tamburini et al., 2020). Intercropping has the potential to counteract landscape simplification, by increasing habitat heterogeneity for beneficial biodiversity at the field level whilst maintaining productivity (Brandmeier et al., 2021). Increasing plant diversity in managed landscapes decreases pest abundance and damage and increases natural pest control (Wan et al., 2020). However, whether these benefits can be optimised by a combination of management at the field and the landscape level is unknown.

At the field level, biodiversity and related ES are directly impacted by the management choices of farmers. In tropical smallholder agriculture, agroecology, a more holistic and sustainable approach to agriculture that addresses both ecological and social aspects of food systems (Wezel et al., 2020), is very important. Agroecology benefits smallholders through, improved food security and nutrition (Bezner Kerr et al., 2021), and climate change adaptation (Snapp et al., 2021). We use the terms agroecological pest management (APM) and agroecological soil management (ASM) to refer to a range of traditional and agroecological practices aimed at reducing pest damage and improving soil health respectively (Table 2.S1). Co-benefits between social and agronomic effects with biodiversity and ES are assumed, but not empirically studied on a wide range of taxa.

Apart from the obvious differences in climate, environment, and agronomic practices compared to large-scale temperate agriculture, smallholders in Africa experience several unique challenges. First, Africa has older soils, which were not exposed to glaciation, and thus experienced longer periods of nutrient leaching and degradation compared to many temperate regions (Hengl et al., 2017). Continued degradation of soil quality is particularly severe in cropped lands, with real risks for agricultural productivity (Borrelli et al., 2017). Secondly, the invasive Fall Armyworm (*Spodoptera frugiperda*) poses additional problems as it is a major pest of several important African crops, including maize, the main staple in many African regions (Stokstad, 2017). Third, the use of synthetic agricultural inputs has increased over the last decades at the cost of human and environmental health. Particularly in sub-Saharan Africa, limited education on the correct use and access to personal protection equipment increase health risks for farmers and reduce potential pest-control benefits (Isgren & Andersson, 2021).

We aimed at investigating combined effects of increased crop diversity by intercropping maize with beans and landscape SNH cover, as well as diversification of APM and ASM across a range of indicators related to biodiversity and ES relevant to crop production in African smallholder agriculture. Our study area in Malawi illustrates many of the challenges faced by smallholder communities in sub-Saharan Africa and in the Global South. Northern Malawi lies in the transnational Miombo woodland ecoregion, a global biodiversity hotspot, which is highly threatened by habitat conversion and overexploitation despite its importance for ES provision (Gumbo et al., 2018; Ribeiro et al., 2020). In Malawi, SNH cover is steadily declining (Chirambo & Mitembe, 2014). With 51% of the population experiencing severe food insecurity (FAO et al., 2021), increasing crop yields and developing agriculture to alleviate poverty is a major priority of government and other stakeholders. Participatory research with farmers identified research questions about APM and how to foster natural enemies and pest control (Enloe et al., 2021), providing the opportunity to study the effects of these practices on functional biodiversity and ES. A research team of small-scale farmers, a non-profit farmer organization and scientists co-designed the study as part of a broader participatory research project. We aimed to test the following hypotheses:

1. We expect that intercropping, diversification of APM and ASM, and increased SNH have positive effects on activity density and diversity of functional taxa and modify species assemblages.
2. Crop species and SNH cover interactively affect pest control and pollination with intercropping and increased SNH positively affecting pest control but negatively affecting bean pollination. Additionally, more APM and ASM is expected to have positive outcomes for ES on fields.
3. (A) Fields with a higher activity density and diversity of natural enemies have reduced pest damage on crops, and (B) a higher bee activity density, bee diversity and soil bacterial diversity improve seed set on beans.

2.2 Methods

Study area and site selection

We conducted our field experiments from February to May 2019 in 24 villages in Mzimba District, in northern Malawi. The villages were distributed across independent gradients of SNH cover in the surrounding landscape (16-75 % semi-natural habitat in a 1 km radius surrounding the study sites: Figure 2.1), as well as diversification of agroecological pest management practices (APM) and agroecological soil management practices (ASM), defined by the number of practices used per hectare (Table 2.S1). Villages were distant from each other by at least 2 km (Figure 2.1). In our system, SNH are unmanaged, naturally occurring grasslands, shrublands and forests containing vegetation typical for the Miombo woodland ecoregion (Ribeiro et al., 2020). Though not actively managed, no protection is enforced in the SNH and they are therefore strongly impacted by day-to-day activities of local communities, such as livestock grazing or extraction of firewood and edible or medicinal plants (Gumbo et al., 2018).

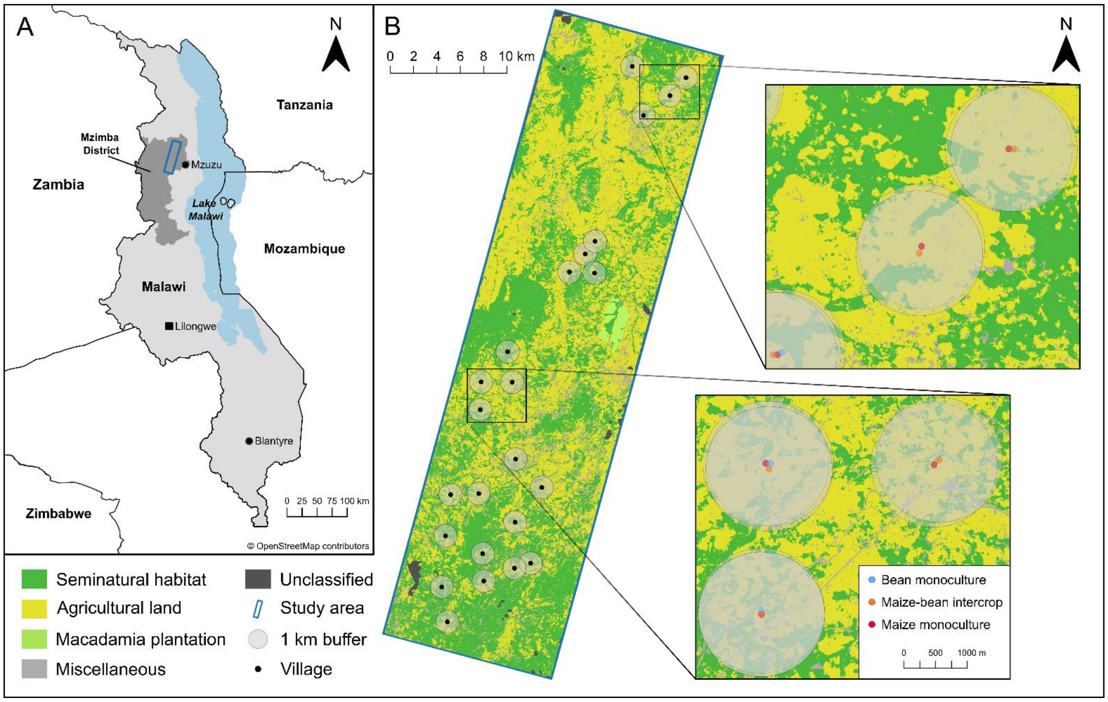


Figure 2.1: Map showing A) the study region within Malawi, and B) the distribution of study sites within the study region (by the location of maize fields). Insets show examples of the distribution of fields within the landscapes, with the 1km buffer around each field.

In each village we selected a maize monoculture and a maize-bean intercropped field (Figure 2.1). In 14 villages, we additionally selected a bean monoculture field, resulting in a total of 62 fields. Malawi is in the seasonal tropics and experiences a marked peak in rainfall from December until the end of March. All selected fields were sown between December 2018 and January 2019, at the onset of the first rains. Fields were solely rain-fed throughout the growing season. Field management activities, including soil preparation and sowing, were done by hand-hoe, as per usual practice in the region. We aimed for consistency between the fields across villages, but since we used smallholder farmers' existing fields, we could not fully control for planting densities and crop varieties (Table 2.S2). Field sizes ranged from 0.08 hectares to 0.80 hectares, with a mean of 0.30 hectares.

Data collection

In two rounds of data collection between the 22nd February and 26th April 2019, we recorded (i) richness and abundance of birds in each village (n=24), (ii) collected various arthropod taxa in all 62 fields, for which we analysed richness (carabids, ants, and bees) and activity densities (carabids, spiders, parasitoid wasps, and bees), and (iii) collected soil bacterial microbiome DNA. To quantify pest control services, we assessed (iv) leaf pest damage during growth of both maize and beans, while during harvest, we assessed (v) pest damage on maize cobs on 40 fields, and (vi) bean seed set on 14 fields. Additionally, we performed a (vii) farmer questionnaire on the diversification of APM and ASM practices of participating households, and (viii) quantified the cover of SNH in a 1 km radius surrounding the fields using satellite imagery and a GIS. For assessing ecosystem service potentials, birds were split into feeding guilds (insectivorous, omnivorous, frugivorous; Table S3). Detailed information of how individual data was collected is provided in Supporting Information 2.1.

Statistical analysis

We tested (i) the effect of crop type, SNH cover, APM and ASM on biodiversity, (ii) the effect crop type, SNH cover, APM and ASM on ecosystem services and (iii) the effect of biodiversity on ecosystem services using linear and linear mixed effects models. Detailed information on the statistical analyses is provided in Supporting Information 2.2. All analyses were performed in R version 4.0.5 (R Core Team, 2020).

2.3 Results

We observed 897 birds of 37 species (Table 2.S3) and collected 256 carabids of 71 (morpho-) species (Table 2.S4), 2460 spiders, 58 different ant species (Table 2.S5), 928 parasitoids and 296 bees of 54 species (Table 2.S6). DNA metabarcoding of the soil bacterial microbiome resulted in over 15,500 OTUs, though after data cleaning and low-abundance filtering, 515 taxa remained (Table 2.S7).

Effects on functional biodiversity

Increasing SNH increased carabid richness in maize and intercropped fields but not in beans (Figure 2.2A; Table 2.1; Table 2.S9). Bee activity densities did not change with crop type or SNH, but there bee richness increased with increasing SNH (Figure 2.2B; Table 2.1). Spider activity densities were highest in bean fields and lowest in maize, with intercropped fields being intermediate (Figure 2.2C; Table 2.1; Table 2.S9). Crop type and SNH interactively affected parasitoid activity densities, with parasitoids in bean fields showing a strong decline with increasing SNH. In maize and intercropped fields, the overall activity density of parasitoids was significantly lower than in beans and remained relatively constant across the SNH gradient (Figure 2.2D; Table 2.1; Table 2.S9). Crop type and SNH interactively affected the soil bacterial Shannon diversity: bacterial Shannon diversity declined with increasing SNH in bean and intercropped fields whereas it slightly increased in maize (Figure 2.2E; Table 2.S9). In addition, bacterial Shannon diversity increased with increased ASM (Figure 2.3A; Table 2.1). Increasing SNH (Figure 2.3B) and to a lesser extent increased diversification of ASM (Figure 2.3C; Table 2.S8) changed the composition of carabid assemblages. SNH, APM or ASM did not affect bird abundance, richness (Table 2.1) or assemblages (Table 2.S8). Carabid activity density, ant richness and assemblages, bee activity density and assemblages, as well as soil bacteria assemblages were not affected by crop type, SNH (or their interaction), APM or ASM (Table 2.1; Table 2.S8).

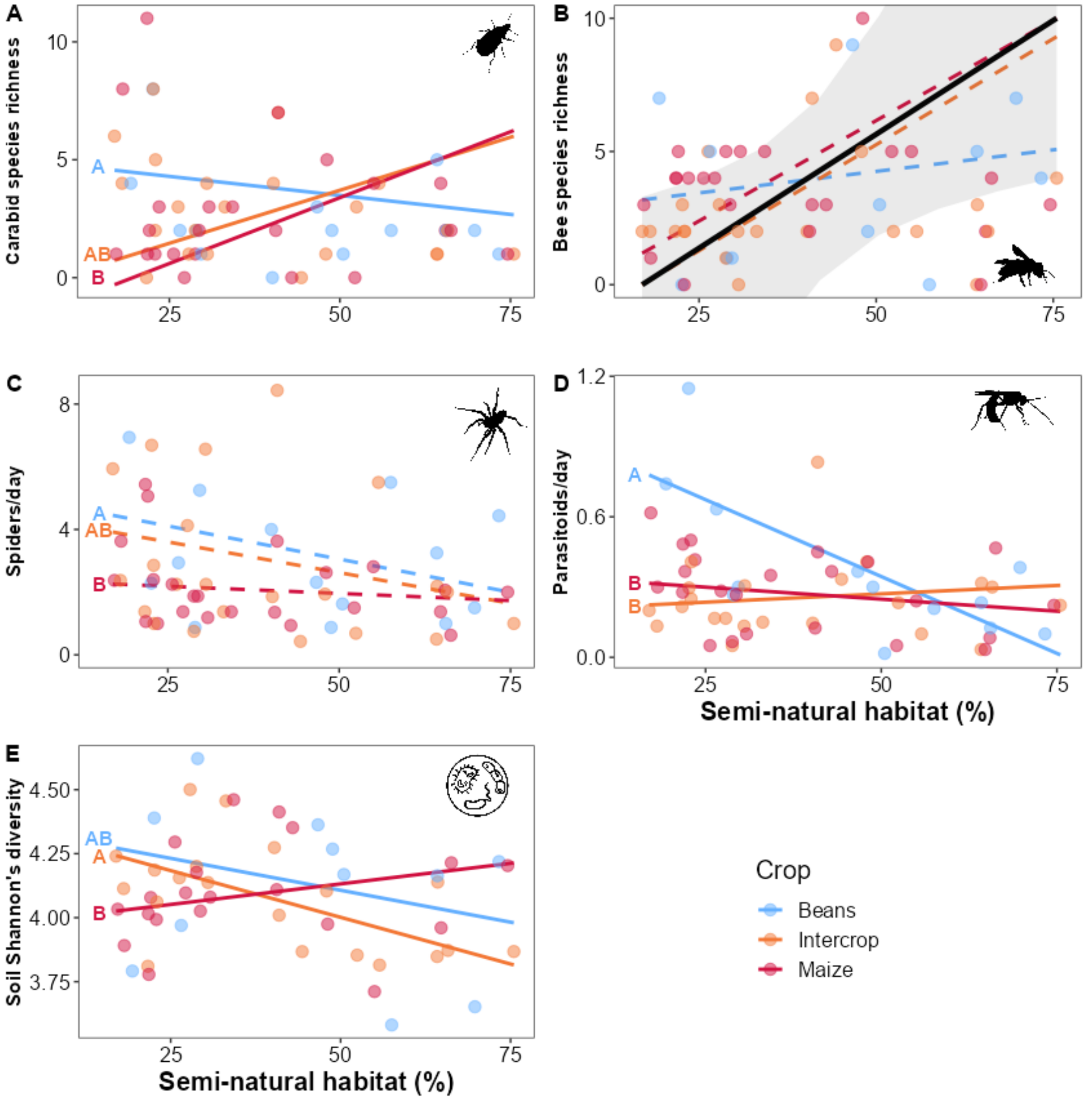


Figure 2.2: Activity density or diversity response to semi-natural habitat (SNH) cover by crop type and different taxa: A) carabid species richness, B) bee species richness, C) spider activity density, D) parasitoid activity density, E) soil bacterial Shannon diversity. Solid colored lines (as in B) represent a significant crop x SNH effect; dashed lines represent predictions of non-significant interactions. A solid black line represents a significant overall SNH effect (with the 95 % confidence interval). Wherever responses to SNH differed significantly between crop types, different letters on the left-hand side indicate these differences (as in C).

Table 2.1: Results from generalized linear Poisson model (GLM; for birds) and the linear mixed effects models (LMM; for all other responses) testing for the effects of crop type (Crop), semi-natural habitat (SNH), and agroecological pest management (APM) and agroecological soil management (ASM) on different responses related to functional biodiversity. DF_{num}: numerator degrees of freedom; DF_{den}: denominator degrees of freedom; R^2_m: marginal R^2; R^2_c: conditional R^2. P-values in bold indicate statistical significance, the number of asterisks (*) show the strength of responses.

Response	**Model type**	**Predictors**	**z-value/ F-value**	**p-value**	DF_{num}/DF_{den}	R^2_m/R^2_c
Bird counts	GLM with Poisson distribution	SNH	-0.16	0.875	1/21	0.07
		APM	1.33	0.185	1/20	
		ASM	0.82	0.413	1/19	
Bird species richness	GLM with Poisson distribution	SNH	0.66	0.513	1/21	0.06
		APM	0.43	0.670	1/20	
		ASM	-0.27	0.787	1/19	
Carabid activity density	LMM	Crop	0.05	0.955	2/36	0.08/0.34
		SNH	0.12	0.731	1/20	
		APM	1.45	0.235	1/41	
		ASM	0.03	0.871	1/44	
		Crop x SNH	1.66	0.204	2/35	
Carabid species richness	LMM	Crop	1.25	0.301	2/33	0.11/0.73
		SNH	1.74	0.199	1/24	
		APM	2.31	0.135	1/51	
		ASM	0.58	0.449	1/50	
		Crop x SNH	4.22	**0.023***	2/33	
Spider activity density	LMM	Crop	3.67	**0.036***	2/34	0.14/0.48
		SNH	1.64	0.215	1/20	
		APM	1.53	0.223	1/45	
		ASM	0.32	0.576	1/48	
		Crop x SNH	0.58	0.566	2/33	
Ant species richness	LMM	Crop	0.65	0.529	2/36	0.12/0.29
		SNH	3.98	**0.060**	1/20	
		APM	3.95	**0.054**	1/39	
		ASM	2.71	0.107	1/42	
		Crop x SNH	0.49	0.615	2/36	

Parasitoid activity density	LMM	Crop	7.30	**0.002****	2/34	0.32/0.52
		SNH	3.79	**0.066**	1/20	
		APM	3.36	**0.074**	1/43	
		ASM	1.35	0.252	1/45	
		Crop x SNH	8.39	**0.001****	2/34	
Bee activity density	LMM	Crop	0.21	0.809	2/38	0.10/0.15
		SNH	2.85	0.105	1/22	
		APM	0.94	0.338	1/39	
		ASM	2.82	0.101	1/41	
		Crop x SNH	0.06	0.946	2/38	
Bee species richness	LMM	Crop	0.45	0.641	2/38	0.19/0.53
		SNH	4.97	**0.036***	1/22	
		APM	0.04	0.848	1/40	
		ASM	0.68	0.415	1/41	
		Crop x SNH	1.16	0.324	2/38	
Soil bacterial Shannon's richness	LMM	Crop	0.68	0.512	2/29	0.17/0.50
		SNH	1.46	0.240	1/21	
		ASM	4.07	**0.049***	1/43	
		Crop x SNH	4.43	**0.021***	2/30	

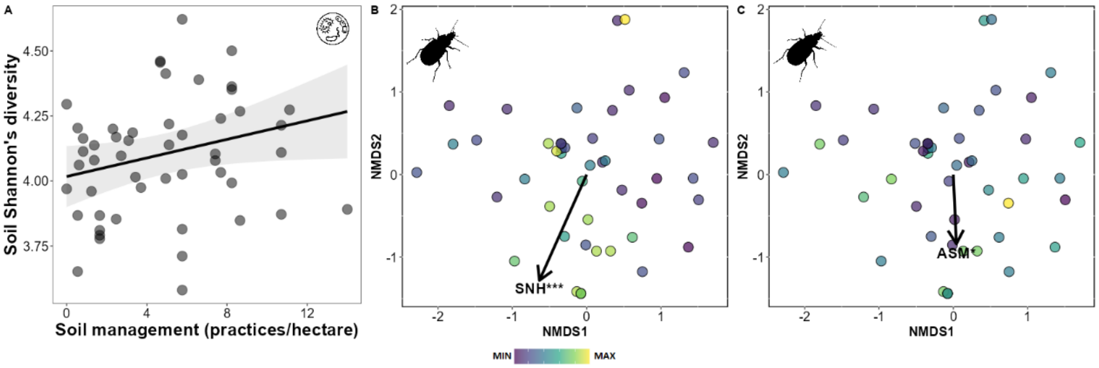


Figure 2.3: Relationship of A) soil bacterial microbiome Shannon diversity to increased diversification of agroecological soil management (ASM), B) carabid assemblages to changing cover of semi-natural habitat (SNH) in the landscape and C) carabid assemblages to the diversification of soil agroecological practices. Non-metric multidimensional scaling (NMDS) plots (plots B and C) indicate relatedness of carabid species assemblages. Vectors show direction of change, and the length of the vector is proportional to the strength of change.

Effects on ecosystem services

We found a positive relation between maize leaf damage and APM (Figure 2.4A), though this effect was not visible in cob damage at harvest (Table 2.2). Generally, the assessed ecosystem services did not differ significantly between monoculture or intercropped fields (Table 2.2), except for bean leaf damage, which was reduced in bean monoculture fields (Figure 2.4B). Increasing APM (Figure 2.4C) and SNH (Figure 2.4D) negatively affected bean seed set, both resulting in a decrease of approximately 0.75 beans per pod per 25% SNH increase. ASM generally did not affect the ecosystem services assessed (Table 2.2).

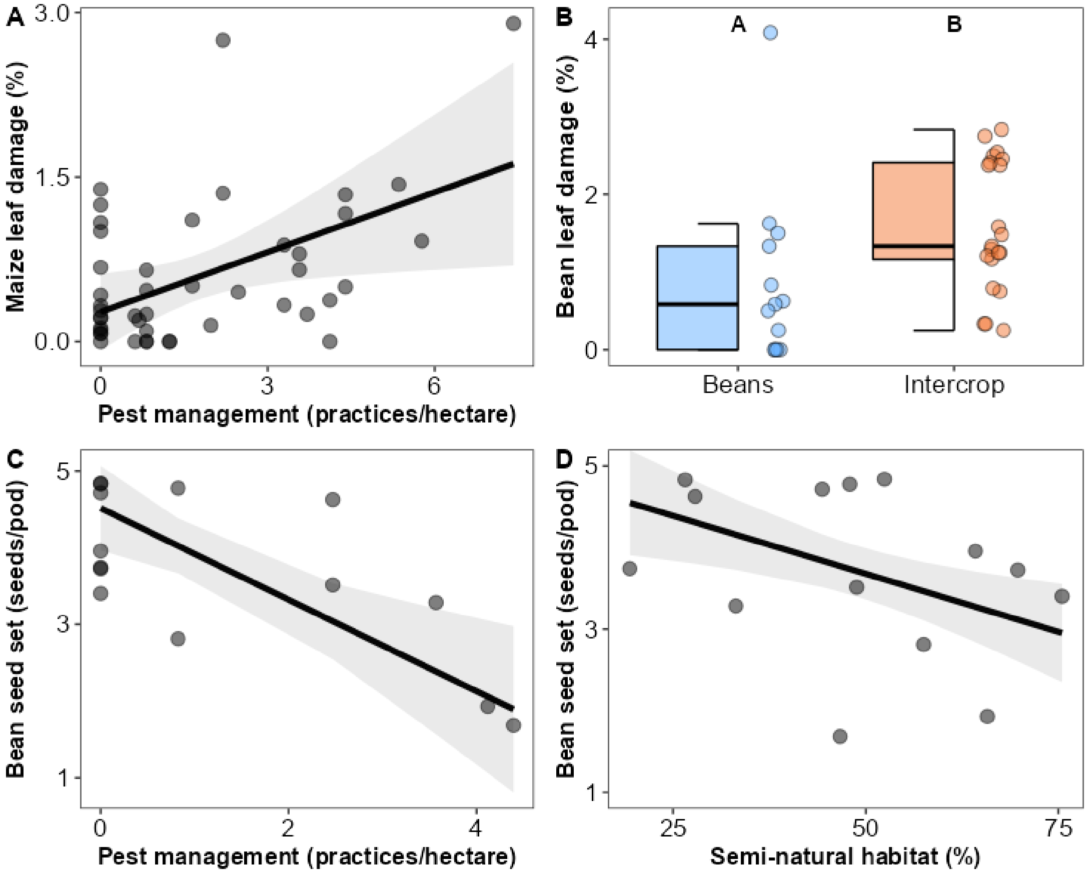


Figure 2.4: Relationship of A) maize leaf damage to pest management practices, B) bean leaf damage to crop type, and bean seed set to C) pest management practices, and D) semi-natural habitat.

Table 2.2: Results of the linear models (LM; in the case of bean seed set) and the linear mixed effects models (LMM; all other responses) testing for the effects of crop type (Crop), semi-natural habitat (SNH), and agroecological pest management (APM) and agroecological soil management (ASM) on different responses related to ecosystem services. DF_{num}: numerator degrees of freedom; DF_{den}: denominator degrees of freedom; R^2_m: marginal R^2; R^2_c: conditional R^2. P-values in bold indicate statistical significance, the number of asterisks (*) show the strength of responses.

Response	Model type	Predictors	F-value	p-value	DF_{num}/DF_{den}	R^2_m/ R^2_c
Maize leaf damage	LMM	Crop	2.62	0.120	1/22	0.31/0.53
		SNH	0.21	0.654	1/20	
		APM	7.72	**0.009****	1/33	
		ASM	2.85	0.100	1/25	
		Crop x SNH	0.84	0.369	1/20	
Maize cob damage	LMM	Crop	0.69	0.416	1/19	0.14/0.18
		SNH	1.14	0.303	1/16	
		APM	1.70	0.208	1/18	
		ASM	0.78	0.389	1/17	
		Crop x SNH	1.04	0.323	1/17	
Bean leaf damage	LMM	Crop	10.60	**0.004****	1/20	0.24/0.32
		SNH	0.05	0.832	1/19	
		APM	0.00	0.978	1/26	
		ASM	0.04	0.847	1/27	
		Crop x SNH	0.70	0.413	1/19	
Bean seed set	LM	Crop	3.10	0.116	1	0.69/0.81
		SNH	5.90	**0.041***	1	
		APM	22.04	**0.001****	1	
		ASM	0.85	0.422	1	
		Crop x SNH	2.43	0.158	1	

2.3.3 Effects of biodiversity on ecosystem services

Activity densities of natural enemies, insectivorous birds, carabids, and parasitoids did not affect damage on maize leaves, maize cobs or bean leaves. Carabid richness was related positively with maize leaf damage, but not with maize cob damage (Figure 2.S2). We found no effects of insectivorous birds or ant richness on damage of maize leaves, maize cobs, or bean leaves. Bee activity density, richness or soil bacteria Shannon richness did not affect bean seed set (Table 2.3).

Table 2.3: Results of the linear models (LM; in the case of bean seed set) and the linear mixed effects models (LMM; all other responses) of measured biodiversity on ecosystem services. DF_{num}: numerator degrees of freedom; DF_{den}: denominator degrees of freedom; R^2_m: marginal R^2; R^2_c: conditional R^2. P-values in bold indicate statistical significance, the number of asterisks (*) show the strength of responses.

Response	Model type	Predictors	F-value	p-value	DF_{num}/DF_{den}	R^2_m/ R^2_c
Maize leaf damage	LMM	Carabid activity density	1.66	0.204	1/41	0.04/0.27
		Spider activity density	0.03	0.866	1/41	
		Parasitoid activity density	0.07	0.786	1/40	
		Insectivorous bird abundance	0.00	0.982	1/22	
Maize leaf damage	LMM	Carabid species richness	4.32	**0.044***	1/41	0.09/0.33
		Ant species richness	0.17	0.682	1/44	
		Insectivorous bird species richness	0.23	0.638	1/22	
Maize cob damage	LMM	Carabid activity density	0.48	0.496	1/32	0.05/0.17
		Spider activity density	1.81	0.188	1/32	
		Parasitoid activity density	0.07	0.794	1/31	
		Insectivorous bird abundance	0.58	0.576	1/18	
Maize cob damage	LMM	Carabid species richness	0.15	0.701	1/29	0.01/0.23
		Ant species richness	0.29	0.592	1/33	
		Insectivorous bird species richness	0.00	0.970	1/19	

Bean leaf damage	LMM	Carabid activity density	2.34	0.136	1/30	0.11/0.11
		Spider activity density	0.49	0.490	1/30	
		Parasitoid activity density	2.19	0.150	1/30	
		Insectivorous bird abundance	0.11	0.737	1/30	
Bean leaf damage	LMM	Carabid species richness	0.48	0.492	1/32	0.02/0.02
		Ant species richness	0.02	0.882	1/32	
		Insectivorous bird species richness	0.43	0.518	1/32	
Bean seed set	LM	Bee activity density	0.15	0.704	1	0.02
		Bee species richness	0.05	0.826	1	
		Soil bacterial richness	0.01	0.937	1	

2.4 Discussion

Although we expected intercropping, semi-natural habitat (SNH) and agroecological practices to affect functional biodiversity and ecosystem services (ES), our results show that the responses are not uniform across different taxa and ES. Consequently, maintaining functional biodiversity and ES on smallholder farms does not have a “one-size fits all” solution but depends on landscape context, crop type and management practices. Though more challenging for making broad recommendations, adapting practices to suit a particular agroecosystem and socio-cultural context is central to agroecological approaches, which are guided by adaptive principles rather than recipes for management (Rosset & Altieri, 2017).

Effects on functional biodiversity

Spider and parasitoid activity densities and carabid richness were higher in bean monoculture fields than in maize or intercropped fields. This is surprising, since in other systems, intercropping has been shown to increase insect predator abundance and richness (Wan et al., 2020). Our results indicate that rather than a monoculture in and of itself, in our system it is maize cultivation in general that seems to be negatively influencing natural enemy abundance and richness. Maize is an input-intensive crop compared to legumes (Norris et al., 2016), even in our relatively unmechanized study system. Specifically, maize is a priority crop for farmers, and often the focus of their labour and available chemical inputs. A subsidy program by the Malawian government for fertilizer has increased the fertiliser input for maize in our study area (Burke, Jayne & Snapp, 2022), despite high fertiliser use being environmentally unsustainable and not providing enduring maize yield benefits to smallholder farmers in Malawi (Ricker-Gilbert & Jayne, 2017).

Crop-type and SNH interactively shaped parasitoid activity density, carabid richness and soil bacterial richness - the relative benefits for biodiversity of bean cultivation compared to maize was much higher in areas with little surrounding SNH. Since farmers have little individual influence on the SNH surrounding their fields, our results suggest that farmers in landscapes with little SNH could maintain or even increase functional biodiversity on their fields by growing grain legumes. In contrast with our expectations, parasitoid activity densities decreased with increasing SNH. The presence of flowering beans in a maize-dominated landscape could provide nectar as a food source as well as pests as hosts for reproduction, concentrating parasitoids there, possibly benefiting parasitism rates of these pests (Damien et al., 2017). For carabids in a maize-dominated agricultural landscape, certain species could benefit from alternative microhabitats or pest species provided by bean fields. Additionally, both intercropped and maize monoculture fields had higher soil bacterial diversity in low SNH landscapes, but not in landscapes high in SNH. However, the causative direction of these differences, with soil properties affecting soil bacteria or vice versa, may not always be clear and require more research (Schmidt et al., 2019).

Increasing SNH increased bee richness, but not abundance, across the three crop types, consistent with other studies showing that SNH is important for maintaining bee communities (Kennedy et al., 2013). This finding is important, because bee richness, more so than abundance, is a driver of pollination services (Garibaldi et al., 2016; Dainese et al., 2019). In contrast, another study in our study system found that bees, especially honeybees, are more abundant in landscapes high in agriculture on a legume crop flowering in the dry season - in other words, a concentration effect (Vogel et al., 2021). In our study only 6% of captured bees were honeybees, and our study was performed in the wet season, when tropical insects are at the peak of their diversity and flower resources are less limiting (Schmitt et al., 2021). In the same study region, increases in richness with increasing SNH cover were observed in butterflies (Vogel et al., *under review*), further indicating that maintaining SNH is crucial to maintain pollinator diversity.

Carabid assemblages showed a significant turnover with increasing SNH, suggesting that as SNH is converted, certain species are being filtered out and replaced by others. Assuming this change is unidirectional (i.e. SNH is converted to agriculture, but not the other way around) this means that to conserve all species found across a wider landscape SNH should be maintained. From a functional perspective, turnover of species with landscape change is significant because species differ in their individual traits, such as body-size or diet preferences which can mediate associated pest control services (Perez-Alvarez et al., 2021), suggesting that even if overall activity densities or richness of predators do not change, landscape changes may still have consequences for functional biodiversity and the delivery of ecosystem services.

Overall, there was little effect of agroecological practices on arthropods, except for carabid assemblages which changed with the increasing implementation of ASM. The number and intensity of soil disturbances can be an important factor distinguishing carabid assemblages (Pisani Gareau, Voortman & Barbercheck, 2020). Changes in carabid assemblages can also change associated pest control services (Perez-Alvarez et al., 2021), but further investigation is necessary to understand if the introduced soil disturbance by ASM results in any meaningful change in pest-control outcomes.

Soil bacterial diversity increased with the increased diversification of soil agroecological practices. Soil management affects soil biodiversity (Schmidt et al., 2019), and diverse cropping systems affect the function of soil microbiota (Song et al., 2007). Biodiverse soils often perform better ecosystem functioning and are more resistant to stress with changing environmental conditions, for example with climate change (Bender, Wagg & van der Heijden, 2016). This quality is especially important in sub-Saharan Africa, as it is one of most vulnerable regions on the planet to impacts of climate change (Serdeczny et al., 2017). Soil-associated practices were shown to benefit smallholder farms as, for example, including soil amendments such as compost increased dietary diversity (Bezner Kerr et al., 2019) and farmers who included crop residues in their soil management regime were almost three times more likely to be food secure (Madsen et al., 2021). Our findings suggest that social and nutritional outcomes might be, in part, mediated by improved functioning of soils in which ASM is more intensively practiced.

Effects on ecosystem services

There was less bean leaf damage in bean monoculture than in maize-bean intercropped fields, in contrast with other systems where mixtures experience less herbivory than monocultures (Wan et al., 2020). However, other studies show the importance of legume cultivation for providing ES and other benefits to Malawian smallholder farmers (Snapp et al., 2010; Mhango, Snapp & Phiri, 2013). Trade-offs occurred for beans and maize damage in intercrops, where the bean plants seem to be disadvantaged in mixtures, possibly linked to lower parasitoid and spider activity, whereas maize plants received similar levels of damage compared to monocultures. Interestingly, increased bean leaf damage in mixtures did not affect seed set, which was roughly the same. However, we saw a decrease in bean seed set with increasing landscape SNH cover. Though no direct relationship was found, it could be that in low SNH areas, increased soil bacterial diversity, better soils, and natural enemy presence in these fields could have contributed to improved plant performance.

APM is proposed as a low-cost, culturally appropriate method of managing the invasive fall armyworm in smallholder farms (Harrison et al., 2019). Surprisingly, pest management was positively associated with maize leaf damage, suggesting that APM failed in decreasing pest damage. However, it is likely that farmers who observed a lot of pest damage performed a larger variety of APM on their fields. Additionally, we found a positive relation between carabid richness and maize leaf damage, indicating that carabids were attracted by increased prey availability. At harvest, there was no effect of APM or carabid richness on cob damage, which is arguably more important and indicates that both APM and carabid richness may have led to effective pest control. In contrast, we see a decrease in seed set of almost three seeds per pod in bean fields with the highest diversity of APM compared to fields with no APM. Possibly, practices aimed at deterring pests also deterred pollinators. The adoption of these practices should be tailored to the crop priorities of the farmer to avoid such trade-offs.

2.5 Conclusions

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

First, we show the importance of maintaining SNH for carabids and bee diversity. Therefore, we encourage stakeholders to increase efforts to maintain the quantity and quality of remaining SNH to conserve biodiversity and the ecosystem services they provide. Sustainable use of the remaining Miombo woodlands should maintain biodiversity as well as resources and ecosystem services essential for the livelihoods of the smallholders (Gumbo et al., 2018).

Second, we find that legume cultivation in low (<~50 %) SNH landscapes benefited pest control taxa, leaf damage and eventually seed set. In a very practical sense, this means that bean cultivation in these areas improves pest control, resulting in higher yields for farmers. As co-benefits, legumes are an important addition to the nutrient-poor Malawian diet (Kamanga et al., 2014), and their cultivation improves soil quality (Mhango, Snapp & Phiri, 2013). Therefore, increased legume cultivation in these landscapes should be encouraged in farmer outreach projects.

Third, we show that diversification of management creates diverse soil bacterial and carabid communities. As diversification of agroecological soil management practices also provides important benefits to soil health and social outcomes (Bezner Kerr et al., 2021), farmers should be encouraged to implement, diversify, and experiment with ASM on their farms as a low-cost alternative to synthetic fertilizers.

Finally, we found limited damage-reducing success of APM, but also reduced bean seed set. Farmers thus need to mind trade-offs and to adapt the implementation of APM to the crop they prioritize. Informed decisions, based on a better ecological understanding of the complex nature of pest and natural enemy dynamics, of which (group of) practices should be used in which contexts, can help farmers focus their labour where it is most important.

Overall, we suggest that an interactive implementation of agroecological practices such as crop diversification with legumes, soil agroecology and the conservation of the remaining semi-natural habitats is important for maintaining biodiversity and ecosystem services on smallholder farms and foster sustainable development of smallholder agriculture in maize-based tropical agroecosystems in sub-Saharan Africa.

Supplementary material 2

Supporting information 2.1:

i. Bird surveys

Bird surveys were conducted using point counts in two rounds of observations for each village (Table 2.S2). The first round of observations was performed when crops were still growing vegetatively. During the second round of observations crops were starting to produce cobs (in the case of maize) and pods (in the case of beans). The second round ended close to harvest time. The same observer performed all bird surveys. In each village, the observer stood for 20 minutes in a central spot between the selected fields where it was possible to observe birds in all directions. Both visual and auditory bird observations were recorded during the 20 minutes. The number of birds observed as well as their species was recorded. Sinclair and Ryan's "Birds of Africa: South of the Sahara" was used to identify unfamiliar birds (Sinclair & Ryan, 2010).

ii. Arthropod sampling

As with the bird surveys, arthropod sampling was conducted in two rounds for both flowering-visiting insects and ground-dwelling arthropods (Table 2.S2). To collect flower-visiting insects, we placed five clusters of yellow, blue, and white pan traps (15 individual traps in total) on an appropriate field edge. We considered a field edge appropriate if it had no woody vegetation overhanging the field edge, and the remaining grassy vegetation was relatively sparse and short (< 50 cm), so that flower-visiting insects could easily spot the traps. The length of the field edge was measured to place one cluster at the center and the other two at 5 m and 10 m on either side of the central cluster but also along the field edge (Figure 2.S1). Pan traps were filled with water mixed with a small amount of non-perfumed detergent to break the water tension and left out in the field for 48 hours. After two days, insects were collected and preserved in 70 % ethanol. In the lab, insects were sorted to order. Bees (Hymenoptera: Apiformes) were pinned, separated into (morpho)species and identified to (sub)genus using the keys in Michener (2007), and Eardley, Kuhlmann & Pauly (2010), and advice from a specialist. We distinguished parasitoid wasps from non-parasitoids and counted their abundance for each sample.

In parallel, ground-dwelling arthropods were collected using 20 pitfall traps in each field. Pitfall traps were arranged in 5 rows of 4 traps from the field edge towards the field center, perpendicular to the row of pan traps (Figure 2.S1). As with the pan traps, the pitfall traps were filled with water and a small amount of detergent. After 24 hours, collected arthropods were stored in 70 % ethanol and sorted to order. Specifically, we counted the abundance of true spiders (Araneae) and carabid beetles (Coleoptera: Carabidae) but omitted ants (Hymenoptera: Formicidae) because pitfall traps are not appropriate for assessing ant densities. Additionally, we identified carabids and ants to (sub)genus or (morpho)species. For carabid beetles, all specimens were mounted, and male genitals were extracted and embedded in 'Lompe-solution' (Lompe, 1989) to allow safe assignment of the specimens to (morpho-)species. As identification literature for African carabid beetles is scarce, we used original descriptions as well as species group revisions together with the old and rather outdated works on African Harpalinae (the single most abundant group in our survey) by Basilewsky (1950, 1951) for identifications. For many of our morphospecies, however, we refrained from giving species level IDs as these would be insecure and could lead to incorrect species records. For the ants, we mounted one specimen per morphospecies present in each trap and identified them to species using the keys in Fisher & Bolton, 2016 and Schmidt & Shattuck, 2014 for the Ponerinae ants specifically, as well as advice from a specialist.

iii. Soil bacterial microbiome sampling and metabarcoding

In each field, during the second round of trap-placing, we took five random subsamples of soil of the top 15 cm of soil using a 5 cm diameter metal soil borer. To preserve DNA for bacterial microbiome analysis, a small subsample of each mixed soil sample was taken in the field and placed in a 10 ml Eppendorf tube containing lysis beads and DNA/RNA shield buffer solution (Zymo Research). The samples were stored at 4°C until analysis.

Genomic DNA for bacteria was extracted using the ZymoBIOMICS™ 96 DNA Kit (Zymo Research) following the manufacturer's instructions. Library preparation and sequencing followed strictly the protocol of Kozich et al. for 16S rDNA (Kozich et al., 2013). As for bioinformatics, VSEARCH v2.15.1 (Rognes et al., 2016) was used to merge forward with corresponding reverse reads (maximum sequence differences of 10 bp), for quality filtering (Emax=1, no ambiguous base pairs), size filtering (between 200 bp and 300 bp), singleton exclusion and de-novo chimera filtering (Edgar & Flyvbjerg, 2015). Using the Unoise2 algorithm (Edgar, 2016b) sequences were denoised and dereplicated into amplicon sequence variants (ASVs). Taxonomic assignment of 16S rDNA sequences was conducted with the RDP v16 reference database with SINTAX using bootstrap levels of 0.8 (Edgar, 2016a), as implemented in VSEARCH. Sequences of each sample were then mapped back to ASVs to obtain taxa counts per sample. Reads identified as chloroplasts or mitochondria were removed.

Reads were transformed to relative abundances, and taxa with less than 0.1% community contribution per sample were removed. Two samples with less than 1500 reads after quality filtering were excluded from further analysis. Three samples were found to be contaminated with foreign material, and where therefore also omitted from analysis.

iv. Leaf damage assessment

We assessed pest damage for 20 plants of each crop in each field. Plants were randomly selected by marking every fifth plant in the central row and the two rows 10 meters from this central row, from the edge inwards, aiming for approximately 6-7 plants per row, until 20 plants were marked. The assessment was done twice, in parallel with the arthropod sampling and bird surveys, once when the crops where still vegetatively growing, and the second time closer to harvest time (Table 2.S2). For maize, we measured the height of the plants and counted the number of leaves (excluding the two bottom leaves) at each sampling time. For each leaf, we estimated herbivory damage through visual inspection according to four categories: < 5 %, 5-25 %, 26-50 % and > 50 %. For beans, the number of true leaves where counted (excluding the cotyledon). The bottom, middle and top leaves (three leaves in total, each containing three leaflets) where assessed for pest damage using the same categories as for maize.

v. Maize cob damage assessment

To assess damage of maize cobs, we revisited the fields at harvest from 18th of April to 25th of May 2019. At 8 fields, we missed the harvest, meaning we collected data on a total of 40 fields, 20 monocrop and 20 intercropped fields. To assess extent of cob damage, we selected 10 plants by taking every second plant used for the leaf damage assessment (as described above). For each cob from each of these plants, we categorized damage in the same categories as before.

vi. Bean seed set assessment

On 7 bean monoculture and 7 intercropped fields, we assessed the seed set of beans between the 2nd of April and the 3rd of May 2019. On each field, we selected 10 plants by taking every second plant used for the leaf damage assessment. For each of these plants, we counted the number of pods produced, and the total number of seeds produced by each plant. To obtain the average seed set per plant, we divided the total number of seeds by the number of pods produced.

vii. *Farmer surveys on agroecological practices*

To quantify the implementation of agroecological practices on and around the fields on which we collected data, we surveyed households participating in our study and neighbouring farms. Surveys were performed from March 8th to March 25th, 2020. One household on which we collected data declined to participate in the survey. Each household that participated in the survey answered questions, translated into their native language (chiTumbuka) concerning the implementation of various pest and soil management practices on the surveyed fields as well as up to 2 other farm fields. (Farmers declined to respond to more than 3 fields due to time constraints and so answered about their 3 largest fields). Pest management practices included: synthetic pesticides, botanical sprays, manual removal, use of ash/sand, and adjusting planting dates. Soil management practices included: intercropping with legumes, crop rotation with legumes, incorporation of legume residue into soil, use of compost or animal manure, agroforestry, pit planting, vetiver grass or other soil conservation methods (Table 2.S1).

For pest and soil management practices separately, we created an area-standardized index by summing the number of practices per field and dividing by field size (in hectares) to obtain the number of practices per hectare of each surveyed field. We then averaged this number over all three fields to obtain the mean number of pest and soil management practices per hectare for each household.

viii. *Quantifying semi-natural area in the landscape*

We used a synergetic remote sensing approach fusing optical (Sentinel-2 and PlanetScope) and radar (Sentinel-1) imagery to classify the land cover in our study region. This approach produced the best overall classification accuracy for a subset of our study area (Kpienbaareh et al., 2021). Following the steps outlined in this publication, four optical imagery fusion pairs, each paired with the combination of radar data from six different dates in the growing season all acquired between January and April 2020, were used to cover the extent of a 1 km radius around all the 62 fields in our study. All optical images used were selected to depict the study region as cloudless as possible. For each of our four fusion pair combinations, we ran a supervised random forest algorithm trained with land cover class data collected through extensive ground-truthing during the growing season of 2019/20 complemented with manually digitized land cover samples of easily discernible land cover classes (e.g. shrubland, water or settlement) via Google satellite images in QGIS 3.12 and Digital Globe images in ArcGIS Pro 2.7. If several classifications were available at a village, the best fit was selected based on overall accuracy and visual inspection of the extent of shrubland in comparison with a high-resolution satellite image. Any remaining gaps in the 1 km radius around the fields were either filled with values from other classifications or, if unavailable, were manually digitized. All land cover pixel values in the 1 km radius around the fields were extracted from the final 3 m resolution classifications using the R package ‘exactextractr’ (Baston, 2022). Resulting land cover class proportions of shrubland, grassland and forest were aggregated to semi-natural habitat (SNH) to be used in statistical analyses. At one village, there was a large overlap of the 1 km radius around fields with the 1 km radii of fields from two other villages. Thus, this village was excluded from any statistical analysis involving landscape.

Supporting information 2.2:

All models were tested for and met the assumptions of normality, 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 original model using the ‘ggeffect’ function from the ‘ggeffects’ package (Lüdecke, 2018).

i. Effect on functional biodiversity

Since our three continuous predictors - SNH proportion within the 1 km radius, the mean household pest management practices per hectare and the mean household soil management practices per hectare - were on different scales, we standardized these variables by z-scaling from -1 to 1 in all models. In all models, testing landscape and agroecological management (except for birds, where crop type was omitted, and soil Shannon’s diversity, where agroecological pest management was omitted), the independent variables used were crop-type (bean monoculture, intercrop, or maize monoculture) and SNH proportion with an interaction term between the two, and diversity of agroecological pest management practices per hectare and diversity of agroecological soil practices per hectare.

To determine how landscape composition and pest and soil management affected birds, we used general linear models with a Poisson distribution. As response variables, we used the sum of individual birds observed across the two observation times and the cumulative species richness in each village. Mean semi-natural habitat proportion, pest management and soil management at village level were used as predictors.

To test the effect of landscape and management on the activity densities of carabids, spiders, parasitoids and bees, we used linear mixed models using the ‘lmer’ function from the ‘lme4’ package (Bates et al., 2019). To calculate activity density, we divided the sum of all trapped individuals by the total number of trapping days (traps retrieved x 2 days). We used the abovementioned independent variables as fixed effects and village as a random intercept to account for the nested design of the study (Bates et al., 2019). Carabid activity density was square root transformed to improve normality. To test the effect of landscape and management on the species richness of carabids, ants, and bees, we used the same model as for activity density but with ‘days’ (total days retrieved traps were active) as an offset in the model to account for the effect of trap losses (and thus unequal sampling effort) on species richness.

We used the package ‘phyloseq’ to import soil bacterial microbiome data into R (McMurdie & Holmes, 2013). As a response variable, we calculated Shannon’s diversity of each soil sample with the relative abundances of the taxa using the package ‘vegan’ (Oksanen et al., 2020). We then used the same mixed model as described above but omitting diversity of agroecological pest management as a fixed effect.

If a dependent variable responded significantly to crop type, a categorical variable, we used the function ‘lsmeans’ from the ‘emmeans’ package to obtain pairwise comparisons between the three crop types (Lenth et al., 2021). If a dependent variable had a significant crop x SNH interaction, we used the ‘emtrends’ function (‘emmeans’ package) to assess differences in trends (i.e. direction of the effects for each crop type) along the SNH gradient per crop.

Apart from assessing activity densities and species richness, we also wanted to know if crop type, SNH proportion and pest- and soil agroecological practices affected species assemblages the various taxa. To assess the response of bird, carabid, ant, bee, and soil bacterial assemblages to the landscape variables, we used a PERMANOVA using the function ‘adonis’ from the ‘vegan’ package (Oksanen et al., 2020). For birds, carabids, bees, and soil bacteria we used Bray-Curtis distances on proportions per (morpho-)species to avoid total differences in densities affecting the results. For ants (presence-absence data), we calculated Jaccard distances. For birds, the PERMANOVA used SNH proportion, pest, and soil management as predictors. For the other taxa, crop was additionally included as a predictor as well as including the call ‘strata=village’ to account for the nested nature of the data. For both bees and carabids, we excluded sites where no individuals were recorded. Additionally, five sites were excluded from the carabid dataset that had no species overlap at all with any other sites. All PERMANOVAs were calculated with 999 permutations.

ii. *Effects on ecosystem services*

To assess the effect of landscape on bean leaf, maize leaf, and maize cob damage, we calculated the mean damage of all leaves or cobs on each plant. Then, we took the mean of all assessed plants per field, to obtain the mean leaf or cob damage per plant for each field. Again, we used mixed models with the aforementioned fixed effects and village as a random intercept. Bean leaf damage was log transformed and maize leaf damage was square root transformed to improve normality.

For bean seed set, we took the mean seed set of each field. Using a linear model, we used the same independent variables as described above. Mean seed set was squared to improve normality.

iii. *Effect of biodiversity on ecosystem services*

To test the response of activity densities on bean leaf, maize leaf, and maize cob damage, we used linear mixed models including z-scaled natural enemy densities (bird abundance of insectivorous bird species, carabid, spider, and parasitoid activity densities) as fixed effects and village as a random intercept. All crop damages were square root transformed to improve normality.

To test the effect of species richness on crop damage, we used linear mixed models including z-scaled natural enemy richness: insectivorous birds, carabid and ant species richness as fixed effects and village as random intercept.

To test the effects of bee activity density and species richness and bacterial diversity on bean seed set, we z-scaled these and used a linear regression model with these factors as fixed effects.

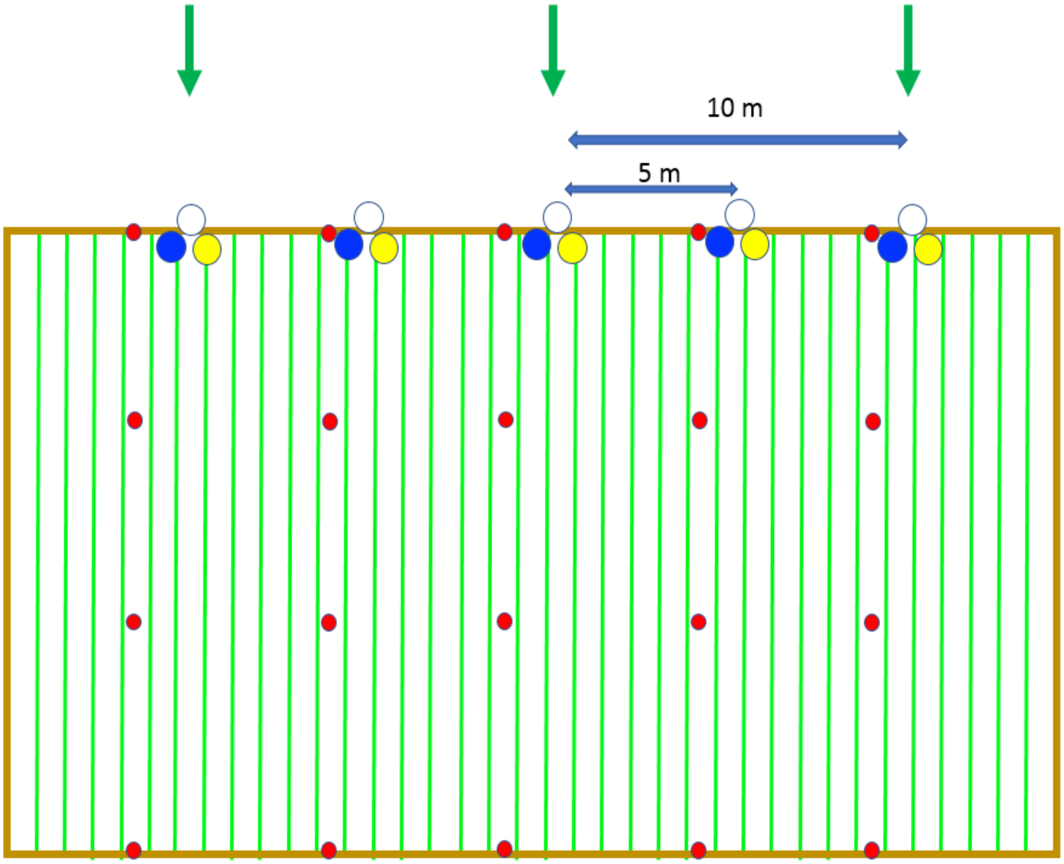


Figure 2.S1: Setup of the pan traps (represented by the yellow, white, and blue circles), pitfall traps (represented by red circles) and the rows used for crop damage assessment (green arrows) in each field.

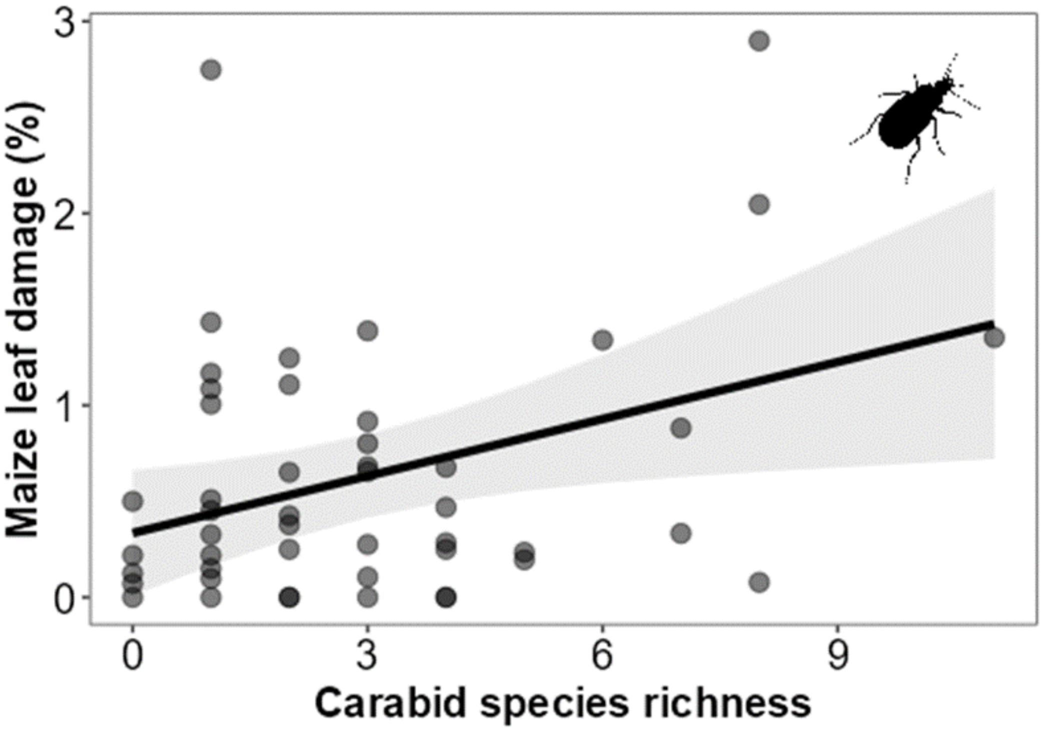


Figure 2.S2: Relationship of carabid species richness to maize leaf damage.

Table 2.S1: Agroecological practices reported by farmers, grouped by either pest- or soil-related agroecological practices.

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

Table 2.S2: Overview of the 62 fields included in the study, showing the crops grown and dates of data collection.

Village number	Cropping type	Bean variety	Bean planting density (plants/m^2)	Maize variety	Maize planting density (plants/m^2)	Date trap collection survey 1	Date trap collection survey 2	Date bean harvest	Date maize harvest
1	Beans mono	Local dwarf	1.25	*NA*	*NA*	06/03/2019	04/04/2019	04/04/2019	*NA*
	Intercrop	Local climbing	1.30	Hybrid	2.35	06/03/2019	04/04/2019	30/04/2019	30/04/2019
	Maize mono	*NA*	*NA*	Hybrid	3.00	06/03/2019	04/04/2019	*NA*	30/04/2019
2	Beans mono	Hybrid dwarf	1.45	*NA*	*NA*	07/03/2019	08/04/2019	08/04/2019	*NA*
	Intercrop	Local climbing	1.60	Hybrid	2.05	07/03/2019	08/04/2019	*Missed*	09/05/2019
	Maize mono	*NA*	*NA*	Hybrid	1.85	07/03/2019	08/04/2019	*NA*	09/05/2019
3	Beans mono	Unknown	Unknown	*NA*	*NA*	07/03/2019	18/04/2019	*Missed*	*NA*
	Intercrop	Local climbing	1.55	Hybrid	1.70	07/03/2019	18/04/2019	*Missed*	02/05/2019
	Maize mono	*NA*	*NA*	Hybrid	1.75	07/03/2019	18/04/2019	*NA*	02/05/2019
4	Beans mono	Hybrid dwarf	1.40	*NA*	*NA*	06/03/2019	04/04/2019	*Missed*	*NA*
	Intercrop	Local climbing	1.50	Hybrid	2.10	06/03/2019	04/04/2019	04/04/2019	30/04/2019
	Maize mono	*NA*	*NA*	Hybrid	17	06/03/2019	04/04/2019	*NA*	30/04/2019
5	Beans mono	Local climbing	1.20	*NA*	*NA*	13/03/2019	04/04/2019	*Missed*	*NA*
	Intercrop	Local climbing	2.25	Hybrid	1.90	13/03/2019	04/04/2019	01/05/2019	01/05/2019
	Maize mono	*NA*	*NA*	Local	2.30	13/03/2019	04/04/2019	*NA*	01/05/2019
6	Beans mono	Hybrid dwarf	2.05	*NA*	*NA*	25/03/2019	08/04/2019	08/04/2019	*NA*
	Intercrop	Local climbing	1.55	Hybrid	1.90	25/03/2019	08/04/2019	08/04/2019	02/05/2019
	Maize mono	*NA*	*NA*	Hybrid	1.60	25/03/2019	08/04/2019	*NA*	02/05/2019
7	Intercrop	Local climbing	2.00	Hybrid	1.75	25/03/2019	18/04/2019	*Missed*	02/05/2019
	Maize mono	*NA*	*NA*	Hybrid	1.90	25/03/2019	18/04/2019	*NA*	02/05/2019
8	Beans mono	Climbing variety of unknown origin	1.70	*NA*	*NA*	13/03/2019	08/04/2019	08/04/2019	*NA*

	Intercrop	Local climbing	2.10	Local	2.00	13/03/2019	08/04/2019	*Missed*	*Missed*
	Maize mono	*NA*	*NA*	Hybrid	1.50	13/03/2019	08/04/2019	*NA*	10/05/2019
9	Beans mono	Hybrid dwarf	1.55	*NA*	*NA*	27/02/2019	08/04/2019	08/04/2019	*NA*
	Intercrop	Local climbing	1.40	Hybrid	1.90	27/02/2019	08/04/2019	18/04/2019	02/05/2019
	Maize mono	*NA*	*NA*	Hybrid	2.70	27/02/2019	08/04/2019	*NA*	10/05/2019
10	Intercrop	Local climbing	1.60	Hybrid	2.10	28/03/2019	25/04/2019	25/04/2019	25/04/2019
	Maize mono	*NA*	*NA*	Hybrid	Unknown	28/03/2019	25/04/2019	*NA*	10/05/2019
11	Intercrop	Climbing variety of unknown origin	1.85	Hybrid	1.70	28/03/2019	25/04/2019	25/04/2019	25/04/2019
	Maize mono	*NA*	*NA*	Hybrid	2.10	28/03/2019	25/04/2019	*NA*	25/04/2019
12	Intercrop	Hybrid climbing	1.40	Hybrid	2.15	22/02/2019	18/04/2019	*Missed*	18/04/2019
	Maize mono	*NA*	*NA*	Hybrid	2.10	22/02/2019	18/04/2019	*NA*	18/04/2019
13	Intercrop	Climbing variety of unknown origin	1.00	Hybrid	1.70	19/03/2019	12/04/2019	12/04/2019	01/05/2019
	Maize mono	*NA*	*NA*	Hybrid	1.60	19/03/2019	12/04/2019	*NA*	01/05/2019
14	Beans mono	Local climbing	2.15	*NA*	*NA*	26/03/2019	12/04/2019	*Missed*	*NA*
	Intercrop	Local climbing	1.35	Local	1.90	26/03/2019	12/04/2019	*Missed*	*Missed*
	Maize mono	*NA*	*NA*	Hybrid	1.60	26/03/2019	12/04/2019	*NA*	06/05/2019
15	Beans mono	Local climbing	2.20	*NA*	*NA*	22/02/2019	12/04/2019	*Missed*	*NA*
	Intercrop	Hybrid dwarf	1.50	Local	3.90	22/02/2019	12/04/2019	*Missed*	06/05/2019
	Maize mono	*NA*	*NA*	Hybrid	1.70	22/02/2019	12/04/2019	*NA*	06/05/2019
16	Beans mono	Local climbing	1.20	*NA*	*NA*	22/02/2019	26/04/2019	*Missed*	*NA*
	Intercrop	Local climbing	1.15	Hybrid	2.10	22/02/2019	26/04/2019	*Missed*	26/04/2019
	Maize mono	*NA*	*NA*	Local	1.80	22/02/2019	26/04/2019	*NA*	26/04/2019

17	Intercrop	Local climbing	1.20	Hybrid	2.20	01/04/2019	26/04/2019	*Missed*	26/05/2019
	Maize mono	*NA*	*NA*	Hybrid	2.10	01/04/2019	26/04/2019	*Missed*	*Missed*
18	Beans mono	Hybrid dwarf	1.40	*NA*	*NA*	14/03/2019	01/04/2019	03/05/2019	*NA*
	Intercrop	Hybrid dwarf	1.70	Hybrid	2.20	14/03/2019	01/04/2019	03/05/2019	13/05/2019
	Maize mono	*NA*	*NA*	Local	1.50	14/03/2019	01/04/2019	*NA*	03/05/2019
19	Intercrop	Hybrid dwarf	1.20	Hybrid	1.54	14/03/2019	01/04/2019	*Missed*	13/05/2019
	Maize mono	*NA*	*NA*	Hybrid	1.50	14/03/2019	01/04/2019	*NA*	03/05/2019
20	Beans mono	Local climbing	1.20	*NA*	*NA*	23/03/2019	11/04/2019	*Missed*	*NA*
	Intercrop	Climbing variety of unknown origin	2.10	Hybrid	2.20	23/03/2019	11/04/2019	*Missed*	*Missed*
	Maize mono	*NA*	*NA*	Local	1.80	23/03/2019	11/04/2019	*NA*	03/05/2019
21	Intercrop	Climbing variety of unknown origin	1.45	Hybrid	2.40	20/03/2019	15/04/2019	*Missed*	15/05/2019
	Maize mono	*NA*	*NA*	Hybrid	1.50	10/03/2019	15/04/2019	*NA*	15/05/2019
22	Intercrop	Local climbing	1.80	Hybrid	2.20	19/03/2019	15/04/2019	*Missed*	15/05/2019
	Maize mono	*NA*	*NA*	Hybrid	1.90	19/03/2019	15/04/2019	*NA*	*Missed*
23	Intercrop	Local dwarf	1.55	Hybrid	2.15	20/03/2019	11/04/2019	*Missed*	03/05/2019
	Maize mono	*NA*	*NA*	Hybrid	1.65	20/03/2019	11/04/2019	*NA*	03/05/2019
24	Beans mono	Hybrid dwarf	2.50	*NA*	*NA*	01/04/2019	26/04/2019	26/04/2019	*NA*
	Intercrop	Climbing variety of unknown origin	2.35	Hybrid	1.70	01/04/2019	26/04/2019	*NA*	26/04/2019
	Maize mono	*NA*	*NA*	Hybrid	1.70	01/04/2019	26/04/2019	*NA*	03/05/2019

Table 2.S3: Bird species found throughout the study period across all villages.

Order	Family	Genus	Species	English name	Feeding guild
Apodiformes	Apodidae	*Apus*	*A. caffer*	White-rumped swift	Insectivore
Passeriformes	Platysteiridae	*Batis*	*B. capensis*	Cape batis	Insectivore
	Nectariniidae	*Chalcomitra*	*C. amethystine*	Amethyst sunbird	Insect- & nectivore
	Campephagidae	*Ceblepyris*	*C. pectoralis*	White-breasted cuckooshrike	Insectivore
	Corvidae	*Corvus*	*C. albus*	Pied crow	Omnivore
	Fringilidae	*Crithagra*	*C. sulphurata*	Brimstone canary	Insect- & granivore
	Dicruridae	*Dicrurus*	*D. adsimilis*	Fork-tailed drongo	Insectivore
	Ploceidae	*Euplectes*	*E. afer*	Yellow-crowned bishop	Insect- & granivore
			E. ardens	Red-collared widowbird	Grani- & nectivore
			E. diadematus	Fire-fronted bishop	Insect- & granivore
			E. orix	Southern red bishop	Insect- & granivore
		Ploceus	*P. cucullatus*	Village weaver	Insect- & granivore
	Estrildidae	*Hypargos*	*H. niveoguttatus*	Red-throated twinspot	Insect- & granivore
		Lagonosticta	*L. rubricata*	African firefinch	Insect- & granivore
		Spermestes	*S. cucullata*	Bronze mannikin	Granivore
			S. nigriceps	Red-backed mannikin	Granivore
		Uraeginthus	*U. angolensis*	Blue waxbill	Insectivore
	Sturnidae	*Lamprotornis*	*L. chalybaeus*	Greater blue-eared starling	Insect- & frugifore
	Laniidae	*Lanius*	*L. collaris*	Southern fiscal	Insect- & granivore
	Melaconotidae	*Melaconotus*	*M. blanchoti*	Grey-headed bushshrike	Insectivore
		Tchagra	*T. australis*	Brown-crowned tchagra	Insectivore
	Motacilidae	*Motacilla*	*M. aguimp*	African pied wagtail	Insect- & granivore
	Passeridae	*Passer*	*P. domesticus*	House sparrow	Granivore
	Cisticolidae	*Prinia*	*P. subflava*	Tawny-flanked prinia	Insectivore
	Pycnonotidae	*Pycnonotus*	*P. tricolor*	Dark-capped bulbul	Frugivore
	Monarchidae	*Terpsiphone*	*T. viridis*	African paradise flycatcher	Insectivore
	Zosteropidae	*Zosterops*	*Z. sengalensis*	Northern yellow white-eye	Insectivore

Pelecaniformes	Ardaidae	*Ardea*	*A. melanocephala*	Black-headed heron	Insect- & carnivore
Cuculiformes	Cuculidae	*Centropus*	*C. grilii*	Black coucal	Insectivore
			C. sengalensis	Senegal coucal	Insect- & carnivore
Accipitriformes	Accipitridae	*Circaetus*	*C. cinereus*	Brown snake eagle	Carnivore
		Melierax	*M. metabates*	Dark chanting goshawk	Carnivore
Coliiformes	Coliidae	*Colius*	*C. striatus*	Speckled mousebird	Grani- & grugivore
Piciformes	Picidae	*Dendropicos*	*D. fuscescens*	Cardinal woodpecker	Insectivore
			D. obsoletus	Brown-backed woodpecker	Insectivore
	Indicatoridae	*Indicator*	*I. indicator*	Greater honeyguide	Insectivore
Columbiformes	Columbidae	*Oena*	*O. capensis*	Namaqua dove	Granivore
		Streptopelia	*S. capicola*	Ring-necked dove	Insect- & granivore
			S. semitorquata	Red-eyed dove	Granivore

Table 2.S4: Carabid (morpho-)species found throughout the study period across all fields.

Subfamily	Genus	(Morpho-)species	Bean monoculture	Intercropped	Maize monoculture
Anthiinae	*Anthia*	*Anthia burchelli*			1
	Atractonotus	*Atractonotus mulsanti*			1
	Cypholoba	*Cypholoba rutata*	1	1	
		Cypholoba tenuicollis	1	2	1
Brachininae	*Brachinus*	*Brachinus sp.1*	1		
	Pherosophus	*Pherosophus insignis*		1	1
		Pherosophus sp.1		1	
	Styphlomerus	*Styphlomerus cf. ovalipennis*		1	
Carabinae	*Calosoma*	*Calosoma sp.*	1		
Cicindelinae	*Lophyra*	*Lophyra neglecta*			5
Ctenodactylinae	*Hexagonia*	*Hexagonia sp.1*	1		
Lebiinae	*Pericalina*	*Pericalina sp.1*			1
	Graphipterus	*Graphipterus tristis*	5	4	23
	Lebia	*Lebia sp.1*			1
		Lebia sp.2			1
	Microlestes	*Microlestes sp.1*		2	
	Piezia	*Piezia sp.1*			1
Licininae	*Callistomimus*	*Callistomimus nairobiensis*	3	2	
	Chlaenius	*Chlaenius cf. sellatus*			1
		Chlaenius dusaultii		1	2
		Chlaenius lastii		4	1
		Chlaenius maculiceps		5	3
		Chlaenius meyeri		2	9
		Chlaenius quadrisignatus	1		2
		Chlaenius varians		1	
		Chlaenius sp.1	1		
		Chlaenius sp.2	1		1
		Chlaenius sp.3	1		2
Harpalinae	*Harpalinae*	*Harpalinae sp.1*	1		
		Harpalinae sp.2			1

		Harpalinae sp.3		1	
		Harpalinae sp.4	1		
		Harpalinae sp.5	1		
		Harpalinae sp.6			1
		Harpalinae sp.7	1		
		Harpalinae sp.8			1
		Harpalinae sp.9		1	1
		Harpalinae sp.10	1	1	2
		Harpalinae sp.11		1	
		Harpalinae sp.12	6	2	2
		Harpalinae sp.13	1		
	Omostropus	*Omostropus sp.1*			1
	Parophonus	*Parophonus holosericeus*	4	2	10
		Parophonus sp.1		3	1
	Siopeles	*Siopeles biseriatus*			1
		Siopelus melancholicus	5	36	13
		Siopeles sp.1	1	4	2
	Stenolophus	*Stenolophus sp.1*			1
Panagaeinae	*Tefflus*	*Tefflus meyerlei*		1	
Platyninae	*Platyninae*	*Platyninae sp.1*	1		
		Platyninae sp.2		1	
		Platyninae sp.3			2
		Platyninae sp.4		4	1
		Platyninae sp.5		1	4
Pterostichinae	*Abacetini*	*Abacetini sp.1*		1	1
	Abacetus	*Abacetus sp.1*			1
		Abacetus sp.2	1		
		Abacetus sp.3		2	
		Abacetus sp.4		3	2
		Abacetus sp.5		3	5
Scaritinae	*Clivini*	*Clivini sp.1*		4	2
	Distichus	*Distichus sp.1*		2	1
	Scarites	*Scarites sp.1*			1
Trechinae	*Trechinae*	*Trechinae sp.1*		1	
		Trechinae sp.2	1		

		Trechinae sp.3		1	1
		Trechinae sp.4	1	1	
		Trechinae sp.5		2	
		Trechinae sp.6			1
	Tachyura	*Tachyura sp.1*	5	11	3
		Tachyura sp.2	1	4	3

Table 2.S5: Ant (morpho)species found throughout the study period across all fields.

Subfamily	**Genus (subgenus)**	**(Morpho)species**
Dolichoderinae	*Axinidris*	*Axinidris* sp1
Ponerinae	*Bothroponera*	*B. ilgii*
		B. sulcate
		Borthoponera sp1
	Brachyponera	*B. sennaarensis*
	Leptogenys	*L. furtive*
		L. intermedia
	Megaponera	*M. analis*
	Mesoponera	*Mesoponera* sp1
	Ophthalmopone	*O. berthoudi*
	Platythyrea	*P. arnoldi*
		P. cribrinodis
	Plectroctena	*P. mandibularis*
	Paltothyreus	*P. tarsatus*
Formicinae	*Camponotus (Tanaemyrmex)*	*C. etiolipes*
		Tanaemyrmex sp1
		Tanaemyrmex sp2
		Tanaemyrmex sp3
	Camponotus (Myrmosericus)	*Myrmosericus* sp1
	Camponotus (Orthonotomyrmex)	*Orthonomyrmex* sp1
	Camponotus (Unknown)	*Camponotus* sp1
	Lepisiota	*L. ambigua*
		Lepisiota sp1
	Polyrhachis	*P. gagates*
Myrmicinae	*Crematogaster*	*C. mimosa*
		Crematogaster sp1
		Crematogaster sp2
	Meranoplus	*M. clypeatus*
		Meranoplus sp1
	Monomorium	*Monomorium* sp1
		Monomorium sp2
	Myrmicaria	*Myrmicaria* sp1
		Myrmicaria sp2
		Myrmicaria sp3

		Myrmicaria sp4
		Myrmicaria sp5
	Ocymyrmex	*O. barbiger*
	Pheidole	*Pheidole* sp1
		Pheidole sp2
		Pheidole sp3
		Pheidole sp4
		Pheidole sp5
		Pheidole sp6
	Tetramorium	*T. sericeiventre*
		T. hortorum
		T. humbloti
		T. notiale
		T. weitzeckeri
		Tetramorium sp1
		Tetramorium sp2
		Tetramorium sp3
		Tetramorium sp4
		Tetramorium sp5
		Tetramorium sp6
		Tetramorium sp7
Pseudomyrmecinae	*Tetraponera*	*Tetraponera* sp1
Dorylinae	*Dorylus*	*Dorylus* sp1
		Dorylus sp2

Table 2.S6: Bee (morpho)species found throughout the study period across all fields.

Family	**Subfamily**	**Genus (subgenus)**	**(Morpho)species**
Apidae	Apinae	*Apis*	*A. mellifera*
		Amegilla	*Amegilla* sp1
		Tetralonia	*T. caudate*
			Tetralonia sp1
		Tetraloniella	*Tetraloniella* sp1
	Xylocopinae	*Braunsapis*	*Braunsapis* sp1
			Braunsapis sp2
		Ceratina	*Ceratina* sp1
			Ceratina sp2
			Ceratina sp3
			Ceratina sp4
			Ceratina sp5
			Ceratina sp6
			Ceratina sp7
		Xylocopa	*Xylocopa* sp1
			Xylocopa sp2
Andrenidae	Andreninae	*Andrena*	*Andrena* sp1
			Andrena sp2
			Andrena sp3
Colletidae	Colletinae	*Colletes*	*Coletes* sp1
	Hylaeinae	*Hylaeus*	*Hylaeus* sp1
Halictidae	Halictinae	*Halictus (Seladonia)*	*Seladonia* sp1
			Seladonia sp2
		Lasioglossum (Ctenonomia)	*Ctenonomia* sp1
			Ctenonomia sp2
			Ctenonomia sp3
			Ctenonomia sp4
		Lasioglossum (Ipomalictus)	*Ipomalictus* sp1
		Lasioglossum (Unknown)	*Lasioglossum* sp1
			Lasioglossum sp2
			Lasioglossum sp3
			Lasioglossum sp4
			Lasioglossum sp5
		Patellapis	*Patellapis* sp1

	Nomiinae	*Lipotriches*	*L. guineensis*
			L. kamerunensis
			Lipotriches sp1
			Lipotriches sp2
			Lipotriches sp3
			Lipotriches sp4
			Lipotriches sp5
			Lipotriches sp6
			Lipotriches sp7
		Nomia	*N. theryi*
			Nomia sp1
		Pseudapis	*Pseudapis* sp1
			Pseudapis sp2
		Steganomus	*Steganomus* sp1
Megachilidae	Megachilinae	*Megachile*	*M. caricina*
			Megachile sp1
Mellitidae	Meganomiinae	*Meganomia*	*Meganomia*
	Melittinae	*Melitta*	*Melitta* sp1
			Melitta sp2
			Melitta sp3

Table 2.S7: 30 most abundant bacteria taxa detected after DNA metabarcoding, data cleaning, and low-abundance filtering, ranked most common to least common.

Taxa rank	**Phylum**	**Lowest taxonomic identification**
1	Acidobacteria	*Gp6*
2		*Gp4*
3	Planctomycetes	Planctomycetaceae
4	Proteobacteria	*Sphingomonas*
5	Firmicutes	*Bacillus*
6	Verrucomicrobia	Spartobacteria
7	Proteobacteria	Betaproteobacteria
8	Unknown	Subdivision 3
9	Proteobacteria	Proteobacterea
10	Thaumarchaeota	*Nitrososphaera*
11	Bacteroidetes	Chitinophagaceae
12	Actinobacteria	Actinobacteria
13		*Gaiella*
14	Acidobacteria	*Gp7*
15	Planctomycetes	WPS-1
16	Acidobacteria	*Gp3*
17	Proteobacterea	Rhizobiales
18	Gemmatimonadetes	*Gemmatimonas*
19	Proteobacterea	Myxococcales
20	Acidobacteria	*Gp6*
21		*Gp1*
22	Proteobacteria	*Bradyrhizobium*
23	Actinobacteria	*Solirubrobacter*
24	Acidobacteria	*Gp10*
25	Proteobacteria	Gammaproteobacteria
26	Acidobacteria	*Gp4*
27	Proteobacteria	Rhodospirillales
28	Firmicutes	*Streptococcus*
29	Actinobacteria	Solirubrobacterales
30	Armatimonadetes	*Gp4*

Table 2.S8: Results of the PERMANOVAs assessing responses by species assemblages to semi-natural habitat and management differences. DF indicate degrees of freedom.

Response (method)	**Response/predictors**	**F-value**	**p-value**	**DF**	**R^2**
Bird species assemblage (Bray-Curtis)	SNH	1.20	0.290	18/22	0.87
	Pest management	0.68	0.747		
	Soil management	0.87	0.575		
Carabid species assemblage (Bray-Curtis)	Crop	0.79	0.800	43/48	0.86
	SNH	2.83	**<0.001*****		
	Pest management	1.11	0.309		
	Soil management	1.74	**0.041***		
Ant species assemblage (Jaccard)	Crop	0.82	0.290	53/58	0.90
	SNH	1.43	0.945		
	Pest management	0.63	0.820		
	Soil management	2.24	0.352		
Bee species assemblage (Bray-Curtis)	Crop	0.93	0.370	45/50	0.89
	SNH	1.51	0.987		
	Pest management	1.29	0.258		
	Soil management	1.01	0.632		
Soil bacteria assemblage (Bray-Curtis)	Crop	0.85	0.339	46/50	0.91
	SNH	1.71	0.203		
	Soil management	1.22	0.302		

Table 2.S9: Contrasts between the three different crop types for those responses where crop differences (with or without interaction with semi-natural habitat) were detected.

Response	Contrast	t-ratio	p-value
Carabid species richness	Bean – intercrop	-2.38	**0.060**
	Bean – maize	-2.76	**0.025***
	Intercrop – maize	-0.48	0.883
Spider activity density	Bean – intercrop	0.83	0.687
	Bean – maize	2.48	**0.047***
	Intercrop – maize	1.92	0.149
Parasitoid activity density	Bean – intercrop	-3.99	**<0.001*****
	Bean – maize	-3.01	**0.013***
	Intercrop – maize	1.08	0.535
Soil bacteria Shannon’s richness	Bean – intercrop	0.56	0.843
	Bean – maize	-1.92	0.151
	Intercrop – maize	-2.88	**0.020***

Searching for flowers: the author and co-author Mwapi Mkandawire searching for female flowers in a pumpkin plot to include in the pollinator exclusion experiment. Flowers with blue tags, as pictured here, were bagged. This prevented pollinators from visiting the flowers, and as a result, these flowers never set fruit.

Chapter 3

Pumpkin fruit set is limited by herbivory and low pollinator richness in a smallholder agricultural landscape

Abstract

Agroecology is proposed as a sustainable alternative to conventional agricultural practices, but little is known about the benefits of diversification of these practices for pollination and pest control services. The presence of pollinators and pests in crop fields is shaped by surrounding landscapes and local management on households. Landscapes and agricultural practices in sub-Saharan Africa are rapidly changing, yet the region is underrepresented in studies about how landscapes and management affect pollinators, herbivory and ultimately crop yields. On 24 smallholder farms in Malawi, 12 which used manual pest management and 12 that did not, located along a gradient of semi-natural habitat and the implementation of soil agroecological practices, we investigated the effects of land-use on pollinators and pest damage. An increasing semi-natural habitat cover in the landscape decreased honeybee abundance but increased the abundance and species richness of non-honeybee pollinators, and had no effect on flower herbivory on pumpkin, a pollinator-dependent crop. Additionally, the implementation of manual pest management negatively affected pollinators, but the use of diversified agroecological soil management practices had positive effects on pollinators and no effect on herbivory. Using a full-factorial hand pollination and exclusion experiment we found that both pollinator limitation and herbivory constrained fruit set, but not fruit quality of pumpkins. Moreover, increasing pollinator species richness improved pumpkin fruit set. We recommend improved protection of remaining semi-natural habitats and increasing soil agroecological practices to ensure pollination services on Malawian smallholder farms.

3.1 Introduction

Land-use change in agricultural landscapes, through the conversion of (semi-)natural habitats and the intensification of agricultural practices, is a major driver of biodiversity loss (Newbold et al., 2015; IPBES, 2019). Crop productivity is dependent on ecosystem services provided by insects, such as pollination and pest control. Abundance and species richness of both pollinators and pests and the delivery of ecosystem services often depends on the composition of the landscape surrounding crop fields (Martin et al., 2019). Loss of semi-natural habitats surrounding crop fields can reduce the abundance and richness of important pollinators (Kennedy et al., 2013) and can increase the abundance of some insect pests (Tamburini et al., 2020). Though the links between land-use, biodiversity, ecosystem services and crops have been well-studied in temperate systems, the same cannot be said for tropical agricultural landscapes cultivated by smallholder farmers, especially in sub-Saharan Africa (Vanlauwe et al., 2014; Otieno et al., 2020a) . This underrepresentation is unfortunate because biodiversity loss is especially rapid in parts of the world that are biodiversity-rich but economically poor, as in many areas in the Global South where smallholder agriculturalists live (Newbold et al., 2015). It is especially these low-income farmers that often lack the means to manage lower productivity with costly synthetic inputs and as such are more impacted by the loss of biodiversity and associated ecosystem services (Steward et al., 2014).

Many crops that provide essential micronutrients, such as legumes and vegetable crops, or important cash crops, such as coffee and cacao, are pollinator dependent. Consequently, many smallholder farmers are directly dependent on pollinators for food security and their livelihoods (Chaplin-Kramer et al., 2014; IPBES, 2016). Unfortunately, both abundance (Koh et al., 2016; Powney et al., 2019) and species richness (Zattara & Aizen, 2021; Carrasco et al., 2021) of some pollinators, as well as natural enemies of pests, are declining; loss of habitat and agricultural intensification are important drivers of this trend (Dicks et al., 2021). The loss of pollinator species richness may be especially problematic, since it is species richness, not necessarily abundance, that is strongly linked to ecosystem service delivery (Dainese et al., 2019).

Pollinator limitation in crops occurs when insufficient pollinator visits or incompatible crop flowers, and crops cannot optimally set fruit or seed. Evidence of pollinator limitation on some crops has already been found in the USA (Reilly et al., 2020), Europe (Holland et al., 2020) and India (Basu, Bhattacharya & Ianetta, 2011). Even though there are some studies comparing ambient pollination to pollinator-excluded crops in sub-Saharan Africa (e.g.: Vogel et al., 2021), the region lacks representation in studies on the effects of landscape on pollinators and the consequences for crops.

Herbivory by insect pests motivates the use of synthetic pesticides. However, pesticides negatively affect human and environmental health and often lose their efficacy over time, due to pests' remarkable ability to evolve pesticide resistance (Ekström & Ekbom, 2011). In sub-Saharan Africa, in particular, lack of access to personal protective equipment and insufficient knowledge on the correct application of pesticides increase costs to human health whilst reducing potential pest-control benefits (Isgren & Andersson, 2021). In contrast to pollinators, the drivers of insect pest abundance are more context dependent, but responses are often elucidated by traits of individual pest species (Tamburini et al., 2020). Pollination and herbivory have often been studied in isolation, with fewer studies focused on the two factors in tandem, despite evidence suggesting that the potential benefits of pollination might be reduced with increasing pest pressure (Lundin et al., 2013; Tamburini et al., 2019). Understanding how landscapes affect pollination and herbivory and knowing which is most responsible for constraining productivity of a particular crop is important for focusing management efforts.

In addition to landscape drivers of insect communities, insects may be directly impacted by management choices of farmers on the farm level: abundance and species richness of beneficial insects may benefit from a more organic or agroecological approach to agriculture (hereafter "agroecology"), compared to conventional agriculture (Bengtsson, Ahnström & Weibull, 2005). Agroecology aims for a more ecological and culturally appropriate approach to farming and has been shown to improve food security (Bezner Kerr et al., 2021) and climate change adaptation (Snapp et al., 2021). Examples of agroecological soil management are intercropping with legumes, mulching, or landscaping fields in such a way that runoff is prevented. An example of agroecological pest management includes the manual removal or squashing of perceived pests. However, the efficacy of such a practice, nor its effect on non-target groups such as pollinators is so far unknown. In general, agroecology aims to harness ecological processes whilst minimising synthetic inputs (Wezel et al., 2020). Therefore, it is assumed that agroecology benefits biodiversity and biodiversity-driven ecosystem services; but empirical evidence of this is still scarce in tropical landscapes.

In our study region in northern Malawi, pumpkin (*Cucurbita pepo*) is valued by smallholders for consumption and sale on local markets (Chagomoka, Afari-Sefa & Pitoro, 2013). Being a monoecious crop, pumpkin is completely dependent on insect pollination to produce any fruit and seed yield. Pumpkin in Malawi is affected by a variety of pest species, though leaf beetles (Chrysomelidae) are considered the most important (Kapeya & Maulana, 2003). Pollinator species richness, but not abundance, in our study region has been shown to increase with increased semi-natural habitat (Vogel et al., *unpublished data*). However, semi-natural habitat in Malawi is in rapid decline (Chirambo & Mitembe, 2014), with unknown effects on pollination services or herbivory rates. In fact, it is totally unknown if either of these factors constrain pumpkin productivity in Malawi. Therefore, we conducted a multifactorial experiment (ambient pollination and herbivory, hand-pollination with ambient herbivory, hand-pollination and herbivory excluded, and a negative control excluding both pollination and herbivory) across 24 landscapes in a sub-Saharan study region dominated by smallholder agriculture to test the following predictions:

1. The abundance and species richness of pollinators will increase while herbivory will decrease with increasing semi-natural habitat in the landscape and with by increasing the number of soil agroecological practices on farms. The use of manual pest management on households will decrease pest damage but will not affect on pollinators.
2. The yield of hand-pollinated and/or excluded flowers will depend on the relative importance of pollinators and herbivores at each farm, depending on the proportion of semi-natural habitat in the landscape and the diversification of agroecological practices.

3.2 Materials and methods

Site selection

This study was part of a broader transdisciplinary and participatory research project, which included trained farmer-researchers, aimed at understanding dynamics between agroecological practices, biodiversity and ecosystem services (Kpienbaareh et al., 2022a). In October 2019, we selected 24 smallholder households with varying implementation of agroecology who agreed to participate in the study in Mzimba district, northern Malawi (Figure 3.1). Sites were at least 2 km apart from each other so that there was no overlap when using 1 km radii. Maize (the main food staple) and tobacco (the main cash crop) are the dominant crops in the region, though legumes (beans, cowpea, groundnut, pigeon pea, bambara groundnut) and various vegetable crops are also grown, often in mixtures. Smallholder farms in this region are typically small, ranging from 0.5 to 1.4 hectares, and fields are managed traditionally by hand (FAO, 2018).

The selected households were located along a gradient of semi-natural habitat (SNH) ranging from 17-74 % SNH in a 1 km radius. We defined semi-natural habitat as the unmanaged, naturally occurring grasslands, shrublands and forests. The semi-natural habitat in our study region contains vegetation typical for the Miombo woodland ecoregion (Ribeiro et al., 2020). Though these semi-natural habitats are unmanaged, they are heavily impacted by activities such as grazing and the collection of firewood (Gumbo et al., 2018). Malawi is located in the seasonal tropics, with a distinct rainy season from approximately November or December until April, which is also the main growing season for crops (Gama et al. 2014).

Six of the participating households owned honeybee hives, but the presence of these hives was not related to semi-natural habit proportion manual pest management or agroecological soil management practices. Hives were not located next to pumpkin fields, nor on neighbouring fields, and owning of hives did not affect honeybee abundance on our plots. Hives managed by our farmers were typical traditional hives (Figure 3.S1), which are hung in trees where they may be passively colonised by a honeybee colony.

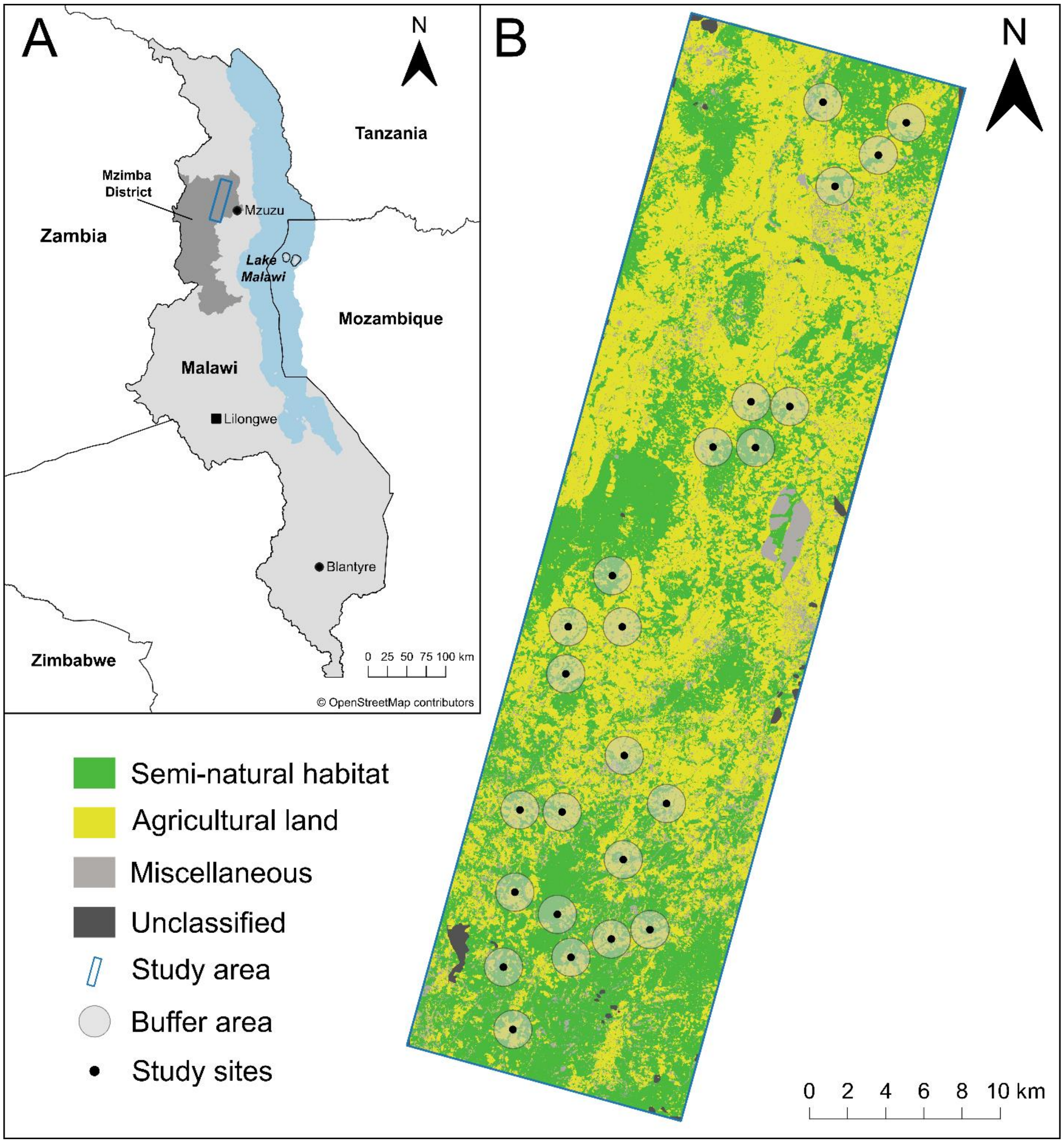


Figure 3.1: Map of the study area showing A) its location in Mzimba District, northern Malawi, and B) a land cover classification map of the study area with the locations of all 24 pumpkin fields as the centers of the respective 1 km buffer areas.

Field preparation

Each farmer was provided with the same local variety of pumpkin seed sourced from a local market. We established a 2 x 15m plot in October 2019 and farmers sowed pumpkin seeds between mid-December 2019 to mid-January 2020, with a density of three seeds every meter, in two rows across the plot. Plots were rain-fed only and not irrigated, in line with typical management in the region. Farmers only used organic compost (called "Bokashi") (Quiroz & Céspedes, 2019), applied twice during the growing season. Field management activities, including soil preparation and sowing, were done by hand-hoe, as per usual practice. Participating farmers reported no use of synthetic pesticides on their farms.

Exclusion experiment

In each pumpkin patch, we marked minimum 8 up to 19 female flowers, with a mean of 12 flowers marked. Of these marked flowers, 2-5 remained open (ambient pollination and ambient herbivory), 2-5 where hand pollinated (supplementary pollination, ambient herbivory), 2-5 were hand pollinated and covered by a mesh bag (optimal pollination, no herbivory) and 2-5 were covered by a mesh bag just before blooming with no further treatment (all insects excluded). Mesh bags were removed after fruit set or when flowers withered, and the fruit was left to develop as normal. All flowers received their respective treatments between 13th of February 2020 and the 3rd of March 2020.

Pollinator recordings

Pollinator densities were assessed in three rounds of transects on each plot between 13th of February and 10th of March. At each transect round, we walked 3 subtransects of 5 minutes per 5 meters, covering the full 15 x 2 meter plot. Like this, all pollinators visiting the flowers were recorded. Pollinators that were not identifiable in the field were captured to be identified at a later time with the keys in Michener (2007) and Eardley, Kuhlmann & Pauly (2010). We considered bee, syrphid and tabanid flower visitors as pollinators, few other flower visitors were observed. All transects were performed by the same researcher to prevent sampling bias.

Flower density and damage assessment

During each transect walk, we counted all open pumpkin flowers blooming in the plot. Male and female flowers were counted separately. At each visit we also checked all flowers for and counted the number of flowers that had herbivory damage. Damage to the petals was recorded separately from damage to the reproductive parts of the flowers.

Pumpkin harvest assessment

All tagged flowers were monitored until harvest or abortion of fruits. First, we recorded whether fruit set occurred or not. When the fruits were harvest-ready, we weighed pumpkins, measured the girth (circumference at widest axis), and counted the number of seeds per fruit.

Landscape analysis

We used a synergetic remote sensing approach fusing optical (Sentinel-2 and PlanetScope) and radar (Sentinel-1) imagery to classify the land cover in our study region (Planet Team, 2017). This approach produced the best overall classification accuracy for a subset of our study area (Kpienbaareh et al., 2021). Following the steps outlined in this publication, four optical imagery fusion pairs, each paired with the combination of radar data from six different dates in the growing season all acquired between January and April 2020, were used to cover the extent of 1 km radii around all 24 pumpkin fields in our study. All optical images were selected to depict the study region as cloudless as possible. As dense cloud cover was common in the growing season, several optical images, from both Sentinel-2 and PlanetScope, were needed. For each of our four fusion pair combinations, we ran a supervised random forest algorithm trained with land cover class data collected through extensive ground-truthing during the growing season of 2019/20. We complemented these with manually digitized land cover samples of easily discernible land cover classes (e.g., shrubland, water or settlement) via Google satellite images in QGIS 3.12 and Digital Globe images in ArcGIS Pro 2.7. If several classifications were available at a study site, the best fit was selected based on overall accuracy and visual inspection of the extent of shrubland in comparison with a high-resolution satellite image. Any remaining gaps in the 1 km radius around the fields were either filled with values from other classifications or, if unavailable, manually digitized. Land cover pixel values were extracted from the final 3 m resolution classifications using the R package ‘exactextractr’ (Baston, 2022). Resulting land cover class proportions of shrubland, grassland and forest were aggregated to semi-natural habitat (SNH) and used in subsequent statistical analyses.

Farmer surveys

To assess the implementation of manual pest management and soil agroecological management practices on the farms on which our pumpkin fields were located, we performed structured interviews from the 8th to 26th of March 2020. Respondents had the study explained to them and gave informed consent prior to answering questions. We asked questions about agroecological practices performed for up to three fields per farm. The questions were posed as a yes or no question (i.e., did you perform x practice on this field?). In addition, farmers were asked if they performed any additional practices that were not prompted in our survey. The questions were asked only to the adults of the household (men or women) who directly managed the plots. Farmers reported squashing or physically removing pests, both which we consider manual pest removal. Farmers reported and nine practices that aimed to maintain soil quality (hereafter: “soil management practices”) namely the planting of vetiver grass hedges (*Chrysopogon zizanioides*), soil landscaping (such as pit planting or terracing), mulching, legume intercropping, the incorporation of legume residue, crop rotation with legumes, the use of manure or compost and agroforestry (Table 3.S1). We conducted a total of 24 interviews, one corresponding to each farm on which data were collected.

To obtain a single value for soil management implementation on each farm, we used a cumulative value for all practices practiced on the household. The Institutional Review Board of Cornell University for Human Subjects Research reviewed and approved the research study design (protocol 1811008425).

Statistical analysis

Since the predictors of proportion of semi-natural habitat and the diversification of pest- and soil management practices were in different units of measurement, we standardized them using z-scores. Although there was variation in the number of flowers across plots, we could not detect any effect of landscape nor management on flower number (Table 3.1). Therefore, flower number was not considered for any further analysis.

We tested the effect of three predictors: semi-natural habitat cover, the implementation of manual pest management and the number of agroecological soil practices. For total pollinator abundance and honeybee abundance, we summed across the three transects per transect round per site and tested them against our three predictors in a negative binomial model. We tested the effect of the three predictors on pollinator cumulative species richness and bee abundance excluding honeybees and fly abundance using a generalized linear model with Poisson distribution. In all these models, we used total number of flowers as an offset to account for local attractiveness of the pumpkin fields. We also analysed the effect of landscape composition on herbivory using the mean proportion of damaged flowers across the three transects in a linear model.

When assessing the effects of hand pollination, exclusion treatments, and landscape on pumpkin harvest metrics, we excluded the negative control (bagged before flowering), since this treatment only produced fruit in a single case. We calculated the proportion of flowers per treatment per plot that set fruit, as well as the proportion of flowers that produced harvestable fruit. Using the ‘lmer’ function from the ‘lme4’ package, we tested the proportion of early fruit set, proportion of harvest, seed set per fruit, fruit weight and fruit size against treatment, the proportion of semi-natural habitat (and its interaction with treatment), as well as and the use of manual pest management and the number of soil management practices in separate linear mixed effects models for each yield parameter, using field as a random factor (Bates et al., 2019). If significant differences in the exclusion treatment were detected, pairwise comparisons between treatments were made using the ‘lsmeans’ function from the ‘emmeans’ package (Lenth et al., 2021).

To analyse the effects of pollinators and herbivory on fruit set, fruit harvest and fruit quality metrics, we tested these in linear mixed effects models against z-transformed pollinator visitation rate (number of pollinators/ number of female flowers), pollinator species richness and herbivory proportion, with field as a random effect. To better understand the relative increase/decrease of early fruit set with increasing pollinator visitation rate, species richness and herbivory, we analysed these factors against the relative difference of the unbagged treatments against the hand pollinated and bagged control within a field using a linear model.

All data analysis was performed in R version 4.0.5 (R Core Team, 2020). All models were validated for the assumptions of normality, 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).

3.3 Results

Across the sampling period, we collected 622 pollinators belonging to eleven bee (morpho)species and five fly morphospecies (Table 3.S1). *Apis mellifera*, the honeybee, was the dominant pollinator on our sites, with 565 individuals (90.8 % of total observations) recorded, followed by syrphid flies (4 morphospecies, 4.5% of total observations). Of the 199 female flowers included in the whole experiment (excluding the negative control), 103 (~52% of flowers) set fruit. In total, 85 (~83% of fruits, ~43% of flowers) of these fruits could be harvested, while 18 could not be harvested since 15 were lost to fungal rot, 2 eaten by mice and 1 damaged too strongly by a hailstorm after fruit set. Of the flowers included in the exclusion experiment, only two were damaged by herbivory during initial flowering stages. Overall, the mean proportion of damaged flowers on fields range 0 - 35%, with only three fields experiencing damage of more than 10%.

Pollinators and herbivory

We found a decline in pollinator abundance (Figure 3.2A), but an increase in pollinator species richness (Figure 3.2M) with increasing proportion of semi-natural habitat. This pattern was driven by the negative relationship between *A. mellifera* abundance with semi-natural habitat proportion (Figure 3.2D), but the increase in abundance of non-honeybee pollinators with increasing semi-natural habitat (Figure 3.2G, Figure 3.2J). The proportion of flowers damaged by herbivory was not affected by the amount of semi-natural habitat in the surrounding landscape (Table 3.1).

The use of manual pest management had a negative effect on pollinator abundance (Figure 3.2B) and species richness (Figure 3.2N). Manual pest management had an especially strong effect on fly pollinators (Figure 3.2K), though honeybees were also negatively affected (Figure 3.2E). However, non-honeybees (Figure 3.2H) nor the proportion of herbivory was not affected by pest management (Table 3.1).

Increasing the number of agroecological soil management practices had positive effects on overall pollinator abundance (Figure 3.2C), the abundance of honeybees (Figure 3.2F), non-honeybees (Figure 3.2I) and fly pollinators (Figure 3.2L). Increasing soil agroecological practices also benefited pollinator species richness (Figure 3.2O). The proportion of flowers damaged by herbivory was not affected by soil management (Table 1).

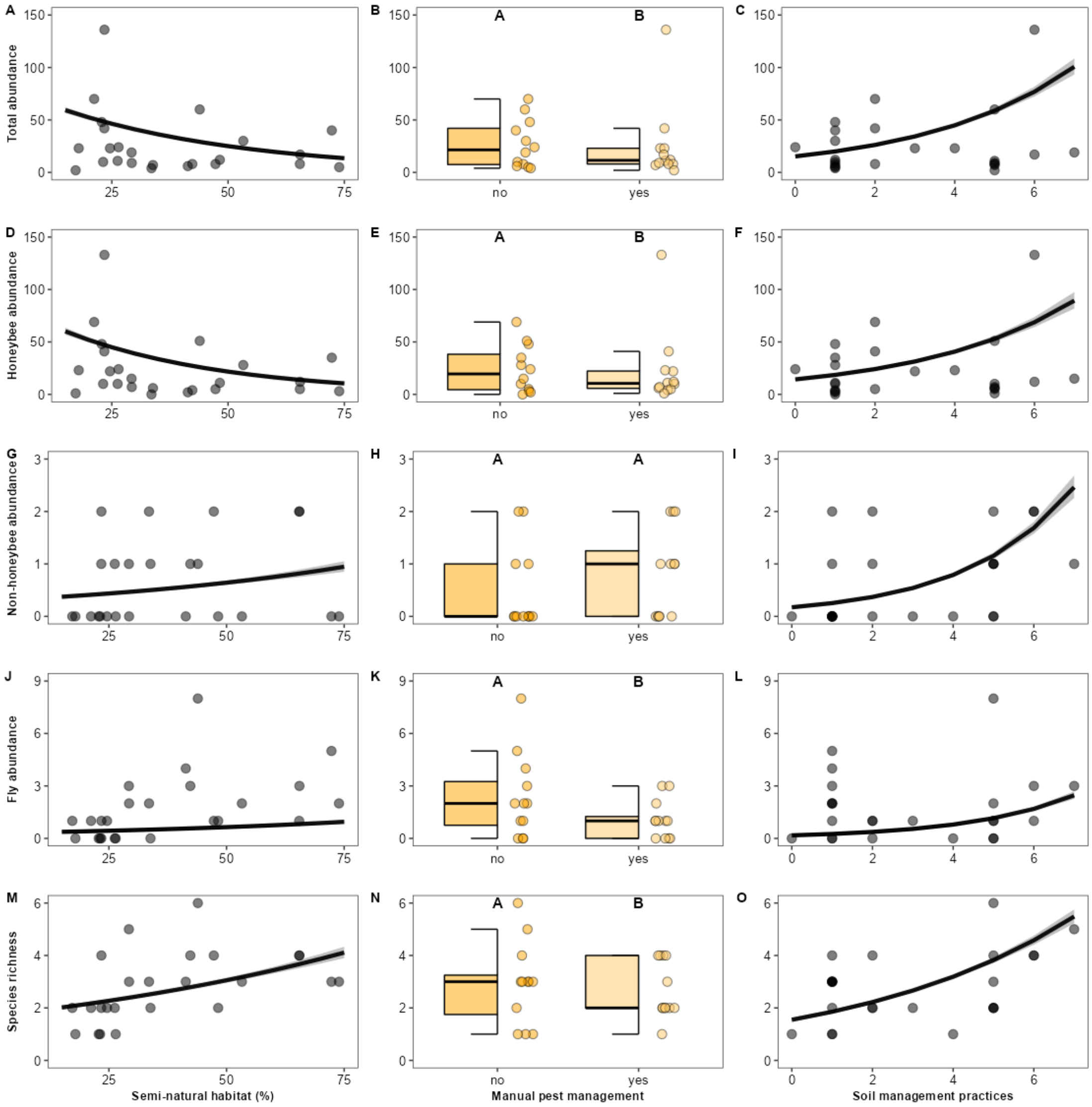


Figure 3.2: Response of total pollinator abundance, honeybee abundance, non-honeybee abundance and pollinator species richness to semi-natural habitat cover, manual pest management and number of agroecological soil management practices. Lines show the direction of the predicted effect, grey areas indicate the 95% confidence interval of the prediction. Boxes indicate the minimum, 1st quantile, median, 2nd quantile and maximum with the data points next to each box. Letters indicate group differences.

Exclusion experiment and pumpkin yield assessment

There was a significant effect of the hand pollination and herbivory exclusion treatment on pumpkin fruit set. Flowers that were hand pollinated and had herbivores excluded had the highest fruit set, whereas ambiently pollinated flowers had the lowest fruit set. Flowers that were hand pollinated but were still exposed to herbivory had an intermediate fruit set (Figure 3.3A; Table 3.S2). Semi-natural habitat or agroecological pest- and soil management practices did not affect fruit set. The exclusion treatment had no effect on seed set, fruit weight or fruit size, but the proportion of semi-natural habitat had a negative effect on all three metrics of fruit quality (Figure 3.3B, C and D). Manual pest management or the number of soil practices had no effect on seed set, fruit weight or fruit size (Table 3.1).

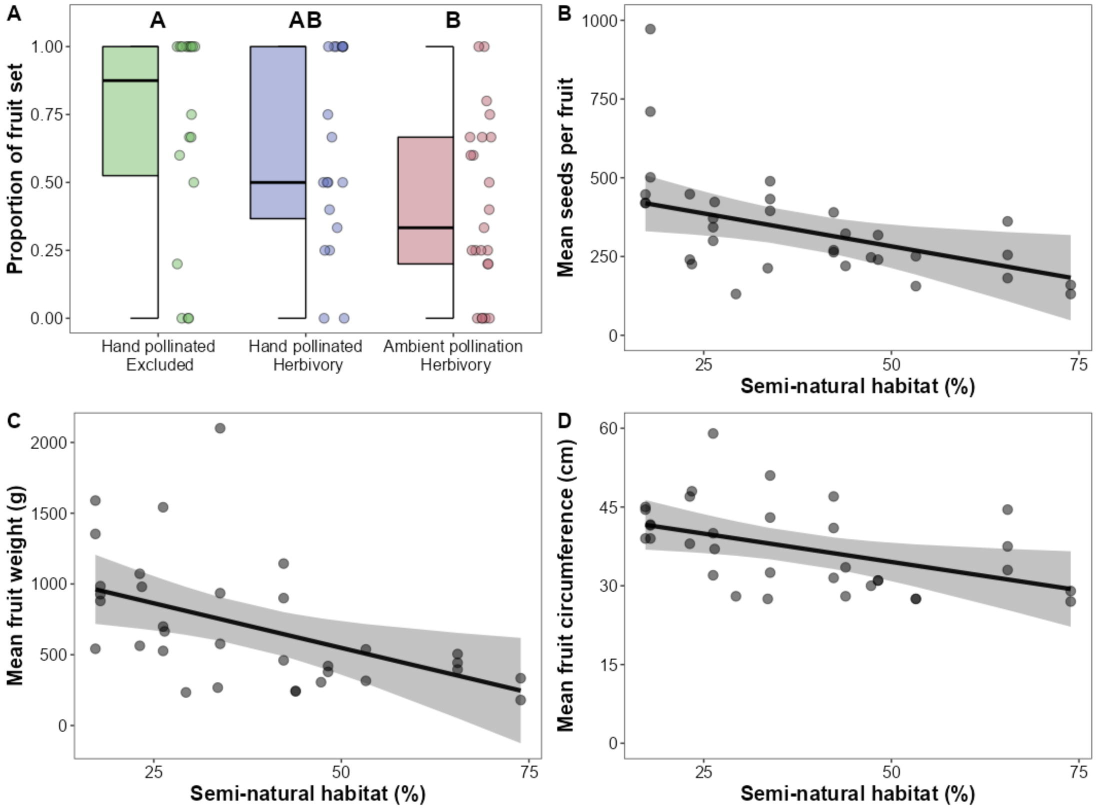


Figure 3.3: Response of A) the proportion of early fruit set by treatment and B) mean seed set, C) mean fruit weight) and D) mean fruit circumference in relation to the proportion of semi-natural habitat. In A, boxes indicate the minimum, 1st quantile, median, 2nd quantile and maximum with the data points next to each box, letters indicate group differences. In B, D and E, grey areas show the 95% confidence interval.

Table 2.1: The results of models assessing the responses of flower abundance, pollinators, herbivory, and pumpkin yield metrics to the proportion of semi-natural habitat (and its interaction with exclusion treatment, in the case of pumpkin yield metrics), manual pest management and number of agroecological soil management practices. Bold p-values indicate significant responses, asterisks indicate the strength of responses. Red indicates a negative trend, whereas green indicates a positive trend.

Response	**Predictors**	**Chi^2/F-value**	**p-value**	**DF$_{num}$/DF$_{den/res}$**	**R^2_m/R^2_c**	**Model type**
Flower abundance	Semi-natural habitat (%)	1.88	0.170	1	0.11	Negative binomial model
	Manual **pest** management	0.05	0.828	1		
	Number of **soil** practices	0.03	0.861	1		
Pollinator abundance	Semi-natural habitat (%)	495.74	**<0.001*****	1	1.00	Negative binomial model
	Manual **pest** management	49.15	**0.0021*****	1		
	Number of **soil** practices	406.49	**<0.001*****	1		
Honeybee abundance	Semi-natural habitat (%)	553.60	**<0.001*****	1	1.00	Negative binomial model
	Manual **pest** management	188.34	**<0.001*****	1		
	Number of **soil** practices	560.02	**<0.001*****	1		
Non-honeybee abundance	Semi-natural habitat (%)	142.48	**<0.001*****	1	1.00	Generalized linear model with Poisson distribution
	Manual **pest** management	0.08	0.778	1		
	Number of **soil** practices	888.28	**<0.001*****	1		
Fly abundance	Semi-natural habitat (%)	1083.91	**<0.001*****	1	1.00	Generalized linear model with Poisson distribution
	Manual **pest** management	589.70	**<0.001*****	1		
	Number of **soil** practices	881.66	**<0.001*****	1		
Pollinator species richness	Semi-natural habitat (%)	271.88	**<0.001*****	1	1.00	Generalized linear model with Poisson distribution
	Manual **pest** management	81.05	**<0.001*****	1		
	Number of **soil** practices	750.01	**<0.001*****	1		

Proportion herbivory	Semi-natural habitat (%)	0.08	0.779	1/20	0.17	Linear model
	Manual **pest** management	3.65	**0.070**	1/20		
	Number of **soil** practices	0.38	0.543	1/20		
Early fruit set	Treatment	3.37	**0.046***	2/34	0.12/0.20	Linear mixed effects model
	Semi-natural habitat (%)	0.00	0.962	1/16		
	Manual **pest** management	0.78	0.392	1/14		
	Number of **soil** practices	0.01	0.925	1/13		
	Treatment*SNH	0.15	0.865	2/36		
Harvestable fruit	Treatment	4.83	**0.014***	2/34	0.16/0.33	Linear mixed effects model
	Semi-natural habitat (%)	0.00	0.948	1/17		
	Manual **pest** management	1.60	0.226	1/14		
	Number of **soil** practices	0.15	0.700	1/14		
	Treatment*SNH	0.23	0.794	2/36		
Seed set	Treatment	0.44	0.653	2/16	0.29/0.68	Linear mixed effects model
	Semi-natural habitat (%)	5.02	**0.048***	1/10		
	Manual **pest** management	0.58	0.461	1/11		
	Number of **soil** practices	0.12	0.737	1/11		
	Treatment*SNH	1.07	0.367	2/15		
Fruit girth	Treatment	1.56	0.230	2/25	0.36/0.36	Linear mixed effects model
	Semi-natural habitat (%)	6.59	**0.017***	1/25		
	Manual **pest** management	1.39	0.250	1/25		
	Number of **soil** practices	0.86	0.364	1/25		
	Treatment*SNH	0.17	0.844	2/25		
Fruit weight	Treatment	0.24	0.787	2/25	0.31/0.31	Linear mixed effects model
	Semi-natural habitat (%)	7.85	**0.009****	1/25		

	Manual **pest** management	1.85	0.186	1/25		
	Number of **soil** practices	0.00	0.992	1/25		
	Treatment*SNH	0.28	0.757	2/25		

Effects of pollinators and herbivory on pumpkin yield

Early fruit set proportion significantly responded to pollinator species richness in interaction with pollination and herbivore exclusion treatments (Table 3.S3). In both non-excluded treatments (hand- and ambiently pollinated flowers without bag), the proportion of flowers that set fruit increased with an increase in the number of pollinator species. However, fruit set of excluded flowers was negatively related to pollinator species richness (Figure 3.4A). Pollinator visitation rate or the proportion of herbivory had no effect on fruit set. Harvestable fruits and fruit quality, in terms of seed set, fruit weight and fruit size were not affected by pollination or herbivory (Table 3.S3).

For the relative differences in fruit set, we found a significant decrease in difference between the ambient treatment, but not the hand pollinated treatment, and the positive control with increasing pollinator richness (Figure 3.4B). Pollinator visitation rate and herbivory did not affect the relative differences between treatments (Table 3.S3).

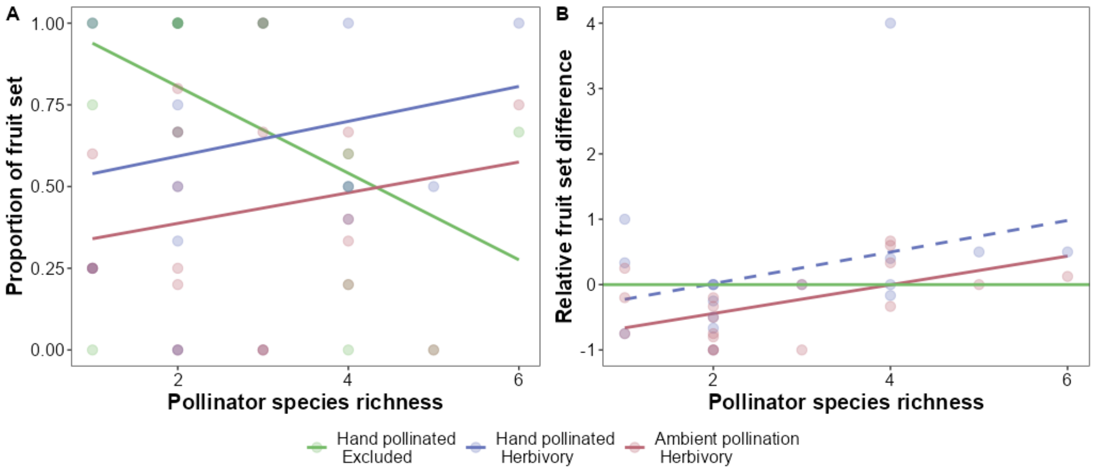


Figure 3.4: A) Responses of the proportion of flowers that set fruit to pollinator species richness by exclusion treatment, and B) relative fruit set difference between the treatments and the positive control (hand-pollinated and excluded) across the pollinator species richness gradient. Significant difference with the control is indicated with a solid line, the dashed line indicates a non-significant difference.

3.4 Discussion

In our tropical smallholder study system, pollinators, but not pest damage, was influenced by land-use and agroecological practices. Pollinator richness increased with increasing semi-natural habitat cover, while, contrary to expectations, pollinator abundance decreased. This was due to the very high abundance of the native honeybee (*A. mellifera*) in landscapes low in semi-natural habitat; when honeybees were not considered, the remaining pollinators, non-honeybees and flies increased in abundance with increasing semi-natural habitat – emphasising a positive effect of semi-natural habitat on these non-managed pollinators. We found similar responses by bees on pigeon pea (Vogel et al., 2021), and of butterfly abundance and species richness in the same study area (Vogel et al., *under review*). These results align with studies that suggest that agricultural landscapes may favour a few, very adaptable, pollinator species (Grab et al., 2019). The high abundance of honeybees in agricultural landscapes could be caused by a higher number of potential beekeepers but could additionally be due to the wide foraging range of honeybees compared to solitary pollinators. Additionally, honeybees are highly generalist and tolerant of disturbance in their habitat (Steffan-Dewenter et al., 2002). Notably, in contrast to temperate agricultural landscapes, up to 90 % of African honeybees are wild-nesting (Requier et al., 2019), and even human-manufactured hives are passively colonised and in our study region are not actively placed near fields for pollination purposes.

There was no relationship between fruit set and semi-natural habitat. However, we did find negative effects of the proportion of semi-natural habitat on fruit weight, size, and seed set. Possibly, areas with soil suitable for agriculture are converted first (Serneels & Lambin, 2001). Therefore, pumpkins perform better in areas with better soils that also have lower semi-natural habitat cover, but a high pollinator species richness compensates for lower fruit set in low semi-natural habitat areas, and possibly, increasing pollinator richness in landscapes low in semi-natural habitat could enhance yields. In contrast with another study in a tropical agroecosystem, we found no relationship between pollinator richness and pumpkin seed set per fruit (Hoehn et al., 2008), but in our study, participating farmers considered unsuccessful fruit production a bigger concern than seed production for pumpkins (*personal communication with farmers*).

The killing of non-target organisms, such as pollinators, is a major disadvantage of conventional pest management involving pesticides (Ekström & Ekbom, 2011). Manually removing or killing pests, considered an agroecological pest management practice, was practiced by half the participating households and is often assumed to be a more sustainable method of pest management (Wezel et al., 2020), but the effects of this method on non-target organisms has been poorly studied. We find that manual pest management did not affect herbivory but did negatively affect pollinator abundance and richness. This negative affect was mediated by the effects of pest control on honeybee and fly pollinator abundance, but not non-honeybee abundance. We suspect that the negative effect on observed on pumpkin-visiting flies in particular, may be because the potential pollinators may not be effectively distinguished from other larviform pests in the larval stage by farmers (as opposed to non-honeybees, whose larvae are not free living and remain inside nests). Previous research in the study area (Enloe et al., 2021), and in other smallholder communities in Africa (Mkenda et al., 2020) reveal that smallholders cannot always effectively identify beneficial insects. In the case of Tabinid and Syrphid flies, this lack would not only negatively affect the pollinating adults but also the larvae as natural enemies of pests. Therefore, it is imperative that smallholders receive more education about beneficial insects on their farms.

Increasing the use of agroecological soil management practices had an even greater positive effect on pollinator abundance (doubled the number of pollinators) and species richness (three-fold increase in species richness), than manual pest management had a negative effect, which lowered the abundance by a quarter, and decreased species richness by a third. This may be linked to planting of alternative crops (i.e., intercropping with legumes, practiced in half the households) suitable to pollinators through the provision of alternative food sources in an area dominated by maize agriculture. Additionally, the incorporated legume residue (10 households), or the use of manure and compost (13 households each), could create more humid microclimates which would be especially beneficial for fly pollinator larvae. In addition, sustainable soil management is key to maintain ground nesting bees such as *Lasioglossum* spp. in agroecosystems (Antoine & Forrest, 2021). Though we found no effect of the number of soil management on pumpkin production, agroecological soil practices had positive food security outcomes for smallholder farmers (Bezner Kerr et al., 2021). Here, we show that agroecological soil management may also have important ecological co-benefits - indicating that increased agroecological soil practices may result in positive outcomes for both smallholders and biodiversity.

The pollinator and pest exclusion experiment showed that both pollinator limitation and herbivory, rather than either factor alone, constrain fruit set in our study region, but only in areas of low pollinator species richness. This is in contrast with studies from other regions that do not find pollinator limitation in pumpkins (Reilly et al., 2020) and shows that pollinator limitation is a context-dependent phenomenon in this crop. Furthermore, in plots with high species richness, ambient pollinated flowers outperformed hand-pollinated and herbivory-excluded flowers. The fact that the excluded treatment declined in fruit set across the species richness gradient is not causal, but rather indicates a co-correlation of an additional factor with species richness. The positive relationship between species richness with the fruit set in open treatments indicate the importance of bee species richness, and not only abundance, for pumpkin yields, as has been found in other crops and in other contexts (Garibaldi et al., 2016; Grab et al., 2019). The positive relationship of richness with fruit set is consistent with other studies that indicate the importance of species diversity for ecosystem services important in crop production (Dainese et al., 2019) and further emphasizes the necessity of maintaining pollinator diversity by protecting remaining semi-natural habitats and employing nature-friendly farming practices such as agroecological soil management practices.

3.5 Conclusion

Our study underpins the important role pollinators play in the productivity of pollinator-dependent crops and indicates that pumpkin fruit set is constrained by pollinator richness and herbivory in a tropical smallholder agricultural landscape. Though the main staple in our study region, maize, is wind-pollinated, most crops that are important for smallholder food diversity and nutrition depend on insect pollinators (Eilers et al., 2011; Chaplin-Kramer et al., 2014) - highlighting the contribution of diverse pollinators to nutritional security in smallholder societies. Therefore, we argue that maintaining and increasing the diversity of pollinators in smallholder agricultural landscapes should be a priority for stakeholders. Remaining semi-natural habitats should be protected. The negative effect of semi-natural habitat on fruit quality needs better understanding so that the relative importance of semi-natural habitat for pollinators and productivity can be better disentangled – we believe soil quality may be an important component. Farmers need to be informed on what constitutes a pest and a beneficial insect to prevent manual removal of pollinators from farms. Additionally increased use of agroecological soil management practices to maintain the abundance and richness of pollinators on their farms should be encouraged in smallholder communities - helping to improve livelihoods and food security in a sustainable way in sub-Saharan Africa (Bezner Kerr et al., 2021).

Supplementary material 3

Figure 3.S1: Typical traditionally manufactured beehive on one of the participating farms - this specific one was uncolonized. Photograph taken in February 2020.

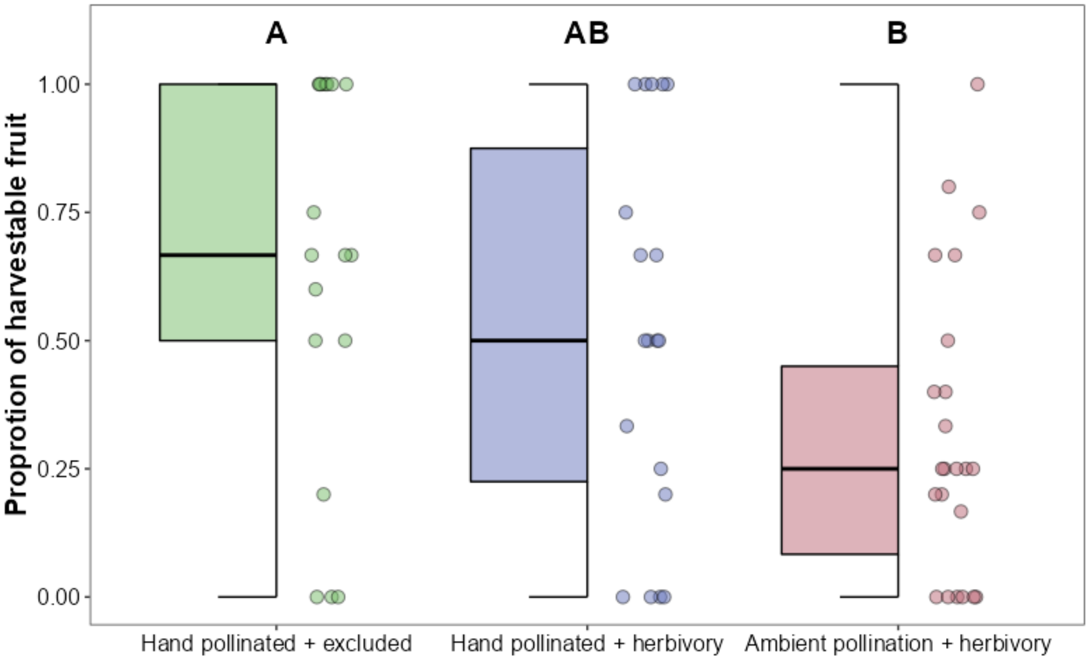


Figure 3.S2: Differences in the proportion of flowers that became harvestable fruit by treatment. Boxes indicate the minimum, 1st quantile, median, 2nd quantile and maximum with the data points next to each box, letters indicate the group difference.

Table 3.S1: (Morpho)species of pollinators recorded across the study period.

Taxon	Family	Genus	Species
Bees	Apidae	*Apis*	*Apis mellifera*
		Pleibena	*Pleibena armata*
	Halictidae	*Halictus*	*Halictus* sp1
		Lasioglossum	*Lasioglossum* sp1
		Nomia	*Nomia* sp1
		Lipotriches	*Lipotriches* sp1
		Pseudapis	*Pseudapis* sp1
	Megachilidae	*Osmia*	*Osmia* sp1
	Unknown	Unknown	Unknown sp1
Flies	Syrphidae		*Syrphidae* sp1
			Syrphidae sp2
			Syrphidae sp3
			Syrphidae sp4
	Tabanidae		*Tabanidae* sp1

Table 3.S2: Contrasts between initial fruit set and harvestable fruit produced by the different treatments of the hand pollination and exclusion experiment.

Response	Contrast		t-ratio	p-value
Fruit set	Hand pollinated + excluded	Hand pollinated + herbivory	0.59	0.828
	Hand pollinated + excluded	Ambient pollination + herbivory	2.49	**0.045***
	Hand pollinated + herbivory -	Ambient pollination + herbivory	1.89	0.157
Harvestable fruit	Hand pollinated + excluded	Hand pollinated + herbivory	0.97	0.597
	Hand pollinated + excluded	Ambient pollination + herbivory	3.07	**0.011***
	Hand pollinated + herbivory	Ambient pollination + herbivory	2.06	0.112

Table S3: Results of models testing the responses of pumpkin harvest metrics to biodiversity. Bold p-values indicate significant responses, asterisks indicate the strength of the responses.

Response	Predictors	F-value	p-value	DF_{num}/DF_{den}	R^2_m/R^2_c	Model type
Early fruit set	Treatment	1.91	0.165	2/33	0.26/0.39	Linear mixed effects model
	Pollinator visitation rate	2.05	0.165	1/23		
	Pollinator species richness	0.00	0.968	1/17		
	Proportion herbivory	1.10	0.308	1/19		
	Treatment*visitation rate	1.49	0.238	2/37		
	Treatment*species richness	3.35	**0.048***	2/31		
	Treatment*proportion herbivory	1.20	0.313	2/33		
Harvestable fruit	Treatment	1.96	0.158	2/32	0.19/0.38	Linear mixed effects model
	Pollinator visitation rate	0.24	0.631	1/16		
	Pollinator species richness	0.05	0.833	1/16		
	Proportion herbivory	0.95	0.342	1/19		
	Treatment*visitation rate	0.45	0.639	2/31		
	Treatment*species richness	2.01	0.151	2/31		
	Treatment*proportion herbivory	0.02	0.979	2/33		
Seed set	Treatment	1.26	0.320	2/11	0.26/0.76	Linear mixed effects model
	Pollinator visitation rate	0.08	0.785	1/12		
	Pollinator species richness	2.39	0.150	1/11		
	Proportion herbivory	0.10	0.757	1/12		
	Treatment*visitation rate	0.23	0.799	2/11		
	Treatment*species richness	1.29	0.314	2/11		
	Treatment*proportion herbivory	0.87	0.446	2/10		
Fruit girth	Treatment	2.26	0.144	2/13	0.20/0.52	Linear mixed effects model
	Pollinator visitation rate	0.36	0.561	1/11		
	Pollinator species richness	0.68	0.430	1/10		
	Proportion herbivory	0.01	0.915	1/10		
	Treatment*visitation rate	1.15	0.346	2/13		
	Treatment*species richness	0.09	0.919	2/12		
	Treatment*proportion herbivory	0.94	0.418	2/12		
Fruit weight	Treatment	0.65	0.536	2/16	0.23/0.35	Linear mixed effects model
	Pollinator visitation rate	0.01	0.908	1/11		
	Pollinator species richness	1.30	0.279	1/10		
	Proportion herbivory	0.00	0.951	1/10		
	Treatment*visitation rate	1.34	0.291	2/16		

	Treatment*species richness	0.06	0.946	2/15		
	Treatment*proportion herbivory	0.86	0.444	2/15		
Relative difference early fruit set (hand pollinated and herbivory excluded vs. hand pollinated and ambient herbivory)	Pollinator visitation rate	1.09	0.316	1/13	0.15	Linear model
	Pollinator species richness	1.02	0.332	1/13		
	Proportion herbivory	0.25	0.623	1/13		
Relative difference early fruit set (hand pollinated and herbivory excluded vs. ambient pollination and herbivory)	Pollinator visitation rate	0.14	0.719	1/14	0.32	Linear model
	Pollinator species richness	6.39	**0.024***	1/14		
	Proportion herbivory	0.03	0.871	1/14		

Thirsty bees: a bee from the genus *Megachile* drinking nectar from a pigeon pea flower, with green pods visible in the background. Pigeon pea flowers during the dry season in Malawi, and therefore could provide important nectar and pollen resources for bees during a period when these resources would otherwise be scarce.

Chapter 4

Higher bee abundance, but not pest abundance, in landscapes with more agriculture on a late-flowering legume crop in tropical smallholder farms

Abstract

Background

Landscape composition is known to affect both beneficial insect and pest communities on crop fields. Landscape composition therefore can impact ecosystem (dis)services provided by insects to crops. Though landscape effects on ecosystem service providers have been studied in large-scale agriculture in temperate regions, there is a lack of representation of tropical smallholder agriculture within this field of study, especially in sub-Sahara Africa. Legume crops can provide important food security and soil improvement benefits to vulnerable agriculturalists. However, legumes are dependent on pollinating insects, particularly bees (Hymenoptera: Apiformes) for production and are vulnerable to pests. We selected 10 pigeon pea (Fabaceae: *Cajunus cajan* (L.)) fields in Malawi with varying proportions of semi-natural habitat and agricultural area within a 1 km radius to study: (1) how the proportion of semi-natural habitat and agricultural area affects the abundance and richness of bees and abundance of florivorous blister beetles (Coleoptera: *Melloidae*), (2) if the proportion of flowers damaged and fruit set difference between open and bagged flowers are correlated with the proportion of semi-natural habitat or agricultural area and (3) if pigeon pea fruit set difference between open and bagged flowers in these landscapes was constrained by pest damage or improved by bee visitation.

Methods

We performed three, ten-minute, 15 m, transects per field to assess blister beetle abundance and bee abundance and richness. Bees were captured and identified to (morpho)species. We assessed the proportion of flowers damaged by beetles during the flowering period. We performed a pollinator and pest exclusion experiment on 15 plants per field to assess whether fruit set was pollinator limited or constrained by pests.

Results

In our study, bee abundance was higher in areas with proportionally more agricultural area surrounding the fields. This effect was mostly driven by an increase in honeybees. Bee richness and beetle abundances were not affected by landscape characteristics, nor was flower damage or fruit set difference between bagged and open flowers. We did not observe a positive effect of bee density or richness, nor a negative effect of florivory, on fruit set difference.

Discussion

In our study area, pigeon pea flowers relatively late - well into the dry season. This could explain why we observe higher densities of bees in areas dominated by agriculture rather than in areas with more semi-natural habitat where resources for bees during this time of the year are scarce. Therefore, late flowering legumes may be an important food resource for bees during a period of scarcity in the seasonal tropics. The differences in patterns between our study and those conducted in temperate regions highlight the need for landscape-scale studies in areas outside the temperate region.

4.1 Introduction

Despite covering 16% of global agricultural area and supporting some of the world's most vulnerable populations, tropical smallholder agriculture has received relatively little attention in agroecological research compared to large-scale agriculture in temperate regions (Steward et al., 2014). Smallholder agriculture often exists within the world's most biodiverse but also threatened landscapes, creating a necessity to develop smallholder agriculture in sustainable ways that can both improve food security, whilst also safeguarding biodiversity and ecosystem functions (Newbold et al., 2015; Samberg et al., 2016).

Insect communities in agricultural fields are driven by field management and the composition of the surrounding landscape (Martin et al., 2019). These insect communities are known to be of large importance to agricultural productivity. Pollination, particularly by bees, is a key ecosystem service that is essential for enhancing the production of fruits and seeds in a majority of crops (Garibaldi et al., 2013). On the other hand, herbivory of crops by insect pests is estimated to cause more than 10% of pre-harvest losses (Oerke, 2006). A recent meta-analysis has shown that pollinator density and richness benefits from a more complex landscape containing more semi-natural habitat (SNH) (Dainese et al., 2019). For insect pests, this pattern is more inconsistent between studies than for pollinators (Karp et al., 2018). Some studies show decreasing pest pressure with increasing semi-natural habitat, often attributed to increased occurrence of natural enemies in landscapes with more semi-natural habitat (Chaplin-Kramer & Kremen, 2012). Others suggest that semi-natural habitats can be a source of pests for crops (Rusch et al., 2013) as, for example, non-crop habitat can be a refuge in which insect pests can survive outside of the growing season, only to recolonize crops once they start growing again (Bianchi, Booij & Tscharntke, 2006; Martin et al., 2019).

Despite being well studied in temperate larger-scale agriculture, larger knowledge gaps still exist on the understanding of landscape effects on beneficial and damaging insects in tropical smallholder agriculture, particularly in Africa (Otieno et al., 2020a). Even if landscape-scale studies in Africa are conducted, they usually focus on more commercially important crops, such as coffee and cotton (Vanlauwe et al., 2014). Crops more important to household food security are understudied in comparison, despite Africa's high rates of food insecurity (Sasson, 2012; Graeub et al., 2016). Food insecurity in Africa is caused in part by large crop losses due to pests, with farmers having limited access to pest management strategies, such as pesticides (Abate, van Huis & Ampofo, 2000). Though pesticide use has increased in Africa in the last decades, pesticide application may not necessarily reduce crop losses by pests despite significant costs to the environment and to human health, particularly in sub-Saharan Africa, where lack of access to safety equipment and knowledge on how to correctly apply pesticides increases personal health risks to farmers and reduces the potential pest-control benefits (Oerke, 2006; de Bon et al., 2014; Isgren & Andersson, 2021). This further highlights the need to understand what drives pest densities on important crops in the region in order to successfully manage them sustainably (De Bon et al., 2014). Particularly, legume crops are an important addition to cereal staple crops for providing food security and nutrition in sub-Saharan Africa (Otieno et al., 2020).

Pigeon pea (Fabaceae: *Cajunus cajan* (L.)) is a legume crop with the potential to improve livelihoods of smallholder farmers due to its unique combination of high nutritional value, drought tolerance and nitrogen-fixing, soil-improving properties (Odeny, 2007). However, the adoption of pigeon pea in our study area of northern Malawi has been constrained by perceived yield losses by farmers due to a flower-feeding blister beetle (Coleoptera: *Melloidae*) (Mhango, Snapp & Phiri, 2013). The most commonly observed blister beetle on pigeon pea is a *Hycleus* species (Appendix 4.1), which often feeds on the entire flower, including the reproductive parts. The damaged flower, therefore, is unable to set fruit and produce any yield. *Hycleus* sp. is common pest on legume crops in Africa (Lebesa et al., 2012). Average production in Malawi, one of the larger pigeon pea growing regions in Africa, is less than a quarter of potential yields (Odeny, 2007). In general, yield losses of pigeon pea due to insect pests range from 10-70% (Otieno et al., 2020), though the blister beetles are viewed as the most constraining to yield (Mhango, Snapp & Phiri, 2013). Pigeon pea can be up to 70% self-pollinating (Saxena, Singh & Gupta, 1990). However, pollination has been shown to significantly improve fruit set of pigeon pea compared to unvisited flowers. In particular, bees of the genera *Megachile* and *Xylocopa* have been found to be responsible for 20-90% of cross-pollination in this crop, with the remainder being pollinated by other bee species or pollinating flies (Fohouo, Pando & Tamesse, 2014; Otieno et al., 2015, 2020b).

We investigated how the proportion of semi-natural habitat and agricultural area within a 1 km radius around ten pigeon pea fields affects (1) the abundance and species richness of bees (Hymenoptera: Apiformes) and the abundance of florivorous blister beetles, and (2) if the proportion of flowers damaged and fruit set difference is correlated with the proportion of agricultural area or semi-natural habitat. Additionally, using an exclusion experiment, we (3) investigated if differences in fruit set between visited (open) and unvisited (bagged) flowers set in these landscapes were constrained by pest damage and or improved by bee visitation.

4.2 Materials & methods

Study area and field selection

We conducted our study from May to August 2019 in Mzimba district, Northern Malawi. We selected ten already existing pigeon pea fields. We were granted verbal permission for conducting the research on each of the farmer's private fields. Their names are: Isobel Lubanda, Adams Tembo, Mercillina Tembo, Ireen Mhoni, Simon Chitaya, Jacob Mvula, Jane Salanda, Lyna Njunga, Goodson Moyo, Moles Thupa. The farmers are not represented by a company or a farming cooperation, but were in contact with the authors through the SFHC (Soils, Food and Healthy Communities) organization. We have no form of written permission for the conduction of the research. In all the ten fields, the pigeon pea crop had been planted at the onset of rains in December 2018, and were initially intercropped with groundnut (Fabaceae:

Arachis hypogaea L.). By the time we began data collection, all the groundnut had already been harvested from all the fields. All pigeon pea fields selected were planted with a local medium-maturing variety. The peak of bloom of this pigeon pea variety is in May in our system. The duration of the flowering period can depend on the climatic conditions, but in our region, the bloom lasted about 4 weeks.

Malawi is located in the seasonal tropics and experiences a marked peak in rainfall from December until the end of February. In the months when we performed our experiment, there was no rainfall, as is typical during this time of year (Mungai et al., 2016). The pigeon pea in our study region is a rain-fed crop and is not irrigated or watered in any way, especially as pigeon pea is considered drought-resistant (Odeny, 2007). All field activities, including land preparation and weeding, were managed traditionally by hand. Farmers did not apply any chemicals such as herbicides and pesticides on their fields.

Fields ranged from 166 m^2 to 577 m^2 in size, with mean field size being 332 m^2. This is representative of field sizes of such a crop in the study region, where the average smallholder total farm size ranges from only 0.5 to 1.4 hectares (FAO, 2018). Field size did not correlate significantly with the proportion of semi-natural area ($F_{2,6}$ = 2.08, R^2 = 0:21, p = 0.683) nor with the proportion of agricultural area ($F_{2,6}$ = 2.08, R^2 = 0:21, p = 0.088) in the 1km radius surrounding our fields. Field margins were vegetated with non-flowering weeds, grass or shrubland. As it was the dry season during data collection, there were no flower margins on the fields. The surrounding agricultural fields where mostly empty, as the main staples in Malawi, such as maize, was already harvested by this time in the season. Surrounding semi-natural habitat was mainly composed of shrubland and forest. Generally, these are not actively managed but may to some extent be exposed to exploitation by people due to economic activities such as collection of firewood and grazing of livestock.

We aimed to choose sites which were at a distance of at least 2 km from each other. However, one site was found to have too large an overlap with two others within a 1km radius, with the center of this field being 883 and 885 m away from the center of the nearest and second-nearest site, respectively. Therefore, this site was subsequently dropped from any landscape analyses (Figure 4.1). The remaining fields were located within two non-correlating gradients of semi-natural habitat (ranging from 2% to 32%), and agricultural area (ranging from 25% to 75%) within a 1 km radius surrounding the fields. ($F_{1,7}$ = 0.56, R^2 = 0:07, p = 0.480). The 1 km radius was chosen, because we wanted our sites to be independent from each other and prevent spatial autocorrelation. Additionally, since bees are central place foragers, and their foraging ranges are limited, most bees would be sensitive to landscape differences within the 1 km radius (Steffan-Dewenter et al., 2002; Zurbuchen et al., 2010). Other habitats in our study area included some built-up areas (such as buildings and roads) and bare rock (mostly on hilltops). Although honeybees are native to the area (Requier et al., 2019), we found no honeybee hives in any of the fields across our study area. Moreover, none of the farmers we worked with kept honeybees on any of their fields. In our study area, honeybees are rarely actively placed in fields by farmers, but rather encouraged to nest nearby by placing traditional beehives near fields where they may be passively colonized by a honeybee colony (Appendix 4.2) (Requier et al., 2019). To our knowledge, there were no such hives placed near any of our study fields.

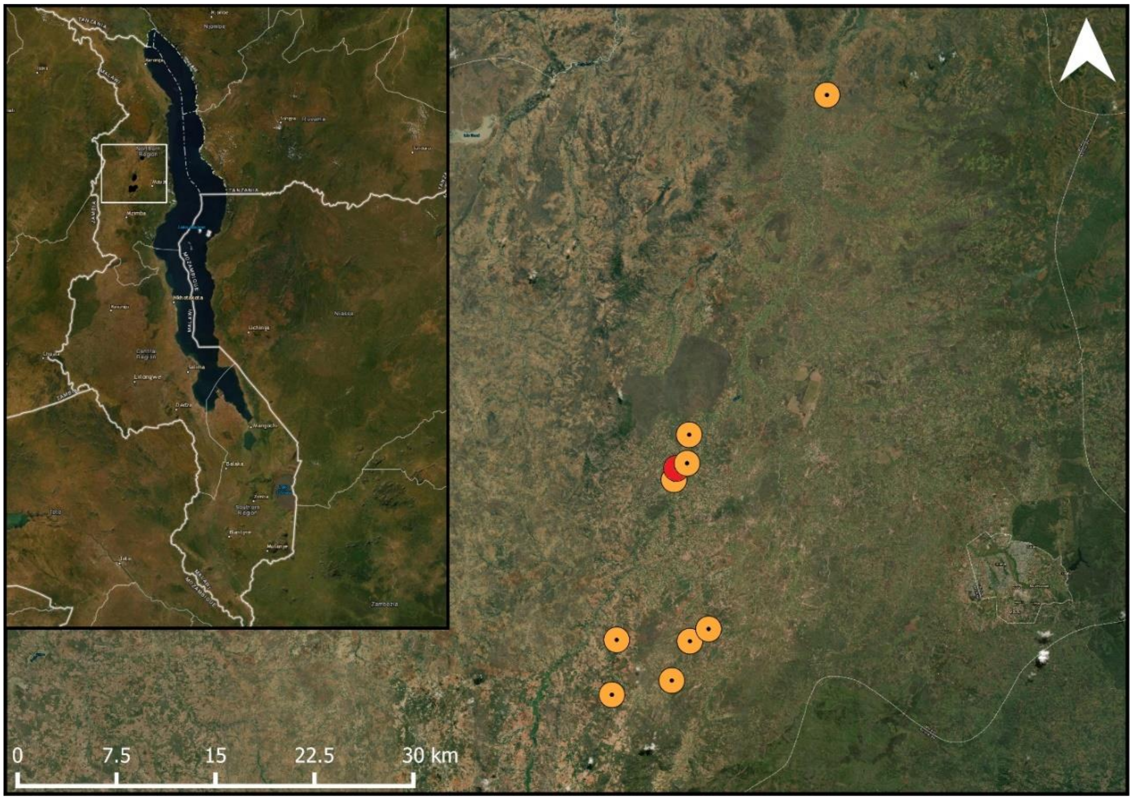


Figure 4.1: Studied pigeon pea fields in the landscape. Map showing the location of the study fields within its one-kilometre buffer within the study area. The study area marked in red had too much overlap within the one-kilometre radius with the adjacent fields. ESRI Satellite is used as a basemap (ArcGIS Pro 2.6; Esri, Redlands, CA, USA).

Landscape analysis

For the land use and land cover classification, we acquired three cloud-free Sentinel-2 satellite images from 2019 from the Copernicus Open Access Hub (https://scihub.copernicus.eu/dhus/#/home). One image was taken on November 8th 2019, and two are from November 15th 2019, which is in the late dry season in Malawi. Though this is not the same time as our field study period, the images still show the general land use and land cover in our study area and we assume this has not changed significantly between May and November. The methodology for land cover analysis involved images pre-processing, supervised maximum likelihood classification, post-classification, and accuracy assessment (Appendix 4.3). First, we pre-processed the Sentinel-2 images, which consisted of the atmospheric correction, image resampling, layer stacking, seamless mosaic, and image subsetting. Then, we conducted Maximum Likelihood classification using training samples generated from fieldwork and Google Earth. The classification includes six classes, which are: (1) bare land/road; (2) shrubland; (3) agricultural land; (4) water/riverbed; (5) settlement; (6) trees/forest. However, in this study, we only used classification (2) shrubland and (6) trees/forest together which we defined as semi-natural habitat (SNH) and (3) agricultural area. Finally, we performed post-classification and accuracy assessment. The overall accuracy of the classification is 85.1%, with a Kappa Coefficient of 0.817. We used tabulate area tools in ArcGIS to get the area and proportion of the types of land use and land cover for all buffer zones of each site (ArcGIS Pro 2.6; Esri, Redlands, CA, USA).

Bee identification

Captured bees were identified to genus or subgenus level with the guides from Michener (2007) and Eardley, Kuhlmann & Pauly (2010) and grouped by (morpho)species. Captured bees are stored at the Biocentre, University of Würzburg, Germany.

Flower exclusion and fruit set data

At each site, we marked 15 pigeon pea plants in a continuous line from the edge of the field inwards. On each plant, we tagged one cluster of flowers as the open control. This cluster was accessible to all visitors, both pollinators and herbivores. On the same plant, we then paired this tagged cluster with another cluster of flowers to which all visitors (pollinators as well as herbivores) were excluded using a 9_12 cm organza bag. The number of flowers in the tagged and bagged clusters where counted. The bags had a mesh size of 0.6 mm - small enough to exclude any insect. Although exclusion of pollinators and pests in different treatments would have been ideal, this could not be done, since the beetles feed on the flowers, during the same time that pollinators are visiting them. Our hypothesis was that if the fields experience high pest pressure, bagged clusters will perform better, as they are protected from herbivory. On the other hand, we assumed that in fields where there is a large amount of ambient pollination and low flower damage by herbivores, the open clusters would outperform the bagged ones. In fields with little ambient pollination, or where the benefits of pollination are cancelled out by pest damage, open and bagged flowers would perform similarly. Plants were tagged and bagged upon the first visit to the field before the flowers had opened and we removed the bags when all the flowers in the cluster had finished blooming, which took approximately two weeks. After removing the bags, the pigeon pea pods were left to mature in the field.

Fruit set data was collected from the 3rd of July to the 2nd of August 2019. To assess fruit set (the proportion of flowers turning into pods) as a measure of pollinator effectiveness, we counted the number of flowers that were originally present on the tagged clusters, and then counted the number of pods formed in the same clusters. The number of pods formed divided by the number of flowers was taken as a measure of fruit set per cluster. In one field, damage by cattle grazing destroyed the tagged plants and we were unable to collect data on fruit set there.

Blister beetle damage assessment

To get a measure of the proportion of flowers damaged by blister beetle herbivory/florivory, we assessed flower damage three times at eight of the sites and twice at two of the sites. We used the open cluster of the 15 pigeon pea shrubs we tagged in each field for this. We counted the number of flowers per cluster and the number of these flowers that showed signs of chewing herbivory typical of blister beetles. With this data we calculated the proportion of flowers damaged by blister beetles.

Data analysis

To test whether landscape composition affected bee and blister beetle abundance, we summed the number of individuals across all three transects. For bee richness, we used the cumulative bee richness across dates per field. We first tested if bee abundance, bee richness and blister beetle abundance were independent of planting density across transects or field size (Appendix 4.4). We then tested how the proportion of semi-natural habitat and agricultural area within the 1 km radius affected bee and blister beetle abundance using a linear regression. To test whether landscape composition affected bee richness, we used the bee richness at each site and again tested this against the landscape variables using a linear regression. To test to what extent our patterns where driven by the presence of honeybees (*Apis mellifera* L.), the most abundant pollinator in our system, we tested bee abundance against the two landscape variables including and excluding honeybees from the analysis.

To test if landscape variables affected blister beetle damage in our fields, we calculated for each of the 15 plants the mean proportion of flowers damaged by herbivory across the flowering season from the three dates. Since our data were zero-inflated (no flowers damaged), we used a negative-binomial mixed model using the `glmer.nb' call from the package `lme4' (Bates et al., 2019). We tested the mean proportion of flowers damaged against the proportion of semi-natural habitat and agricultural area. Since we had repeated measures within fields, we used field as a random factor in this model.

To test whether landscapes affected the differences in fruit set between bagged and open clusters, we calculated the proportion of flowers that set fruit for each cluster. Then, we subtracted the proportion of fruit set of the bagged cluster from that of the open cluster. Again, using the package `lme4' (Bates et al., 2019), we calculated mixed effects models testing the difference in fruit set against the two landscape variables, using field as a random factor to account for repeated measures per field. In this analysis, we had to exclude 31 out of 120 plants due tampering or missing tags.

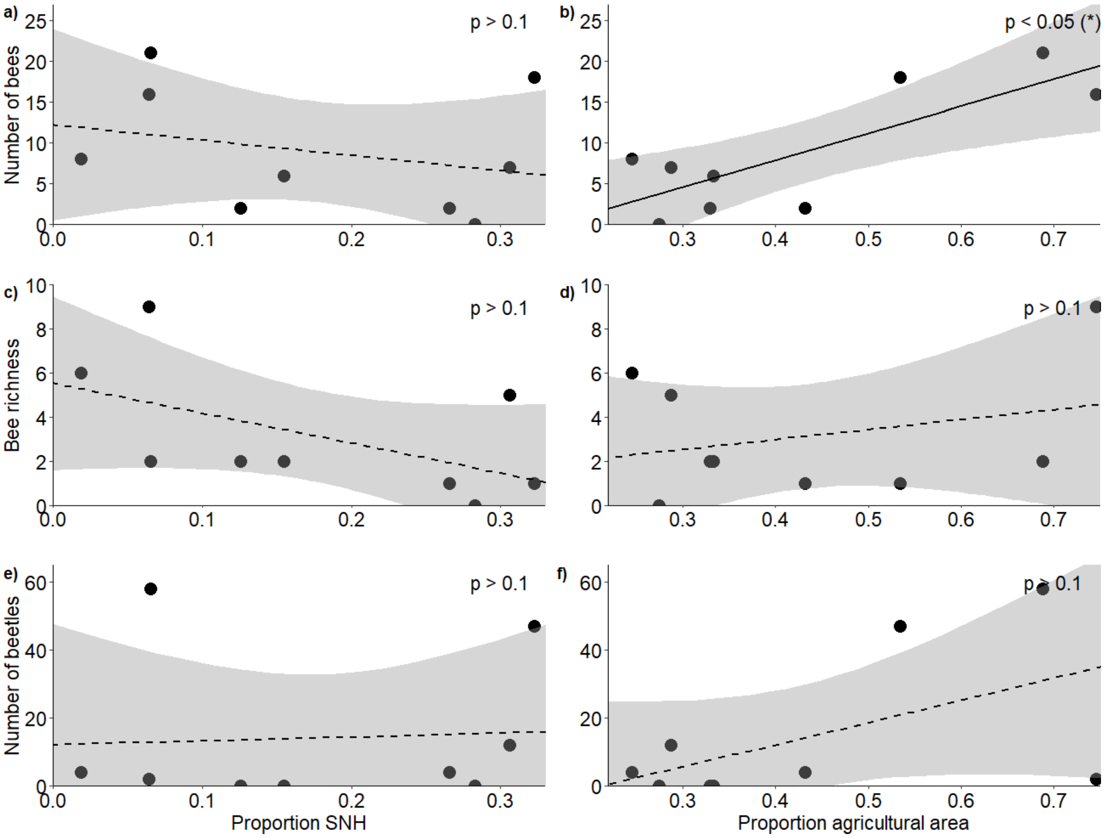
Finally, to calculate the effect of bee visitation and beetle damage on fruit set difference between the bagged and open clusters, we used mixed models. To do this, we took the total number of bees recorded at each site, and divided this by the total number of pigeon pea shrubs across our transects. This gives us bee density per crop plant, which we used as a proxy for bee visitor density per pigeon pea shrub. We then calculated the effect of bee density, bee richness and the proportion of flowers damaged per plant on the difference in fruit set between the paired clusters, using field as a random factor to account for nestedness. We chose to use flower damage, rather than beetle abundance or density in this model because we deemed it a more concrete representation of the pest pressure the plants experienced, though blister beetle abundance and the proportion of damage was correlated ($F_{1,418} = 4.88$, $R^2 = 0.01$, $p = 0.028$). In this analysis, we had to exclude 34 out of 135 pigeon pea shrubs due to tampering or missing tags.

All models were tested for and met the assumptions of distributions, normality (of residuals) and heteroscedasticity. All statistical analyses were performed in R version 4.0.1 (R Core Team, 2020).

4.3 Results

Landscape effects on bee abundance, bee richness, and blister beetle abundance

In total, we observed 84 bees of 13 species (Appendix 4.5) and 127 blister beetles across the five hours of transects during our study period. The proportion of semi-natural habitat within a 1 km radius of the fields did not affect bee abundance ($F_{2,6} = 5.53$, $R^2 = 0.65$, $p = 0.775$) (Figure 4.2A) or richness ($F_{2,6} = 1.38$, $R^2 = 0.32$, $p = 0.203$) (Figure 4.2C), and neither did it affect blister beetle abundance ($F_{2,6} = 1.58$, $R^2 = 0.35$, $p = 0.538$) (Figure 4.2E). The proportion of agricultural area positively affected bee abundance ($F_{2,6} = 5.53$, $R^2 = 0{:}65$, $p = 0.0209$) (Figure 4.2B), though this pattern was primarily driven by higher honeybee densities at high-agricultural area sites, as solitary bees alone did not respond significantly to landscape factors. The pattern was additive, as honeybee densities alone did also not show significant patterns, and it was just the analysis with honeybees and solitary bees together that showed a result (Appendix 4.6). However, agricultural area did not affect bee richness ($F_{2,6} = 1.38$, $R^2 = 0.32$, $p = 0.683$) (Figure 4.2D) nor blister beetle abundance in the fields ($F_{2,6} = 1.58$, $R^2 = 0.35$, $p = 0.127$) (Figure 4.2F) (Table 4.1).



(Previous page) Figure 4.2: Response of bees and blister beetles to landscape variables. Relationship (±95% CI) between the proportion of semi-natural habitat in the surrounding landscape and (A) bee abundance, (C) bee richness and (E) blister beetle abundance, as well as the relationship between the proportion of agricultural area and (B) bee abundance, (D) bee richness and (F) blister beetle abundance.

Table 4.1: Model summaries of animal responses to landscape composition.
Model summary of linear models assessing bee and blister beetle responses to landscape composition (proportion semi-natural habitat and proportion agricultural area) (n = 9)

Response	**F-statistic (2,6)**	**Multiple R^2**	***p*-value**	**Predictor**	**t-value**	***p*-value**
Bee abundance	5.53	0.65	0.043	**SNH**	-0.30	0.775
				Agricultural area	3.11	**0.021***
Bee richness	1.38	0.32	0.321	**SNH**	-1.43	0.203
				Agricultural area	0.43	0.683
Blister beetle abundance	1.58	0.35	0.281	**SNH**	0.65	0.538
				Agricultural area	1.77	0.127

Landscape effects on blister beetle damage and fruit set difference

The proportion of flower damage ranged from zero to 0.36, with a mean of 0.06. There was no effect of the proportion of semi-natural habitat nor agricultural area on the proportion of flowers damaged by blister beetles on the tagged open clusters (Appendix 4.7). The number of open clusters that a higher proportion of damage than 0.05 varied from 2 to 12 clusters per site, but this did not correlate to either proportion of semi-natural habitat ($F_{2,6} = 0.01$, $R^2 = 0.001$, $p = 0.923$) or agricultural area ($F_{2,6} = 0.01$, $R^2 = 0.001$, $p = 0.998$). The proportion of fruit set on open clusters ranged from 0 (none of the flowers set fruit) to 1 (all flowers set fruit) with a mean fruit set proportion of 0.37. The proportion of fruit set on bagged clusters also ranged from 0 to 1 with a mean fruit set proportion of 0.26. Fruit set difference (open-bagged) ranged from -1 to 1 and had a mean of 0.11. There was no effect of the landscape variables on the fruit set difference between the open and bagged flower clusters (Table 4.2) (Appendix 4.7).

Table 4.2: Summaries of the models assessing the landscape composition on the proportion of damaged flowers and fruit set difference.

Summary of the linear mixed models assessing the effect of landscape composition (proportion semi-natural habitat and proportion agricultural area) on the proportion of damaged flowers and the difference in fruit set between the open and the bagged treatment.

Response	Total number of observations	Number of groups (n)	Predictor	z-value	*p*-value
Proportion damaged flowers	135	9	**SNH**	0.05	0.960
			Agricultural area	-0.78	0.439
Difference in fruit set (open - bagged)	89	8	**SNH**	-1.83	0.125
			Agricultural area	-0.19	0.853

Effects of bees and blister beetle damage on fruit set difference

We observed no effects of bee density or bee richness nor of blister beetle damage on the proportional difference in fruit set (Table 4.3) (Appendix 4.8).

Table 4.3: Model assessing the effect of bees and blister beetles on fruit set difference.

Summaries of the linear mixed model assessing the effect of bee density, bee richness and proportion of damaged flowers on the difference in fruit set between bagged and open flower clusters.

Response	Total number of observations	Number of groups (n)	Predictor	t-value	*p*-value
Fruit set differences (open – bagged)	101	9	**Bee density**	0.36	0.734
			Bee richness	1.45	0.196
			Proportion of flowers damaged	1.92	0.058

4.4 Discussion

In our study, we aimed to investigate how differences in landscape composition may drive ecosystem services and disservices on smallholder farms in the tropics. We find that increasing agricultural area surrounding our crop increases the abundance of bees, driven primarily by an increase in honeybees, on our studied fields. This seems in contrast with most studies that indicate that increasing semi-natural habitat in the surrounding area increases pollinator abundance in crop fields (Kennedy et al., 2013). Another study on pigeon pea, conducted in Kenya, also showed that fields located closer to semi-natural habitat also had a lower abundance of pollinators (Otieno et al., 2011), indicating that such a pattern may be more common in the African seasonal tropics. In our system, pigeon pea flowers during May, which is well into the dry season in our study system (Mungai et al., 2016). In general, bee abundance in our study system was low, which is expected in the seasonal tropics where the peak in insect activity is usually on the onset of the wet season, which in our study area would be around December (Kishimoto-Yamada & Itioka, 2015). Since abundances were mostly driven by honeybees, it can be assumed this could be due to the larger number of colonies nesting in agricultural areas compared to areas with less agricultural area. Relative to solitary bees, honeybees also have a larger foraging range, which means they may be more successful in finding resource-rich flowering fields in a resource-poor environment over larger distances from their nests. Additionally, they recruit colony mates to forage there, which is not the case for solitary bees, which do not live in colonies and have more limited foraging ranges (Steffan-Dewenter & Kuhn, 2003; Zurbuchen et al., 2010). Considering the resource scarcity during our study period, it is reasonable to observe higher densities of bees in agricultural areas, where there are still some flowering crops providing resources to bees, which would be almost absent in semi-natural areas during this time of year.

Aside from one site, most of our sites showed similar performance between bagged and open clusters. In our study, damage by blister beetles did not predict differences in fruit set between bagged and open flower clusters. Though we do not rule out that blister beetles contribute to losses in fruit set, our data suggests blister beetles are not as significant a pest on pigeon pea in our study area as commonly believed. Farmers often state blister beetles as a significant constraint to growing pigeon pea in our study area, perhaps because they are conspicuous (Mungai et al., 2016). In our study, we used existing pigeon pea fields, and did not plant the fields specifically. Since no pigeon pea fields existed in areas where farmers did not grow pigeon pea due to extensive pest damage, we did not investigate those areas where blister beetle densities are perceived to be highest. It could be that the contrast between our sites is not large enough to observe possible differences since these higher extremes are not included. This could contribute to the fact that we did not observe any differences in blister beetle abundance on pigeon pea fields and resulting flower damage within the scope of our study, and pest damage was similar across sites.

Increasing bee densities did not improve the fruit set of open-pollinated flower clusters compared to bagged clusters. This is in contrast with many studies showing improved agricultural production with increased flower visitation, particularly on small farms like those in our study system (Garibaldi et al., 2016), and also on an earlier study on pigeon pea (Otieno et al., 2011). Additionally, we did not find an effect of bee richness on fruit set, which is also not consistent with other studies on pollinator dependent crops (Garibaldi et al., 2016; Dainese et al., 2019). In our study, higher bee abundances were mostly driven by increased honeybee abundance. Previous studies indicate that honeybee visitation often does not benefit crop yield (Garibaldi et al., 2013), which could explain the lack of increased fruit set in our sites with higher bee abundance. Numerous studies have shown that pollination and pest damage may interactively shape crop yields (Lundin et al., 2013; Bartomeus, Gagic & Bommarco, 2015). In our study, such effects may also be at play, but we cannot distinguish them since we were unable to test the interactive effects due to low sample size.

In our study area, honeybees were the most abundant bees, and therefore important in driving higher bee abundances in agricultural areas. In contrast to temperate systems, in Africa, up to 90% of honeybee colonies occur in the wild, and honeybee keeping as a practice is still underdeveloped and small-scale, with no impact of humans on breeding (Requier et al., 2019). Therefore, like both social and solitary wild bees in temperate systems, honeybees in our system have conservation value as a part of the local bee biodiversity (Dietemann, Pirk & Crewe, 2009). Though bee visitation did not directly benefit fruit set of this particular crop, the fact that a crop flowers during this time of year may still be important, as this could provide an important flower resource, particularly for social bees, that are still active during this season of scarcity in our study system. If it helps individual bees and honeybee colonies to survive this time of the year, it may benefit farmers on the long run if these pollinator populations are conserved until the next growing season when the farmers may be growing early flowering crops that are more strongly pollinator dependent.

4.5 Conclusions

Many studies show the effect of landscape composition on the abundance and richness of pollinators and pests, and that particularly in the case of pests, these patterns are not always consistent (Kennedy et al., 2013; Karp et al., 2018). Our study shows that these patterns may be quite different in tropical smallholder agriculture compared to better studied tropical agroforestry and temperate annual cropping systems. Differences in patterns in comparison to temperate systems highlight the necessity to study different climatic and growing contexts better. Our study indicates that late-flowering crops provide an important floral resource during a scarce period in the seasonal tropics and are therefore an important component in sustainable agriculture in these parts of the world.

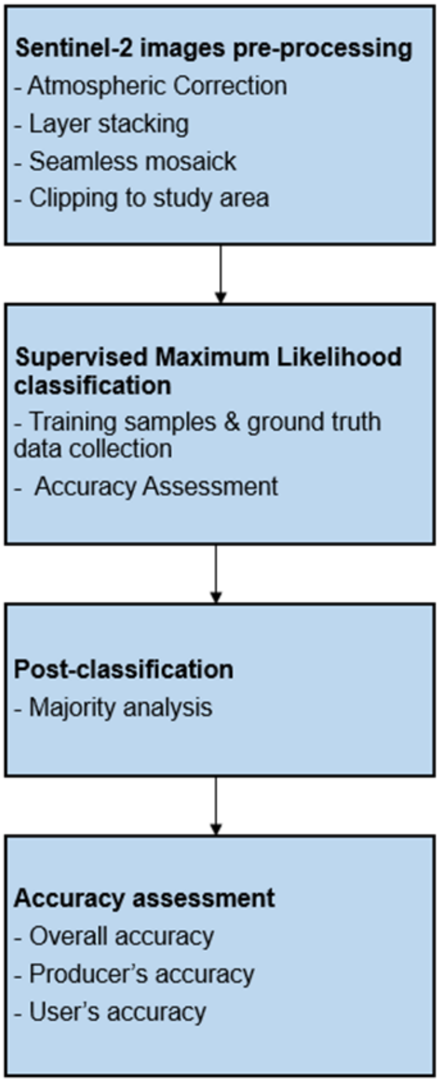
Appendix 4

Appendix 4.1: Blister beetle found on pigeon pea flowers.

Photograph of the *Hycleus* spp. found feeding on pigeon pea flowers. Photo taken in May 2019 at one of the study sites.

Appendix 4.2: Traditional beehive.

Photograph of a traditional honeybee hive as the farmers in our study area make them. They are hung in trees and not colonies are not actively placed in them –Farmers wait until they are colonized. The photo taken in February 2020 on a farm in Chiluzwazwa Ngwira, Mzimba district, Northern Malawi (not one of the study sites included in this study).



Appendix 4.3: Flowchart of land use and land cover classification approach.

Appendix 4.4: Model summary of linear models assessing bee and blister beetle responses to planting density and field area (n=10)

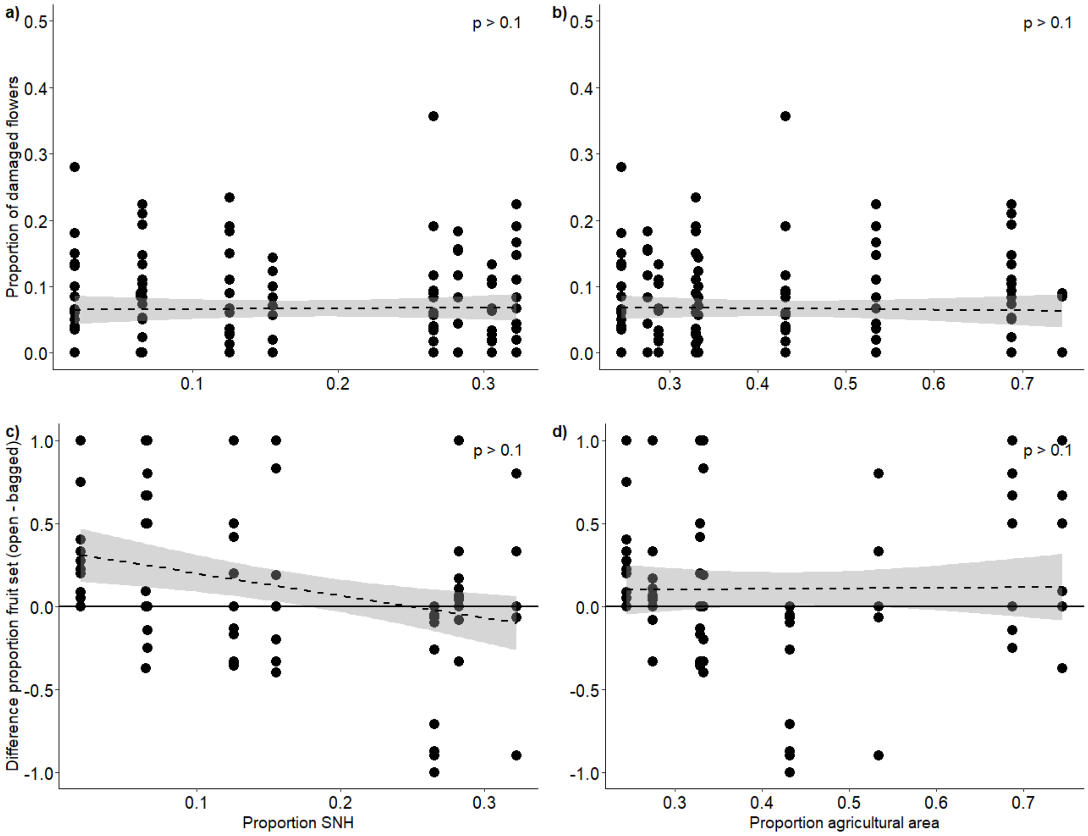
Response	F-statistic (2,7)	Multiple R^2	p-value	Predictor	t-value	p-value
Bee abundance	1.89	0.35	0.220	**Shrubs per 75m**	-1.08	0.316
				Field area	1.69	0.135
Bee richness	0.03	0.01	0.9681	**Shrubs per 75m**	-0.12	0.912
				Field area	0.24	0.82
Blister beetle abundance	1.81	0.34	0.233	**Shrubs per 75m**	-1.388	0.208
				Field area	1.39	0.206

Appendix 4.5: Bee species collected across all sites and transects. Captured bees are stored in the Biocentre of the University of Würzburg.

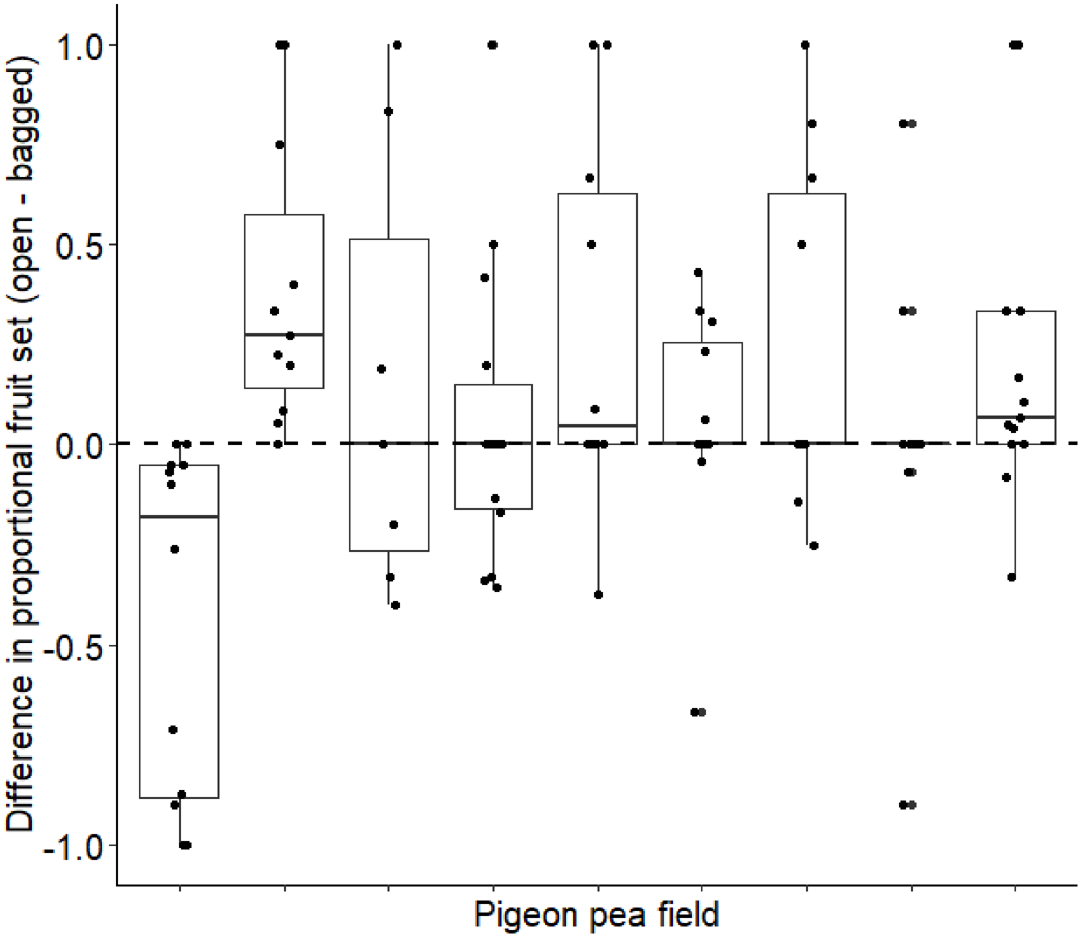
Family	**Genus (subgenus)**	**Species**	**Number of individuals**
Apidae	Apis	*A mellifera* (Linneus)	52
	Xylocopa	*Sp1*	3
		Sp2	1
Megachilidae	Megachile	*M. caricina* (Cockerel)	1
		Sp1	4
		Sp2	2
		Sp3	1
		Sp4	6
		Sp5	2
		Sp6	5
		Sp7	2
		Sp8	1
Halictidae	Nomia (Crocisaspedia)	*Sp1*	4
Total			**84**

Appendix 4.6: Model summary of linear models assessing the response of solitary and honeybee abundance responses to landscape composition (proportion semi-natural habitat and proportion agricultural area) (n=9).

Response	**F-statistic (2,6)**	**Multiple R^2**	**p-value**	**Predictor**	**t-value**	**p-value**
Solitary bee abundance	1.45	0.33	0.506	**SNH**	-1.39	0.240
				Agricultural area	0.57	0.588
Honeybee abundance	1.91	0.39	0.228	**SNH**	0.70	0.510
				Agricultural area	1.95	0.099



Appendix 4.7: Relationship between proportional fruit set difference and bee visitation and blister beetle damage. Relationship (+95% CI) between the difference in fruit set between open and bagged clusters and a) bee density, b) bee richness and c) proportional damage by blister beetles. Points above the horizontal line indicate plants where the open clusters performed better than bagged clusters, points below the horizontal line indicate plants where bagged clusters performed better than open clusters.



Appendix 4.8: Proportional fruit set difference per site. Fruit set difference between open and bagged clusters at the 9 sites where this was measured. Points above the horizontal line indicate plants where the open clusters performed better than bagged clusters, points below the horizontal line indicate plants where bagged clusters performed better than open clusters (*n* = 101).

African emigrant: or *Catopsilia florella* drinking nectar from the flowers of a weed growing on field edges in Mzimba district, Malawi. A ubiquitous generalist and a strong disperser, this species was by far the most commonly observed butterfly in our study region.

Chapter 5

Local and landscape scale conversion of woodland to farmland and agroecological practices shape butterfly communities in tropical smallholder landscapes

Abstract

1. The conversion of (semi-)natural habitat (SNH) to farmland and the subsequent management has strong, often negative, impacts on biodiversity. In tropical smallholder agricultural landscapes, the impacts of agriculture on insect communities, both through landscape conversion and subsequent land management, is understudied. Agroecological management has social and agronomic benefits for smallholders. Although ecological co-benefits 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 (semi-natural) shrubland and smallholder-managed farmland sites located across a gradient of SNH proportion within a 1 km radius and increasing agroecological pest and soil management practices as well as flowering plant species richness on farmlands.
3. Farmland had lower butterfly abundances and approximately half the species richness than shrubland. Farmland communities had, on average, a larger wingspan than shrubland communities. Surprisingly, increasing SNH decreased the abundance of butterflies in both habitats, but this effect was driven by the presence of the most dominant species who made up 66 % of all butterflies. In contrast, species richness increased with increasing SNH proportion. Butterfly species assemblages were distinct between shrub- and farmland and shifted across the SNH gradient.
4. Farmland butterfly abundance, but not species richness, increased with increasing flowering plant species richness on farms. Increasing agroecological pest management per hectare decreased the abundance of the dominant species, but not of rarer species. However, increasing agroecological soil management increased the abundance of these rarer species.
5. *Synthesis and applications:* We show that diversified agroecological soil practices and flowering plant richness benefits butterflies on farmland sites. However, negative effects of woodland conversion, both on landscape and local scales on butterflies suggest that on-farm measures will have limited effects if remaining semi-natural habitats continue to decline. Therefore, we call for more active protection of remaining semi-natural habitats, in tandem with agroecological practices such as increased soil services and flowering plants to conserve butterflies whilst benefiting smallholders.

5.1 Introduction

Converting natural habitats to agriculture and subsequently intensifying the agricultural landscapes - with monocultures of few genetically similar crops, increased use of synthetic inputs, and increased mechanisation - 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 change and subsequent agricultural management (but see: Jew et al., 2015; Tommasi et al., 2021; Schmitt et al., 2021), even though climatic, geographical and management differences may play an important role (Crossley et al., 2021).

Butterflies (Lepidoptera: Rhopalocera) are indicators of environmental change (Hill et al., 2021), and are amongst 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, conversion from natural to agricultural habitats can result in butterfly communities with distinct species composition and traits (Schmitt et al., 2021), which has implications for butterfly conservation across the wider landscape. Since landscape change does not affect all butterfly species equally, this results in shifts in community life-history traits. For instance, increasing land-use intensity favour large-winged butterflies (Börschig et al., 2013). Additionally, species with higher habitat or larval host plants 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 (Steffan-Dewenter & Tscharntke, 2000; Börschig et al., 2013; Gossner et al., 2016).

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 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 remaining woodland remnants are heavily exploited by human activities (Gumbo et al., 2018). However, an overall characterisation and understanding of how entomofauna in this region is affected by landscape change 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) as well as deforestation for charcoal and brick production due to rising rates of urbanization (Petersen et al., 2021). 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 (Bezner Kerr et al., 2021). Agroecological pest management practices include, for example, using botanical sprays or covering affected crops with ash to smother pests. Although agroecological practices avoid the use of synthetic pesticides, other 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 intercrops, may positively affect farmland butterfly abundance, in part because they focus on diversification of crops (Table 5.S1). Agroecological systems that include multiple practices or components tend to have higher positive food security outcomes for smallholder farmers (Bezner Kerr et al., 2021). The ecological co-benefits of diversified agroecological practices on insects are often assumed, but not tested. Particularly, studies assessing the impacts of the diversification of agroecological pest or soil practices on butterflies are lacking. In addition to agroecological practices, vegetation characteristics, such as flowering plant species richness, have 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.

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 predictions:

1. Local habitat type (shrub- or farmland) and the proportion of semi-natural habitat in the surrounding landscape interactively affect butterfly abundance, species richness and assemblages, as well as life-history traits. We expect a higher abundance and species richness in shrub- than in farmlands and an increase in abundance and species richness with an increasing proportion of semi-natural habitat in the landscape. Life history traits will shift from specialised smaller-winged species with a narrow range of larval host plants and habitat preferences in shrubland to more generalised species with larger wings and less specialised larval host plants and habitat preferences in farmland with decreasing semi-natural habitat in the landscape.
2. The implementation of agroecological soil management as well as increasing the richness of flowering plants increases farmland butterfly abundance and species richness. On the other hand, agroecological pest management practices reduce butterfly abundance and species richness on farms.

5.2 Materials and methods

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 the main growing season.

Within our study region, we chose 24 smallholder farms in villages surrounded by varying proportions of semi-natural habitat in a 1 km radius (15 - 75 %) (Figure 5.1). All chosen farms were representative of our study region. Maize (the main food staple) and tobacco (the main cash crop) are dominant crops, though legumes and vegetable crops were also grown, often in mixtures. Smallholder farms in this region are typically small, ranging from 0.5 to 1.4 hectares, and fields are managed traditionally by hand (FAO, 2018). We considered these farms as the “farmland” and the butterflies there as “farmland butterflies”.

In contrast, “shrubland”, which we also considered a part of the surrounding semi-natural habitat, was the grassy or bushy shrubland and forests that border villages. These shrubland habitats are part of the Miombo-Mopane ecoregion (Ribeiro et al., 2020). These habitats have no official protection status. Additionally, they are not actively 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 or materials for traditional medicines (Gumbo et al., 2018).

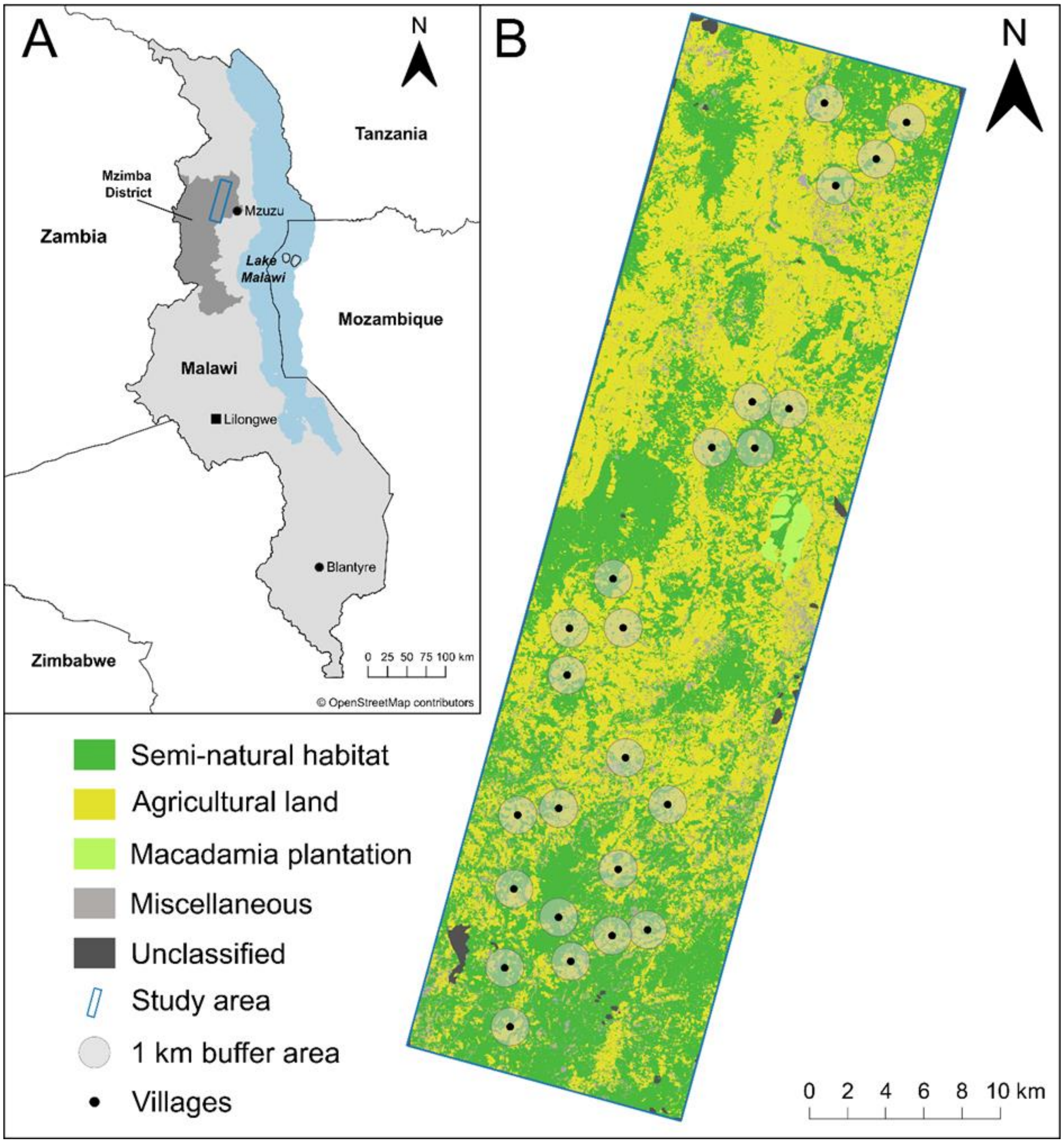


Figure 5.1: Map of the study area showing A) its location in Mzimba District, northern Malawi, and B) the land cover classification map of the study area with all 24 villages. Villages are shown using the locations of the starting points of the third subtransects of the first farmland transect walks as the centre of the respective 1 km buffer area.

Data collection

Throughout the study period in November 2019 to February 2020, we 1) quantified butterfly communities using 5 rounds of transect walks on all 24 farms and surrounding shrubland. We then 2) assigned life-history traits to the butterflies observed during the study. We performed 3) landscape analysis to quantify the proportion of semi-natural habitat in a 1 km radius around all sites. Additionally, we performed 4) farmer interviews to quantify the number of agroecological pest- and soil management practices performed on farmland sites. Detailed information of how individual data was collected is described in Supporting Information 5.

Statistical analysis

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

To test the effect of habitat-change on butterflies we used the following predictors: local habitat type (shrub- vs. farmland) and the proportion of semi-natural habitat in the landscape, with an interaction term between the two. To test the effect of farmland management on farmland butterflies, we used the following predictors: diversity of pest management practices per hectare, diversity of soil management practices per hectare 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 (shrub- 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. As these are count data, we used generalised linear mixed models with a Poisson distribution using the function ‘glmer’ from the ‘lme4’ package to these response variables against the landscape predictors, with village as a random effect to account for the nestedness of the paired transects (Bates et al., 2019). To assess the effect of landscape on butterfly life-history traits, we calculated community weighted means of female wingspan for each site, as well as the proportion of the butterfly community represented by the three different larval host plant specialisations or habitat specialisations. These responses were then tested against the landscape predictors using linear mixed models, again with village as a random effect.

To test if farm- and shrubland species communities became more similar or different along the semi-natural habitat 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 semi-natural habitat gradient (Oksanen et al., 2020). Then, to test whether proportional species assemblage (β-diversity) overall differed with habitat type and increasing semi-natural habitat, 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.

For farmland butterflies, we used the same response variables (total butterfly abundance, *C. florella* abundance, non- *C.florella* abundance and species richness) in a generalised linear model with a Poisson distribution to test the effect of on-farm management.

All models were tested for the assumptions of normality, 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).

5.3 Results

In total, we counted 5242 individual butterflies, belonging to 70 different taxa (Table 5.S2), with 34 taxa represented on farmland habitats and 66 taxa found in shrubland habitats. The most common butterfly was *Catopsilia florella* (Pieridae) with 3457 individuals, accounting for 66 % of all recorded butterflies in our study.

Butterfly community and life history trait responses to habitat type and semi-natural habitat

On a village scale, shrubland had higher butterfly abundance than farmland (Figure 5.2A), with both the most common species, *C. florella* and other butterflies (Figure 5.2B) being more abundant in shrublands. Shrubland habitats also had a higher species richness than farmland (Figure 5.2C; Table 5.1), as well as a different species assemblage (Figure 5.S2; Table 5.S3).

With increasing semi-natural habitat in the landscape, butterfly abundance decreased (Figure 5.2A), whereas butterfly species richness increased (Figure 5.2C) in both habitat types. This decrease in butterfly numbers across the semi-natural habitat gradient was caused by a decrease of the most common species, *C. florella* (Table 5.1), while the abundance of other butterfly species increased with increasing semi-natural habitat in farmland habitats and stayed constant across the semi-natural habitat gradient in shrubland (Figure 5.2B; Table 5.1). Even though differences between farmland and shrubland butterfly communities did not significantly increase or decrease across the semi-natural habitat gradient ($F_{1/22} = 0.33$, $p = 0.574$), the species assemblage overall showed proportional species turnover across the semi-natural habitat gradient (Table 5.S3).

The proportion of individuals whose larvae are mono- (0 - 12.5 %), oligo- (19.4 - 96.4 %), or polyphagous (3.6 - 80.6 %) was not significantly affected by habitat type or the proportion of semi-natural habitat or their interaction (Table 1).

Forest habitat specialists were the least represented in the butterfly community (0 - 28 %) but were significantly more common in farmlands compared to shrublands and increased with increasing semi-natural habitat in the landscape (Table 5.1). Savanna specialists were better represented in the community (19 - 96 %), but did not respond to habitat type, semi-natural habitat or their interaction (Table 5.1). Habitat generalists, representing 3 - 74 % of the butterfly community also did not respond to increasing semi-natural habitat, but were better represented in shrubland than in farmland habitats (Table 5.1).

The community weighted means of female wingspan showed no change with increasing semi-natural habitat in the landscape (Table 5.1), but overall, butterflies in farmlands were significantly larger than shrubland butterflies (Figure 5.2D).

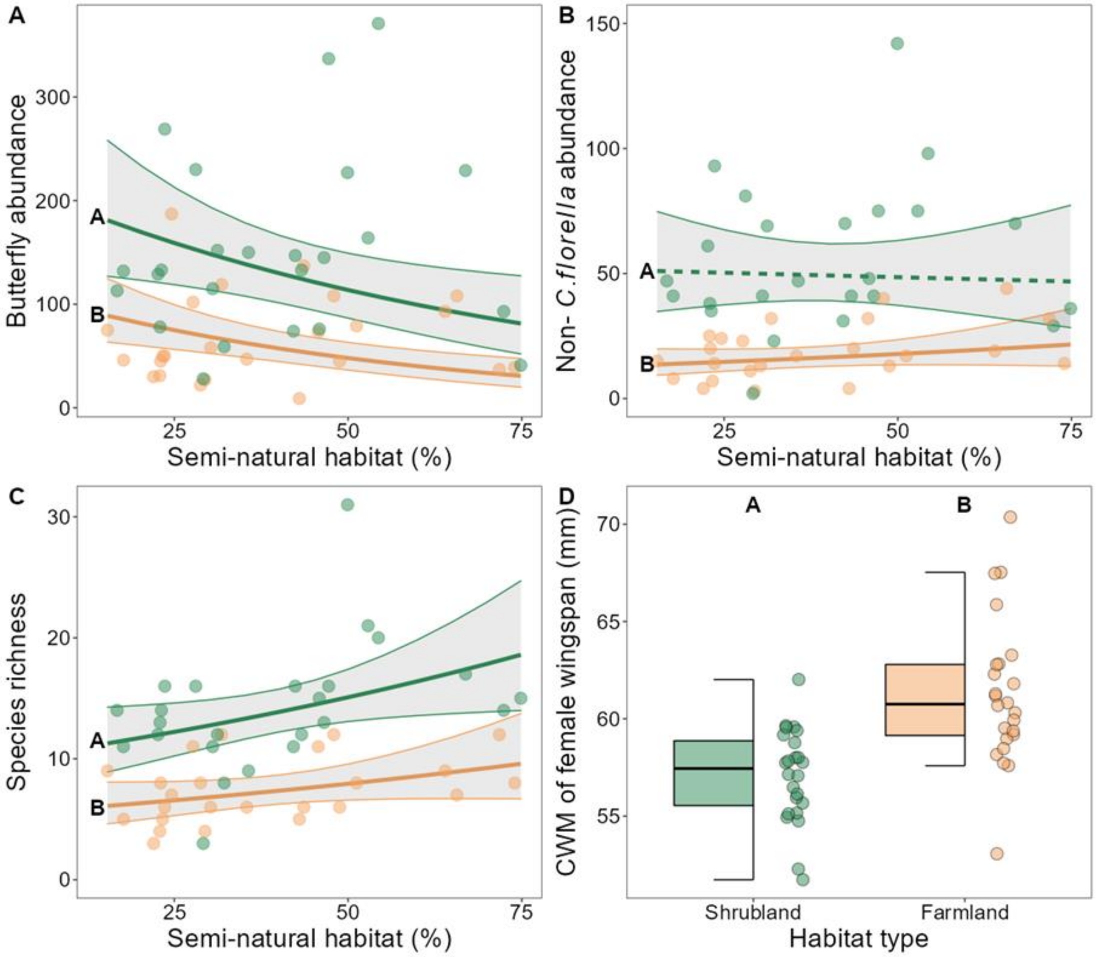


Figure 5.2: A) total butterfly abundance, B) non- *C.florella* abundance and C) species richness in response to habitat type (shrubland in green, farmland in orange) and the proportion of semi-natural habitat (SNH) within a 1 km radius. Significant differences between shrub- and farmland are indicated with letters, significant changes across the semi-natural habitat are indicated with a solid line, non-significant trends with a dashed line. Grey areas around the lines show the 95% confidence interval. D) shows differences between the community weighted means (CWM) of female wingspan between shrub- and farmland habitat types, 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.

Table 5.1: The results of the generalized linear mixed models (GLMERs) with a Poisson distribution (in the case of butterfly count analyses) and linear mixed models (LMMs) (in the case of trait analyses) assessing the responses of the butterfly community life-history traits to habitat type, the proportion of semi-natural habitat (SNH) in the landscape and their interaction.

Response	**Predictors**	**Chi^2-value**	**p-value**	**Df$_{num}$/Df$_{den\|resid}$**	**R^2_m/ R^2_c**
Total butterfly abundance	SNH	12.78	**<0.001*****	1/43	0.37/0.99
	Habitat type	735.34	**<0.001*****	1/43	
	Type x SNH	4.96	**0.027***	1/43	
***C. florella* abundance**	SNH	11.71	**<0.001*****	1/43	0.31/0.99
	Habitat type	354.10	**<0.001*****	1/43	
	Type x SNH	16.92	**<0.001*****	1/43	
Non-*C. florella* abundance	SNH	7.63	0.555	1/43	0.49/0.96
	Habitat type	383.15	**<0.001*****	1/43	
	Type x SNH	7.76	**0.006****	1/43	
Butterfly species richness	SNH	8.02	**0.014***	1/43	0.33/0.35
	Habitat type	46.70	**<0.001*****	1/43	
	Type x SNH	0.02	0.879	1/43	
Female wingspan (community weighted means)	SNH	1.17	0.291	1/23	0.33/0.35
	Habitat type	22.35	**<0.001*****	1/22	
	Type x SNH	0.69	0.416	1/23	
Proportion of monophagous species	SNH	3.32	**0.081**	1/24	0.09/0.31
	Habitat type	0.39	0.540	1/22	
	Type x SNH	0.11	0.738	1/23	
Proportion of oligophagous species	SNH	0.81	0.377	1/25	0.03/0.40
	Habitat type	0.38	0.542	1/22	
	Type x SNH	0.43	0.521	1/23	
Proportion of polyphagous species	SNH	0.30	0.592	1/24	0.01/0.37
	Habitat type	0.24	0.632	1/22	
	Type x SNH	0.34	0.569	1/23	
Proportion of forest specialists	SNH	6.65	**0.016***	1/24	0.21/0.47
	Habitat type	6.98	**0.015***	1/22	
	Type x SNH	0.06	0.811	1/22	
	SNH	4.07	**0.054**	1/26	0.13/0.58
	Habitat type	1.19	0.288	1/22	

Proportion of savannah specialists	Type x SNH	0.17	0.685	1/22	
Proportion of habitat generalists	SNH	1.23	0.213	1/24	0.10/0.46
	Habitat type	5.92	**0.024***	1/22	
	Type x SNH	0.25	0.622	1/22	

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

Increasing the number of agroecological pest management practices per hectare decreased total butterfly abundance (Figure 5.3A), due to a decrease of abundance of *C. florella*, but not of the other butterfly species (Table 5.2). In contrast, on farms with more agroecological soil management practices per hectare the abundance of butterflies other than *C. florella* increased (Figure 5.3E; Table 5.2). Increasing flowering plant species richness on farms had a positive effect on butterfly abundance (Figure 5.3C; Figure 5.3F; Table 5.2). Species richness did neither change with increasing pest or soil management practices nor with flowering plant species richness (Table 5.2).

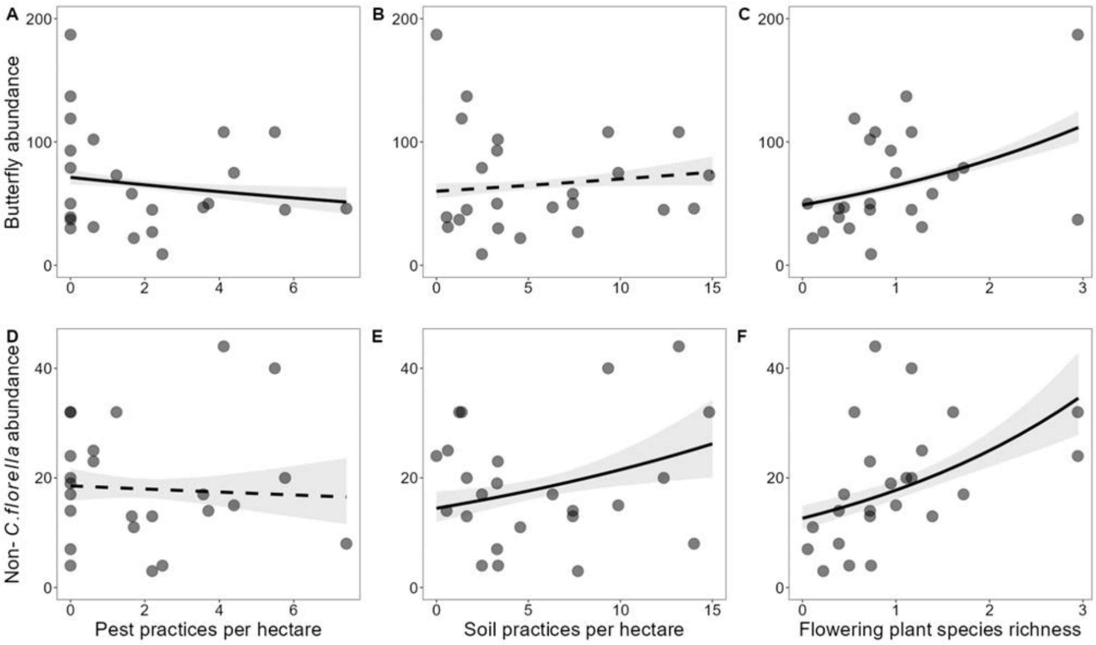


Figure 5.3: Responses of total farmland butterfly abundance and non- *C. florella* butterfly abundance to traditional pest management practices per hectare (A, D), traditional soil management practices per hectare (B, E) and flowering plant species richness along the transects on farms (C, F). Significant effects are indicated with solid lines, dashed lines indicate a non-significant relationship. Grey areas show the 95% confidence interval.

Table 5.2: 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.

Response	**Response/predictors**	**z-value**	**p-value**	**Df_{num}/Df_{den}**	**R^2**
Total butterfly abundance	Agro-ecological **pest** management practices per hectare	-2.45	**0.015***	1/22	0.98
	Agro-ecological **soil** management practices per hectare	1.94	**0.056**	1/21	
	Flowering plant species richness	9.50	**<0.001*****	1/20	
***C. florella* abundance**	Agro-ecological **pest** management practices per hectare	-2.55	**0.011***	1/22	0.97
	Agro-ecological **soil** management practices per hectare	0.52	0.606	1/21	
	Flowering plant species richness	7.51	**<0.001*****	1/20	
Non-*C. florella* abundance	Agro-ecological **pest** management practices per hectare	-0.49	0.625	1/22	0.82
	Agro-ecological **soil** management practices per hectare	2.85	**0.006****	1/21	
	Flowering plant species richness	5.87	**<0.001*****	1/20	
Butterfly species richness	Agro-ecological **pest** management practices per hectare	-0.50	0.620	1/22	0.14
	Agro-ecological **soil** management practices per hectare	0.84	0.412	1/21	
	Flowering plant species richness	1.67	0.101	1/20	

5.4 Discussion

Our study shows the negative effects of semi-natural habitat decline on butterfly communities and that habitat conversion on a local scale interacts with landscape-scale declines in a biodiversity-rich ecoregion in sub-Saharan Africa. However, we also show that agroecological soil management practices and maintaining flowering plant species richness on farmlands have potential to mitigate some of these negative effects, but only if semi-natural areas in the region are simultaneously protected.

Butterfly community and life-history trait responses to habitat type and semi-natural habitat

In contrast to studies that examine discrete landscapes or rely on a surrounding landscape gradient only, to our knowledge this study is the first to investigate the interactive effects of the two landscape types with a surrounding landscape gradient in sub-Saharan Africa. Our results show a lower butterfly abundance and species richness in farmlands compared to shrublands. This finding is consistent with study results elsewhere in Africa (Jew et al., 2015) and adds to the understanding that maintaining semi-natural habitats is essential for butterfly abundance and species richness. The importance of shrublands 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 shrubland 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). This difference in species assemblages highlights the need to maintain shrublands in Africa to maintain butterfly diversity.

We observed a shift from smaller butterflies in shrubland, 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 shrubland 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 shrubland is converted to farmland. In contrast to expectations, we observed a higher proportion of habitat generalists in shrubland than in farmland and a higher proportion of forest specialists in farmland than in shrubland. One explanation for this could be that shrubland habitats had more variation within the habitat than farmland habitats, catering to habitat generalists.

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 (Gumbo et al., 2018), degrading the biodiversity. Miombo woodlands are particularly rich in plant diversity and endemism, but also one of the most at-risk biomes globally (Laurance, Sayer & Cassman, 2014). Therefore, we expected an increase in butterfly abundance and species richness with increasing semi-natural habitat in the landscape. Contrary to our expectations, we observed a decrease in abundance, but an increase in species richness with increasing semi-natural habitat. This seems counter-intuitive since species richness is often correlated with abundance. However, in our system, a single dominant species *Catopsilia florella* (Pieridae), drove abundance patterns. Non- *C. florella* butterflies, in contrast, increased with increasing semi-natural habitat in the landscape, possibly also driving the increasing species richness observed. In addition, we observed significant, albeit small, increase in the proportion of forest specialists in both habitats with increasing proportion of semi-natural habitat. In contrast, areas with little semi-natural habitat in the surrounding landscape had limited butterfly species richness, even in the remaining shrubland habitats, with a reduction of approximately 30% in the shrubland with the least amount of surrounding semi-natural habitat compared to the shrubland sites surrounded by the most semi-natural habitat. This loss in species richness could be explained by a decline in habitat quality and negative effects of lower connectivity in these fragmented habitats (Brückmann et al 2011), and suggests that more active protection of remaining Miombo woodlands in Malawi will be necessary to maintain biodiversity.

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 (Johnson, 2004; Goldblatt & Manning, 2006; Butler & Johnson, 2020). Pollinators have been shown to be drivers of plant species richness (Wei et al., 2021), and therefore the reduction of 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). 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, in order to better understand the possible consequences of disappearing butterfly diversity, both as pollination partners as well as larvae-host plant relationships. This relationship between semi-natural habitat in the landscape and species richness, as well as the observed shift in species assemblages across the semi-natural habitat gradient indicate that maintaining semi-natural habitat in the landscape will be essential to preserve butterfly species diversity in this region. 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).

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 per hectare reduced *C. florella* abundance on farms. *C. florella* a migratory species with a wide host-plant breath, 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, 2019), 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 the use of 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 would improve habitat suitability for a larger range of butterfly species. In addition, healthy soils could promote crop health, which mediates plant-butterfly interactions by increasing the quality of farmed plants for butterflies as a food source. 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 study 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.

In addition, we found that increases in 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) and we indicate similar effects in agro-ecosystems in our study region. In temperate systems, set-aside habitats such as flower strips show promising benefits for butterfly abundance and species richness, mediated by an increase in flowering plant species richness (Steffan-Dewenter & Tscharntke 1997, Wix, Reich & Schaarschmidt, 2019). Given the financial and temporal constraints on farmers in our study region, we do not necessarily suggest set-aside habitats in our context. 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. This practice could be a relatively simple, cost- and labour-effective measure and would, in combination with better protection of remaining surrounding semi-natural habitats, contribute to the preservation of butterfly abundance on smallholder farms and might also promote other ecosystem services such as natural pest control.

5.5 Conclusions

Mitigating the negative effects of agriculture for biodiversity is a huge challenge. Butterfly communities are sensitive to changes in the environment and therefore a good indicator of processes affecting biodiversity (Woodhall 2020). The global South, and particularly the Miombo woodland ecoregion in southern Africa, is biodiversity-rich but economically poor, making it difficult to balance the needs to maintain unique biodiversity whilst also improving the livelihoods of its largely agrarian population (Gumbo et al., 2018). Agroecology is often proposed as a socially just tool for improving the livelihoods of the rural poor (Bezner Kerr et al., 2021), but its ecological benefits have not been widely tested in Africa. Our results reveal that increasing diversification of agroecological practices aimed at improving soils, as well as increasing flowering plant species richness on farms, shows promising benefits for conserving butterfly abundance on farms. However, farmland habitats overall had lower butterfly abundance and species richness than semi-natural shrublands, as well as different butterfly species assemblages and community life-history traits. Additionally, areas with less semi-natural habitat in the landscape showed locally decreased butterfly species richness, as well as decreased abundance of the non-dominant butterfly species on farmlands in particular. This reduced farmland species richness indicates that on-farm measures aimed at conserving butterflies will have limited success if remaining semi-natural habitats are 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 semi-natural habitats 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 on farms could be a practical solution to mitigate the negative effects of agriculture on butterfly communities, whilst also benefiting the livelihoods of rural smallholders.

Supplementary material 5

Supporting Information 5

1. *Transect walks*

To quantify the butterfly community in farm- and shrublands five paired transect walks were carried out on all farms and the surrounding shrubland (Figure S1). The precise location of the transect within each habitat varied from visit to visit. The distance between the farm- and shrubland transect was at most 1 km (58 - 702 m, mean: 266 m), so that we could consider them part of the same village landscape, and they wouldn't be too close to the farms in the study. The order in which villages were visited each round of transects was random, and the order in which farm- and shrubland transects were walked within the study site was also random.

We performed variable transect walks with a length of ~ 300m, divided into 6 subtransects of ~ 50m (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 minutes per 50 m subtransect adding up to 18 minutes 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.

2. *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 specialisation and habitat specialisation. For the wingspan of each species, we took the mean of the wingspan range reported for female individuals. For larval host-plant specialisation, 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.

3. *Landscape analysis*

We used a synergetic remote sensing approach fusing optical (Sentinel-2 and PlanetScope) and radar (Sentinel-1) imagery to classify the land cover in our study region (Planet Team, 2017). This approach produced the best overall classification accuracy for a subset of our study area (Kpienbaareh et al., 2021). Following the steps outlined in Kpienbaareh 2021, four optical imagery fusion pairs, each paired with the combination of radar data from six different dates in the growing season obtained between January and April 2020, were used to cover the extent of 1 km radii around the 240 transect walks in our study. In each transect, we used the starting point of the third subtransect as the center of the 1 km radius (Figure S1). All optical images were selected to depict the study region as cloudless as possible. As dense cloud cover was common in the growing season, several optical images, from both Sentinel-2 and PlanetScope, were needed. For each of our four fusion pair combinations, we ran a supervised random forest algorithm trained with land cover class data collected through extensive ground-truthing during the growing season of 2019/20. We complemented these with manually digitized land cover samples of easily discernible land cover classes (e.g. shrubland, water or settlement) via Google satellite images in QGIS 3.12 and Digital Globe images in ArcGIS Pro 2.7. If several classifications were available at a village, the best fit was selected based on overall accuracy and visual inspection of the extent of shrubland in comparison with a high-resolution satellite image. Any remaining gaps in the 1 km radius around the fields were either filled with values from other classifications or, if unavailable, manually digitized. Land cover pixel values were extracted from the final 3 m resolution classifications using the R package ‘exactextractr’ (Baston, 2022). Resulting land cover class proportions of shrubland, grassland and forest were aggregated to semi-natural habitat (SNH) and used in subsequent statistical analyses.

4. *Farmer surveys*

To assess the implementation of agroecological agricultural practices on the farms on which butterflies were assessed, we performed structured interviews from 8th to 26th 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 S1). The questions were posed as a yes or no question (did you perform x 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. Farmers reported up to five different 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”) per field (Table S1). A total of 24 interviews, who all managed the farms on which data was collected, were included in later analysis.

To obtain a single value for pest and soil management implementation on each farm, we calculated the number of practices per hectare for each field, and then took the mean across all fields on the farm.

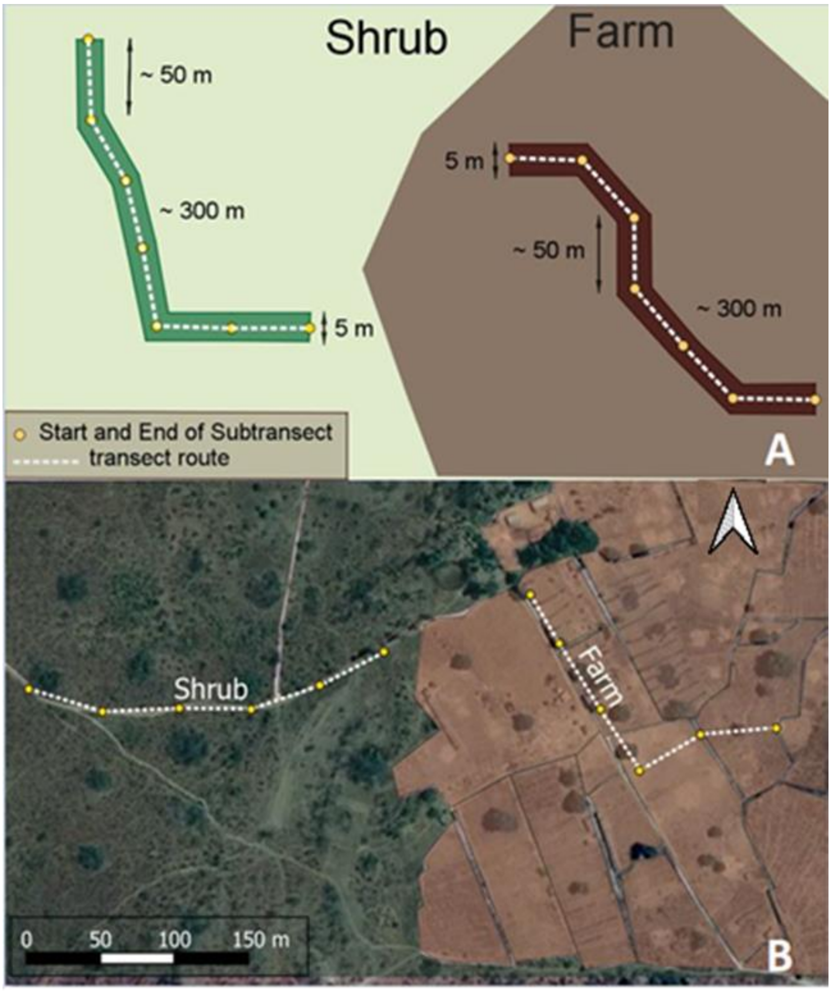


Figure 5.S1: Transect walks were each conducted in the shrub- and the farmland. Every transect had a width of 5 m and a total length of about 300 m (divided into 6 subtransects of 50 m each). Every village was sampled 5 times. A) shows the scheme of the transect method and B) a transect walk at a particular site on a satellite picture. The white line shows the transect route. The beginning and the end of a subtransect are indicated by yellow dots.

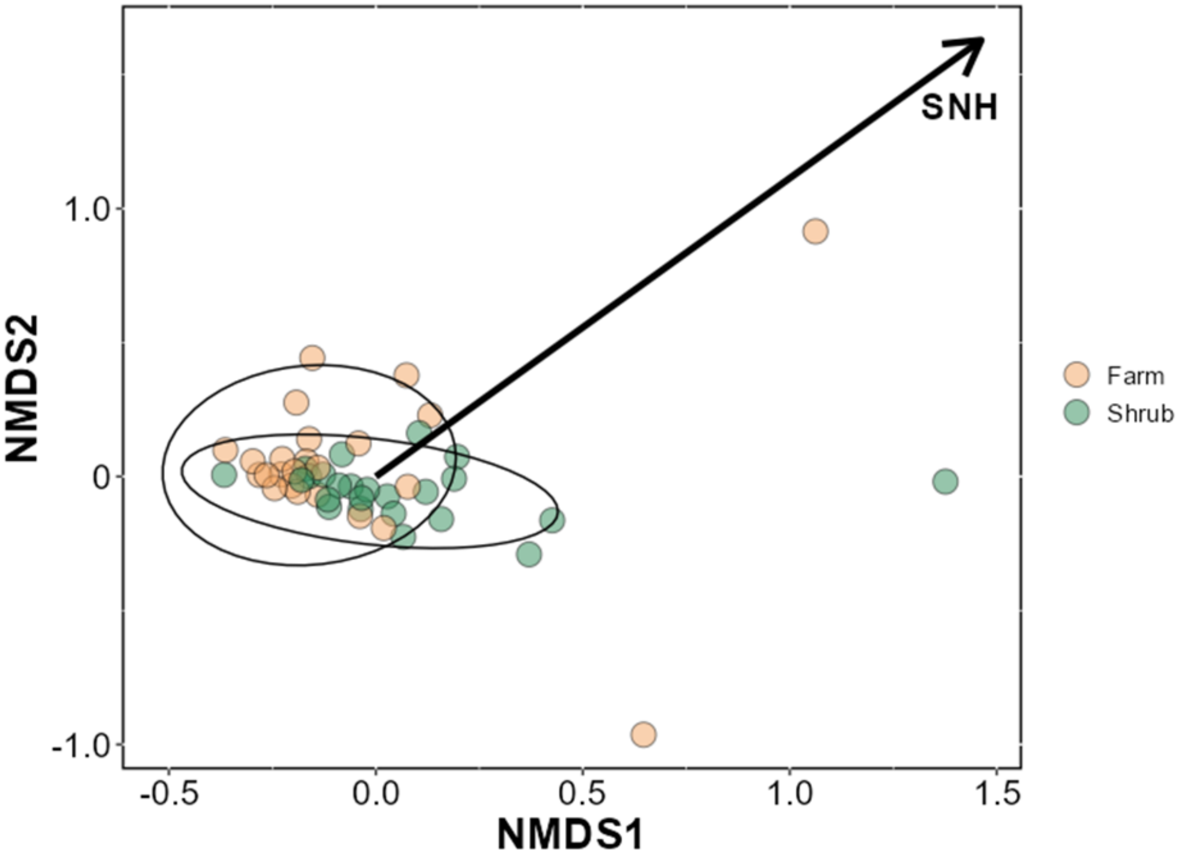


Figure 5.S2: NMDS plot of the butterfly species assemblages in farmland (orange) and shrubland (green). The clustering of the two habitat types is indicated by the ellipses. The direction of change with increasing proportion of semi-natural habitat (SNH) in a 1 km radius is indicated with a vector.

Table 5.S1: Agroecological practices reported by farmers, grouped by either pest- or soil-related agroecological practices.

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

Table 5.S2: Butterfly species found during the study period.

Family	**Subfamily**	**Genus**	**Species**
Hesperiidae	Pyginae	*Abantis*	*Abantis tettensis*
		Spialia	*Spialia dromus*
	Hesperiinae	*Acada*	*Acada beseriata*
		Borbo	*Borbo* sp.
		Unknown	Hesperiinae sp.
	Coeliadinae	*Coeliades*	*Coeliades forestan*
		Unknown	Coeliadinae sp.
Lycaenidae	Polyommatinae	*Anthene*	*Anthene amarah*
			Anthene lemnos
			Anthene sp.
		Azanus	*Azanus jesous*
			Azanus natalensis
		Euchtrysops	*Euchtrysops malathana*
			Euchtrysops sp.
		Leptotes	*Leptotes pirithous*
			Leptotes sp.
		Pseudonacaduba	*Pseudonacaduba sichela*
		Tuxentius	*Tuxentius gregorii*
		Zintha	*Zintha hintza*
	Aphanaeinae	*Axiocerses*	*Axioxerses croesus*
			Aziocerses tjoane
		Cigaritis	*Cigaritis natalensis*
		Crudaria	*Crudaria* sp.
	Theclinae	*Deudorix*	*Deudorix dinomenes*
		Hypolycaena	*Hypolycaena lochmophila*
	Lycaeninae	Unknown	Lycaeninae sp.
Pieridae	Pierinae	*Belenois*	*Belenois aurota*
			Belenois creona
		Colotis	*Colotis antevippe*
			Colotis lais
			Colotis pallene
			Colotis sp.
	Coliadinae	*Catopsilia*	*Catopsilia florella*
		Eurema	*Eurema brigitta*

			Eurema hecabe
			Eurema sp.
Nymphalidae	Heliconiinae	*Acraea*	*Acraea induna*
			Acraea natalica
			Acraea neobule
			Acraea serena
			Acraea utengulensis
			Acraea sp.
		Pardopsis	*Pardopis puncatissima*
		Phalanta	*Phalanta phalantha*
		Unknown	Heliconiinae sp.
	Satyrinae	*Bicyclus*	*Bicyclus safitza*
			Bicyclus sp.
		Melantis	*Melantis leda*
		Ypthima	*Ypthima asterops*
	Nymphalinae	*Catacroptera*	*Catacroptera cloanthe*
		Hypolimnas	*Hypolimnas misippus*
		Junonia	*Junonia artaxia*
			Junonia hierta
			Junonia natalica
			Junonia oenone
			Junonia terea
		Precis	*Precis antilope*
	Charaxinae	*Charaxes*	*Charaxes guderiana*
			Charaxes phaeus
			Charaxes sp.
		Unknown	Charaxinae sp.
	Limenitidinae	*Hamunumida*	*Hamunumida daedalus*
		Neptis	*Neptis laeta*
		Pseudacraea	*Pseudacraea boisduvalii*
Papilionidae	Papilioninae	*Graphium*	*Graphium angolanus*
			Graphium Leonidas
		Papilio	*Papilio demodocus*
			Papilio nireus
			Papilio sp.

		Unknown	Papilioninae sp.

Table 5.S3: Results of the Bray-Curtis distances PERMANOVA testing the effect of habitat type and semi-natural habitat (SNH) in a 1 km radius on butterfly species assemblages.

Response	**Predictors**	**F-value**	**p-value**	**DF_{num}/DF_{den}**	**R^2**
Butterfly assemblage	SNH	3.47	**0.005****	45/48	0.87
	Habitat type	3.55	**0.002****		

A Malawian smallholder farm: a typical smallholder farm from a remote area in our study region. A collection of buildings where the usually multigenerational household lives, surrounded by relatively small fields where crops are grown. To the left the family grows maize, intercropped with pumpkin. Behind the buildings some fruit trees, in this case mango, are growing. On the slopes behind the farm the semi-natural habitats are present.

Chapter 6

General Discussion

Biodiversity is at risk globally, threatening the ecosystem services they provide. In the Global South, the declines in ecosystem services could endanger the livelihoods of the almost two billion farmers who depend on smallholder farming (Steward et al., 2014). My research, performed in an underrepresented but biodiverse region in sub-Saharan Africa, Northern Malawi, shows that agroecological practices performed by smallholder farmers affect biodiversity and ecosystem services on crops important for food security. For example, we found that growing legumes had positive effects on natural enemy activity and lowered crop damage, but that these effects were mediated by landscape context. We also found evidence that the diversification of agroecological soil management benefits the diversity of soil bacteria and pollinators on farms. Perhaps without being aware of it, smallholders in regions such as Malawi are stewards of the unique biodiversity in their landscapes and should be actively involved in decision making and discussions about conservation. In addition, we found surprising responses of biodiversity to landscape and management drivers – for example, we found that in the dry season in the flowering crop pigeon pea, bee abundance was higher in areas high in agriculture at the landscape scale (Vogel et al., 2021). Such results, which contrasted with results from similar studies performed primarily in the Global North (e.g. Kennedy et al., 2013), indicate that the consequences of different land-use and agricultural management are not uniform globally, but instead context-dependent. Without proper understanding of the drivers of biodiversity and ecosystem services in Malawi and more generally in the tropics, evidence-based recommendations for smallholders and other stakeholders will be impossible. In this thesis, we aimed to investigate two aspects driving biodiversity on crops – semi-natural habitat at the local and landscape scale and local agroecological practices and use these to formulate management applications that would be mutually beneficial for both smallholders and biodiversity

6.1 Importance of semi-natural habitats

The Miombo woodland ecoregion is a global biodiversity hotspot under threat – in our study region of Malawi, the cover of natural habitat is decreasing by an alarming ~2.5% annually (Chirambo & Mitembe, 2014). However, the consequences of these landscape-scale changes in semi-natural habitat cover biodiversity and ecosystem services to crops are not well characterised in the Miombo woodland ecoregion (Ribeiro et al., 2020), despite the potential negative outcomes for vulnerable smallholders in the region. Our research aimed to address this knowledge gap and to that end we investigated the effects of landscape-scale semi-natural habitat cover on several important taxa and their ecosystem services.

For several taxa, we found contrasting responses between abundance (or activity density), species richness and species assemblages to increasing semi-natural habitat cover in the landscape. For example, in chapters 3 and 5, we found that pollinator abundance decreased (driven by a single, highly dominant species - the honeybee for bees and *Catopsilia florella* for butterflies), but species richness increased, with increasing semi-natural habitat cover. This contrasts with other contexts, where increasing semi-natural habitat increased pollinator abundance. For example, in Brazil and the USA, increasing abundance of semi-natural habitat increased bee abundance on cotton (Cusser et al., 2019), and in Sweden (Raderschall et al., 2021), honeybee and bumblebee densities increased with increasing semi-natural habitat proportion. Additionally, global synthesis showed overall abundance and richness increased with increasing habitats surrounding fields (Kennedy et al., 2013). Our results highlight the possible context-dependence of these responses. In butterfly communities, we also observed a local effect of habitat differences – semi-natural shrubland had a higher abundance and species richness than farmlands within the same landscape. Interestingly, habitat type also affected community traits such as the proportion of habitat specialists and generalists as well as butterfly wingspan. Additionally, we found that the compositions of carabid (Chapter 2) and butterfly (Chapter 5) species assemblages changed with increasing semi-natural habitat in the landscape. This contrast between the responses in abundance, richness, traits, and assemblage compositions begs the question: if the aim is to conserve biodiversity and maintain ecosystem services, which aspect of biodiversity is most important to consider?

The relative contribution of abundance and species richness for ecosystem service delivery is difficult to disentangle in real-world systems, not in the least because the two are often correlated. In the past, a high abundance of a few, common species was found to be most important for ecosystem service delivery (Winfree et al., 2015). Similarly, in our system, we found higher parasitoid activity in bean fields in areas low in semi-natural habitat (Chapter 2), where we also found lower pest damage in bean fields. Additionally, bee abundance was increased on pigeon pea in agriculture-rich areas (Chapter 4; Vogel et al., 2021), though we could not demonstrate a pollination benefit. In butterflies, local conversion of shrubland to farmland changed butterfly community wingspan size (Chapter 5). Responses in community traits are significant because trait shifts, including pollinator body sizes, is important for ecosystem service delivery (Gagic et al., 2015; Wood et al., 2015). More recently, Dainese et al., (2019) has convincingly shown that species richness, rather than abundance or species dominance, is the most reliable predictor of ecosystem service delivery. Indeed, the exclusion study on pumpkin (Chapter 3) provides evidence that increased pollinator species richness resulted in increased fruit set, demonstrating a direct benefit of conserved species richness to smallholder farmers. Often, protecting biodiversity is synonymous with protecting species richness. We found increased species richness of butterflies (Chapter 5) in shrublands compared to farmland on a local scale, as well as increasing bee (Chapters 2 and 3) and butterfly (Chapter 5) species richness with increasing semi-natural habitat cover at a landscape scale, demonstrating the value of these habitats for the conservation of species richness.

Species richness as the only metric of biodiversity, however, also has its limitations. Under land-use change, certain species may be replaced by others – meaning species richness may remain static. Often specialist species may be replaced by generalists and therefore, changes in biodiversity in response to decreasing semi-natural habitat cover might be more clearly detected by investigating changes in the composition of assemblages (Hillebrand et al., 2018), as we did in chapters 2 and 5. In chapter 2, carabid species assemblages changed across the semi-natural habitat cover gradient, and in chapter 5, shrub- and farmland butterfly species assemblages were distinct as well as shifting in response to increasing semi-natural habitat cover in the landscape. In Malawi, change in habitat cover is mostly unilateral – semi-natural forest habitats are converted to agricultural area, but very little is reforested. Additionally, studies on reforestation show that species assemblages may take decades to recover even as richness increases during recovery (Rozendaal et al., 2019). Interestingly though, evidence from our study region in Malawi shows that agroecological intensification farmers allowed more land to lay fallow as agroecology resulted in higher yields per hectare (Kpienbaareh et al., 2022b). During Scenario Planning Workshops conducted with participating farmers and their communities in April 2022, farmers also reported that since using agroecology, they needed smaller fields to grow the same amount of crop (*personal communication with farmers*). Over time the reduced land-use intensity could create semi-permanent steppingstone habitats within the agricultural landscape, demonstrating a possible indirect benefit of agroecology for biodiversity. My results demonstrating changes in assemblages with increasing semi-natural habitat cover, therefore, underscore the necessity to maintain semi-natural habitats to conserve the full scope of biodiversity in northern Malawi.

Despite the positive outcomes of increasing semi-natural habitat for biodiversity, some trade-offs with crop yield were detected. For example, bean seeds per pod decreased with increasing semi-natural habitat, despite increases in bee richness in these areas (Chapter 2). Additionally, there was a decrease in pumpkin fruit size and seed set with increasing semi-natural habitat, though fruit set was not affected (Chapter 3). Though we could not find a direct cause for these correlations, we suspect it might be due to the possibility of better soil conditions in areas that tend to be dominated by agriculture – after all, land-use is not random and more fertile areas would be converted to agriculture first (Serneels & Lambin, 2001). However, this does not take away from the fact that increased semi-natural habitat cover was important for biodiversity and should be conserved. If negative relationships between semi-natural habitat cover and seed set in pumpkin and bean are mediated by soil quality as suspected, it is implausible that continued removal of these habitats will contribute to improved seed set in these landscapes. In fact, exactly the opposite might be the case if biodiversity and ecosystem services decrease with further losses semi-natural habitat. For example, on pumpkin, we found that increased pollinator richness compensated for decreased fruit set in fields high semi-natural habitat cover in the landscape (Chapter 3), demonstrating that ecosystem services possibly compensate for poorer soils in some contexts if biodiversity is conserved. Instead, we recommend that farmers in landscapes high in semi-natural habitat cover, but potentially low in soil quality, focus their efforts on appropriate soil management as a method to improve yields.

6.2 Putting legumes in context

The growing of grain legumes, particularly in intercrop with cereal crops, is a traditional practice widely implemented throughout sub-Saharan Africa (Snapp et al., 2002), and has been identified as a key agroecological practice for sustainable intensification in the region (Kuyah et al., 2021). Growing legumes has numerous benefits to smallholder farmers. Firstly, legumes are protein-rich and thus contribute to household nutritional security. Secondly, they can play an important part in maintaining soil fertility through nitrogen fixation. Lastly, certain species of legume, such as pigeon pea, are particularly suited to semi-arid environments and might therefore contribute to climate change adaptation (Snapp et al., 2021). Recognising the importance of legumes for smallholders in sub-Saharan Africa, we performed two studies on legumes. First, we investigated the effects of crop-type, land-use and agroecological practices on biodiversity and ecosystem services in a bean-maize intercropping system (Chapter 2), and second, we investigated the effects of land-use on bee pollinators and pest pressure on pigeon pea (Chapter 4). In the maize-bean intercropping system, we additionally tested for interactive effects of crop type and with landscape scale semi-natural habitat cover. With this approach, we demonstrate that the effects local management (crop type) can interact with effects on the landscape-scale. These potential interactions between local- and landscape-scale effects are so far little explored in the existing literature, but are important to understand how management can be tailored to the landscape context and make appropriate recommendations.

In my study in chapter 2, we found surprising benefits of bean cultivation for biodiversity and ecosystem services, even compared to maize-bean intercropped fields. Previous studies indicate that the increased crop diversity through intercropping benefits ecosystem services such as pest control (Wan et al., 2020). However, in my study, bean monocultures had the highest carabid richness, parasitoid and spider activity densities and soil bacterial Shannon's richness of all three crop types, with the intercropped system representing an intermediate response, and beans in monoculture had significantly less pest damage than intercropped beans. Interestingly, the response of biodiversity was mediated by land-use context: carabid richness, parasitoid activity density and soil bacteria Shannon's richness on beans was highest on fields with low surrounding semi-natural habitat cover (<50%). This reveals two things: one, that monocultures *per se* are not problematic in smallholder farms and that the growing of a legume crop in a maize-dominated landscape enhances biodiversity and pest control, second, that the benefits of an agroecological practice are context-dependent and should therefore be tailored to the needs and situation of the smallholder farmer (Gliessman, 2018).

On pigeon pea fields, we found another surprising response to land-use differences, bee abundance increased with increasing agricultural area cover in the landscape (Chapter 4; Vogel et al., 2021). Again, the context of the system is important to understand these dynamics. Pigeon pea in our study area flowers in May, which is at the onset of dry season, after the main harvesting time in April. Therefore, we likely observed a concentration effect – bees gather on the remaining flowering resource (i.e. the flowering pigeon pea), in a landscape where flowering resource is otherwise scarce since all other crops are already harvested and native spontaneous vegetation predominantly already ceased flowering. Thus, the planting of pigeon pea may support pollinators in landscapes and in times, where alternative resources are scarce.

6.3 Dynamics of pests and pest management

Insect pests are considered a major constraint to reliable agricultural production. Understanding pest population dynamics is a major challenge for ecologists because their responses to changes in land-use depend strongly on the life-history traits of the pest in question (Tamburini et al., 2020), making it difficult to identify general pest management strategies. Unfortunately, high crop losses to pests are strongly associated with food-insecure regions, such as sub-Saharan Africa (Savary et al., 2019). This problem in sub-Saharan Africa is compounded by limited coping strategies of farmers, a favourable climate for the reproduction of pests and the introduction of invasive pests such as the Fall Armyworm (Matova et al., 2020). Though still low compared to the rest of the globe, pesticide use in sub-Saharan Africa is increasing, despite its costs to the environment and human health (Isgren & Andersson, 2021). Intensive and inappropriate pesticide use has the potential to aggravate pest outbreaks in the long term: firstly by destroying top-down control by natural enemies, that are also indiscriminately killed by pesticides, and secondly due to the evolution of genetic resistance to pesticides in pest populations (Savary et al., 2019). Agroecological pest management could provide a nature-based solution to the pest management issues (Wezel et al., 2014). Previous work in Malawian smallholder communities identified an interest of participating farmers in pests and agroecological pest management, but also highlighted limits in ecological knowledge about natural enemies of pests (Enloe et al., 2021).

In my thesis, we investigated pest damage patterns of in a maize-bean cropping system (Chapter 2), pumpkin (Chapter 3) and pigeon pea (Chapter 4). In addition, we investigated the effects of diversification of agroecological pest control maize-bean cropping systems (Chapter 2) and the effects of manual pest management, an agroecological pest management practice, on pollinators and pest damage (Chapter 3). In pumpkin, pests contributed to lowered fruit set in our study area (Chapter 3). Unfortunately, the implementation of manual pest management did not lower the proportion of damaged pumpkin flowers but did lower the abundance and richness of pollinators. Particularly, there was a negative effect on fly pollinators but not on non-honeybees, we suspect that this could be because the free living syrphid and tabanid larvae (as opposed to larvae of bees that live inside nests) are not distinguishable from pests by smallholder farmers. Smallholders may have limited knowledge on beneficial insects (Enloe et al., 2021), and therefore, agroecological pest management may be implemented inappropriately in some cases – highlighting the need for educating smallholders on what constitutes pests.

Similar to Baudron et al., (2019) in Zimbabwe, we found that higher pest damage during growth did not predict grain damage at harvest in maize in Malawi (Chapter 2). Additionally, though a higher diversity of agroecological pest management practices were applied to maize with more damage to growth, we do not see a reduction in maize damage at harvest. This indicates that applying pest management in response to observed pest damage may not result in expected pest control benefits on yields. As long as pest damage stays under an acceptable threshold, the labour invested in pest management may better be invested elsewhere (Dara, 2019). Additionally, there was lower pest damage on beans in monoculture than in intercrop, possibly mediated by higher natural enemy activities in the bean monoculture fields - indicating that the planting of legume crops in maize-dominated landscapes might be helpful to mitigate pest pressure through the attraction of natural enemies without active pest management (Chapter 2). Across my studies, we found no evidence that increasing semi-natural habitat cover or increased diversity of agroecological pest management decreased pest damage on the investigated crops. In fact, bean seed set was negatively affected by increased agroecological pest management diversification (Chapter 2), possibly due to the negative effects of pest management on pollinators (Chapters 3 & 5).

However, there are limitations to this approach. Firstly, we primarily investigated the proportional damage to crops, and as such could not detect damage caused by individual pest species, or the abundance of these pests. Since individual pest traits affect pest responses (Tamburini et al., 2020), investigating individual pest species in more detail will be an important field of future research to inform better pest management strategies in our system. Secondly, though we investigated the effects of an individual practice on pumpkin (Chapter 3) we mainly investigated the effect of agroecological pest management *diversification* (Chapter 2 & 5). This makes it difficult to elucidate the effects of individual practices, and as such structured research into the efficacy of individual practices and trade-offs with beneficial organisms are sorely needed.

6.4 Benefits of diverse agroecological soil management

Soil management is a key component of agroecological farming and reduces the reliance on unsustainable synthetic fertilizers (Wezel et al., 2020). From an agronomic perspective, the introduction of legumes, for example, can improve nitrogen and phosphorous cycling in degraded tropical soils (Garland et al., 2018). Implementing key agroecological soil practices benefits smallholder farmers beyond agronomic benefits. For example, households from the same communities where we collected data, were almost three times more likely to be food secure if they incorporated legume residue in the soil after harvest (Madsen et al., 2021). Additionally, a large-scale intervention project involving over 400 households in Malawi found that intercropping was associated with food security (Figure 6.1), and that agroecological soil amendments benefitted dietary diversity (Bezner Kerr et al., 2019b). Furthermore, a review by Bezner Kerr et al., (2021) found that agroecological systems implementing multiple components (i.e. a higher diversity of agroecological practices) were more likely to have positive outcomes for food and dietary security. Direct co-benefits of diversification of agroecological practices for biodiversity and ecosystem services are assumed, but not often empirically tested. In my thesis, we aimed to address this knowledge gap.

Figure 6.1: maize intercropped with soy, Mzimba district, Malawi. Legume intercropping is a common practice across our study region and helps maintain soil nutrients such as nitrogen. Our studies show that increasing the number of agroecological soil management practices on farms can benefit biodiversity, especially pollinators.

Across several of our studies, we provide evidence that increased diversification of agroecological soil management benefits biodiversity. Diversification increased soil bacteria Shannon's diversity (Chapter 2), as well as the abundance of non-dominant butterfly species

(Chapter 5). Also increasing the number of agroecological soil management practices at a farm level increased the abundance and species richness of pumpkin pollinators (Chapter 3). Furthermore, increased agroecological soil management changed carabid species assemblages (Chapter 2). With this, we demonstrate that diversified soil agroecological management could be a key component for conserving functional biodiversity on tropical smallholder farms. Though there was no direct effect of diversified agroecological soil management for ecosystem services, increased pollinator richness improved fruit set in pumpkin (Chapter 3). As such, diversified agroecological soil management provided an indirect benefit to pumpkin yield by increasing pollinator richness. However, increasing the diversity of soil management practices did not benefit all investigated taxa, and therefore, may not be appropriate to conserve these taxa on farmlands. For these taxa, alternative conservation measures should be identified.

As with agroecological pest management, my approach cannot identify the mechanism behind the observed benefits of diversified agroecological soil management, as we cannot identify which specific practice is responsible for the measured effects on biodiversity. As ground dwelling arthropods, one can assume that carabid assemblages are affected by soil disturbances introduced by some practices such as tillage, as has been found in other systems (Pisani Gareau, Voortman & Barbercheck, 2020). The introduction of manure, aeration of the soil and the planting of diverse crops such as nitrogen-fixing legumes could all have been responsible for the increased Shannon’s diversity of soil bacteria (Lakshmanan, Selvaraj & Bais, 2014). As for pollinators, we suspect that increased diversity and covering of flowering (leguminous) crops benefited their abundance and/or diversity (Wix, Reich & Schaarschmidt, 2019). Further research is needed to better understand the mechanisms and tailor the practices to specific conservation goals. However, the established benefits of the diversification of agroecological soil management practices for smallholders (Bezner Kerr et al., 2021), and the benefits for biodiversity demonstrated here warrants the upscaling and increased promotion of soil agroecology within smallholder communities.

6.5 Practical recommendations for decision makers in Malawi and beyond

Our data shows that land-use and agroecological practices on biodiversity and ecosystem services affect biodiversity and ecosystem services on tropical smallholder farms in a variety of ways. From this evidence, there are several concrete steps that can be taken by stakeholders at various levels, such as government, agricultural extension agencies and NGOs as well as the farming communities themselves to protect biodiversity and maintain ecosystems services in agricultural landscapes.

Figure 6.2: wild foods collected from semi-natural habitats in Mzimba district, Malawi. On the left, edible mushrooms, on the right, beetle larvae, which are fried and consumed as a relish.

Though some recommendations go beyond the scope and influence of a single smallholder farmer, we believe that the smallholder communities should be involved in decision making about the landscapes that they occupy and be informed about the potential effects of their own practices, so that they can make informed decisions tailored to their needs and priorities (Wezel et al., 2020). Within the FARMS4biodiversity project, stakeholders, particularly smallholder farming communities themselves, contributed knowledge and were regularly included in discussions about the project and informed about the results generated (Kpienbaareh et al., 2022a). As an example: that Scenario Planning workshops that took place in April 2022 in Malawi smallholder communities discussed their experiences and perceptions regarding landscape-scale declines in semi-natural habitats in their own communities. Farmers themselves reported observing negative effects of semi-natural habitat decline, such as decreased access to wild foods such as mushrooms and bushmeats, and medicinal plants normally found in surrounding semi-natural habitats. Farmers mentioned that they were motivated to maintain forests around their communities (*personal communication with farmers*, figure 6.2). Similar approaches could also be successful in engaging smallholder farmers and other stakeholders elsewhere and can empower farmers to make more informed decision making in affairs that directly affect them.

At the government and policy levels, there is a responsibility to increase protection of remaining semi-natural habitats, even outside protected habitats, by tackling the causes of deforestation in Malawi. As our data show (Chapters 2, 3 & 5), high semi-natural habitat cover is essential for biodiversity. Additionally, these habitats are important to maintain the ecosystem services and resources that the Miombo woodlands themselves provide to rural communities (Gumbo et al., 2018). Currently, natural habitats in the Malawi suffer from poor legal protection and poor enforcement of legal protections (Syampungani et al., 2009). Though technically illegal, harvesting fuelwood primarily for cooking, is a major driver of forest decline in Malawi. With only 2% of the rural population having access to electricity (which is itself unreliable and prone to frequent blackouts) (Taulo, Gondwe & Sebitosi, 2017), for smallholders, there simply is no feasible alternative until the energy access of rural communities is addressed. Therefore, my results call on the government and other stakeholders to address this problem to ensure the conservation of biodiversity and to maintain ecosystem services for smallholders. Firstly, address the energy needs of Malawi's communities by providing access to fuelwood alternatives such as electric stoves and a reliable, preferably renewable source of electricity. Secondly, remaining (semi-)natural habitats need stronger legal protection and these protections need to be enforced. Thirdly, degraded areas should be restored, possibly reforested with native trees and finally, local communities should be actively involved in the preservation and restoration and educated about the value of natural habitats in their landscapes.

The Malawian government has so far primarily attempted to improve rural livelihoods by increasing access to inputs, such as through the Farm Input Subsidy Programme (FISP). However, the benefits of these programmes are contested (Messina, Peter & Snapp, 2017). Though Malawi has seen a moderate increase of about 50% in maize yield since 2006, the number of undernourished people has only decreased by 0.1% in the same period (Mkindi et al., 2020). This demonstrates that food insecurity in Malawi is not adequately addressed by simply increasing yields with environmentally unsustainable inputs, but rather that an alternative, holistic approach is necessary to address the challenges facing smallholder communities. Instead, we argue that agroecological intensification, especially through the diversification of soil agroecological practices, is a more sustainable path forward, as agroecology has demonstrated benefits to smallholder farmers (Mkindi et al., 2020; Snapp et al., 2021; Bezner Kerr et al., 2021) whilst simultaneously promoting functional diversity (Chapters 2, 3 & 5). Therefore, we recommend that agroecological practices should be a key component of government agricultural extension programmes aimed at improving livelihoods of smallholder communities.

An example of an agroecological practice, legume cultivation, especially in areas low in semi-natural habitat cover, benefitted pollinators (Chapter 3) and natural enemies of pests, and had higher pest control (Chapter 2). As legume cultivation has a variety of other dietary and agronomic benefits, this practice should be upscaled and actively encouraged in smallholder communities, in the best case supported by incentives. Similarly, diversified soil agroecological practices should be encouraged to foster on-farm biodiversity (Chapters 2, 3 & 5), as well as increasing on-farm flowering plant diversity to increase pollinators (Chapter 5). Further participatory research and farmer experimentation are needed to find effective agroecological pest control strategies for smallholder farmers, as we could not find evidence that agroecological pest management practices lowered pest damage (Chapters 2 & 3). Outreach to farming communities should also aim to increase the ecological knowledge of farmers about the benefits of natural enemies and pollinators, and how to distinguish beneficial organisms from potential pests.

In summary, the main recommendations are:

1. Protection and recovery of semi-natural habitats through stronger legal protection and by addressing the drivers of deforestation - which will need to include poverty alleviation and improved access to reliable electricity.
2. Encourage the growing of legumes to increase the activity of pollinators and natural enemies of pests, especially in areas low in semi-natural habitat cover.
3. More research and experimentation into the drivers of pests on crops and appropriate agroecological control strategies for endemic and invasive pests.
4. Encourage diversified agroecological soil management practices to maintain biodiversity above- and belowground.
5. Increase on-farm flowering plant diversity through increased flowering crop diversity and tolerating weeds that benefit pollinators such as butterflies.

Though the research was focussed on northern Malawi, we believe the above-mentioned recommendations to be applicable to other countries in the Miombo-woodland ecoregion and more broadly in throughout sub-Saharan Africa and the Global South. However, despite the ecological, climatic, and cultural diversity of sub-Saharan Africa, the region is still underrepresented in applied ecological research (Steward et al., 2014; Nuñez et al., 2019).

Therefore, we believe more research is needed throughout sub-Saharan Africa to test the consistency of the results described here between regions and agricultural systems.

Agrobiodiversity: a very small selection of the wide variety of animals that can be found on smallholder farms in Malawi. Clockwise, starting from the top left: A carpenter bee (*Xylocopa* sp.) feeds on the flower of a *Tephrosia* sp. Extracts from *Tephrosia* spp. are used by smallholder farmers as a botanical pesticide. As its name suggests, the village indigobird (*Vidua chalybeate*) is commonly found around smallholder villages. A small bee from the family *Megachilidae* rests on a pigeon pea leaf. The red-lipped snake (*Crotaphopeltis hotamboeia*) is only mildly venomous and primarily hunts frogs. This *Ammophila* sp. sleeps by clasping a stem with its jaws. It is a predator of caterpillars, including potential pests. A smallholder farmer shows the author an adult insect from the order Neuroptera. Larvae of this order are specialized predators and may contribute to natural pest control on farms.

Chapter 7

Conclusion

Agricultural intensification has increased food production globally, but has come at a tremendous cost to biodiversity, threatening ecosystem services on which that same agriculture depends. As a result, pushing for further intensification, particularly in the Global South, endangers those regions that are still invaluably high in biodiversity, whilst at the same time exchanging short term productivity gains against long-term maintenance of essential agroecosystem processes. In sub-Saharan Africa in particular, the push for industrialised agriculture in smallholder communities has additionally increased disparities between the "haves" and "have-nots" and is therefore not delivering on promised benefits (Mkindi et al., 2020). Clearly, our current food systems are incapable of providing enough nutritious food for all in a way that can continue sustainably into the future. Agroecology as an alternative system could have many benefits both for smallholder farmers and the environment.

In this thesis, we investigated the potential for agroecological practices to maintain biodiversity and ecosystem services on smallholder farms in a region undergoing rapid landscape-scale deforestation. Increasing semi-natural habitat on the landscape scale decreased abundances, but increased species richness of pollinators. The cultivation of legumes, especially in maize-dominated landscapes, increased the activity of natural enemies, and bean-only fields had less damage than those planted in mixtures. The use of agroecological pest management strategies were not successful in reducing pest damage, and negatively impact pollinators, highlighting the need for a better understanding of pest dynamics and of the effectiveness of individual management practices. However, we found benefits of household diversification of agroecological soil management for the Shannon's diversity of soil bacteria as well for butterflies and other pollinators. In pumpkin, we found evidence that increased diversity of pollinators increased fruit set and as such, directly provided an ecosystem service to smallholder farmers. Our results show that to maintain biodiversity and ecosystem services in a tropical smallholder landscape, a twofold approach is needed: firstly, remaining semi-natural habitats needs to be protected and restored, and secondly, on-farm diversification of soil management practices and legume cultivation need to be encouraged and scaled up. Our work is a small addition to the growing body of evidence that shows that nature-based solutions are the way forward for the sustainable development of smallholder agricultural landscapes in a way that benefits the biodiversity and the smallholder communities living within them.

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Author contributions

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Participated in	**Author initials (Responsibility decreasing from left to right)**						
Study design	CV	ISD	KP	AI	TM	TC	RBK
Data collection	CV	TC	TM				
Farmer survey	RBK						
Bird survey and identification	TM						
Sorting and counting of arthropods	CV						
Bee and ant identification	CV						
Carabid identification	FB						
Cleaning and preparation of bacterial DNA data	AK						
Landscape analysis	GK						
Data analysis	CV	FB	KP	AI			
First draft of manuscript	CV						
Editing of manuscript	ALL						

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Participated in	**Author initials (Responsibility decreasing from left to right)**			
Study design	CV	ISD	KP	AI
Field preparation and data collection	CV	TM	MM	
Farmer survey	RBK	LD		
Pollinator collection & identification	CV			
Landscape analysis	GK			
Data analysis	CV	KP	AI	ISD
First draft of manuscript	CV			
Editing of manuscript	ALL			

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Participated in	Author initials (Responsibility decreasing from left to right)		
Study design	CV	ISD	KP
Data collection	CV	TLC	
Bee identification	CV		
Landscape analysis	XS		
Data analysis	CV	KP	ISD
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Study design	ISD	VM	JK	CV
Data collection	VM	MM		
Farmer survey	RBK			
Butterfly identification	VM			
Landscape analysis	GK			
Data analysis	CV	VM		
First draft of manuscript	CV	VM		
Editing of manuscript	ALL			

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Publication List

Publications as part of the doctoral thesis

Vogel C, Chunga TL, Sun X, Poveda K, Steffan-Dewenter I. 2021. Higher bee abundance, but not pest abundance, in landscapes with more agriculture on a late-flowering legume crop in tropical smallholder farms. *PeerJ* 9:e10732. http://doi.org/10.7717/peerj.10732

Vogel C, Poveda K, Iverson I, Chunga T, Mkandawire T, Boetzl FA, Küstner G, Keller A, Bezner Kerr R, Steffan-Dewenter I. (Under review.) The effects of crop type, landscape composition and agroecological practices on biodiversity and ecosystem services in tropical smallholder farms. *Journal of Applied Ecology*

Vogel C & Mayer V, Mkandawire M, Küstner G, Bezner Kerr R, Krauss J, Steffan-Dewenter I. (Under Review) Local and landscape scale conversion of woodland to farmland and agroecological practices shape butterfly communities in tropical smallholder landscapes. *Journal of Applied Ecology.*

Vogel C, Mkandawire T, Mkandawire M, Küstner G, Bezner Kerr R, Iverson A, Poveda K, Steffan-Dewenter I. (In Preparation) Pumpkin fruit set is limited by herbivory and low pollinator richness in a smallholder agricultural landscape.

Additional publications

Kpienbaareh D, Bezner Kerr R, Amoak D, Chunga T, Dakishoni L, Enloe S, Gondwe T, Iverson A, Kanyimbo P, Küstner G, Lupafya E, Luginaah I, Mehreteab T, Mayer V, Mhoni I, Mkandawire M, Mkandawire T, Moyo P, Munthali P, Nagothu US, Nyantakyi-Frimpong H, Poveda K, Shumba L, Steffan-Dewenter I, Tembo Y, **Vogel C**, Wang J. 2022. Transdisciplinary agroecological research on biodiversity and ecosystem services for sustainable and climate resilient farming systems in Malawi. *Advances in Ecological Research* (Special Issue: Pluralism in Ecosystem Governance.).

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Presentations

06/2022	**Vogel C,** Bezner Kerr R, Iverson A, Poveda K, Steffan-Dewenter I. The effects of landscape and agroecology on biodiversity and ecosystem services in smallholder farms in sub-Saharan Africa. Talk. European Conference of Tropical Ecology (*Gesellschaft für Tropenökologie*). Montpellier, France.
09/2021	**Vogel C,** Poveda K, Iverson I, Chunga T, Mkandawire T, Boetzl FA, Küstner G, Keller A, Bezner Kerr R, Steffan-Dewenter I. The effects of crop type, landscape composition and agroecological practices on biodiversity and ecosystem services in Malawian smallholder farms. Talk. Landscape 2021 (*ZALF*). Online.

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