Impact of human land use on bee diversity and plant-pollinator interactions in Tanzania savannah ecosystems

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"If the bee disappeared off the surface of the globe, then man would have only four years of life left. No more bees, no more pollination, no more plants, no more animals, no more man."

Albert Einstein

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Affidavit

Declaration

I, Julius Vincent Lasway certify that the thesis entitled **“Impact of human land use on bee diversity and plant-pollinator interactions in Tanzanian savannah ecosystems”** results from my own work. I also certify that I did not receive any help or support from any commercial consulting firm and that all sources and materials applied are listed and specified in the thesis. Further to that, I certify that this thesis has not been submitted as part of another examination process neither in identical nor in similar form.

Ich, Julius Vincent Lasway, bestätige, dass die vorliegende Arbeit mit dem Titel “**Impact of human land use on bee diversity and plant-pollinator interactions in Tanzanian savannah ecosystems**” auf meiner eigenen Arbeit beruht. Ich bestätige auch, dass ich keine Hilfe oder Unterstützung durch ein kommerzielles Beratungsunternehmen erhalten habe und dass alle verwendeten Quellen und Materialien in der Arbeit aufgeführt und spezifiziert sind. Ferner versichere ich, dass diese Arbeit weder in identischer noch in ähnlicher Form im Rahmen eines anderen Prüfungsverfahrens eingereicht worden ist.

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Summary

One of the pronounced global challenges facing ecologists is how to feed the current growing human population while sustaining biodiversity and ecosystem services. To shed light on this, I investigated the impact of human land use on bee diversity and plant-pollinator interactions in Tanzania Savannah ecosystems. The thesis comprises the following chapters:

Chapter I: General Introduction

This chapter provides the background information including the study objectives and hypotheses. It highlights the ecological importance of bees and the main threats facing bee pollinators with a focus on two land-use practices namely livestock grazing and agriculture. It also highlights the diversity and global distribution of bees. It further introduces the tropical savannah ecosystem, its climate, and vegetation characteristics and explains spectacular megafauna species of the system that form centers of wildlife tourism and inadequacy knowledge on pollinators diversity of the system. Finally, this chapter describes the study methodology including, the description of the study area, study design, and data collection.

Chapter II: Positive effects of low livestock grazing intensity on East African bee assemblages mediated by increases in floral resources

The impact of livestock grazing intensity on bee assemblage has been subjected to research over decades. Moreover, most of these studies have been conducted in temperate Europe and America leaving the huge tropical savannah of East Africa less studied. Using sweep netting and pan traps, a total of 183 species (from 2,691 individuals) representing 55 genera and five families were collected from 24 study sites representing three levels of livestock grazing intensity in savannah ecosystem of northern Tanzania. Results have shown that moderate livestock grazing

slightly increased bee species richness. However, high livestock grazing intensity led to a strong decline. Besides, results revealed a unimodal distribution pattern of bee species richness and mean annual temperature. It was also found that the effect of livestock grazing and environmental temperature on bee species richness was mediated by a positive effect of moderate grazing on floral resource richness. The study, therefore, reveals that bee communities of the African savannah zone may benefit from low levels of livestock grazing as this favors the growth of flowering plant species. A high level of livestock grazing intensity will cause significant species losses, an effect that may increase with climatic warming.

Chapter III: Agricultural intensification with seasonal fallow land promotes high bee diversity in Afrotropical drylands

This study investigated the impact of local agriculture intensification on bee diversity in the Afro tropical drylands of northern Tanzania. Using sweep netting and pan traps, a total of 219 species (from 3,428 individuals) representing 58 genera and six families were collected from 24 study sites (distributed from 702 to 1708 m. asl) representing three levels of agriculture intensity spanning an extensive gradient of mean annual temperature. Results showed that bee species richness increased with agricultural intensity and with increasing temperature. However, the effects of agriculture intensity and temperature on bee species richness were mediated by the positive effects of agriculture and temperature on floral resource richness used by bee pollinators. Moreover, results showed that variation of bee body sizes increases with agricultural intensification, “that effect”, however, diminished in environments with higher temperatures. This study reveals that bee assemblages in Afrotropical drylands benefit from agriculture intensification in the way it is currently practiced. Further intensification, including year-round irrigated crop monocultures and extensive use of agrochemicals, is likely to exert a negative impact on bee diversity and pollination services, as reported in temperate regions. Moreover, several bee species were restricted to natural savannah habitats. Therefore, to conserve bee communities in Afro tropical drylands and guarantee pollination services, a mixture of savannah and agriculture, with long periods of fallow land should be maintained.

Chapter IV: Impact of land use intensification and local features on plants and pollinators in Sub-Saharan smallholder farms

For the first time in the region, this study explores the impact of land-use intensification on plants and pollinators in Sub-Saharan smallholder farms. The study complemented field surveys of bees with a modern DNA metabarcoding approach to characterize the foraged plants and thus built networks describing plant-pollinator interactions at the individual insect level. This information was coupled with quantitative traits of landscape composition and floral availability surrounding each farm. The study found that pollinator richness decreased with increasing impervious and agricultural cover in the landscape, whereas the flower density at each farm correlated with pollinator richness. The intensification of agricultural land use and urbanization correlated with a higher foraging niche overlap among pollinators due to the convergence of individuals' flower-visiting strategies. Furthermore, within farms, the higher availability of floral resources drove lower niche overlap among individuals, greater abundance of flower visitors shaped higher generalization at the networks level ($H2^{I}$), possibly due to increased competition. These mechanistic understandings leading to individuals’ foraging niche overlap and generalism at the network level, could imply stability of interactions and the pollination ecosystem service. The integrative survey proved that plant-pollinator systems are largely affected by land use intensification and by local factors in smallholder farms of Sub-Saharan Africa. Thus, policies promoting nature-based solutions, among which the introduction of more pollinator-friendly practices by smallholder farmers, could be effective in mitigating the intensification of both urban and rural landscapes in this region, as well as in similar Sub-Saharan contexts.

Chapter V: A synopsis of the Bee occurrence data of northern Tanzania

This study represents a synopsis of the bee occurrence data of northern Tanzania obtained from a survey in the Kilimanjaro, Arusha, and Manyara regions. Bees were sampled using two standardized methods, sweep netting and colored pan traps. The study summed up 953 species occurrences of 45 species belonging to 20 genera and four families (Halictidae, Apidae, Megachilidae, and andrenidae) A. This study serves as the baseline information in understanding the diversity and distribution of bees in the northern parts of the country. Understanding the richness and distribution of bees is a critical step in devising robust conservation and monitoring strategies for their populations since limited taxonomic information of the existing and unidentified bee species makes their conservation haphazard.

Chapter VI: General discussion

In general, findings obtained in these studies suggest that livestock grazing and agriculture intensification affects bee assemblages and floral resources used by bee pollinators. Results have shown that moderate livestock grazing intensity may be important in preserving bee diversity. However, high level of livestock grazing intensity may result in a strong decline in bee species richness and abundance. Moreover, findings indicate that agriculture intensification with seasonal fallow lands supports high floral resource richness promoting high bee diversity in Afrotropical drylands. Nonetheless, natural savannahs were found to contain unique bee species. Therefore, agriculture intensification with seasonal fallow should go in hand with conserving remnant savannah in the landscapes to increase bee diversity and ensure pollination services. Likewise, findings suggest that increasing urbanization and agriculture cover at the landscape level reduce plant and pollinator biodiversity with negative impacts on their complex interactions with plants. Conversely, local scale availability of floral resources has shown the positive effects in buffering pollinators decline and mitigating all detrimental effects induced by land-use intensification. Moreover, findings suggest that the impact of human land use (livestock grazing and agriculture) do not act in isolation but synergistically interacts with climatic factors such as mean annual temperature, MAT. The impact of MAT on bee species richness in grazing gradient showed to be more detrimental than in agriculture habitats. This could probably be explained by the remaining vegetation cover following anthropogenic disturbance. Meaning that the remaining vegetation cover in the agricultural gradient probably absorbs the solar radiations hence reducing detrimental effect of mean annual temperature on bee species richness. This one is not the case in grazing gradient since the impact of livestock grazing is severe, leaving the bare land with no vegetation cover. Finally, our findings conclude that understanding the interplay of multiple anthropogenic activities and their interaction with MAT as a consequence of ongoing climate change is necessary for mitigating their potential consequences on bee assemblages and the provision of ecosystem services. Morever, future increases in livestock grazing and agriculture intensification (including year-round crop irrigated monocultures and excessive use of agrochemicals) may lead to undesirable consequences such as species loss and impair provision of pollination services.

Zusammenfassung

Eine der größten globalen Herausforderungen für Ökologen ist die Beantwortung der Frage, wie die wachsende menschliche Bevölkerung ernährt und gleichzeitig die biologische Vielfalt und die Ökosystemleistungen erhalten werden können. Um dies zu beleuchten, habe ich die Auswirkungen der menschlichen Landnutzung auf die Bienenvielfalt und die Wechselwirkungen zwischen Pflanzen und Bestäubern in den Ökosystemen der Tansania-Savanne untersucht. Die Arbeit umfasst die folgenden Kapitel:

Kapitel I: Allgemeine Einführung

Dieses Kapitel enthält die Hintergrundinformationen, einschließlich der Studienziele und Hypothesen. Es hebt die ökologische Bedeutung von Bienen und die Hauptbedrohungen für Bienenbestäuber hervor, wobei der Schwerpunkt auf zwei Landnutzungspraktiken liegt, nämlich Viehbeweidung und Landwirtschaft. Außerdem werden die Vielfalt und die globale Verbreitung der Bienen herausgearbeitet. Des Weiteren werden das Ökosystem der tropischen Savanne, sein Klima und seine Vegetationscharakteristika vorgestellt und die spektakulären Megafauna-Arten des Systems erläutert, die Zentren des Wildtiertourismus bilden, sowie die unzureichenden Kenntnisse über die Vielfalt der Bestäuber in diesem System. Schließlich wird in diesem Kapitel die Methodik der Studie beschrieben, einschließlich der Beschreibung des Untersuchungsgebiets, des Studiendesigns und der Datenerhebung.

Kapitel II: Positive Auswirkungen einer geringen Beweidungsintensität auf ostafrikanische Bienengemeinschaften, vermittelt durch eine Zunahme der floralen Ressourcen

Die Auswirkungen der Weideintensität auf die Bienenbestände sind seit Jahrzehnten Gegenstand von empirischen Untersuchungen. Die meisten dieser Studien wurden jedoch in den gemäßigten Breiten Europas und Amerikas durchgeführt, während die riesigen tropischen Savannen Ostafrikas weniger untersucht wurden. Mit Hilfe von Wurfnetzen und Schwenkfallen wurden insgesamt 183 Arten (von 2.691 Individuen) aus 55 Gattungen und fünf Familien an 24 Untersuchungsstandorten, die drei Stufen der Viehweideintensität im Savannen-Ökosystem im Norden Tansanias repräsentieren, gesammelt. Die Ergebnisse zeigen, dass eine mäßige Beweidung mit Weidevieh den Artenreichtum der Bienen leicht erhöht. Eine hohe Beweidungsintensität führte jedoch zu einem starken Rückgang. Außerdem zeigten die Ergebnisse ein unimodales Verteilungsmuster des Bienenartenreichtums und der mittleren Jahrestemperatur. Es wurde auch festgestellt, dass die Auswirkungen von Viehbeweidung und Umwelttemperatur auf den Bienenartenreichtum durch eine positive Auswirkung von mäßiger Beweidung auf den Reichtum an floralen Ressourcen vermittelt wurden. Die Studie zeigt daher, dass Bienengemeinschaften in der afrikanischen Savanne von einer geringen Beweidung durch Vieh profitieren können, da dies das Wachstum blühender Pflanzenarten fördert. Eine hohe Beweidungsintensität führt zu erheblichen Artenverlusten, die sich infolge der Klimaerwärmung noch verstärken können.

Kapitel III: Intensivierung der Landwirtschaft mit saisonalem Brachland fördert hohe Bienenvielfalt in afrotropischen Trockengebieten

In dieser Studie wurden die Auswirkungen der Intensivierung der lokalen Landwirtschaft auf die Bienenvielfalt in den afrotropischen Trockengebieten im Norden Tansanias untersucht. An 24 Untersuchungsstandorten (zwischen 702 und 1.708 m ü.N.N.), die drei Intensitätsstufen der Landwirtschaft repräsentieren und einen weiten Gradienten der Jahresmitteltemperatur abdecken, wurden 219 Arten (von 3.428 Individuen) gesammelt, die 58 Gattungen und sechs Familien repräsentieren. Die Ergebnisse zeigten, dass der Artenreichtum der Bienen mit der Intensität der Landwirtschaft und mit steigender Temperatur zunahm. Die Auswirkungen der Intensität der Landwirtschaft und der Temperatur auf den Artenreichtum der Bienen wurden jedoch durch die positiven Auswirkungen der Landwirtschaft und der Temperatur auf den Reichtum der von den Bienenbestäubern genutzten Blütenressourcen vermittelt. Außerdem zeigten die Ergebnisse, dass die Variation der Körpergröße der Bienen mit der Intensivierung der Landwirtschaft zunimmt, diese jedoch in Umgebungen mit höheren Temperaturen abnimmt. Diese Studie zeigt, dass die Bienengemeinschaften in afrotropischen Trockengebieten von der Intensivierung der Landwirtschaft, wie sie derzeit praktiziert wird, profitieren. Eine weitere Intensivierung, einschließlich ganzjährig bewässerter Monokulturen und intensiver Einsatz von Agrochemikalien, wird sich wahrscheinlich negativ auf die Bienenvielfalt und die Bestäubungsleistung auswirken, wie dies auch in den gemäßigten Regionen beobachtet wurde. Außerdem war das Vorkommen einiger Bienenarten auf natürliche Savannenlebensräume beschränkt. Um die Bienengemeinschaften in afrotropischen Trockengebieten zu erhalten und die Bestäubungsleistungen zu gewährleisten, sollte daher eine Mischung aus Savanne und Landwirtschaft mit Langzeitig-Brachflächen beibehalten werden.

Kapitel IV: Auswirkungen der Intensivierung der Landnutzung und lokaler Gegebenheiten auf Pflanzen und Bestäuber in kleinbäuerlichen Betrieben südlich der Sahara

In dieser Studie werden zum ersten Mal in der Region die Auswirkungen der Intensivierung der Landnutzung auf Pflanzen und Bestäuber in kleinbäuerlichen Betrieben südlich der Sahara untersucht. Hierbei wurden Felduntersuchungen von Bienen um einen modernen DNA-Metabarcoding-Ansatz ergänzt, um die beflogenen Pflanzen zu charakterisieren und so Netzwerke aufzudecken, die die Interaktionen zwischen Pflanzen und Bestäubern auf der Ebene einzelner

Insekten beschreiben. Diese Informationen wurden mit quantitativen Merkmalen der Landschaftszusammensetzung und der Blütenverfügbarkeit in der Umgebung der einzelnen landwirtschaftlichen Betriebe verknüpft. Die Studie ergab, dass der Reichtum an Bestäubern mit zunehmendem Landschaftsanteil an undurchlässiger und landwirtschaftlicher Fläche abnahm, während die Blütendichte mit dem Reichtum an Bestäubern korrelierte. Die Intensivierung der landwirtschaftlichen Nutzung und die Urbanisierung korrelierten mit einer stärkeren Überlappung der Nischen für die Nahrungssuche von Bestäubern, was auf die Konvergenz der Strategien der Individuen bei der Suche nach Blüten zurückzuführen ist. Darüber hinaus führte innerhalb der landwirtschaftlichen Betriebe die höhere Verfügbarkeit von Blütenressourcen zu einer geringeren Nischenüberschneidung zwischen den Individuen, während eine größere Anzahl von Blütenbesuchern zu einer stärkeren Generalisierung auf der Ebene der Netzwerke führte ($H2^{I}$), was möglicherweise auf einen erhöhten Wettbewerb zurückzuführen ist. Diese mechanistischen Erkenntnisse, die zur Überlappung der Nischen der Individuen bei der Nahrungssuche und zum Generalismus auf der Netzwerkebene führen, könnten die Stabilität der Interaktionen und der Ökosystemdienstleistung Bestäubung implizieren. Die integrative Untersuchung hat gezeigt, dass die Bestäubersysteme in den kleinbäuerlichen Betrieben Afrikas südlich der Sahara weitgehend von der Intensivierung der Landnutzung und von lokalen Faktoren beeinflusst werden. Daher könnten politische Maßnahmen zur Förderung naturbasierter Lösungen, zu denen auch die Einführung bestäuberfreundlicher Praktiken durch Kleinbauern gehört, die Intensivierung sowohl städtischer als auch ländlicher Landschaften in dieser Region wie auch in ähnlichen Kontexten südlich der Sahara wirksam abmildern.

Kapitel V: Ein Überblick über die Daten zum Bienenvorkommen im Norden Tansanias

Diese Studie gibt einen Überblick über die Daten zum Bienenvorkommen im Norden Tansanias, die im Rahmen einer Erhebung in den Regionen Kilimanjaro, Arusha und Manyara gewonnen wurden. Die Bienen wurden mit zwei standardisierten Methoden erfasst: mit Keschern und Farbschalen. Im Rahmen der Studie wurden 953 Individuen aus 45 Arten aus 20 Gattungen und vier Familien (Halictidae, Apidae, Megachilidae und Andrenidae) nachgewiesen. Diese Studie dient als Grundlage für das Verständnis der Vielfalt und Verbreitung von Bienen in den nördlichen Teilen des Landes. Das Verständnis des Reichtums und der Verbreitung von Bienen ist ein entscheidender Schritt bei der Entwicklung robuster Erhaltungs- und Überwachungsstrategien für deren Populationen, da die begrenzten taxonomischen Informationen über die vorhandenen und nicht identifizierten Bienenarten deren Erhaltung ungewiss erscheinen lassen.

Kapitel VI: Allgemeine Diskussion

Im Allgemeinen deuten die Ergebnisse dieser Studien darauf hin, dass die Beweidung mit Vieh und die Intensivierung der Landwirtschaft Auswirkungen auf die Bienenbestände und die von Bienenbestäubern genutzten Blütenressourcen haben. Die Ergebnisse haben gezeigt, dass eine mäßige Beweidungsintensität für die Erhaltung der Bienenvielfalt von Bedeutung sein kann. Eine hohe Beweidungsintensität kann jedoch zu einem starken Rückgang des Artenreichtums und der Abundanz von Bienen führen. Außerdem deuten die Ergebnisse darauf hin, dass die Intensivierung der Landwirtschaft mit saisonalem Brachland einen hohen Reichtum an floralen Ressourcen aufweist, der eine hohe Bienenvielfalt in afrotropischen Trockengebieten fördert. Nichtsdestotrotz zeigte sich, dass natürliche Savannen eine einzigartige Artenzusammensetzung aufweisen. Daher sollte die Intensivierung der Landwirtschaft mit saisonalem Brachland mit der Erhaltung von Savannenresten in den Landschaften einhergehen, um die Bienenvielfalt zu erhöhen und die Bestäubungsleistung sicherzustellen. Ebenso deuten die Ergebnisse darauf hin, dass die zunehmende Urbanisierung und landwirtschaftliche Nutzung auf Landschaftsebene die biologische Vielfalt von Pflanzen und Bestäubern verringert, was sich negativ auf ihre komplexen Interaktionen mit Pflanzen auswirkt. Umgekehrt hat sich die Verfügbarkeit von Blütenressourcen auf lokaler Ebene als positiv erwiesen, da sie den Rückgang der Bestäuber abpuffert und alle durch die Intensivierung der Flächennutzung verursachten negativen Auswirkungen abmildert. Darüber hinaus deuten die Ergebnisse darauf hin, dass die Auswirkungen der menschlichen Landnutzung (Viehbeweidung und Landwirtschaft) nicht isoliert wirken, sondern synergetisch mit Klimafaktoren wie der mittleren Jahrestemperatur (MAT) zusammenwirken. Die Auswirkung von MAT auf den Artenreichtum der Bienen in Weidegebieten erwies sich als nachteiliger als in landwirtschaftlich genutzten Lebensräumen. Dies könnte wahrscheinlich durch die verbleibende Vegetationsdeckung nach einer anthropogenen Störung erklärt werden. Das bedeutet, dass die verbleibende Vegetationsdeckung im landwirtschaftlichen Gradienten wahrscheinlich die Sonneneinstrahlung absorbiert und damit die nachteiligen Auswirkungen der mittleren Jahrestemperatur auf den Artenreichtum der Bienen verringert. Dies ist im Weidegradienten nicht der Fall, da die Auswirkungen der Beweidung durch das Weidevieh schwerwiegend sind und kahles Land ohne nennenswerte Vegetationsbedeckung zurücklassen. Unsere Ergebnisse lassen den Schluss zu, dass ein Verständnis des Zusammenspiels verschiedener anthropogener Aktivitäten und ihrer Interaktion mit MAT als Folge des fortschreitenden Klimawandels notwendig ist, um die potenziellen Folgen für die Bienenbestände und die Bereitstellung von Ökosystemleistungen zu mildern. Darüber hinaus können die künftige Zunahme der Viehbeweidung und die Intensivierung der Landwirtschaft (einschließlich ganzjährig bewässerter Monokulturen und übermäßiger Einsatz von Agrochemikalien) zu unerwünschten Folgen wie dem Verlust von Arten und Bestäubungsleistungen führen.

Chapter I

General Introduction

Objectives and hypotheses of the studies

The main objective of this thesis is to investigate the impact of human land use on bee assemblages and plant-pollinator interaction in Tanzania savannah ecosystems. The thesis has four specific objectives that form the basis of four chapters/studies.

The first specific objective that forms the first study of this thesis (chapter II) investigate the impact of livestock grazing on bee diversity. In this study, the effect of livestock grazing intensity on bee assemblages along the temperature gradient of the savannah ecosystem of northern Tanzania was examined. The study further disentangled the direct and indirect effects of livestock grazing intensity and mean annual temperature on bee species richness and the species composition of bee communities.

The second specified objective that forms the second chapter (chapter III) of this thesis examines the impact of local agriculture intensification on bee diversity in Afrotropical drylands. To achieve this research purpose, the study hinges on four hypotheses that suggest; i) High agricultural intensity negatively affects bee species richness and abundance; ii) Bee species richness increase with ambient temperature; iii) The effect of agriculture on bee species richness is indirect, i.e., mediated by a change in their potential floral resources (plant species richness). Alternatively, agriculture directly (e.g., plowing, weed extirpating, or pesticide application) rather than indirectly impacts bee species richness; and iv) Increases in temperature and agricultural intensity lead to a change in the bee body size distribution.

The third specified objective that forms chapter IV of this thesis investigates the impact of land-use intensification and local features on plants and pollinators in Sub-Saharan smallholder farms. The study combined a DNA metabarcoding-based approach with field monitoring and land use analysis to investigate how different features of the surrounding landscape affect the plant-pollinator communities in smallholder farms of Northern Tanzania. The study hypothesized to find a negative effect of land use intensification on plants and pollinators richness and alteration of the foraging preferences and structural properties of the plant-bee interaction networks.

The last (fourth) specific objective that forms chapter V of this thesis gives a synopsis of the bee occurrence data of northern Tanzania from a survey conducted in Kilimanjaro, Arusha, and Manyara regions. This study set out the first-ever checklist of bee species of the tropical savannah of northern Tanzania. However, other species data obtained from this survey will be published in subsequent papers.

Ecological importance of bees, land-use intensification, and global pattern of bee diversity

▪ Ecological importance of bees

Insect pollinators particularly bees are extremely important component of global biodiversity (Potts et al., 2010). Through pollination services, bees play a vital role in maintaining the functionality of natural ecosystems, maintaining wild plant communities, enhancing agricultural productivity, and hence promoting human well-being (Klein, Vaissiere, et al., 2007; Potts et al., 2016; Ollerton et al., 2011). About ninety percent of all flowering plant reproduction, 87% of the major food crops, and 35% of global food production depend on animal pollination and in particular on bee pollinators (Klein et al., 2007). Therefore, the need for conserving bee diversity and abundance is apparent to ensure ecosystem healthy and functioning.

Accumulating evidence suggests a global decline in bee-pollinators richness and abundance in different parts of the world with negative consequences for pollination services (Potts et al., 2010). The global decline of bees is associated with various factors such as, habitat loss and fragmentation, invasive species, diseases, and climate change (Brown & Paxton, 2009; Potts et al., 2010; Potts et al., 2016; Winfree et al., 2009). Decline in bee-pollinators makes their fundamental characteristics, such as distribution dynamics and evolutionary history be poorly understood. Because some of them disappears (extinct) even before their discovery (Lasway et al., 2021b). Understanding bee-pollinators distribution is key to evolutionary studies of origin and diversification. Besides, understanding their distribution and how specific group is responding to threats such as human-induced phenomena and climate change will elevate their conservation efforts (Orr et al., 2021).

- **Land-use intensification**

Land-use intensification, particularly agriculture expansion and livestock grazing, are assumed to be major global drivers for pollinators' decline (Potts et al., 2010). These anthropogenic activities aim at accommodating the exponential increase of the human population that increases food demand (Laurance et al., 2014; Ma et al., 2019). However, improper management of these activities may lead to habitat loss and fragmentation. Global agriculture expansion has been associated with the loss of natural habitats and intensified agricultural practices such as pesticides application, loss of crop diversity, and agriculture mechanization resulting in loss of pollinators diversity and its associated ecosystem services (Goulson et al., 2015; Potts et al., 2016; Steffan-Dewenter & Westphal, 2008). On the other hand, the global expansion of livestock grazing is considered an utmost threat to bee diversity (Brown & Paxton, 2009; Potts et al., 2010, 2016; Winfree et al., 2009). Higher livestock grazing intensity decimates vegetation cover, causes severe soil compaction, and ultimately soil erosion (Lazaro et al., 2016; Petanidou & Ellis, 1996). These impacts may affect bee assemblages, both directly or indirectly. Direct through trampling that destroys nests of ground-nesting bees (Lazaro et al., 2016; Tadey, 2015) or damaging nests in twigs or branches of plants (Potts et al., 2009). Conversely, the indirect impact is through reducing the floral resources hence interrupting bee-plant interaction networks (Tadey, 2015). Understanding the mechanisms through which livestock grazing and agriculture intensification may affect bee assemblages and plant-pollinator interactions is critical for informed management decisions and pollinators conservation planning.

▪ Global pattern of bee diversity

Global databases provide checklists that give a clear picture of global bee distribution (Orr et al., 2021). From the five global databases, Orr et al., (2021) made a bee species richness distribution model (Fig. 1a) and found that large hotspots of richness are apparent in Southwestern USA, Mediterranean Basin into the Middle East, and Australia with a weak signal of species richness in South Africa. Contrasting species-rich arid-temperate areas, the humid tropics and even arid tropical areas including large parts of tropical East Africa are generally poor in species richness. However, there is a lack of studies of bee diversity for many tropical areas and particularly for Africa. In this context, Orr et al., (2021) also showed a bee sampling distribution map (Fig. 1b) indicating that few samplings of bees have been conducted in the tropical East Africa region. This finding is consistent with that of Saunders et al., (2020) that showed that most studies on bees have been conducted in temperate Europe and America that are unlikely the globally representative leaving information of bee assemblage in tropical East African drylands largely unknown.

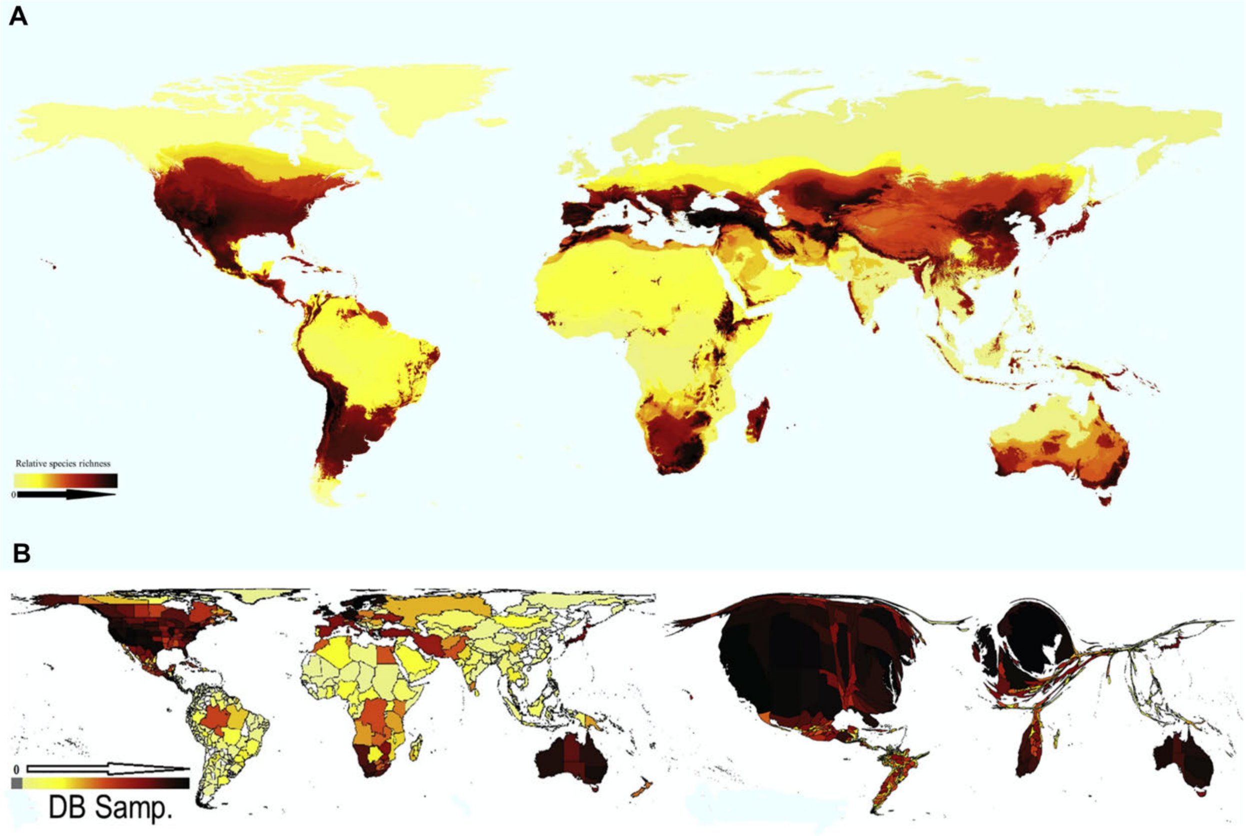


Fig. 1 | A, High resolution bee species richness distribution model. The map shows species richness distribution based on checklists and data points from global data bases. Areas of higher projected species richness are darker compared with areas of the lowest richness. **B,** Sampling intensity of bees for different countries (left) and cartogram showing sampling intensity in different continent (right). *Figure adapted from Orr et al., (2021).*

Tropical savannah ecosystems

Tropical savannah ecosystems cover about 20% of the earth's land surface (Broxton et al., 2014), (Fig. 2) harboring high biodiversity that provides ecosystem goods and services to millions of inhabitants in the world (Osborne et al., 2018). The ecosystem is characterized by warm temperature all year round and seasonal water availability, with rainfall typically confined to two seasons (Osborne et al., 2018; Skarpe, 1996). The dominant vegetation of this biome are grasses and dispersed trees that do not form a closed canopy allowing sunlight to reach the ground. This ecosystem covers almost half of Africa with more than 13 million square kilometers (Osbone et al., 2018) (Fig. 2). Since a large part of this system (tropical savannah) is dominated by grasses, it is sometimes referred to as tropical grassland (Osborne et al., 2018).

Tropical savannah ecosystems are ecologically important as they provide habitat for high diverse of living things including migratory birds and several threatened and endangered species of plants and animals (Abel et al., 2021). They are homes to diverse endemic flora and fauna, including charismatic megafaunas that are centers of wildlife tourism in Africa. Tropical savannah ecosystems are referred to as biodiversity hotspots as they are species-rich ecosystems with biodiversity levels of many taxa comparable to those of tropical rain forests. They represent some of the most iconic and spectacular examples of complex terrestrial food webs (Osborne et al., 2018). However, as humans increasingly dominate the earth, anthropogenic drivers are increasing and causing rapid vegetation change across the Afrotropical savannah system threatening biodiversity and ecosystem services such as pollination.

Land cover changes and transformation to agriculture and livestock grazing are among anthropogenic drivers threatening tropical savannah ecosystems in recent decades (Osborne et al., 2018), leading to their degradation at an even quicker pace. Despite the fact that tropical savannahs are well known for their high diverse megafauna. Yet, little is known about wild bee pollinators of the system and the potential impacts that face their survival. In this study, I am interested in identifying wild bee pollinators of East African tropical savannah, their response to anthropogenic land-use changes and climate. It is apparent that if we do not know what we have in terms of species richness, where they live, and how abundant they are. It is almost impossible to measure their decline and generate a prioritized and meaningful conservation strategy.

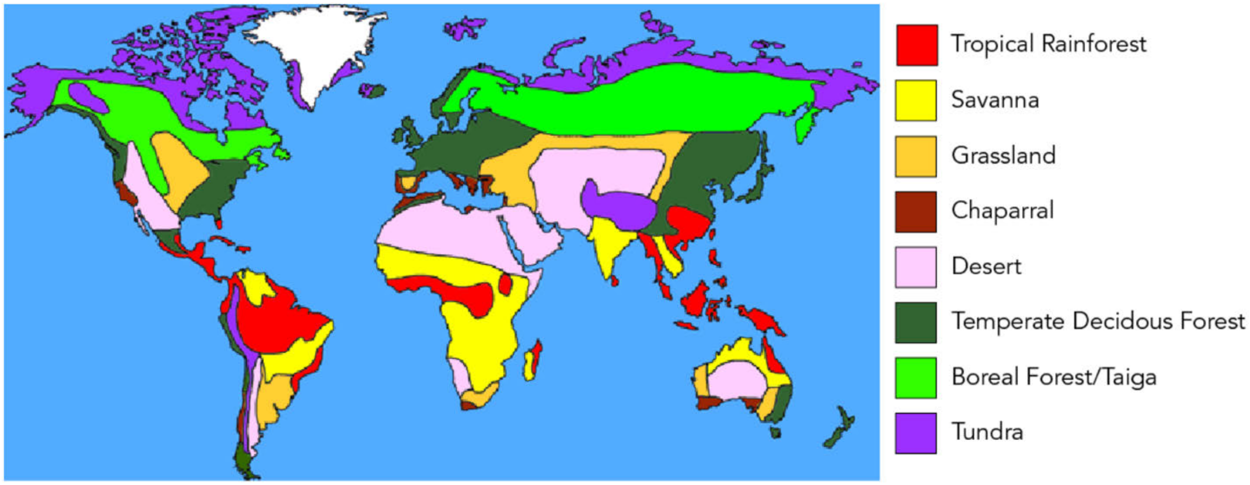
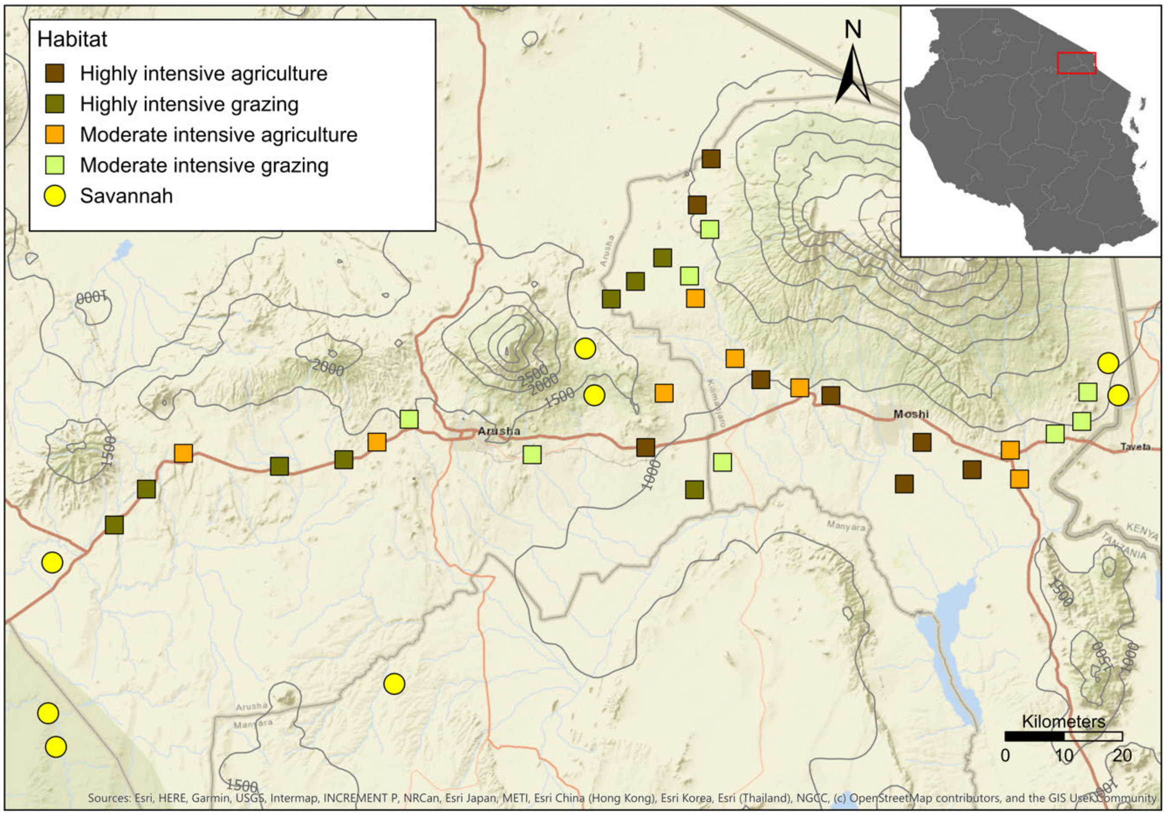


Fig. 2 | Major terrestrial biomes. *Figure adapted from: H.J. de Blij and P.O. Miller*

Description of the Study Area

This study was conducted in savannah ecosystem of northern Tanzania, in the lowlands of Mt. Kilimanjaro and Mt. Meru, and the areas of Tarangire National Park in Kilimanjaro, Arusha, and Manyara regions, respectively (Fig. 3). The study area is characterized by a tropical climate with extensive dry periods (Gebrechorkos et al., 2019a). The elevation of the study area ranges between 702m and 1708m above sea level (asl) with the mean annual temperature spanning from 18°C to 26°C (depending on elevation) with maxima temperatures regularly exceeding 40°C (own unpublished data). The area experiences bimodal rainfall with a long rainy season between ca. March and May and a short rainy season typically in November and December (C. A. Foley & Faust, 2010). The dominant natural vegetation of this dryland is composed of grasses interspersed with herbs and scattered trees (dominated by *Commiphora* and *Acacia*) (tropical savannah). Outside of the protected areas, non-native tree species like *Acrocarpus flaxinifolius*, *Leucaena leucocephala*, and *Grevillea robusta* can be found. The study area was categorized into five habitats (natural savannah, moderate livestock grazing intensity, highly livestock grazing intensity, moderate intensive agriculture and highly intensive agriculture). Eight replicates study sites of each different habitat were distributed across the entire study area to minimize spatial autocorrelation (Fig. 3). The eight replicates of each habitat made a total of forty study sites which spanned two land use gradients (livestock grazing gradient and agriculture gradient).



Sources: Esri, HERE, Garmin, USGS, Intermap, INCREMENT P, NRCan, Esri Japan, METI, Esri China (Hong Kong), Esri Korea, Esri (Thailand), NGCC, (c) OpenStreetMap contributors, and the GIS User Community

Fig. 3 | Map of the study area. Study sites are indicated by different colors depending on the grazing and agriculture intensity (see legend). The two larger mountains on the map are Mt. Kilimanjaro (upper right) and Mt. Meru (center). The small map in the upper right corner shows the location of the study area within Tanzania.

Depiction of land use gradients (livestock grazing and agriculture)

a) Grazing gradient

The characterization of grazing gradient was done based on information on the distribution of protected areas such as National Parks, visual inspection of on-site signs of obvious grazing like shortened tufts of grass, the presence or absence of livestock footprints and by calculating the distance between study sites to bomas (livestock enclosures holding large herds of livestock) and non-boma villages (where families hold only single or few individuals (<10) of livestock). Study sites with signs of high livestock grazing intensity were very near to bomas (average distance 0.09 ± 0.05 (SD) km; distance to non-boma village = 1.9 ± 1.9 km), while study sites with moderate livestock grazing intensity were near to non-boma villages (average distance = 0.25 ± 0.05 (SD) km; distance to boma village = 25.3 ± 27.6 km). Study sites with low livestock grazing intensity were far from both boma and non-boma villages (average distance to boma = 22.3 ± 18.4 (SD) km; distance to non-boma village = 9.4 ± 11.5 km) and they were confined within the protected areas boundaries such as Tarangire and Arusha National Park.

b) Agriculture gradient

Characterization of agriculture gradient. was based on the field sizes, use of heavy agricultural machines, regular use of herbicides, and crop diversity cultivated in the farmlands. Moderate intensive agriculture study sites were composed of subsistence farming characterized by small field sizes (mostly less than 1 ha) of mixed crops such as maize, beans, and sunflower. Crop areas are intermingled with patches of savannah habitats, and typically only small agriculture machines such as small tractors and planters are used. Highly intensive agricultural intensity habitat was characterized by large monoculture fields of wheat, maize, or barley as the major crops. Heavy agricultural machines and chemical fertilizers and herbicides are regularly used during the growing time of the crops. Distances between study sites habitats were at least 3 km, which is far larger than the flying distance of most bee species (Wright et al., 2015; Zurbuchen et al., 2010).

Data collection

Data were collected from June 2018 to March 2020 in 40 replicate study sites distributed equally among the five selected habitats following grazing intensity (GI) and agricultural intensification gradient. Each study site was composed of two study plots positioned ca. 150 m apart. Each study plot had a size of 50 x 50 m, where bees and floral resources were sampled and quantified. We collected four types of data: First, we collected data on bee pollinators using two standardized methods (UV-reflecting colored pan traps and standardized random work) (Fig. 4a and 4b). All specimens collected were temporarily stored in 70% ethanol before being sorted and mounted into pins. All mounted bees were later identified to species level following the nomenclatural system established by Michener (2007) with an exception to the Halictidae family; Second, we collected data on plant species used by bees (this measure corresponds to the floral resource used by bees rather than on site total number of plant species); Third, we measured inter-tegular distance (ITD) of each individual bee collected during the study. The ITD is used as a proxy of bee body sizes. This data was obtained using a digital microscope (Dino-Lite digital handheld microscope Taiwan, with a precision of 0.001mm) (Fig 4c); and fourth, we collected data on the mean annual temperature (MAT). This data was collected by using Thermochron iButton data loggers (DS1921G; ± 0.5 °C resolution; Maxim Integrated Products, USA) that were placed on all study sites at 2 m height above the ground (on a branch of a shrub/tree) to record the ambient temperature over one year (Fig. 4d) (Classen et al., 2015).

Fig. 4 | (a) Collection of bee specimens using hand net and (b) pan trap cluster with three different colored pan traps. (c) Measurement of the inter tegular distance (ITD) of collected bee specimens using Dino-Lite digital microscope. (d) Temperature sensor i-button positioned on the branch of a tree to record the ambient temperature on study sites.

Chapter II

Positive effects of low livestock grazing intensity on East African bee assemblages mediated by increases in floral resources

Summary

Livestock grazing is widespread and increasing in the African grasslands with largely unknown consequences for bee pollinators. Here we assessed the direct and indirect impacts of livestock grazing intensity on bee assemblages in East African grasslands. We tested if the effect of grazing intensity on bee assemblage is depending on temperature. We collected data on 24 study sites representing three different levels of livestock grazing intensity in northern Tanzania. Ordinary linear models and path analysis were used to test the effect of grazing and temperature on floral resources and bee diversity. Non-metric multidimensional scaling (NMDS) and permutational MANOVA were used to analyze changes in bee community composition with grazing intensity and temperature. We found that moderate livestock grazing slightly increased bee species richness while high grazing intensity led to a strong decline. Further, bee species richness was highest at moderate temperatures and significantly lower in colder and very hot environments. Results from path analysis showed that the effect of livestock grazing and environmental temperature on bee species richness was mediated by a positive effect of moderate grazing on floral resource richness. Livestock grazing led to a significant change in the species composition of bee communities. This effect was stronger in environments with very high temperatures. Our study reveals that bee communities of African savannah zone may benefit from low levels of livestock grazing as this proliferates the growth of flowering plant species. However, livestock grazing at high intensity will cause significant species losses and turnover of bee species communities; effects which may increase with climatic warming.

Keywords: bee assemblage, bee community composition, bee species richness, East Africa, floral resources, livestock grazing intensity.

Introduction

Bees play a vital role through their pollination services in maintaining the functionality of natural ecosystems, enhancing agricultural productivity, and hence promoting human well-being (Klein, Vaissiere, et al., 2007; Potts et al., 2016; Ollerton et al., 2011). About 90% of all flowering plant reproduction, including wild plants, food crops, and livestock fodders, depends on animal pollination, in particular on bee-pollinators (Hanley et al., 2015; Klein, Vaissière, et al., 2007; Ollerton et al., 2011). Accumulating evidence suggests a decline in abundance and richness of bee-pollinators in different parts of the world with negative consequences for pollination services (Bartomeus et al., 2013; Dainese et al., 2019; Potts et al., 2016). The global expansion of livestock grazing, particularly in dryland areas, is considered a major threat to bee diversity (Brown & Paxton, 2009; Potts et al., 2010, 2016; Winfree et al., 2009). However, conditions and mechanisms through which grazing affects bee abundance and diversity are little understood and it remains unclear how grazing effects may interact with increasing temperatures in the course of climate change (Deutsch et al., 2008; Gebrechorkos et al., 2019b).

Livestock grazing is a dominant form of land use globally, and nearly 25% of the earth's terrestrial land surface is utilized for grazing purposes (Ma et al., 2019). Despite being the global-prevalent form of land use, livestock grazing poses a significant negative effect on bee assemblages (Davidson et al., 2020; Tadey, 2015; Potts et al., 2009). Higher livestock grazing intensity decimates vegetation cover, causes severe soil compaction, and ultimately soil erosion (Lazaro et al., 2016; Petanidou & Ellis, 1996). The negative effects of livestock grazing on bee assemblage can either be direct or indirect. Livestock grazing may pose a direct negative effect on bee assemblage through trampling that destroys nests of ground-nesting bees (Lazaro et al., 2016; Tadey, 2015) or damaging nests in twigs or branches of plants (Potts et al., 2009). Conversely, livestock grazing can cause an indirect negative effect by reducing the floral resources, hence interrupting bee-plant interaction networks (Tadey, 2015). Contrary to higher livestock grazing intensity, studies from temperate ecosystems support the view that moderate livestock grazing intensity can even have positive effects on bee species richness and abundance (Lazaro et al., 2016; Tadey, 2015; Vulliamy et al., 2006). At moderate grazing intensity, the growth of grasses and dominant shrubs is suppressed; a situation that often promotes the growth of diverse plant communities (Herrero-Jáuregui & Oesterheld, 2018; Tadey, 2015), hence supporting high bee diversity (Lazaro et al., 2016; Tadey, 2015; Vulliamy et al., 2006). In that regard, understanding the mechanisms through which grazing may affect pollinator assemblage is critical for informed management decisions and bee conservation planning.

A particular concern regarding the influence of livestock grazing intensity on bee pollinators is how the livestock grazing interacts with climatic conditions, in particular temperature. As bees are ectotherms, their metabolic, activity, abundance, and species diversity are modulated by ambient temperature (Classen et al., 2015; Deutsch et al., 2008). However, tropical dryland areas are characterized by temperatures that may exceed the optimum or even the critical thermal maxima of even warm-adapted species (Sunday et al., 2014a) such that both positive and negative effects of ambient temperature on bee diversity can be expected (Classen et al., 2015; Hamblin et al., 2018; Papanikolaou et al., 2017a, 2017b). In addition to the independent effect of ambient temperature on bee communities, it may also interact with the effects of livestock grazing and cause a synergistic impact on bee communities. This would be the case if livestock grazing has stronger effects in warmer habitats than cooler habitats. Such interactive effects are of particular concern, as they may indicate that more extreme changes in biodiversity can be expected than currently predicted by “climate-only” or “land-use-only” models (Peters et al., 2019).

Despite that livestock grazing constitutes the major land use type in the drylands of Afrotropical grasslands and is expected to further increase in the near future, (Basu et al., 2016; Bystriakova et al., 2018; Rojas-Downing et al., 2017), there is no single well-replicated study that has attempted to elucidate the effect of livestock grazing intensity on the bee abundance and diversity of the Afrotropical savannah. Hitherto, most of the studies have been conducted in temperate regions (Davidson et al., 2020; Kearns & Oliveras, 2009; Kimoto et al., 2012; Lazaro et al., 2016; Minckley, 2014; Shapira et al., 2020; Tadey, 2015; Van Klink et al., 2016; Vulliamy et al., 2006; Yoshihara et al., 2008) leaving the effects of grazing intensity on bee assemblage in Afrotropical savannah largely unknown. In this study, we examined the effect of livestock grazing intensity on bee species richness and abundance along a temperature gradient in the Afrotropical savannah of northern Tanzania. Furthermore, we disentangled the direct and indirect effects of livestock grazing intensity on bee species richness and the species composition of bee communities.

Methods

Study area description

This study was conducted in northern Tanzania, in the areas surrounding Tarangire National Park, the lowlands of Mt. Meru, and Mt. Kilimanjaro in the Manyara, Arusha, and Kilimanjaro regions (Fig. 1). The study region is characterized by a seasonal tropical climate with extensive dry periods (Gebrechorkos et al., 2019a). The altitude of the study region ranges between 890m to 1576m asl. The mean annual temperature of the study region ranges between 19.2^{o}C and 24.2^{o}C. The area has two rainy seasons: a long rainy season between ca. March and May and short rainy season November and December (C. A. Foley & Faust, 2010). The dominant natural vegetation cover of this dryland area are grasses and herbs interspersed with some scattered trees (dominated by *Acacia* and *Commiphora*). The areas outside the protected areas contain several non-native trees such as *Grevillea robusta*, *Acrocarpus flaxinifolius*, and *Leucaena leucocephala*. The soil type of the region originates from the volcanic activities of Mt. Meru and Mt. Kilimanjaro. We selected three habitats in the study region corresponding to different levels of livestock grazing intensity (GI): First, natural savannah habitat situated in protected areas with low GI. Second, savannah habitat with moderate livestock grazing intensity outside of protected areas but with only moderate to low densities of livestock and, third, savannah habitat with high livestock grazing intensity in unprotected areas dominated by high densities of livestock and livestock grazing as the major land-use type (Fig. A1 in Appendix 1).

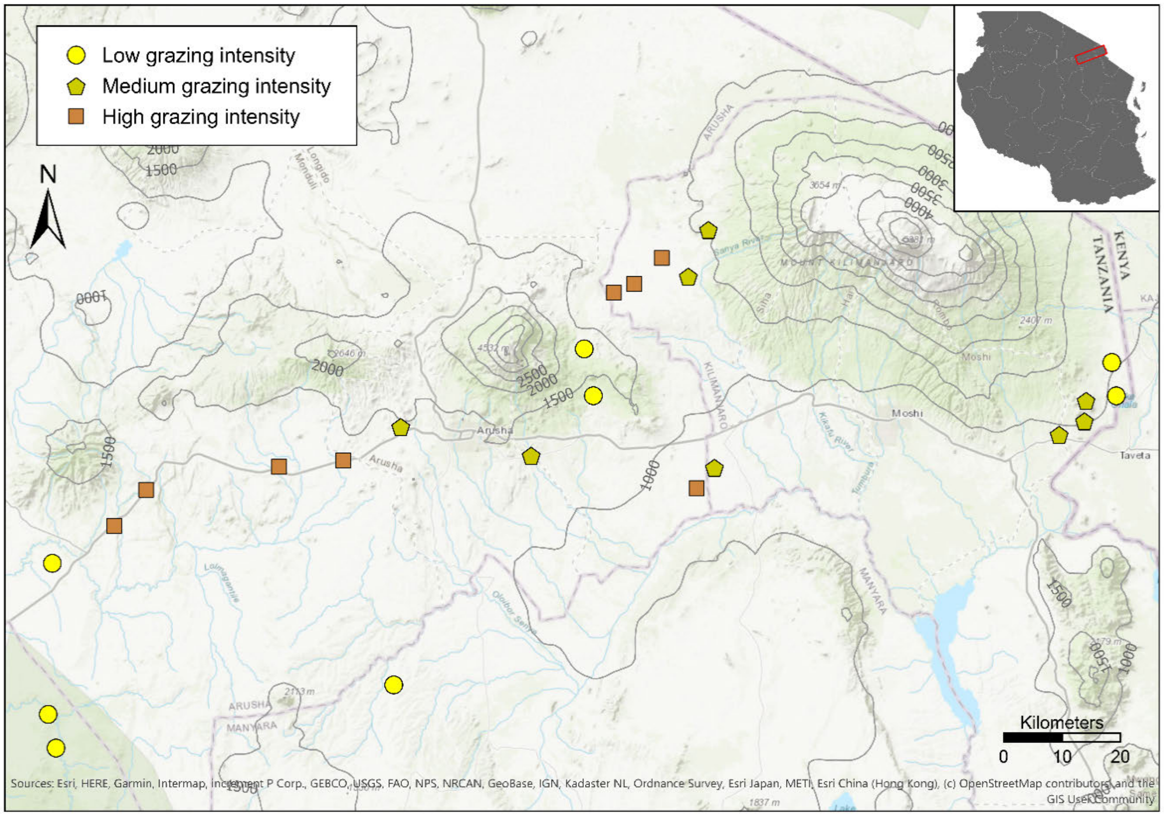


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Fig. 1 | Map of the study area. Study sites are indicated by different colors and symbols depending on the grazing intensity (see legend). The two larger mountains on the map are Mt. Kilimanjaro (upper right) and

Mt. Meru (center). The small map in the upper right corner shows the location of the study area within Tanzania.

Data collection

Data were collected from August 2018 to March 2020 on 24 study sites equally distributed among the three levels of livestock grazing intensity (8 replicates for each level): low, medium, and high grazing intensity (Fig. 1). The characterization of grazing intensity was done based on information on the distribution of protected areas such as National Parks and total protected private lands, visual inspection of on-site signs of obvious grazing like shortened tufts of grass, the presence or absence of livestock footprints and by calculating the distance between study sites to bomas (livestock enclosures and living grounds of families holding large herds of livestock) and non-boma villages (where families hold only single or few individuals (<10) of livestock). Study sites with signs of intensive grazing activity were very near to bomas (average distance 0.09 ± 0.05 (SD) km; distance to non-boma village = 1.9 ± 1.9 km), while study sites with moderate livestock grazing intensity were near to non-boma villages (average distance = 0.25 ± 0.05 (SD) km; distance to boma village = 25.3 ± 27.6 km). Study sites with low livestock grazing intensity were far from both boma and non-boma villages (average distance to boma = 22.3 ± 18.4 (SD) km; distance to non-boma village = 9.4 ± 11.5 km). Distances among study sites were for all pairs of study sites larger than 3 km, which is larger than the flying distance of most bee species (Rader et al., 2011; Wright et al., 2015; Zurbuchen et al., 2010b). We distributed the study sites of different grazing intensity across the whole study region. This study design minimized spatial autocorrelation among replicates. In each study site, we established two smaller plots of 50 x 50 m in which bees and floral resources were sampled and quantified. The distance between the centers of these two study plots in each study site was approximately 150m.

Sampling of bees

We employed two standardized methods (clusters of colored pan traps and a standardized random walk) to sample bees on each study site (Prendergast et al., 2020; Westphal et al., 2008). For each of the two plots per study site, four pan trap clusters, each containing three pan traps of three different UV reflecting colors (yellow, blue, and white) (Classen et al., 2015; Elzay & Baum, 2021; Westphal et al., 2008) (Fig.A2a in Appendix 1) were installed to passively collect bees. Four clusters of pan traps (two with 35 cm and two with 120 cm tall poles) were positioned diagonally from each other on two 50 m parallel transects with an interspace distance of 30 m (Fig. A2b in Appendix 1). Pan traps were installed at two different heights, at the level of the herbaceous layer (35 cm from the ground) and the shrub layer level (120 cm above ground distance). The distance between the two pan trap clusters was 30 m (Fig. A2b in Appendix 1). Pan traps were filled with soapy water and left in the field to passively collect bees for 48 hours. A drop of soap per ca. 1 l was used to break the surface tension of water so that bees landing on the pan trap were more likely to be captured. After 48 hours, samples were collected from pan traps and preserved in 70% ethanol for further processing in the lab (sorting and mounting). Pan trap sampling was conducted in three different seasons on each study site to cover three main seasons of the year (dry season, short rain, and long rain season). This summed up to 3456 pan trap hours per study site and 82944 pan trap hours for the whole study.

In addition to pan trap sampling, a standardized random walk was used to sample bees. This method involves walking randomly slowly within plots using a sweep net to actively collect bees from flowers. A random walk was conducted for 2 hours in each study site (one hour per 50 x 50 m study plot), excluding handling and recording time. Bee sampling was conducted from 9:00 am to 5:00 pm time which bees are expected to be most active (Prado et al., 2017). As for pan trapping, 2 hours transect walks were conducted in the three major seasons on each study site. This summed up to 6 hours of active collection per study site and 144 hours for the whole study. Sampling was restricted to days with low wind speed and no or only very little rainfall. All specimens collected in a day were temporarily stored in 70% ethanol before being mounted on the same day. Species richness was calculated per study site by summing up the cumulative number of bee species collected by both sampling methods across all three sampling seasons.

Quantification of bee–plant interactions and species richness of bee-visited plants

In each study site, we recorded all plant species visited by bees during transect walks. This measure corresponds to the plant species used by bees rather than the total number of plant species on sites (Carman & Jenkins, 2016; Weiner et al., 2011). Plant species were counted as a bee-visited plant in case we observed a bee sitting or walking on the flower (not just flying over it) (Weiner et al., 2011). Plant species that could not be identified in the field were temporarily stored in plastic bags before taken to the National Herbarium of Tanzania (Arusha) for identification.

Environmental parameters

Temperature data were recorded using temperature sensors (iButton) (Classen et al., 2015). On each study site, a Thermochron iButton datalogger (DS1921G; ± 0.5 °C resolution; Maxim Integrated Products, USA) was placed on a branch of a shrub/tree at 2 m height above ground level to record the ambient temperature (Classen et al., 2015) (Fig. A2c in Appendix 1). An overlay plastic funnel was hanged 10 cm above the sensor for radiation shielding. Temperature sensors were set to take records in 60 minutes intervals. Sensors were left in the field for the entire period of the data collection and revisited every three months for data reading. Mean annual temperature

(MAT) was then calculated by averaging all individual temperature measurements per study site. High-resolution data on mean annual precipitation (MAP) was obtained from CHELSA (Climatologies at high resolution for the earth's land surface areas) (Karger et al., 2017) based on the geographic coordinates of each study site. The CHELSA Bioclim data has a resolution of 30 arcsec (Karger et al., 2017).

Statistical analyses

Data were analyzed using R version 4.0.3 (http://cran.r-project.org/). We used ordinary linear models to explore the effect of grazing intensity (GI) and MAT on bee assemblages (bee species richness and abundance). Mean annual temperature was added as a linear and quadratic term to model potential unimodal relationships between MAT and bee assemblages. We also included interaction effects between MAT × GI and $MAT^2 \times GI$ to test for the possible interaction of temperature and grazing intensity. We used the dredge function in MuMIn R package to select the best-supported model based on the Akaike information criterion (AIC) value (Burnham & Anderson, 2004). Since our sample size was relatively small, we used the AIC with a second-order bias correction (AICc) instead of the standard AIC.

We used path analysis (Shipley, 2016) to examine causal relationships and to disentangle the direct and indirect effect of MAT and GI on bee species richness (Classen et al., 2015; Njovu et al., 2019). Direct effects are those effects that go directly from one variable to another, while indirect effects occur when the relationship between two variables is mediated by one or more variables (Shipley, 2016). Based on the ecological understanding of bees, we constructed a conceptual path diagram (Fig. 3b) assuming both direct and indirect effects of MAT and GI on bee species richness. We pre-select possible path combinations by analyzing the two endogenous variables of the path model (bee species richness and floral resource richness) with all explaining variables, i.e., MAT, GI in case of floral resource richness; MAT, GI, and floral resource richness in case of bee species richness. The full (most inclusive) model for bee species richness was:

$SP_b \sim GI + MAT + MAT^2 +$ bee-visited plant species

For floral resource richness, we constructed the following full model:

$SP_p \sim GI + MAT + MAT^2$

We used the 'dredge' function to construct and evaluate the full and all nested model (including the null model) and ranked them based on the Akaike Information Criterion (AIC_C). For all combinations of competitive models ($\Delta AIC_C < 2$), we conducted path analyses and derived path coefficients, their statistical significance, and multiple coefficients of determination (R^2) of explanatory variables. For path analysis, the r package 'piecewise SEM' was used.

To visualize the effect of MAT and GI on the species composition of bee communities, non-metric multidimensional scaling (NMDS) was applied based on a dissimilarity matrix calculated with the Sorensen index of dissimilarity (Oksanen et al., 2018). Using the ordisurf function of the R package *vegan* we modeled MAT isotherms to be plotted in the ordination graph. To test the effect of MAT, GI, and their interaction on the bee species community composition, the adonis function of the R package *vegan* was used. The test was based on the same dissimilarity matrix used for the NMDS. The adonis function calculates the statistical significance for effects of explanatory variables through a permutation procedure (permutational multivariate analysis of variance) (Anderson, 2001; McArdle & Anderson, 2001) with the number of permutations set to 999. We started with adonis model testing for an interactive effect of MAT and GI and successively simplified it by deleting non-significant explanatory variables from the model.

Results

We sampled a cumulative total of 2,691 bee individuals and sorted them into 183 species representing 55 genera and in all five Afrotropical bee families comprising Apidae, Megachilidae, Halictidae, Andrenidae, and Colletidae. Findings revealed that study sites experiencing a moderate livestock grazing intensity had higher cumulative numbers of bee species (135 species) and abundance (1,109 individuals) than sites experiencing low (105 species, 691 individuals) and high grazing intensity (83 species, 891 individuals) (Fig. 2a, Table A1 in Appendix 1). Grazing and mean annual temperature (MAT) had significant additive effects on bee species richness. The highest mean species richness was observed at moderate grazing intensity and the lowest richness at the highest grazing intensity with species richness levels at low grazing intensity lying slightly below those of moderate grazing intensity (Fig. 2b, c). Bee species richness showed at all three levels of grazing intensity unimodal relationships with MAT (Fig. 2c): Bee species richness increased with MAT from 19°C to 22°C but decreased at temperatures exceeding 22°C. Multi-mode inference revealed no significant support for models assuming an interaction of MAT and GI,i.e., the effect of grazing on bee species richness was consistent along the temperature gradient for models including only one explanatory variable.

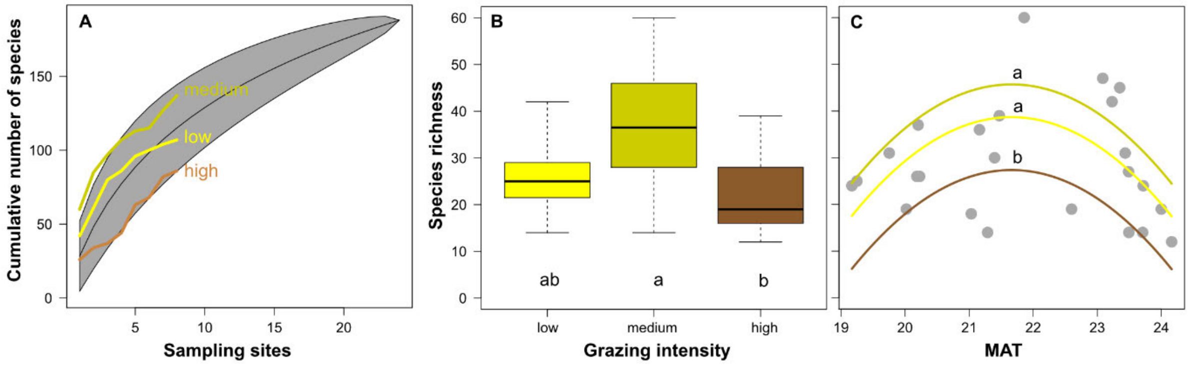

Fig. 2 | Species richness changes with grazing intensity. A, The cumulative number of species increases with the number of sampled study sites and did not reach the asymptote. The bold black line shows species accumulation curves across all study sites (grey polygon: 95% CI). Shorter lines show values for individual grazing intensity categories. B, Mean species richness per study site differed among grazing intensity categories (ANOVA, $F_{2,21} = 4.03$, $P = 0.03$). C, Species richness as a function of temperature and grazing intensity. In B and C, factor levels that significantly ($P < 0.05$) differ from each other in pairwise comparisons are indicated by different letters.

Results from path analysis suggested that climate and grazing intensity determine bee diversity largely by modifying the floral resource richness across study sites. Grazing intensity and temperature were both important predictors of the floral resource richness: The floral resource richness was highest at moderate grazing intensity and significantly lower at low and high grazing intensity (Fig. A1 and Table A2 in Appendix 1). At the same time, it showed a unimodal relationship with MAT (Fig. A2). The species richness of bees linearly increased with the floral resource richness (Fig. A3). Direct effects of MAT or GI on bee species richness were less supported by the data. A second, competitive path model (ΔAIC = 1.3) showed the same relationships depicted in the best-supported path model (Fig. 3) and included a positive effect of MAT on bee species richness.

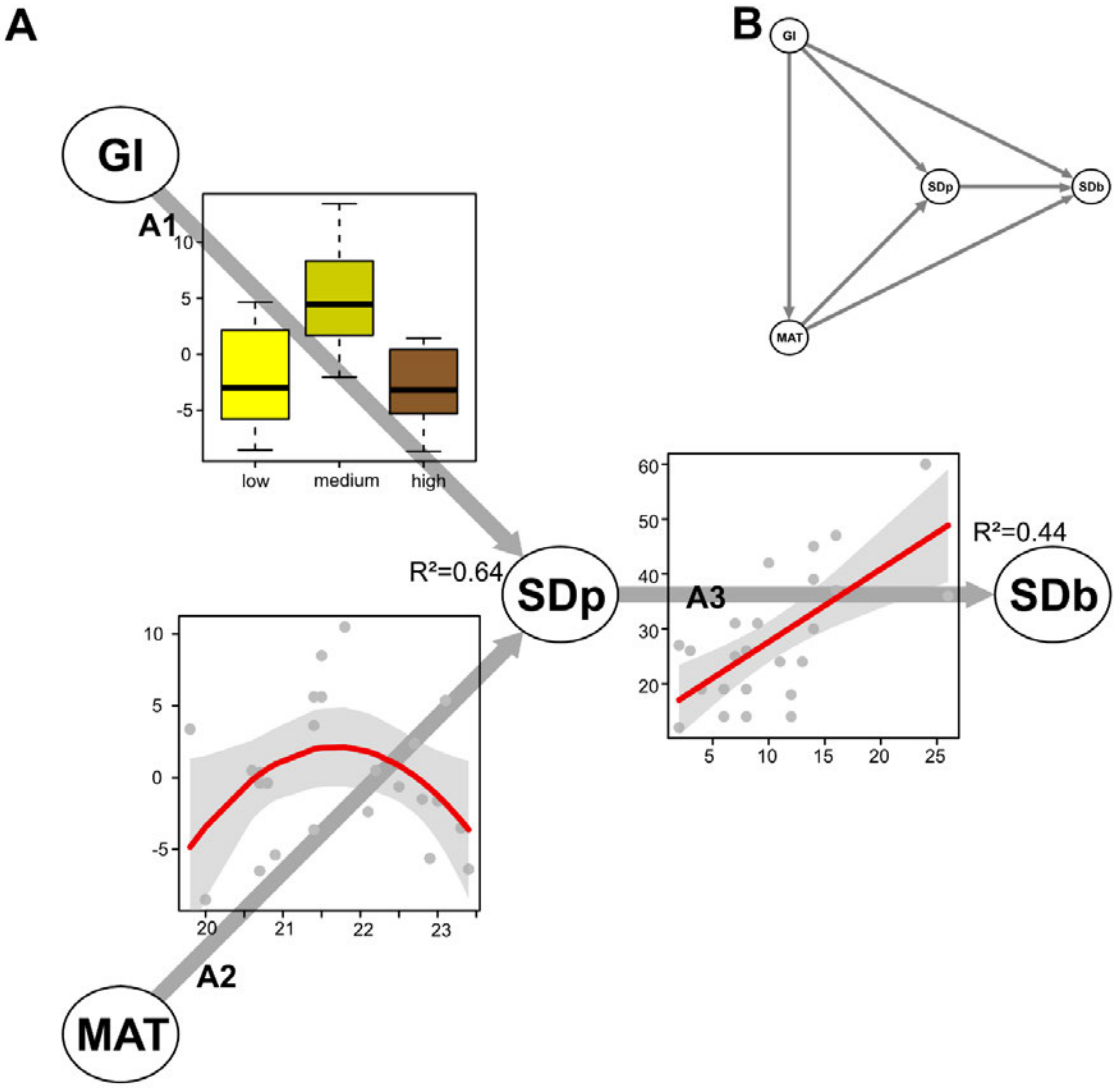

Fig. 3 | Path model showing the direct and indirect effects of grazing and MAT on bee species richness. A, The best supported path model shows that grazing intensity (GI) and mean annual temperature (MAT) indirectly affect the species richness of bees (SDb) by their effects on the floral resource richness (SDp) rather than by direct effects. Inlet figures on arrows depict the relationships between GI and SDp (A1), between MAT and SDp (A2) and between SDp and SDb (A3). In all figures the explanatory variable is shown on the x-axis and the response variable on the y-axis. A1 and A2 show the relationship between GI and SDp and between MAT and SDp after controlling for the effects of MAT and GI, respectively. Grey dots show data points; red lines show predictions of ordinary linear models; grey polygons depict 95% confidence intervals. B, The most inclusive path model illustrating all considered relationships among exogenous and endogenous variables.

A permutational MANOVA analysis revealed a significant interactive effect of grazing intensity and MAT on the composition of bee communities (effect of GI: F = 2.03, *P* = 0.001; MAT: F = 2.86, *P* = 0.001; GI x MAT: F = 1.83, *P* = 0.002), suggesting that the effect of GI on the composition of bee communities is depending on MAT. Study sites situated in warmer environments showed more distinct species communities along the grazing intensity gradient than those in colder environments (Fig. 4).

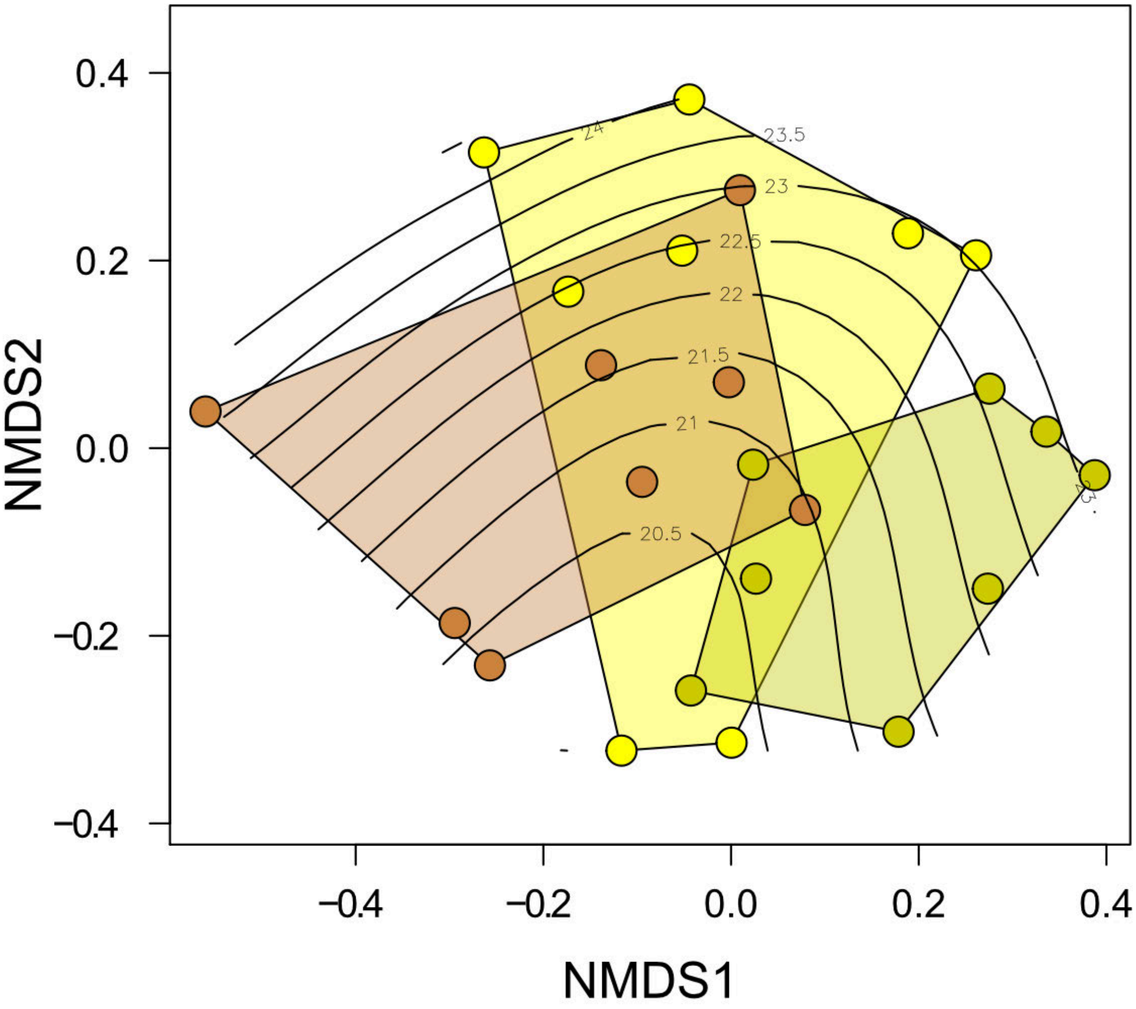

Fig. 4 | Variation in the composition of bee species communities. The ordination shows the results of non-metric multidimensional scaling of a dissimilarity matrix based on the Sorensen dissimilarity measure. Bee communities from study sites with low grazing intensity are shown in yellow, those from moderate sites with moderate grazing intensity in green, and those from sites with high grazing intensity in brown. In the background, contour lines of MAT are displayed (isotherms; in °C). The curvature suggests that communities of different grazing intensity living in areas of lower MAT tend to be more similar than those at high MAT, illustrating the significant interaction between MAT and GI.

Discussion

We found that the species richness of bees slightly increased by moderate grazing intensity. However, higher levels of livestock grazing intensity were associated with strong declines in bee species richness and abundance. Bee species richness showed a unimodal relationship with ambient temperature with lower numbers of species in the lower and higher parts of the temperature range. Changes in bee species richness with the intensity of livestock grazing were mediated by interactive effects of grazing and temperature on the floral resources used by bee pollinators.

Our finding that moderate livestock grazing may even increase bee species richness is consistent with studies conducted in extratropical regions (Lazaro et al., 2016; Lázaro et al., 2016). This effect, theoretically related to the intermediate disturbance hypothesis (Grime, 1973; Svensson et al., 2012), suggests local species diversity is maximized when the ecological disturbance is neither too rare nor too frequent (Kershaw & Mallik, 2013). Results of our path analysis suggest that low grazing intensity first leads to an expansion of floral resources that has a positive effect on bees; at higher intensities of grazing, floral resource richness strongly declined again, leading to the lowest numbers of mean bee species richness. The increase of floral resources was facilitated by the reduction of grass cover at low grazing intensity and the proliferation of flowering herbs (Dorrough et al., 2004; Vesk & Westoby, 2001; Vulliamy et al., 2006), from which bees benefit. Higher richness of plants at moderate grazing intensity is associated with the increase in amount and diversity of bee nesting substrate (Murray et al., 2012; Potts et al., 2003; Vulliamy et al., 2006) and offers higher spatial-temporal stability of food resources from which bee species could benefit.

Higher intensity of livestock grazing was associated with a loss of flowering plant species, affecting a decline in both bee abundance and richness. This could be driven by a general reduction in food resource availability of polylectic bees or a loss of certain food plant species of oligolectic bees at highest grazing intensity (Elwell et al., 2016; Hoiss et al., 2013) Since bees feed exclusively on nectar and pollen, the availability of floral resources is a major driver of bee communities (Vulliamy et al., 2006).

Irrespective of the high abundance of ground-nesting bees in local communities (1234 individuals from 116 species), we did not observe a direct impact of grazing intensity on bee species richness, i.e., an effect which was not mediated by a change in floral resources. Such a relationship would be plausible if the movement and feeding activity of livestock in study sites leads to the destruction of nesting sites (Hopfenmüller et al., 2020; Kearns & Oliveras, 2009; Lazaro et al., 2016; Tadey, 2015). Restricting the analysis to ground-nesting bees only, did not change the lack of support of a direct effect of GI (not shown) suggesting that in the East African grasslands, the effect of livestock grazing is mostly mediated by changes in the flowering plant communities. The impact of livestock grazing on ground-nesting bees vary regionally depending on livestock density (Van Klink et al., 2016; Odanaka & Rehan, 2019).

We found that temperature had a strong influence on bee species richness and abundance. Mean bee species richness and abundance sharply increased up to 22° C above which both bee richness and abundance declined monotonically. Increased bee species richness and abundance with temperature were expected, because, under warm temperatures, bee foraging activity and net energy gain are higher than in cold temperatures (Classen et al., 2015). The finding of a unimodal relationship may suggest that current temperatures in parts of the study region have already exceeded optimum temperatures for bees. Future increases in temperature through climate change will therefore likely lead to a further decrease in species richness and abundance with potential consequences for pollination services.

We found that livestock grazing caused a stronger change in bee species community composition at higher temperatures (i.e. lower elevated studied drylands) than in areas characterized by low temperatures. This finding is contrary to many studies that idiosyncratically found the effect of either temperature (Abrahamczyk et al., 2011) or grazing intensity (Kimoto et al., 2012; Shapira et al., 2020) on bee species community composition. The more dissimilar species community composition with grazing intensity at higher temperatures could indicate a lower resilience of the bee communities to recover to the original state after disturbance (Peper et al., 2011; Davey et al., 2013). The interacting effect of temperature and grazing intensity on bee species community composition suggests that this environmental stressor does not act in isolation but rather synergistically with climatic effects (Peters et al. 2019). Rota et al., (2017) and Herrero-Jáuregui & Oesterheld, (2018) also explained the interactive effects of grazing and climatic variables in predicting species community composition. They found that precipitation modulated the effect of livestock grazing on bee species composition.

Conclusion

We conclude that livestock grazing at moderate levels may be salient in preserving diverse flowering plant assemblages that consequently attract more bee species richness. However, high levels of livestock grazing intensity lead to a strong decline in the species richness of plant and bee assemblages. Our study therefore strongly speaks for setting upper limits to livestock grazing in the drylands of tropical East Africa as an insect conservation strategy. While we did not find support for an interaction between temperature and livestock grazing on species richness, the unimodal relationship between temperature and the richness of both floral resources and bees underscores the fragility of current bee and plant assemblages to further climatic warming. Further warming may push species assemblages in many dryland areas of East Africa beyond the peak of the unimodal distribution, which will probably contribute to a further decline of tropical bee pollinators. The understanding of the relationship between grazing intensity and bee assemblage is critical for developing conservation and management plans. Besides, knowledge about facilitates the protection and management of potentially threatened species. Furthermore, the results of this study suggest that understanding the interplay of the multiple anthropogenic drivers is necessary for mitigating their potential consequences on bee communities and the provision of pollination services.

Supplementary materials

Appendix 1:

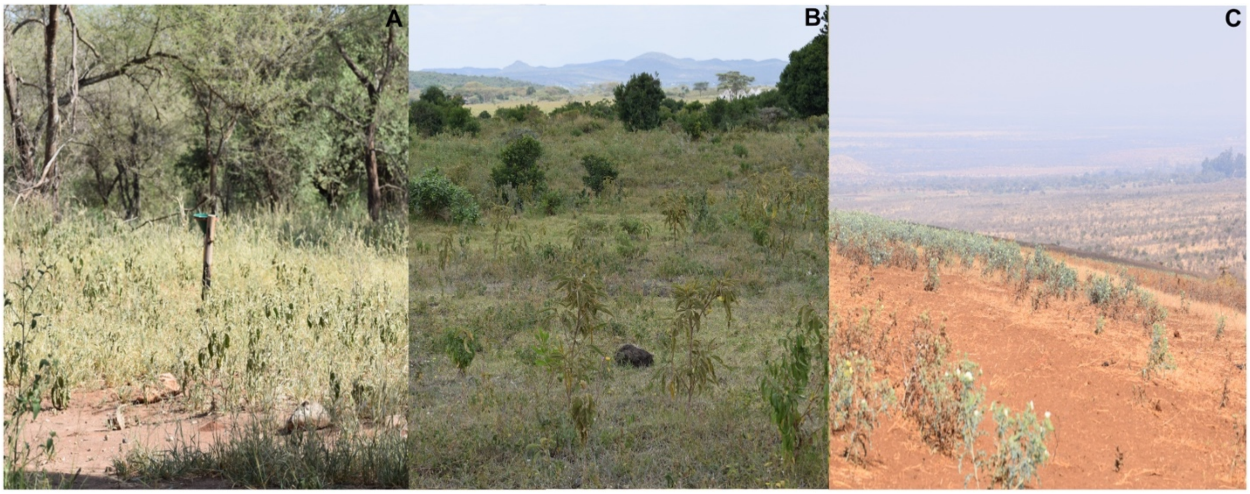

Figure A1| Study sites distributed across the study region. A, Study site characterized by low livestock grazing intensity. These sites were distributed in the protected areas, i.e., at Arusha National Park, Tarangire National Park, and Lake Challa (private land set aside for wildlife conservation). The areas are characterized by natural vegetation mostly *Acacia* and *Commiphora* woody plants, few herbs, and tall grasses with no livestock. B, Study sites characterized by moderate livestock grazing intensity. These areas contain a high abundance and diversity of proliferated herbs with moderate livestock (goat, sheep, and cattle) density. C, Study sites characterized by low plant abundance and diversity due to high livestock grazing intensity. These sites are distributed in the areas dominated by Maasai tribe, typically holding large quantities of livestock.

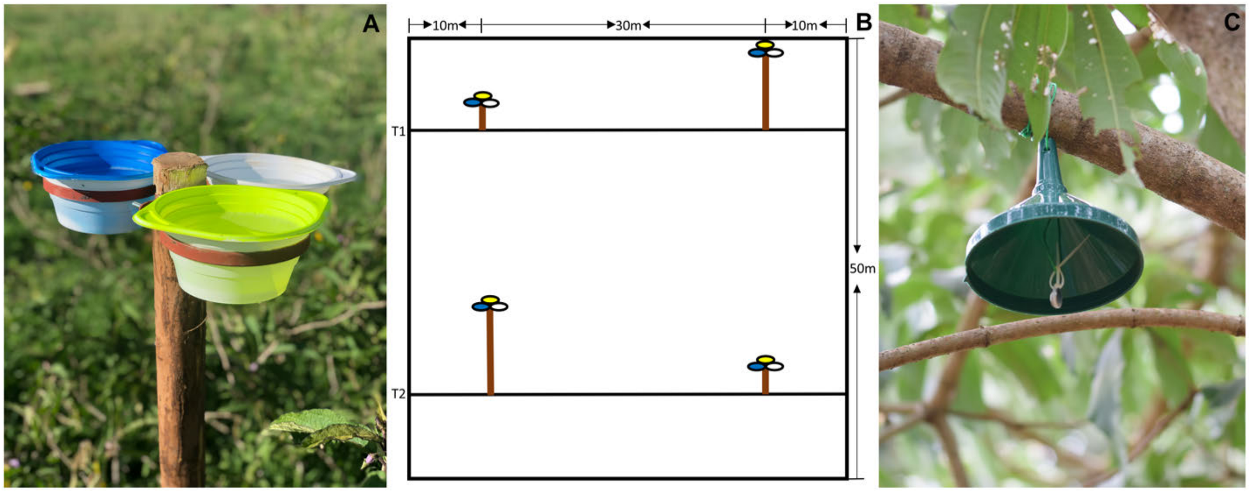

Figure A2|A, One-pan trap cluster with three ultraviolet reflecting colored pan traps (blue, white, and yellow). B, Schematic map of a study plot with the four pan trap clusters on two transect lines (T1 and T2). The four pan trap clusters are hanged on two different height poles (two on 35cm height pole, and two on 120cm height pole). The different height pan trap clusters were positioned diagonally from one another. C, Temperature sensor positioned on the branch of a tree (2 m above the ground) for record air temperature. The overlaying funnel above the sensor provides shielding from direct sunlight.

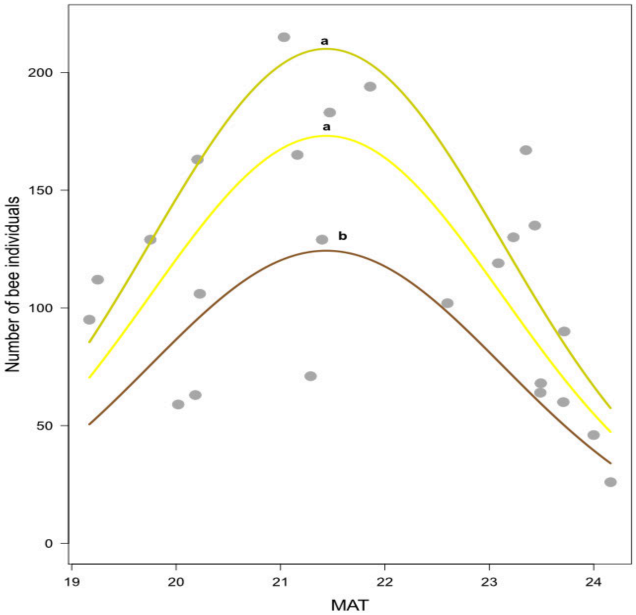

Figure A3| Bee abundance as a function of temperature and grazing. Factor levels which significantly ($P < 0.05$) differ from each other in pairwise comparisons are indicated by different letters.

Table A1 List of bee species and data on the total number of collected individuals per species in habitats of low, moderate and high grazing intensity.

S/no	**Bee species**	**Low grazing intensity**	**Moderate grazing intensity**	**High grazing intensity**
1	*Acunomia senticosa*	1	0	0
2	*Acunomia somalica*	0	1	0
3	*Acunomia theryi*	0	2	0
4	*Afranthidium sp*	0	1	0
5	*Afronomia fimbriata*	1	0	0
6	*Afronomia sjostedti*	1	0	0
7	*Amegilla acraensis*	0	1	1
8	*Amegilla atrocincta*	1	2	0
9	*Amegilla calens*	6	18	7
10	*Amegilla fallax*	0	0	1
11	*Amegilla nigritarsis*	0	1	0
12	*Amegilla nubica*	1	0	4
13	*Amegilla obscuritarsis*	5	5	5
14	*Amegilla punctifrons*	0	2	0
15	*Amegilla terminata*	0	1	0
16	*Andrena africana*	1	0	0
17	*Andrena notophila*	0	0	4
18	*Andrena sp*	0	2	0
19	*Anthidiellum sp*	0	0	1
20	*Anthidiellum(Chloranthidiellum) sp*	0	1	0
21	*Anthidium sp1*	1	1	0
22	*Anthidium sp2*	1	1	0
23	*Anthidium sp3*	1	3	0
24	*Anthophora armata*	0	0	1
25	*Anthophora oldi*	0	1	0
26	*Anthophora rufozonata*	0	0	1
27	*Apis mellifera ssp monticola*	22	25	32
28	*Apis mellifera ssp scutellata*	181	293	319
29	*Austronomia sp1*	4	1	6
30	*Austronomia sp2*	7	1	1
31	*Braunsapis bouyssoui*	3	0	1
32	*Braunsapis facialis*	6	2	3
33	*Braunsapis langenburgensis*	0	0	1
34	*Braunsapis trochanterata*	2	3	0
35	*Ceratina sp*	2	1	0
36	*Ceratina sp1*	0	3	0
37	*Ceratina sp2*	0	0	2
38	*Ceratina inermis*	0	5	2

39	*Ceratina moerenhouti*	1	12	7
40	*Ceratina nasalis*	4	3	4
41	*Ceratina nyassensis*	18	9	18
42	*Ceratina paulyi*	0	2	0
43	*Ceratina penicillata*	0	1	0
44	*Ceratina sp5*	6	5	0
45	*Ceratina tanganyicensis*	1	0	0
46	*Coelioxys sp1*	0	1	1
47	*Coelioxys sp2*	1	0	1
48	*Coelioxys sp4*	1	0	0
49	*Coelioxys sp5*	0	1	0
50	*Colletes sp*	5	1	1
51	*Crocisaspidia chandleri*	0	2	0
52	*Crocisaspidia forbesi*	0	1	1
53	*Eucara macrognatha*	0	1	0
54	*Haetosmia sp*	0	0	1
55	*Heriades sp1*	2	0	4
56	*Heriades sp2*	1	0	0
57	*Hoplitis sp*	0	0	1
58	*Hypotrigona gribodoi*	0	1	1
59	*Lasioglossum (Afrodialictus) bellulum*	21	78	176
60	*Lasioglossum (Afrodialictus) sp1*	0	1	0
61	*Lasioglossum (Ctenonomia) atricrum*	3	20	6
62	*Lasioglossum (Ctenonomia) radiatulum*	0	0	1
63	*Lasioglossum (Ctenonomia) scobe*	0	19	0
64	*Lasioglossum (Ctenonomia) sp1*	1	4	2
65	*Lasioglossum (Ctenonomia) sp2*	7	0	2
66	*Lasioglossum (Ctenonomia) sp3*	5	6	4
67	*Lasioglossum (Ctenonomia) sp4*	1	0	4
68	*Lasioglossum (Ctenonomia) transvaalense*	15	22	14
69	*Lasioglossum (Ipomalictus) bowkeri*	3	9	1
70	*Lasioglossum (Ipomalictus) matopiense*	43	6	99
71	*Lasioglossum (Ipomalictus) rubritarse*	7	21	6
72	*Lasioglossum (Ipomalictus) sp1*	0	5	0
73	*Lasioglossum (Ipomalictus) sp2*	0	7	7
74	*Lasioglossum (Ipomalictus) sp8*	0	2	0
75	*Lasioglossum (Ipomalictus) sp1*	0	5	0
76	*Lasioglossum (Ipomalictus) sp2*	2	1	0
77	*Lasioglossum (Ipomalictus) sp4*	1	0	0
78	*Lasioglossum (Ipomalictus) sp9*	1	1	6
79	*Lasioglossum (Ipomalictus) spA nr hancocki*	0	11	5
80	*Lasioglossum (Ipomalictus) spA nr rubritarse*	1	9	1
81	*Lasioglossum (Ipomalictus) spB nr hancocki*	0	9	0

82	*Lasioglossum (Ipomalictus) spC nr hancocki*	0	35	1
83	*Lasioglossum (Ipomalictus) sp13*	6	2	0
84	*Lasioglossum (Oxyhalictus) acuiferum*	11	2	17
85	*Lasioglossum (Sellalictus) deceptum*	0	2	0
86	*Lasioglossum (Sellalictus) sp1 nr deceptum*	0	1	0
87	*Lasioglossum calliceras*	0	2	0
88	*Leuconomia atripes*	4	10	2
89	*Leuconomia rufitarsis*	0	1	1
90	*Liotrigona bottegoi*	1	0	0
91	*Lipotriches ablusa*	0	1	0
92	*Lipotriches cribrosa*	2	1	0
93	*Lipotriches hylaeoides*	0	21	0
94	*Lipotriches pallidicincta*	0	3	0
95	*Lipotriches patellifera*	0	1	0
96	*Lipotriches sp*	17	6	10
97	*Lipotriches welwitschi*	0	4	0
98	*Lithurgus pullatus*	21	25	2
99	*Macrogalea candida*	85	125	8
100	*Macronomia armatula*	2	0	0
101	*Macronomia femorata*	3	0	0
102	*Macronomia swalei*	1	2	0
103	*Macronomia trochanterica*	1	4	0
104	*Macronomia vulpina*	0	7	0
105	*Maynenomia sp*	1	0	0
106	*Maynenomia sp1*	0	5	3
107	*Megachile (Paracella) sp*	0	0	2
108	*Megachile angulata*	0	1	0
109	*Megachile aurifera*	0	1	1
110	*Megachile basalis*	2	2	1
111	*Megachile bucephala*	1	2	1
112	*Megachile cincta*	0	1	0
113	*Megachile demeter*	0	1	0
114	*Megachile discolor*	1	0	0
115	*Megachile eurymera*	1	0	0
116	*Megachile familiaris*	4	2	4
117	*Megachile frontalis*	11	26	10
118	*Megachile malangensis*	1	6	2
119	*Megachile mossambica*	0	2	0
120	*Megachile nasalis*	4	2	1
121	*Megachile rufoscopacea*	0	4	0
122	*Megachile sp1*	1	0	0
123	*Megachile sp2*	1	0	0
124	*Megachile venusta*	0	2	1

125	*Megachile wahlbergi*	3	0	2
126	*Meliponula togoensis*	8	17	0
127	*Meliturgula fuliginosa*	4	1	0
128	*Meliturgula scriptifrons*	5	1	0
129	*Nomioides micheneri*	0	0	1
130	*Noteriades sp*	0	0	2
131	*Nubenomia reichardia*	5	0	1
132	*Ochreriades sp2*	0	0	1
133	*Othinosmia sp*	3	1	0
134	*Pachyanthidium cordatum*	1	1	0
135	*Pachyhalictus (Dictyohalictus) retigerus*	0	1	0
136	*Pachymelus sp*	2	1	0
137	*Pachymelus sp.n*	4	0	0
138	*Pachynomia flavicorpa*	2	5	0
139	*Patellapis itigiensis*	1	0	0
140	*Plebeina armata*	0	4	0
141	*Plebeina lendliana*	0	4	0
142	*Pseudapis interstitinervis*	1	1	1
143	*Pseudapis pandeana*	5	2	10
144	*Seladonia foana*	1	2	2
145	*Seladonia hotoni*	2	1	5
146	*Seladonia jucunda*	5	13	8
147	*Steganomos junodi*	1	4	1
148	*Stenoheriades sp*	3	0	0
149	*Stictonomia aliceae*	0	1	0
150	*Systropha arnoldi*	4	9	0
151	*Systropha krigei*	4	1	0
152	*Systropha sp1*	1	4	0
153	*Systropha sp2*	2	1	0
154	*Tetralonia exlarge*	0	1	0
155	*Tetralonia labrosa*	1	2	0
156	*Tetralonia macrognatha*	2	4	1
157	*Tetralonia minuticornis*	0	1	0
158	*Tetralonia nigropilosa*	3	3	1
159	*Tetralonia obscuriceps*	10	3	1
160	*Tetralonia sp2*	1	2	0
161	*Tetralonia sp1*	1	7	0
162	*Tetraloniella abessinica*	2	0	0
163	*Tetraloniella inermis*	0	0	1
164	*Tetraloniella katangensis*	0	1	0
165	*Tetraloniella sp*	0	1	0
166	*Tetraloniella vansoni*	0	1	0
167	*Thrinchostoma sjoestedti*	2	1	0

168	*Thyreus meripes*	1	0	0
169	*Thyreus tschoffeni*	0	2	0
170	*Trinomia cirrita*	5	3	9
171	*Trinomia orientalis*	1	15	2
172	*Trinomia triodonta*	0	3	3
173	*Xylocopa caffra*	0	2	0
174	*Xylocopa erythrina*	0	0	1
175	*Xylocopa flavicollis*	0	1	0
176	*Xylocopa flavorufa*	0	3	0
177	*Xylocopa hottentota*	1	0	0
178	*Xylocopa inconstans*	1	0	3
179	*Xylocopa scioensis*	0	5	0
180	*Xylocopa somalica*	1	4	1
181	*Xylocopa subjuncta*	1	1	0
182	*Zonalictus kivuicola*	10	0	0
183	*Zonalictus nomioides*	1	3	1
	TOTAL NUMBER OF INDIVIDUALS	691	1109	891
	TOTAL SPECIES	105	135	83

Table A2 List of plant species interacted with bees in each grazing intensity (i.e low, moderate and high grazing intensity.

S/no	**Floral resource**	**Low grazing intensity**	**Moderate grazing intensity**	**High grazing intensity**
1	*Abutilon hirtum*	0	0	1
2	*Abutilon palmeri*	0	1	2
3	*Achyranthes aspera*	6	10	0
4	*Agave sisalana*	0	0	1
5	*Ageratum conyzoides*	1	5	2
6	*Amaranthus hybridus*	0	0	1
7	*Amaranthusthus viridis*	0	1	0
8	*Argemone mexicana*	0	1	0
9	*Aspilia mossambicensis*	0	3	4
10	*Bidens pilosa*	0	42	6
11	*Bidens schimperi*	0	0	1
12	*Boerhavia cocciinea*	0	0	16
13	*Boerhavia sp*	0	0	3
14	*Buphthalmum saticifolium*	0	0	7

15	*Cajanus cajan*	0	1	0
16	*Caylucea abyssinica*	0	1	0
17	*Chamaecrista nictitans*	0	1	0
18	*Cirsium vulgare*	1	0	0
19	*Commelina benghalensis*	0	3	10
20	*Commicarpus plumbagineus*	3	3	0
21	*Commiphora africana*	0	0	1
22	*Conyza bonariensis*	0	2	0
23	*Conyza pyrrhopappa*	8	0	0
24	*Crotalaria agatiflora*	0	3	0
25	*Crotalaria brachycarpa*	2	0	0
26	*Crotalaria incana*	15	0	0
27	*Crotalaria sp*	0	2	0
28	*Cucumis dipsaceus*	0	3	0
29	*Cucurbita maxima*	0	5	0
30	*Cynodon dactylon*	2	5	0
31	*Cyperus sp*	2	0	1
32	*Cytisus villosus*	0	11	0
33	*Daphne gridium*	0	0	2
34	*Desmodium intortum*	4	3	0
35	*Ductyloctenium aegytium*	0	1	0
36	*Euphorbia geniculata*	0	2	0
37	*Felicia sp1*	2	0	0
38	*Galega officinalis*	0	3	0
39	*Galinsoga parviflora*	0	1	4
40	*Glycine wightii*	3	3	0
41	*Gutenbergia cordifolia*	13	19	0
42	*Gynandropsis gynandra*	2	0	0
43	*Hedyotis diffusa*	40	4	34
44	*Helianthus annuus*	0	19	0
45	*Helichrysum sp*	0	10	3
46	*Heliotropium steudneri*	0	6	2
47	*Hellidrison sp*	0	2	0
48	*Heteropogon contortus*	0	1	0
49	*Hibiscus calyphyllus*	1	0	0
50	*Hirpicium diffusum*	0	1	6

51	*Hoslundia opposita*	1	6	0
52	*Hypoestes forskaolii*	0	7	3
53	*Hypoestes sp1*	12	10	0
54	*Hypoestes sp2*	3	0	0
55	*Hypoestis sp3*	1	0	0
56	*Hyptis suaveolens*	0	2	3
57	*Indigofera arrecta*	5	2	0
58	*Indigofera spinosa*	0	1	0
59	*Indigofera subcorymbosa*	2	0	0
60	*Indigofera tinctoria*	0	2	0
61	*Jacobaea vulgaris*	0	1	1
62	*Justicia flava*	0	0	1
63	*Lamium flexuosum*	0	12	8
64	*Lantana camara*	0	1	3
65	*Launaea cornuta*	0	1	0
66	*Leonotis africana*	1	0	0
67	*Leucas martinicensis*	19	2	11
68	*Lippia javanica*	6	1	7
69	*Ludwigia abyssinica*	1	0	0
70	*Malvaceae sp*	0	3	0
71	*Melissa officinalis*	3	0	0
72	*Nicandra physalodes*	0	2	0
73	*Ocimum basilicum*	22	2	0
74	*Ocimum gratissimum*	19	8	9
75	*Ononis spinosa*	3	0	0
76	*Opuntia ficus-indica*	0	1	0
77	*Oxygonum sinuatum*	0	2	55
78	*Panicum maximum*	0	9	0
79	*Parthenium hysterophorus*	0	2	1
80	*Pavonia senegalensis*	0	1	0
81	*Plectanthus barbatus*	0	2	0
82	*Psiadia punctata*	10	0	0
83	*Ricinus communis*	0	1	0
84	*Schkuhria pinnata*	0	0	9
85	*Senecio doronicum*	1	2	0
86	*Sida rhombifolia*	0	4	0

87	*Sida sp.*	0	1	0
88	*Solanum elaeagnifolium*	15	0	9
89	*Solanum incanum*	8	3	11
90	*Solanum lycopersicum*	0	3	0
91	*Sphaeranthus suaveolens*	0	6	0
92	*Tagetes minuta*	0	4	0
93	*Tanacetum vulgare*	0	8	2
94	*Tephrosia vogelii*	0	11	0
95	*Thelypteris vailantii*	0	1	0
96	*Thevetia peruviana*	0	4	0
97	*Tithonia diversifolia*	0	1	0
98	*Tribulus terrestris*	3	0	5
99	*Trichodesma zeylanicum*	0	11	0
100	*Tridax procumbens*	0	5	0
101	*Triptelis vaillantii*	1	0	0
102	*Unknown sp*	3	9	12
103	*Urochloa mosambicensis*	0	2	0
104	*Vernonia baldwinii*	11	2	0
105	*Vicia sativa*	0	1	0
106	*Vigna sinensis*	0	1	0
107	*Vigna unguiculata*	0	5	0
108	*Waltheria indica*	0	3	0
109	*Zea mays*	0	1	0
110	*Ziziphus mucronata*	2	0	0
	NUMBER OF INTERACTION	257	347	257
	INTERACTED FLORAL RICHNESS	39	79	37

Chapter III

Agricultural intensification with seasonal fallow land promotes high bee diversity in Afrotropical drylands

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Summary

1. The exponential increase of the human population in tandem with increased food demand has caused agriculture to be the global-dominant form of land use. Afrotropical drylands are currently facing the loss of natural savannah habitats and agricultural intensification with largely unknown consequences on bee pollinators. Here we investigate the effects of agricultural intensification on bee assemblages in the Afrotropical drylands of northern Tanzania. We disentangled the direct effects of agricultural intensification and temperature on bee richness from indirect effects mediated by changes in floral resources.
2. We collected data from 24 study sites representing three levels of agriculture intensity and spanning an extensive gradient of mean annual temperature in northern Tanzania. We used ordinary linear models and path analysis to test the effects of agriculture intensity and ambient temperature on bee species richness, bee species composition, and body-size distribution of bee communities.
3. We found that bee species richness increased with agricultural intensity and with increasing temperature. The effects of agricultural intensity and temperature on bee species richness were mediated by positive effects of agriculture and temperature on the richness of floral resources used by bee pollinators. During the off-growing season, agricultural land was characterized by an extensive period of fallow land holding a very high density of flowering plants with unique bee species composition. The increase of bee diversity in agricultural habitats paralleled an increasing variation of bee body sizes with agricultural intensification that, however, diminished in environments with higher temperatures.
4. *Synthesis and applications*. Our study reveals that bee assemblages in Afrotropical drylands benefit from agriculture intensification in the way it is currently practiced. However, further land

use intensification, including year-round irrigated crop monocultures and excessive use of agrochemicals is likely to exert a negative impact on bee diversity and pollination services, as reported in temperate regions. Moreover, several bee species were restricted to natural savannah habitats. To conserve bee communities and guarantee pollination services in the region, a mixture of savannah and agriculture, with long periods of fallow land, and should be maintained.

Keywords: Afrotropical dryland; agricultural intensification; bee abundance; bee body size; bee species richness; forage resources; northern Tanzania; species community composition.

Introduction

Eighty-seven percent of the major food crops and 35% of global food production depend on animal pollination and in particular on bee pollinators . There is great concern regarding the global decline of bees with negative upshot for pollination services (Dainese et al., 2019; Potts et al., 2016). Land-use intensification, particularly agriculture expansion, is assumed to be a major driver (Potts et al., 2010). Global agriculture expansion has been associated with the loss of natural habitats and intensified agricultural practices, resulting in loss of bee diversity and its associated ecosystem services (Goulson et al., 2015; Potts et al., 2016; Steffan-Dewenter & Westphal, 2008). Agriculture intensification could also limit the availability of floral resources for bee pollinators (Dicks et al., 2021). A scenario that could trigger changes in bees morphological functional traits such as body size reduction due to low food supplied to larvae (Filipiak, 2018; Tommasi et al., 2021). Understanding the variation of bee body size is crucial for its conservation efforts as it correlates with many ecological relevant variables such as foraging range and thermoregulatory characteristics (Greenleaf et al., 2007). However, most studies on agricultural intensification impacts on bee assemblage and body size variation were conducted in temperate regions, while the consequences on bee pollinators in the tropical regions are still little understood. This is particularly true for tropical dryland habitats that host a large diversity of bees and show a rather small ecological resilience (Millard et al., 2021; Peters et al., 2019), and which increasingly experience temperatures near the critical thermal limits of organisms (Deutsch et al., 2008; Sunday et al., 2014).

The exponential increase of the human population in tandem with increased food demand has caused agriculture to be the global-prevalent form of land use (Ramankutty et al., 2018). Intensification of agriculture through increased field sizes, agricultural mechanization, external inputs such as herbicides and chemical fertilizers, and decreased crop diversity are among practices performed to increase food production (Almusaed, 2016; Palma et al., 2015). On the other hand, these practices are increasingly becoming one of the cardinal pressures that directly and indirectly affect bee survival (Sanchez-Bayo & Goka, 2014). Some direct effects of agricultural intensification on bees are evidenced through the use of herbicides that cause direct intoxication (Potts, 2016), plowing and compaction that destroy nests of ground-nesting bees (Kim et al., 2006), or impairing nests in branches or twigs of non-crop plants (Sutter et al., 2017). Conversely, agricultural intensification could indirectly affect bees through decreasing floral resource availability via reduced weed cover and loss of non-crop habitats. These habitats provide forage resources and nesting sites for bees, hence, their loss interrupts bee-plant interactions (Roulston & Goodell, 2011).

A special concern regarding the impact of agricultural intensification on bees is how agricultural intensification interacts with higher temperatures in the course of global change. Bees are ectotherms and their body metabolism and activity pattern are increasing with ambient temperature (Classen et al., 2015; Deutsch et al., 2008 Soroye et al., 2020). However, some terrestrial habitats in the tropics hold temperatures that may already surpass optimum temperatures or even critical thermal limits of species (Deutsch et al., 2008; Sunday et al., 2014). Therefore, both negative and positive effects of temperature on bee assemblage can be contemplated (Classen et al., 2015; Hamblin et al., 2018; Mayr et al., 2020). Temperature may also interact with the effects of agricultural intensification e.g. stronger effects of intensification in warmer habitats cause a synergistic impact on bee assemblage (Millard et al., 2021). Such synergistic effects of global change drivers are of high concern, as they are little incorporated in the estimations of global change effects (Oliver & Morecroft, 2014; Peters et al., 2019).

Although agriculture is a major land-use type on earth (Ramankutty et al., 2018) and is expected to increase in Afrotropical drylands (Laurance et al., 2014; Millard et al., 2021; Newbold et al., 2017), few studies have attempted to elucidate the effect of agricultural intensification on bee species assemblage and functional traits (body size) in the region (Otieno et al., 2015; Stein et al., 2018; Tommasi et al., 2021). Hitherto, most of studies have been conducted in temperate Europe and America (Saunders et al., 2020) that are unlike to be globally representative, leaving the effects of agriculture on bee assemblage in tropical East African drylands largely unknown. Additionally, studies on wild bee communities in Afrotropical drylands with a perspective shift from considering a single stressor to quantifying multiple, compounding pressures such as agricultural intensification and temperature are even scarcer (Kammerer et al., 2021).

Therefore, in this study, we investigated the effects of local agricultural intensification on bee diversity, community composition, and body size distributions along a temperature gradient in the Afrotropical dryland of northern Tanzania. Furthermore, the study aimed at understanding the drivers of bee species richness by disentangling the direct effects of agricultural intensification and temperature on bee species richness from indirect effects that are mediated by a change in floral resources. We hypothesized that:

1) Highly agricultural intensity negatively affects bee species richness and abundance.
2) Bee species richness increase with ambient temperature. The effects of temperature and agriculture are interactive, i.e., stronger effects of agricultural intensity on bee species richness are supposed to occur in warmer habitats.
3) The effect of agriculture on bee species richness is indirect, i.e., mediated by a change in their potential floral resources (plant species richness). Alternatively, agriculture directly (e.g., plowing, weed extirpating, or pesticide application) rather than indirectly impacts bee species richness.

4) Increases in temperature and agricultural intensity lead to a change in the bee body size distribution.

Methods

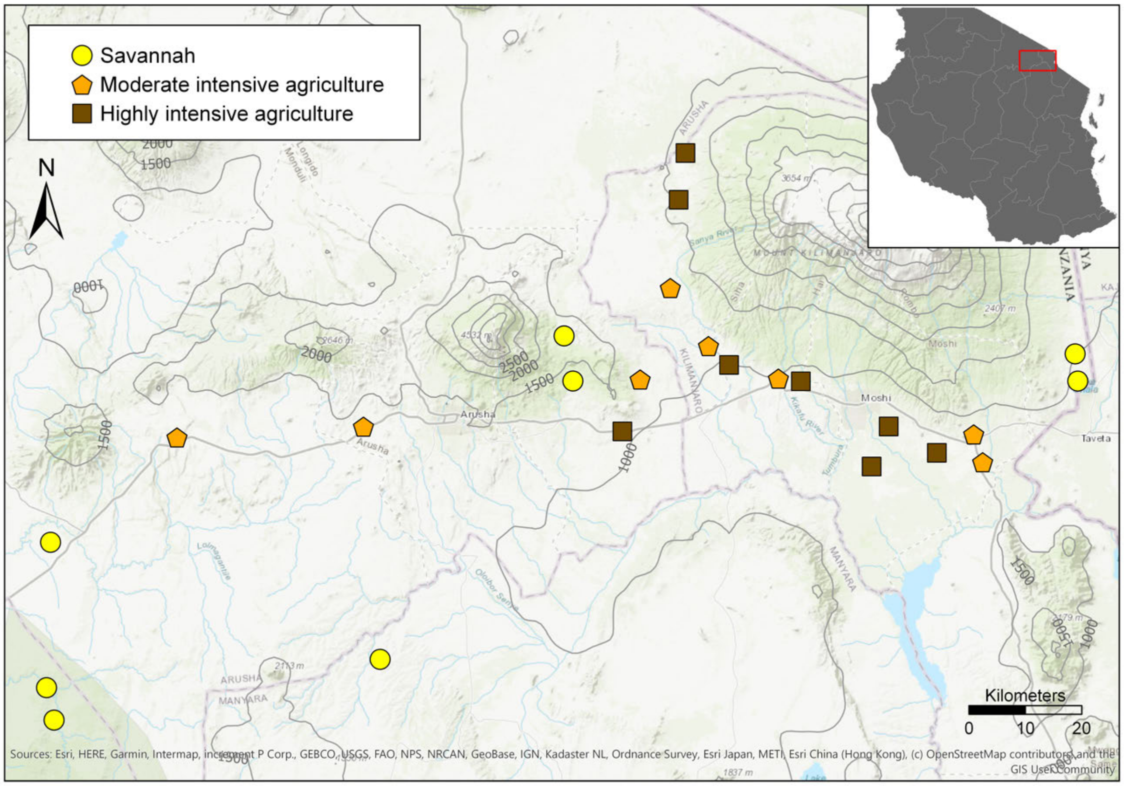
Description of the Study Area

We conducted this study in northern Tanzania, in the lowlands of Mt. Kilimanjaro and Mt. Meru, and the areas of Tarangire National Park in Kilimanjaro, Arusha, and Manyara regions, respectively (Fig. 1). The study area is characterized by a tropical climate with extensive dry periods (Gebrechorkos et al., 2019a). Study area elevation ranges between 702m and 1708m above sea level (asl) with the mean annual temperature spanning from 18^{o}C to 26^{o}C (depending on elevation) with maxima temperatures regularly exceeding 40°C (own unpublished data). The area experiences bimodal rainfall with a long rainy season between ca. March and May and a short rainy season typically in November and December (C. A. Foley & Faust, 2010). The dominant natural vegetation of this dryland is composed of grasses interspersed with herbs and scattered trees (dominated by *Commiphora* and *Acacia*) (tropical savannah). There are several non-native trees outside the protected areas, including *Acrocarpus flaxinifolius*, *Leucaena leucocephala*, and *Grevillea robusta*. Planting and harvesting calendar of typical crops (wheat, maize, barley, sorghum, beans, and sunflower) in the study area follow the rainfall patterns (Rowhani et al., 2011). Planting usually happens after the first rains, in February, and harvest is at the end of the long rainy season between mid-July to early August (Rowhani et al., 2011). Following crop harvesting, fields are customarily abandoned until the next coming annual rain season. During this period the fields are dominated by proliferated herbs. However, due to the relatively low use of herbicides, even during the planting and when the crops are in the fields (growing season), flowers can be found on fields.

Data collection

We collected data from August 2018 to March 2020 in 24 replicate study sites distributed equally among the three selected habitats following a gradient of agricultural intensification (AI) (Fig. 1). The first habitat was natural savannah representing low-intensity agricultural habitat, situated in the protected areas of the Tarangire National Park, Arusha National Park, and Lake Challa wildlife management area. This habitat served as a control site characterized by the absence of agricultural activities and natural conditions with minimum anthropogenic disturbances. Conversely, the habitat is characterized by rolling grasslands with scattered native trees, shrubs, and herbs. Moderate intensive agriculture, the second habitat type, was composed of subsistence farming characterized by small field sizes (mostly less than 1 ha) of mixed crops such as maize, beans, and sunflower. Crop areas are intermingled with patches of savannah habitats, and typically only small agriculture machines such as small tractors and planters are used. The third habitat type was defined as highly intensive agriculture. This habitat type is characterized by large monoculture fields of wheat, maize, or barley as the major crops. Heavy agricultural machines and chemical fertilizers are regularly used during the growing time of the crops.

Distances between study sites were at least 3 km, which is far larger than the flying distance of most bee species (Wright et al., 2015; Zurbuchen et al., 2010a). Replicates of different habitat were distributed along the entire study region to minimize spatial autocorrelation. Each study site was composed of two study plots positioned ca. 150 m apart. Each study plot had a size of 50 x 50 m, where bees and floral resources were sampled and quantified.



Sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), (c) OpenStreetMap contributors, and the GIS User Community

Fig. 1 | A map of the study area. The map shows the distribution of study sites with different colors and symbols representing different land use intensity classes (see legend). The two big mountains on the map are Mt. Meru (center) and Mt. Kilimanjaro (upper right). In the upper right corner, the small map shows the location of the study area in northern Tanzania.

Bee sampling

Two standardized sampling methods (UV-reflecting colored pan traps and standardized random walks) were employed to sample bees (Lasway et al., 2021b; Prendergast et al., 2020). Twelve pan traps in four clusters (each cluster with three different UV-reflecting colors, white, yellow, and blue) were installed in each plot to passively collect bees (Fig. A1a in Appendix) (Classen et al., 2020; Elzay & Baum, 2021). For each plot, four pan trap clusters (two with 120 cm height poles and two with 35 cm) were positioned diagonally on two 50 m parallel transects separated with 30 m interspatial distance (Fig. A1b in Appendix). Pan trap clusters were installed at different heights; a level of the shrub layer (120 cm above ground distance) and the herbaceous layer (35 cm from the ground) to maximize capturing bees flying at different heights. Pan traps were filled with unscented soapy water and left in the field for 48 hours to passively collect bees (Classen et al., 2020). A drop of scentless liquid soap per ca. 1 liter was used to break the surface tension of water so that bees landing on the pan trap were more likely to be captured. Scentless soap also helps to avoid any influence in sampling. Bees were collected from the pan traps after 48 hours and temporarily preserved in 70% ethanol before being further processed in the lab. In each study site, we conducted pan trap sampling in three different main seasons of the year; long rainy season, dry season, and short rain season. The pan trap sampling effort summed up to 3,456 hours per study site and 82,944 hours for the entire study.

Besides pan trap sampling, we used a standardized random walk method to sample bees. This method involves walking randomly at a relatively slow pace within plots using a hand net to actively collect bees foraging on flowers. Using this method, we collected bees for 2 hours on each study site (one hour per each 50 x 50 m study plot), excluding handling and recording time. Random walks were conducted anytime between 9:00 am and 5:00 pm when bees are expected to be active (Classen et al., 2020). On each study site, a two-hour random walk was conducted in three main seasons of the year (long rainy season, dry season, and short rainy season), this summed up to 6 hours of active bee collection for each study site and in total 144 hours for the whole study. We restricted random walk sampling to days with no or very little rainfall and low wind speed. All specimens collected were temporarily preserved in 70% ethanol before being mounted and identified. All bees were identified following the nomenclatural system established by Michener (2007) with exception of the Halictidae family. Bee identification to species levels was mainly performed by two experts on Afrotropical bees (C.E., A.P.). However, few were identified by

J.V.L. We calculated species richness per study site by summing up the cumulative number of bee species collected by both sampling methods across all three sampling seasons.

Quantification of bee-visited plants

All plant species visited by bees during random walks were recorded in each study site. This measure corresponds to the plant species used by bees by way of an alternative to the on-site total number of plant species (Classen et al., 2020; Tucker & Rehan, 2017). Plant species were recorded as bee visited blooms of flowering plants, i.e. in case, we observed a bee walking or landing on a flower (not just flying over it) (Tucker & Rehan, 2017). Flowering plant species that could not be identified in the field were taken to the National Herbarium of Tanzania for morphological identification.

Measurement of body mass

The inter-tegular distance (ITD; in mm) was measured as a proxy for bees' body size (Classen et al. 2017) using a digital microscope (Dino-Lite digital handheld microscope Taiwan, with a precision of 0.001mm). The ITD measures the miniature distance between the two tegulae, i.e., the small-scale-like sclerites covering the base of the fore wing in bees. For each study site, we calculated the mean and standard deviation of the ITD using measures of all sampled individuals.

Environmental parameter

Data on temperature on study sites were recorded using temperature sensors (iButton) (Classen et al., 2015). For each study site, a Thermochron iButton data logger (DS1921G; ± 0.5 °C resolution; Maxim Integrated Products, USA) was placed at 2 m height above the ground (on a branch of a shrub/tree) to record the ambient temperature (Classen et al., 2015). An overlay plastic funnel was hung 10 cm above the sensor for protecting it from direct solar radiation (Fig. A1c in Appendix). Temperature sensors were set to take records in 60 minutes intervals. Sensors were left in the field for the entire year and visited every three months for data reading and maintenance (if any). Mean annual temperature (MAT) per study site was obtained by averaging all individual temperature measurements.

Statistical analyses

We analyzed the data using R version 4.0.3 (http://cran.r-project.org/). Ordinary linear models were used to explore the effect of agricultural intensity (AI) and MAT on bee species richness and abundance. MAT was added as a first and second-degree polynomial term to model potential monotonic or unimodal relationships between MAT and the species richness and abundance of bees. We tested for both additive and interactive effects of temperature and agriculture intensity on bee species richness. The *dredge* function in the *MuMIn* R package was used to select the best-supported model based on Akaike information criterion (AIC) values (Burnham & Anderson, 2004). Our sample size was relatively low, a situation that compelled the use of AIC with a second-order bias correction (AICc) instead of the normal AIC. The obtained *P-value* from the best model summary *F* test was used to evaluate the significance level of estimated parameters.

Path analysis (Shipley, 2016) was used to examine causal relationships and disentangle the direct effect from indirect effects of MAT and AI on floral resource richness and bee species richness. Direct causal effects represent effects that go directly from one variable to another, while indirect effects occur when the relationship between two or more variables is mediated by one or two variables (Shipley, 2016). We postulated and constructed a conceptual path diagram (Fig. 3b), based on the ecological understanding of bees, assuming both direct and indirect effects of AI and MAT on bee species richness. Possible path combinations were pre-selected by analyzing two endogenous variables of the path model (bee species richness and floral resource richness) with all explaining variables, i.e., AI, MAT, and MAT^2. The most inclusive full model for bee species richness was:

$$SD_b \sim AI + MAT + MAT^2 + AI{:}MAT + AI{:}MAT^2 + \text{floral resource richness}$$

For floral resource richness, the following full model was constructed:

$$SD_p \sim AI + MAT + MAT^2 + AI{:}MAT + AI{:}MAT^2$$

The '*dredge*' function of the R package '*MuMIn*' was used to rank models based on the AIC_C. For all combinations of competitive models ($\Delta AIC_C < 2$), we conducted a formal path analysis and derived path coefficients, their statistical significance, and multiple coefficients of determination (R^2) for the two response variables. For formal path analysis, the r package '*piecewise SEM*' was used.

Finally, we performed a linear model to explore the effect of AI and MAT on the variation of bee body size. Similar to species richness, MAT was added as a first and second-degree polynomial term to model the potential relationships between MAT and body size variation and tested for both additive and interaction effects of the two predictor variables on the bee body size variation.

Results

We sampled a cumulative total of 3,428 bee individuals and sorted them into 219 species representing 58 genera and six families: Andrenidae (5 species), Apidae (76 species), Colletidae (4 species), Halictidae (86 species), Megachilidae (47 species), and Melittidae (1 species). Findings revealed that habitats experiencing highly intensive agriculture had the highest cumulative bee species richness (146 species) and abundance (1,639 individuals). Species richness values were relatively similar to habitats experiencing moderate intensive agriculture (140 species, 1098 individuals) but higher than in savannah habitats (105 species and 691 individuals) (Fig. 2a, Table A1 in Appendix). Additionally, species community composition in high and moderate intensive agriculture habitats showed unique bee species in both agricultural habitats (with 17% each) and savannah habitats (12%) (Fig. A2 in Appendix). Nonetheless, there were considerable overlaps in bee species, with 16 species overlapping between savannah and highly intensive agriculture, 11 species between savannah and moderate intensive agriculture, and 39 species overlapping between moderate and highly intensive agriculture.

Agricultural intensity and MAT showed significant additive effects on mean bee species richness. The mean bee species richness was higher in high and moderate intensive agricultural habitats, while the savannah habitat showed a lower mean number of species (Fig. 2b). Conversely, bee species richness showed a monotonic increase with MAT from 18.5°C to 25.5°C (Fig. 2c). Besides, multi-model inference revealed no significant support for models assuming an interactive effect of AI and MAT, suggesting that the effect of agriculture on bee species richness was consistent along the temperature gradient (and vice versa).

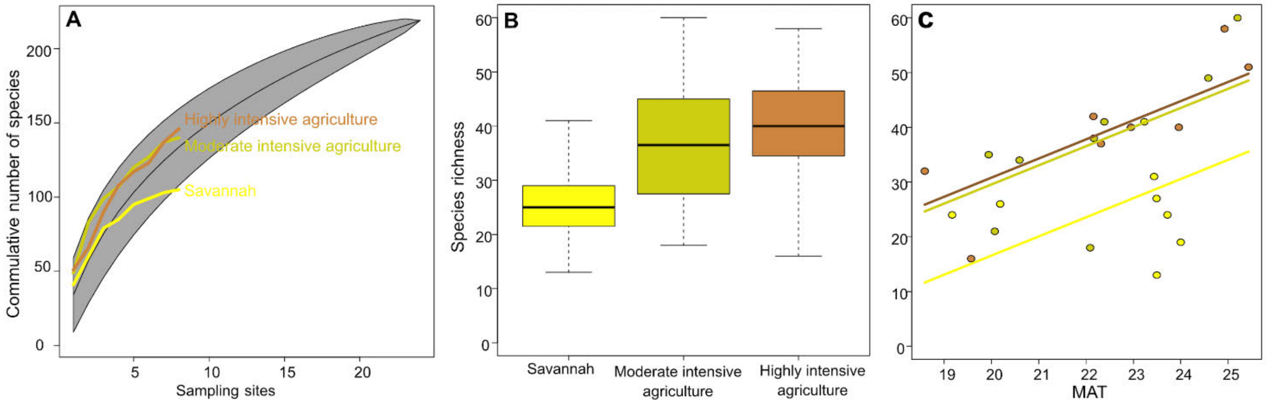


Fig. 2 | Bee species richness changes with agricultural intensification. A, Cumulative number of bee species richness increases with the number of sampled study sites but did not reach an asymptote. Species accumulation curves were shown by the bold black line across all study sites (grey polygon: 95% CI). Individual habitat type values were shown by shorter colored lines. B, Mean bee species richness per study site differed among habitats (ANOVA, $F_{2,21}$ = 3.18, P = 0.062). C, Species richness as a function of agricultural intensity and mean annual temperature ($R^2 = 0.53$, $F_{3,20} = 7.465$, $P = 0.001$; $P_{AI} = 0.007$; $P_{MAT} = 0.002$).

Results from path analysis suggest that agricultural intensity and climate determined bee diversity mainly by modifying the floral resource richness across habitats. Temperature and agriculture intensity were both significant predictors of the floral resource richness: Floral resource richness increased significantly with agricultural intensity (Fig. 3,A1 and Table A2 in Appendix) and MAT (Fig. 3,A2) ($R^2 = 0.43$, $F_{3,20} = 4.963$; $P_{AI} = 0.004$; $P_{MAT} = 0.05$). Bee species richness linearly increased with the floral resource richness (Fig. 3,A4) ($R^2 = 0.57$, $F_{2,21} = 13.65$; $P_{Sdp} = 0.001$). Data also strongly support a direct positive effect of MAT on bee species richness (Fig 3,A3) ($R^2 = 0.57$, $F_{2,21} = 13.65$; $P_{MAT} = 0.04$). However, we did not detect a direct effect of AI on the bees' species richness. A competitive (second-best supported) path model ($\Delta AIC = 0.32$) was highly similar to the best-supported path model (Fig. 3) but additionally included a positive effect of MAT on bee species richness.

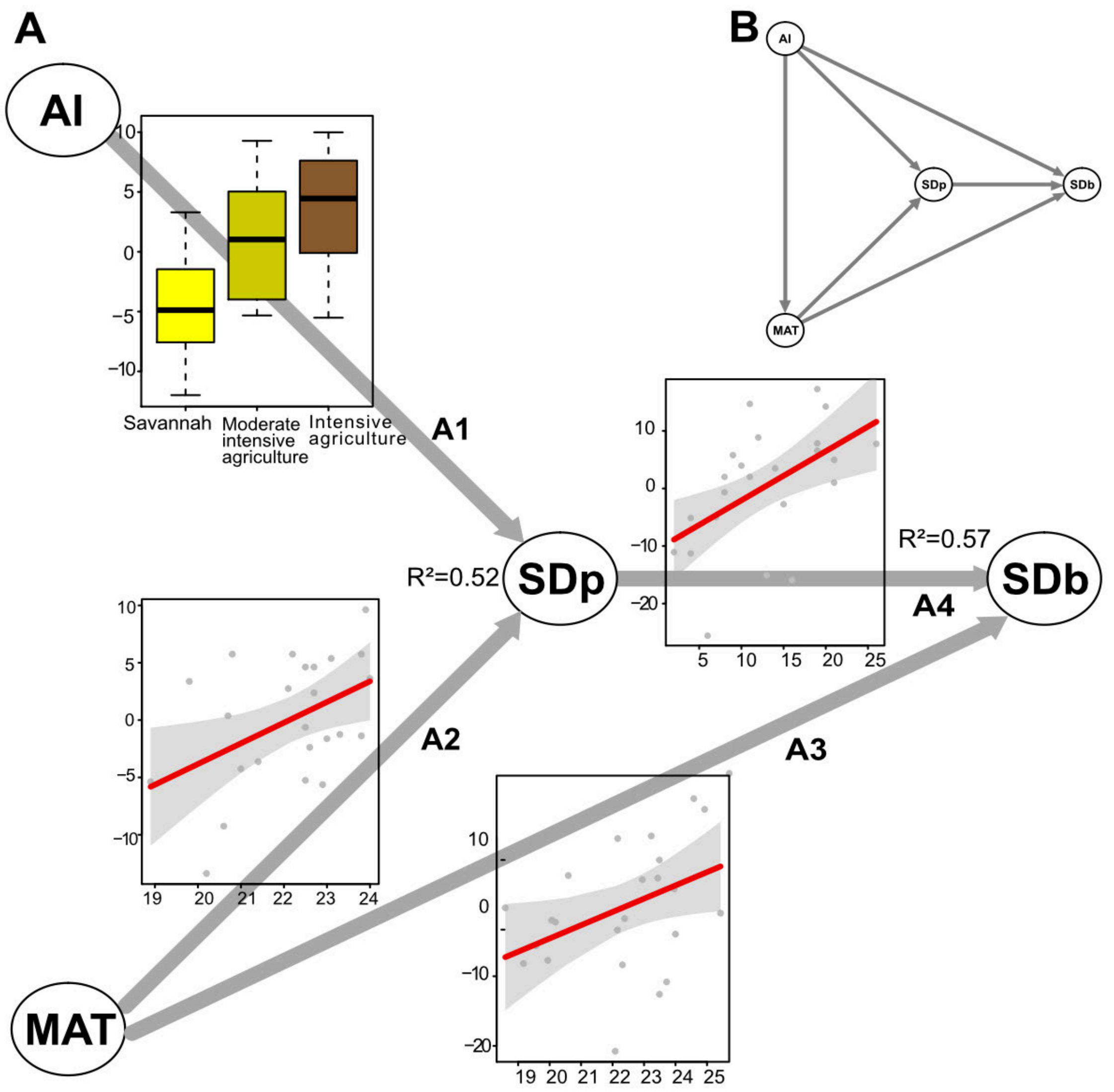


Fig. 3 | Path model showing the direct and indirect effects of MAT and AI on floral resource richness and species richness of bees. A The best-supported path model shows that the effect of mean annual temperature (MAT) and agriculture intensity (AI) on species richness of bees (SDb) is mainly mediated by floral resource richness (SDp). In addition, MAT exerts a direct effect on bee species richness. The inlet figures on arrows depict the relationships between AI and residual SDp (A1), MAT and residual SDp (A2), MAT and residual SDb (A3), and SDp and residual SDb (A4). In all figures, the explanatory variable is shown on the x-axis and the response variable on the y-axis. A1-A A4 show relationships between the response and explanatory variable after controlling for all other effects in the model. Grey dots show data points while red lines and grey polygons show predictions of ordinary linear models and 95% confidence intervals, respectively. B, The most inclusive path model illustrating all considered relationships among exogenous and endogenous variables.

Agricultural intensity and MAT had no significant effects on the mean ITD (R^2 = 0.04, $F_{3,20}$ = 0.299; P_{AI} = 0.381; P_{MAT} = 0.834), but the variation in body sizes significantly increased with agricultural intensification (Fig. 4a). Agricultural intensification and MAT had a significant interactive effect on the variation in ITD. This interaction suggests that the relationship only holds for environments at the cooler edge of the thermal gradient while we observed no difference in the variation in bee body sizes in areas experiencing high temperatures (Fig. 4b).

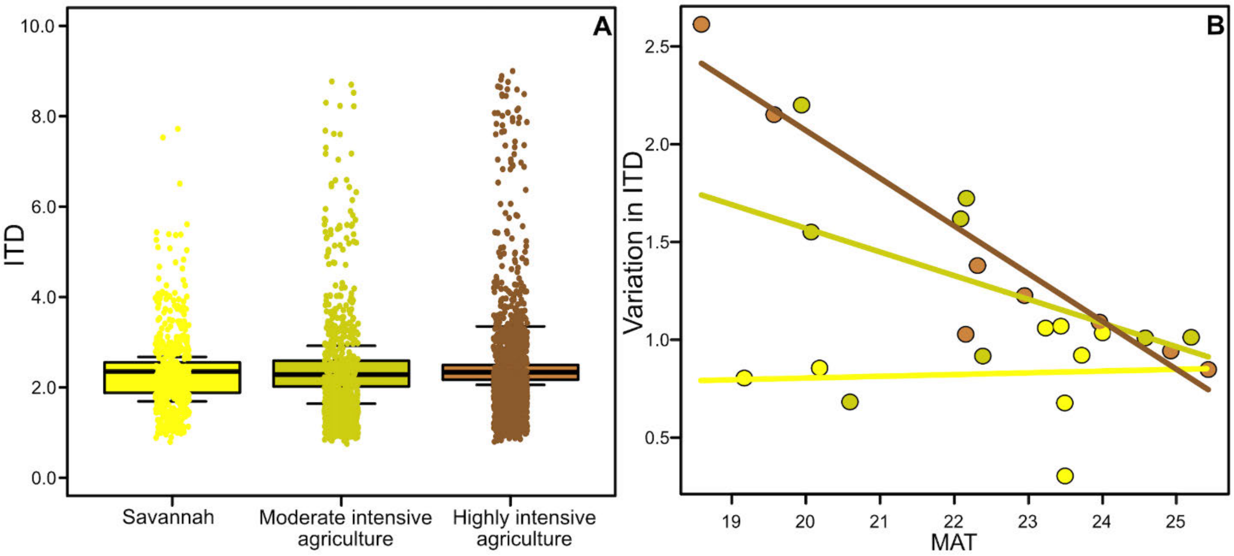


Fig. 4 | Bee body mass changes with agriculture intensification. A**,** Average bee body mass was similar across the land use intensity gradient. B, The variation in bee body size (ITD) showed to be affected by the interaction effect of agriculture with temperature (ANOVA, $F_{5,18}$ = 7.09, P < 0.001; $P_{\mathrm{AI:MAT}}$ = 0.038).

Discussion

Contrary to our expectation, we found that agricultural intensification in the tropical drylands of East Africa was associated with an increase in bee species richness and abundance, and an increased variation of bee body sizes. Bee species richness and abundance also increased with environmental temperature, but we detected no evidence for an interactive effect of temperature and agricultural intensification on bee species richness. Changes in bee species richness along temperature and land-use gradients were mediated by the positive effects of agriculture and temperature on the floral resources that are used by bee pollinators.

Our findings that overall bee species richness and abundance increased with agricultural intensification was unexpected and is inconsistent with most studies conducted along agricultural intensification gradients in temperate Europe and America (Coutinho et al., 2018; Ekroos et al., 2020; Le Féon et al., 2010; Steffan-Dewenter & Westphal, 2008). However, a similar pattern was reported by Classen et al. (2015) on the foothill of Mt. Kilimanjaro. The authors observed that habitat disturbance through agriculture did not impact bee species richness patterns. Furthermore, the study reported increased flower richness and abundance in agricultural habitats that promote high bee diversity (Classen et al. 2015). Contrasting findings supporting an observation that effects of agricultural intensification on bees and other pollinators are diverse, and differ between taxonomic groups, landscape types, climatic regions, and specificities of agriculture systems (Tscharntke et al., 2005; Winfree et al., 2011).

Changes in bee species richness with agricultural intensity were mediated by the positive effect of agriculture and temperature on the floral resources used by bee pollinators. Higher diversity of floral resources in highly intensive agricultural sites is often correlated with larger bee communities (Ellis & Barbercheck, 2015). Eighty percent of global agriculture depends on rainfall (Kijne et al., 2003), and most parts of Tanzania consist of drought-prone ecosystems (Gebrechorkos et al., 2019). Therefore, crop cultivation in the study area is practiced mainly during the long rainy season when water is available for crop growth and development. Following crop harvesting (between mid-July and early August), the land is left fallow for several months until the next annual rain season (Abass et al., 2014). Over this time, fallow fields are dominated by proliferated annual herbs and grass cover (Verhulst et al., 2004; Massante et al., 2019), which can flourish even with small amounts of rainfall, and thus provide forage resources for bee pollinators (Tucker & Rehan, 2017). Besides, abandoned agriculture fields increase bee nesting substrate, offering higher spatial-temporal stability of food resources and nesting sites from which bees could benefit (Nicholls & Altieri, 2013; Requier & Leonhardt, 2020; Steffan-Dewenter & Tscharntke, 2001)

This long period of fallow land with climate fostering bee activity strongly contrasts with the conditions of intensified agriculture in many temperate regions (Fig. 5). Here, crops are cultivated from spring to summer, in the time of the year when the temperature is high enough for crop production (Sloat et al., 2020). Before and after the harvesting period, low temperatures do not support the activity of ectothermic bees and the growth of their floral resources (Borghi et al., 2019).

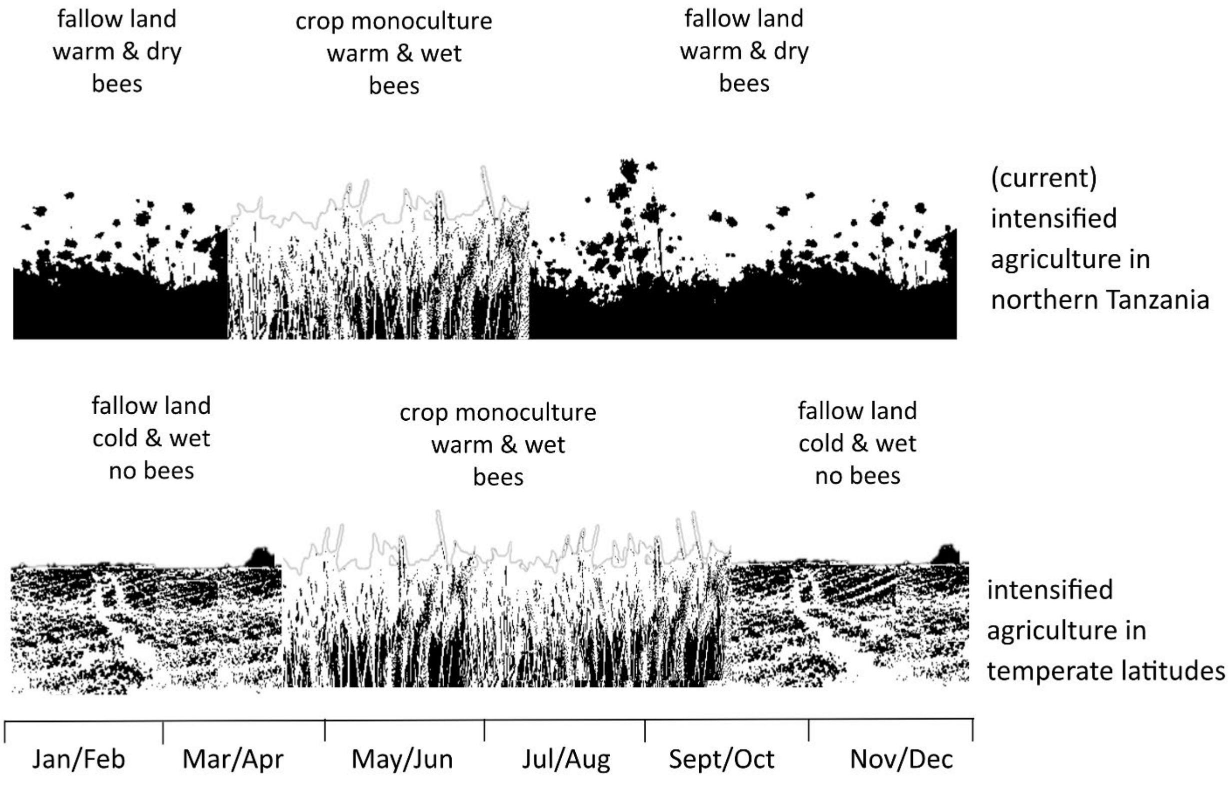


Fig. 5 | Intensified agriculture as currently practiced in the study region in comparison to intensified agriculture at higher latitudes. High temperatures throughout the year in the tropics lead to the proliferation of herbs and grasses in the period following crop harvesting. The condition is not the same in the temperate region, where after crop harvesting temperatures are low.

Irrespective of the findings that agricultural habitats host an average high number of bee species richness. Relatively low bee species richness in savannah habitat can be explained by diverse floral resources richness and continuous matrix of grasses (Ratnam et al., 2011) that set upper (food resource) limits to the number of bee species to coexist in the area (Ratnam et al., 2011; Moylett et al., 2020). Nonetheless, both habitats (savannah and agricultural) showed to contain unique bee species. Therefore, conservation of savannah natural ecosystem is also necessary for conserving bee communities of afro tropical drylands.

We did not observe a direct effect of agricultural intensification on bee species richness. Such a relationship would be plausible if plowing or weed extirpating would lead to the destruction of bee nesting sites for both ground and pith nesting bees or if pesticides application would cause species extinctions on sites. Conversely to intensive agricultural practices in temperate latitudes, many smallholder and intensive farmers in Tanzania still manually extirpate weeds (Classen et al., 2015; Tommasi et al., 2021). This practice reduces the impact of soil compaction on ground-nesting bees (Classen et al., 2015) and avoids agrochemical run-offs (Tommasi et al., 2021). These practices conserve habitats of ground-nesting bees and reduce potential direct impact of pesticides on insects that may lead to their mortality. On the flip side, manually weeded practice contributes to the maintenance of diverse floral resources in agricultural lands and at the field margins that attract more bee pollinators.

Our study shows that the current agriculture practice with prolonged periods of fallow land promotes high bee diversity. However, we expect that future intensification, including year-round crop monoculture with artificial water supply (irrigation), could subsequently result in loss of long periods of fallow land and may result in a strong decline in bee diversity. Nonetheless, increased use of pesticides and heavy machines, would have a strong negative impact on bee diversity and pollination services as reported in temperate latitudes where the decline in bee species richness and abundance due to agriculture intensification is alarming (Potts et al., 2010).

The study indicates temperature had a positive influence on bee species richness. Mean bee species richness sharply increases from 18.5°C to 25.5°C. However, increases in bee species richness with temperature were expected, because, under warm temperatures, bee foraging activities and net energy gain are higher than in cold temperatures (Classen et al., 2015). Additionally, biological processes that shape species richness such as species interactions and evolutionary rates in ectothermic organisms depend on temperature (Puurtinen et al., 2016). In that regard, temperature-mediated speciation rates or enhanced negative density-dependent mortality at higher temperatures may increase the pool of coexisting species of warm ecosystems. Despite the high temperatures which are already reached in East African dryland habitats in parts of the year, no decrease in bee species richness at higher temperatures was observed. This could have been expected because day temperatures in the East African drylands may approach the upper thermal limits of insects (Deutsch et al., 2008; Sunday et al., 2014). Nevertheless, future warming of these ecosystems may push temperatures beyond the critical thermal limits of even the warm-adapted bees.

We found the variation in body size of bees increased with agricultural intensification. This observation is consistent with Le Féon et al., (2010), who also observed large-bodied-size bees (bumblebees) increased in frequency with agriculture intensification. Increased floral resource diversity with agricultural intensity offers a higher amount of forage resources and nesting sites that attract diverse bee fauna with various morphological traits (Laha et al., 2020; Rollin et al., 2019), including small and large-bodied size bees that require more food resources for their offspring (Müller et al., 2006). Observed large-sized bees in highly intensive agriculture sites could also be explained by their larger foraging range and flight ability (Greenleaf et al., 2007). This trait enables large-sized bees to fly to the far proximity looking for rewards obtained from diverse floral resources. Because of this, it is probably that the observed large-sized bees are non-resident of the area. The higher variation of bee body sizes with agricultural intensification vanished in hot environments, where high temperatures may act as an environmental filter of large-sized bees with reduced cooling properties (Goulson, 2010; Theodorou et al., 2021).

One potential caveat of this study is that the methodology of sampling bees and plants could have biased some of the resulting patterns. The distribution of flowering plants in the savannah can be extremely patchy, as the scarce flowering trees or bushes (e.g. *Acacia* trees) between grasses attract a very high diversity of bees but only flower over a very short time period. In contrast, the distribution of flowers in the fallow land on agricultural sites is rather homogenous and less patchy in space and time, which could have facilitated the sampling of a larger number of bees in the agricultural habitats than in the savannah.

Conclusion

Our study concludes that the current agricultural intensification practice with long periods of seasonal fallow land is crucial in preserving diverse flowering plant communities and bee species richness with varying body sizes in the tropical drylands of East Africa. Our study, therefore, supports the view that the impact of agriculture intensification on bee communities depends on the studied region and the reference practiced agricultural system. The monotonic increase of bee species richness with temperature underscores a positive effect of temperatures within the range of temperatures currently reached in the East African study region. Nonetheless, an unbounded increase in temperature, as a consequence of ongoing climate change, may lead to undesirable consequences such as species loss of bee communities and floral resources with consequent negative impacts on pollination services.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declaration of competing interest

The authors declare no conflict of interest.

Supplementary materials

Appendix 1:

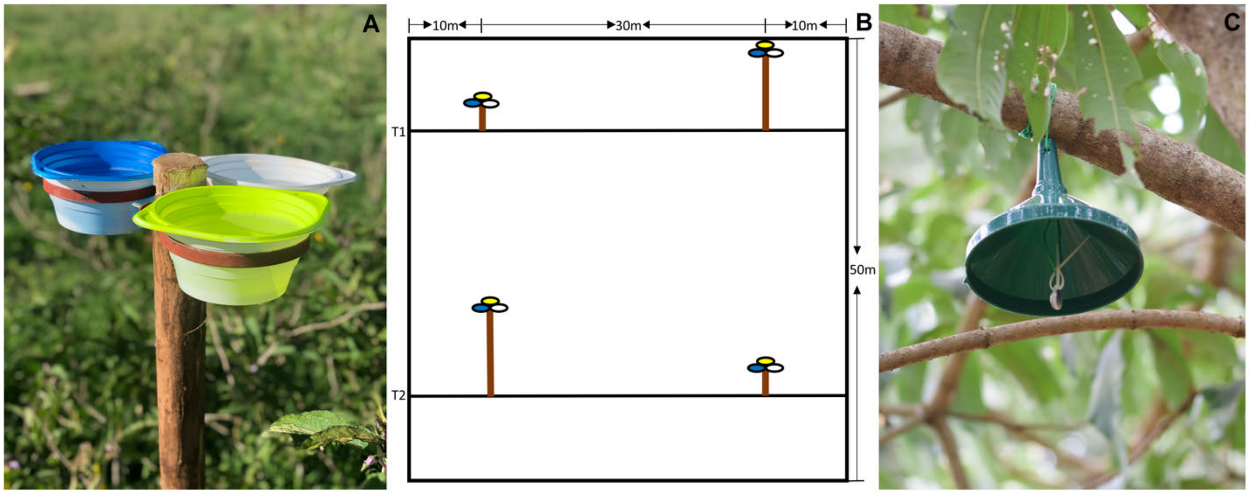


Figure A1 | A, One-pan trap cluster with three ultraviolet reflecting colored pan traps (blue, white, and yellow). B, Schematic map of a study plot with the four pan trap clusters on two transect lines (T1 and T2). The four pan trap clusters are hanged on two different height poles (two on 35cm height pole, and two on 120cm height pole). The different height pan trap clusters were positioned diagonally from one another. C, Temperature sensor positioned on the branch of a tree (2 m above the ground) for record air temperature. The overlaying funnel above the sensor provides shielding from direct sunlight.

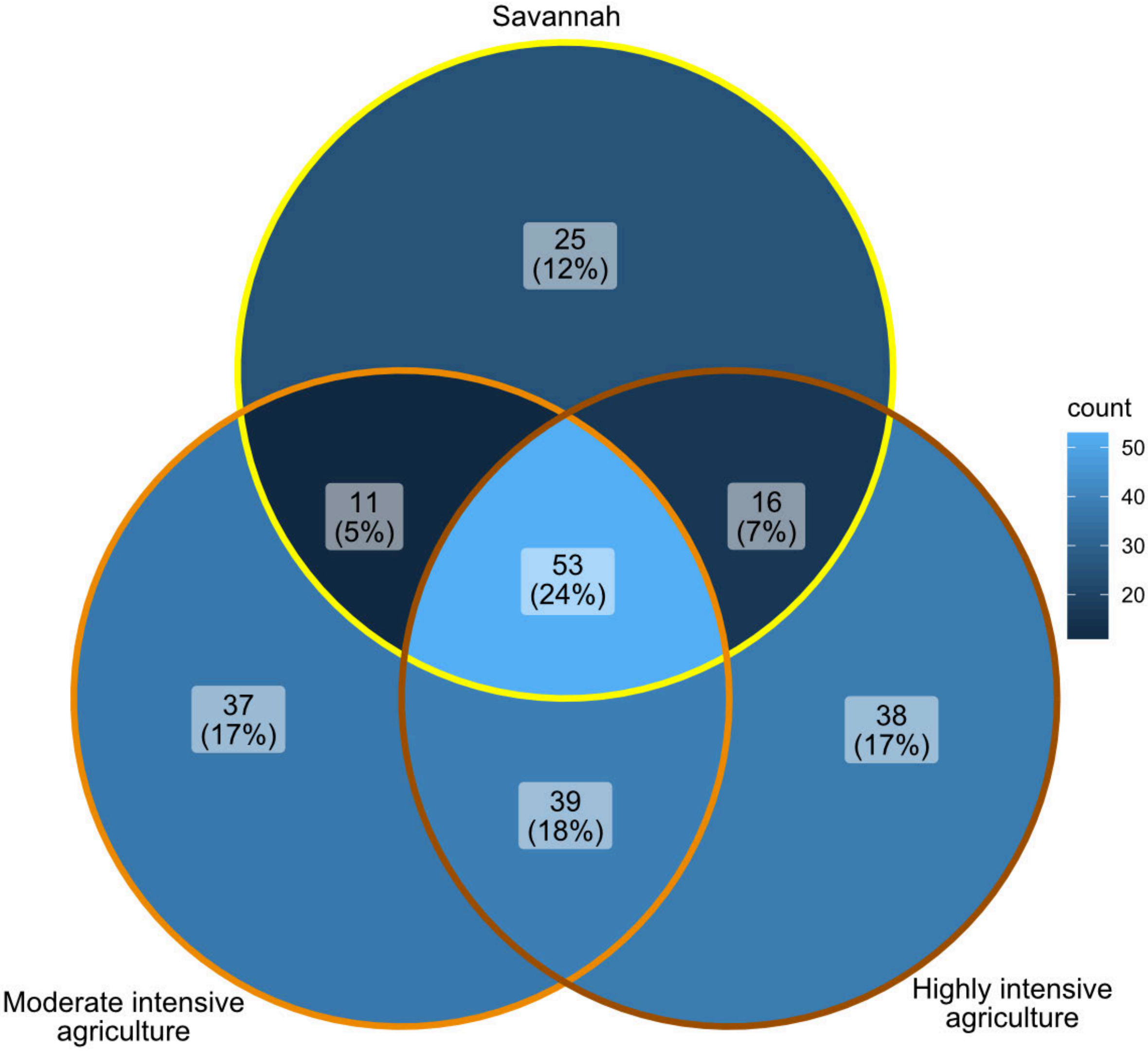


Figure A2 | Venn diagram illustrating the unique and overlapped bee species among habitats following the gradient of agricultural intensification. Highly and moderate intensive agriculture habitats showed a high number of unique bee species community composition while savannah habitat showed fewer unique bee species. Similarly, high species overlapped is observed in agricultural habitats than in savanna. Note that the cumulative total of all the unique and overlapped species matches 219 sampled bee species.

Table A1 | List of bee species and data on the total number of collected individuals per species in habitats of savannah, moderate and highly intensive agriculture.

S/no	**species name**	**Savannah**	**Moderate intensive agriculture**	**Highly intensive agriculture**
1	*Acunomia senticosa*	1	0	0
2	*Acunomia somalica*	0	1	1
3	*Acunomia theryi*	0	5	2
4	*Afranthidium sp*	0	1	1
5	*Afranthidium sp1*	0	1	0
6	*Afranthidium sp2*	0	1	0
7	*Afronomia fimbriata*	1	0	0
8	*Afronomia sjostedti*	1	0	0
9	*Amegilla acraensis*	0	1	1
10	*Amegilla aspergina*	0	0	1
11	*Amegilla atrocincta*	1	0	1
12	*Amegilla calens*	6	13	28
13	*Amegilla discolor*	0	1	0
14	*Amegilla kaimosica*	0	0	2
15	*Amegilla nubica*	1	1	0
16	*Amegilla obscuritarsis*	5	6	4
17	*Amegilla punctifrons*	0	1	3
18	*Amegilla sp1*	0	0	1
19	*Amegilla terminata*	0	0	1
20	*Andreana notophila*	1	0	0
21	*Andrena africana*	0	1	3
22	*Andrena notophila*	0	0	9
23	*Anthidiellum sp5*	0	0	1
24	*Anthidiellum(Chloranthidiellum) benguelense*	0	1	0
25	*Anthidium sp*	0	1	0
26	*Anthidium sp1*	1	0	0
27	*Anthidium sp2*	1	1	0
28	*Anthidium sp3*	1	0	0
29	*Anthophora auone*	0	1	0
30	*Anthophora matopoensis*	0	1	0
31	*Anthophora sp1*	0	0	2
32	*Anthophora sp2*	0	1	0
33	*Apis mellifera ssp monticola*	22	32	53
34	*Apis mellifera ssp scutellata*	181	258	438
35	*Austronomia sp1*	4	4	4
36	*Austronomia sp2*	7	0	4
37	*Braunsapis bouyssoui*	3	5	2
38	*Braunsapis facialis*	6	8	0
39	*Braunsapis somatotheca*	0	1	0

40	*Braunsapis trochanterata*	2	1	1
41	*Capicola sp*	0	0	2
42	*Ceratina sp*	2	0	7
43	*Ceratina sp1*	0	2	1
44	*Ceratina sp2*	0	0	4
45	*Ceratina inermis*	0	6	2
46	*Ceratina lineola*	0	1	0
47	*Ceratina moerenhouti*	1	0	3
48	*Ceratina nasalis*	4	1	0
49	*Ceratina nigriceps*	0	0	1
50	*Ceratina nyassensis*	18	17	10
51	*Ceratina paulyi*	0	1	0
52	*Ceratina sp5*	6	0	1
53	*Ceratina tanganyicensis*	1	0	2
54	*Ceratina(Pithitis) sp1*	0	0	2
55	*Ceratina(Pithitis) sp2*	0	0	1
56	*Coelioxys sp2*	1	0	0
57	*Coelioxys sp3*	0	1	0
58	*Coelioxys sp4*	1	1	1
59	*Colletes sp*	5	1	0
60	*Compsomelissa nigrinervis*	0	1	0
61	*Crocisaspidia chandleri*	0	1	1
62	*Crocisaspidia forbesi*	0	2	1
63	*Ctenoplectra albolimbata*	0	0	1
64	*Euaspis abdominalis*	0	1	0
65	*Eucara macrognatha*	0	2	0
66	*Heriades sp1*	2	0	3
67	*Heriades sp2*	1	1	0
68	*Hylaeus sp1*	0	1	0
69	*Hylaeus sp2*	0	0	1
70	*Hylaeus sp3*	0	1	0
71	*Hypotrigona gribodoi*	0	4	0
72	*Lasioglossum (Afrodialictus) bellulum*	21	75	153
73	*Lasioglossum (Ctenonomia) atricrum*	3	7	16
74	*Lasioglossum (Ctenonomia) radiatulum*	0	1	0
75	*Lasioglossum (Ctenonomia) scobe*	0	59	17
76	*Lasioglossum (Ctenonomia) sp1*	1	7	1
77	*Lasioglossum (Ctenonomia) sp2*	7	3	0
78	*Lasioglossum (Ctenonomia) sp3*	5	3	3
79	*Lasioglossum (Ctenonomia) sp4*	1	0	0
80	*Lasioglossum (Ctenonomia) transvaalense*	15	153	36
81	*Lasioglossum (Ipomalictus) bowkeri*	3	12	106
82	*Lasioglossum (Ipomalictus) hancocki*	0	1	0
83	*Lasioglossum (Ipomalictus) matopiense*	43	7	1
84	*Lasioglossum (Ipomalictus) rubritarse*	7	44	22

85	*Lasioglossum (Ipomalictus) sp1*	0	1	0
86	*Lasioglossum (Ipomalictus) sp2*	0	9	5
87	*Lasioglossum (Ipomalictus) sp8*	0	5	11
88	*Lasioglossum (Ipomalictus) sp.nov nr hancocki*	0	1	5
89	*Lasioglossum (Ipomalictus) sp2*	2	2	1
90	*Lasioglossum (Ipomalictus) sp4*	1	0	0
91	*Lasioglossum (Ipomalictus) sp5*	0	1	0
92	*Lasioglossum (Ipomalictus) sp6*	0	1	0
93	*Lasioglossum (Ipomalictus) sp9*	1	1	1
94	*Lasioglossum (Ipomalictus) spA nr hancocki*	0	0	1
95	*Lasioglossum (Ipomalictus) spA nr rubritarse*	1	2	31
96	*Lasioglossum (Ipomalictus) spB nr hancocki*	0	7	18
97	*Lasioglossum (Ipomalictus) sp13*	6	0	2
98	*Lasioglossum (Oxyhalictus) acuiferum*	11	5	39
99	*Lasioglossum (Sellalictus) deceptum*	0	4	1
100	*Lasioglossum (Sellalictus) diloloense*	0	2	0
101	*Lasioglossum (Sellalictus) mirifrons*	0	1	2
102	*Lasioglossum (Sellalictus) niveostictum*	0	0	1
103	*Leuconomia atripes*	4	9	7
104	*Leuconomia rufitarsis*	0	2	5
105	*Liotrigona bottegoi*	1	0	0
106	*Lipotriches cribrosa*	2	0	0
107	*Lipotriches hylaeoides*	0	1	1
108	*Lipotriches pallidicincta*	0	0	4
109	*Lipotriches panganina*	0	1	0
110	*Lipotriches patellifera*	0	1	3
111	*Lipotriches sp*	17	3	10
112	*Lithurgus pullatus*	21	3	20
113	*Macrogalea candida*	85	36	52
114	*Macronomia armatula*	2	0	0
115	*Macronomia femorata*	3	2	1
116	*Macronomia lamellicornis*	0	2	8
117	*Macronomia swalei*	1	0	0
118	*Macronomia trochanterica*	1	0	0
119	*Macronomia vulpina*	0	6	1
120	*Maynenomia sp*	1	0	0
121	*Maynenomia sp1*	0	4	1
122	*Megachile angulata*	0	2	1
123	*Megachile aurifera*	0	2	1
124	*Megachile basalis*	2	3	3
125	*Megachile bucephala*	1	1	1
126	*Megachile cincta*	0	1	0
127	*Megachile curtula*	0	0	1
128	*Megachile demeter*	0	6	4
129	*Megachile discolor*	1	0	1

130	*Megachile eurymera*	1	0	1
131	*Megachile familiaris*	4	1	5
132	*Megachile fervida*	0	0	3
133	*Megachile frontalis*	11	14	36
134	*Megachile malangensis*	1	5	8
135	*Megachile mossambica*	0	0	4
136	*Megachile nasalis*	4	0	3
137	*Megachile rufipennis*	0	0	2
138	*Megachile rufoscopacea*	0	10	4
139	*Megachile sinuata*	0	0	1
140	*Megachile sp1*	1	0	0
141	*Megachile sp16*	0	0	1
142	*Megachile sp2*	1	1	0
143	*Megachile venusta*	0	2	1
144	*Megachile wahlbergi*	3	2	2
145	*Meliponula ferruginea*	0	0	4
146	*Meliponula togoensis*	8	3	3
147	*Meliturgula fuliginosa*	4	0	0
148	*Meliturgula scriptifrons*	5	0	0
149	*Nomia scitula*	0	0	2
150	*Noteriades sp*	0	0	1
151	*Nubenomia reichardia*	5	14	3
152	*Ochreriades sp1*	0	0	1
153	*Othinosmia sp*	3	1	5
154	*Othinosmia sp1*	0	1	0
155	*Pachyanthidium benguelense*	0	2	1
156	*Pachyanthidium cordatum*	1	0	0
157	*Pachymelus sp*	2	1	2
158	*Pachymelus sp.n*	4	0	1
159	*Pachynomia amoenula*	0	1	3
160	*Pachynomia flavicorpa*	2	2	0
161	*Patellapis itigiensis*	1	0	1
162	*Patellapis rutshuruensis*	0	0	1
163	*Patellapis virungae*	0	0	2
164	*Plebeina lendliana*	0	1	0
165	*Pseudapis interstitinervis*	1	0	3
166	*Pseudapis neumayeri*	0	3	0
167	*Pseudapis pandeana*	5	12	3
168	*Pseudapis usambarae*	0	1	0
169	*Schwarzia emmae*	0	0	1
170	*Seladonia africana*	0	1	1
171	*Seladonia foana*	1	1	1
172	*Seladonia hotoni*	2	3	2
173	*Seladonia jucunda*	5	16	37
174	*Seladonia lucidipennis*	0	1	0

175	*Seladonia sp1*	0	1	0
176	*Seladonia togoensis*	0	1	0
177	*Steganomos junodi*	1	15	25
178	*Stelis sp*	0	0	1
179	*Stenoheriades sp*	3	0	0
180	*Systropha arnoldi*	4	2	5
181	*Systropha krigei*	4	2	97
182	*Systropha sp1*	1	0	0
183	*Systropha sp2*	2	4	5
184	*Tetralonia labrosa*	1	3	8
185	*Tetralonia macrognatha*	2	0	3
186	*Tetralonia minuticornis*	0	1	1
187	*Tetralonia nigropilosa*	3	8	12
188	*Tetralonia obscuriceps*	10	5	5
189	*Tetralonia sp*	1	0	3
190	*Tetralonia sp1*	1	2	4
191	*Tetralonieilla sp1*	0	0	1
192	*Tetraloniella abessinica*	2	0	0
193	*Tetraloniella inermis*	0	1	2
194	*Tetraloniella junodi*	0	1	0
195	*Tetraloniella katangensis*	0	0	1
196	*Tetraloniella minuticornis*	0	2	2
197	*Thrinchostoma sjoestedti*	2	0	0
198	*Thyreus delumbatus*	0	0	1
199	*Thyreus hyalinatus*	0	1	0
200	*Thyreus meripes*	1	0	0
201	*Thyreus tschoffeni*	0	0	3
202	*Thyreus vachali*	0	1	0
203	*Trinomia cirrita*	5	3	3
204	*Trinomia orientalis*	1	15	38
205	*Trinomia triodonta*	0	3	3
206	*Xylocopa caffra*	0	7	15
207	*Xylocopa erythrina*	0	0	1
208	*Xylocopa flavicollis*	0	3	0
209	*Xylocopa flavorufa*	0	1	20
210	*Xylocopa hottentota*	1	1	5
211	*Xylocopa inconstans*	1	6	7
212	*Xylocopa nigrita*	0	5	1
213	*Xylocopa scioensis*	0	2	6
214	*Xylocopa senior*	0	0	1
215	*Xylocopa somalica*	1	5	4
216	*Xylocopa subjuncta*	1	0	0
217	*Zonalictus kabetensis*	0	0	2
218	*Zonalictus kivuicola*	10	4	0
219	*Zonalictus nomioides*	1	2	0

Abundance	**691**	**1098**	**1639**
Richness	**105**	**140**	**146**

Table A2 | List of plant species and the number of interactions with bees per habitat.

S/No	Plant species	Savannah	Moderate intensive agriculture	Highly intensive agriculture
1	*Abutilon theophrasti*	0	0	4
2	*Acacia (Vachellia) nelotica*	0	1	0
3	*Achyranthes aspera*	6	1	3
4	*Achyranthes sp*	0	0	5
5	*Ageratum conyzoides*	1	11	9
6	*Amaranthus hybridus*	0	0	1
7	*Arctium minus*	0	0	2
8	*Aristida congesta*	0	1	0
9	*Aspilia mossambicensis*	0	23	1
10	*Bidens pilosa*	0	24	34
11	*Bidens schimperi*	0	5	1
12	*Boerhavia sp*	0	0	1
13	*Brassica carinata*	0	0	1
14	*Caesalpinia decapetala*	0	0	4
15	*Cajanus cajan*	0	0	2
16	*Calotropis procera*	0	0	2
17	*Senna obtusifolia*	0	2	1
18	*Cirsium vulgare*	1	0	0
19	*Clitoria sp*	0	1	0
20	*Clitoria ternatea*	0	2	5
21	*Commelina benghalensis*	0	1	4
22	*Commicarpus plumbagineus*	3	1	0
23	*Conyza bonariensis*	0	1	4
24	*Conyza pyrrhopappa*	8	0	0
25	*Crotalaria agatiflora*	0	3	3
26	*Crotalaria brachycarpa*	0	0	0
27	*Crotalaria incana*	15	3	6
28	*Crotalaria pallida*	0	0	2
29	*Crotalaria retusa*	0	5	0
30	*Crotalaria spectabilis*	0	0	11
31	*Cucumis dipsaceus*	0	2	2
32	*Cucurbita maxima*	0	0	2
33	*Cycnium tubulosum*	0	1	0
34	*Cynodon dactylon*	2	0	0
35	*Cyperus sp1*	2	1	0
36	*Cyphostemma cirrhosum*	0	0	3
37	*Daphne gnidium*	0	7	0

38	*Desmodium intortum*	4	0	0
39	*Digera muricata*	0	2	1
40	*Emilia abyssinica*	0	0	6
41	*Euphorbia geniculata*	0	1	21
42	*Felicia sp1*	2	0	0
43	*Galinsoga parviflora*	0	1	0
44	*Glycine max*	0	3	2
45	*Glycine wightii*	3	0	19
46	*Gutenbergia cordifolia*	13	7	21
47	*Gutenbergia sp1*	0	8	0
48	*Gynandropsis gynandra*	2	0	0
49	*Hedyotis diffusa*	40	7	7
50	*Helianthus annuus*	0	1	6
51	*Helichrysum sp*	0	6	0
52	*Heliotropium steudneri*	0	1	1
53	*Heteropogon contortus*	0	1	0
54	*Hibiscus calyphyllus*	1	0	0
55	*Hoslundia opposita*	1	14	0
56	*Hypoestes sp1*	12	2	1
57	*Hypoestes sp2*	3	0	0
58	*Hypoestis sp3*	1	0	0
59	*Hyptis suaveolens*	0	39	26
60	*Indigofera arrecta*	5	7	8
61	*Indigofera garckeana*	0	2	0
62	*Indigofera spinosa*	0	0	1
63	*Indigofera subcorymbosa*	2	0	0
64	*Ipomoea kituiensis*	0	0	4
65	*Ipomoea pandurata*	0	0	2
66	*Jatropha curcas*	0	2	0
67	*Justicia sp*	0	1	13
68	*Lablab purpureus*	0	1	2
69	*Lamium flexuosum*	0	10	0
70	*Launaea cornuta*	0	2	3
71	*Leonotis africana*	1	0	0
72	*Leonotis sp*	0	0	1
73	*Leucas martinicensis*	19	4	1
74	*Lippia javanica*	6	7	6
75	*Ludwigia abyssinica*	1	0	0
76	*Macroptilium atropurpureum*	0	3	0
77	*Marrubium vulgare*	0	0	4
78	*Melissa officinalis*	3	0	0
79	*Melilotus officinalis*	0	2	0
80	*Mimosa pigra*	0	0	7
81	*Nicandra physalodes*	0	2	0
82	*Ocimum basilicum*	22	22	17

83	*Ocimum filamentosum*	0	3	0
84	*Ocimum gratissimum*	19	8	17
85	*Ononis spinosa*	3	0	0
86	*Oxalis latifolia*	0	1	0
87	*Oxygonum sinuatum*	0	5	9
88	*Panicum miliaceum*	0	0	1
89	*Cenchrus purpureum*	0	0	1
90	*Phaseolus vulgaris*	0	8	0
91	*Pisum sativum*	0	0	7
92	*Plectranthus barbatus*	0	0	13
93	*Psiadia punctata*	10	0	0
94	*Reseda alba*	0	0	1
95	*Rhynchosia minima*	0	0	3
96	*Richardia brasiliensis*	0	0	10
97	*Ricinus communis*	0	0	2
98	*Salvia verbenacea*	0	1	0
99	*Senecio doronicum*	1	0	0
100	*Senna occidentalis*	0	1	0
101	*Sesbania sesban*	0	0	1
102	*Sida fallax*	0	1	7
103	*Sida rhombifolia*	0	6	6
104	*90id asp.*	0	0	1
105	*Solanum elaeagnifolium*	15	4	0
106	*Solanum incanum*	8	10	8
107	*Solanum lycopersicum*	0	0	2
108	*Sphaeranthus suaveolens*	0	8	4
109	*Sphaeranthus ukambensis*	0	3	2
110	*Tephrosia vogelii*	0	6	1
111	*Thevetia peruviana*	0	0	1
112	*Tribulus terrestris*	3	0	2
113	*Trichodesma zeylanicum*	0	8	20
114	*Tridax procumbens*	0	4	41
115	*Tridax sp*	0	0	3
116	*Tripteris vaillantii*	1	0	0
117	*Unknown sp*	3	30	1
118	*Vachellia drepanolobium*	0	0	10
119	*Verbascum thapsus*	0	1	0
120	*Vernonia baldwinii*	11	2	0
121	*Vicia sativa*	0	2	0
122	*Vigna sinensis*	0	1	0
123	*Vigna vexillata*	0	2	0
124	*Waltheria indica*	0	0	1
125	*Zinnia elegans*	0	1	0
126	*Ziziphus mucronata*	2	0	0

Total number of interactions	**255**	**370**	**468**
Interacted floral richness	**38**	**70**	**76**

Chapter IV

Impact of land use intensification and local features on plants and pollinators in Sub-Saharan smallholder farms

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Summary

Sub-Saharan African crop production largely relies on smallholder farms, located both in urban and agricultural landscapes. In this context, the investigation of plant and pollinator diversity and their interactions is of primary importance since both these factors are threatened by land use intensification and the consequent loss of natural habitats. In this study, we evaluated for the first time how plant and pollinator insect assemblages and interactions in Sub-Saharan farming conditions are shaped by land use intensification. To do that, we complemented biodiversity field surveys in Northern Tanzania with a modern DNA metabarcoding approach to characterize the foraged plants and thus built networks describing plant-pollinator interactions at the individual insect level. Moreover, we coupled this information with quantitative traits of landscape composition and floral availability surrounding each farm. We found that pollinator richness decreased with increasing impervious and agricultural cover in the landscape, whereas the flower density at each farm correlated with pollinator richness. The intensification of agricultural land use and urbanization correlated with a higher foraging niche overlap among pollinators due to convergence of individuals' flower visiting strategies. Furthermore, within farms, the higher availability of floral resources drove lower niche overlap among individuals, while a greater flower visitors abundance shaped higher generalization at the networks level ($H2^{I}$), possibly due to increased competition. These mechanistic understandings leading to individuals' foraging niche overlap and generalism at the network level, could imply stability of interactions and of the pollination ecosystem service. Our integrative survey proved that plant-pollinator systems are largely affected by land use intensification and by local factors in smallholder farms of Sub-Saharan Africa. Thus, policies promoting nature-based solutions, among which the introduction of more pollinator-friendly practices by smallholder farmers, could be effective in mitigating the intensification of both urban and rural landscapes in this region, as well as in similar Sub-Saharan contexts.

Keywords: Bees; DNA metabarcoding; Ecosystem services; Hoverflies; Plant-pollinator interaction; Sustainability

Introduction

Anthropogenic land use conversion and intensification are among the major drivers of landscape changes and habitat loss in natural and semi-natural contexts (J. A. Foley et al., 2005; Graitson et al., 2020). At the global scale, the growing population trend is leading to land use intensification, with negative effects on several ecosystem services such as pollination (IPBES, 2016; United Nations, 2019). Human wellbeing is intimately linked to pollination, not only for the agri-food production and food security issues, but also for the quality of fruit resulting from this service (Classen et al., 2014; Elisante et al., 2020; Smith et al., 2015; Stein et al., 2017) In this context, the scientific community concurs that pollinators largely contribute to the sustainable development of the planet, being relevant in the achievement of United Nations Sustainable Development Goals (Patel et al., 2021). The efficiency of pollination is positively linked to the abundance and diversity of some insects, mainly bees and hoverflies (Dainese et al., 2019), which is in turn influenced by local and landscape variables. For example, bee richness was found to decline in agricultural sites that are surrounded by progressively higher built-up surfaces (Bennett & Lovell, 2019). A similar pattern was also observed considering agricultural intensification that causes a dramatic decrease of pollinator richness, following the loss of semi-natural patches surrounding the farms (Deguines et al., 2014).

To date, most of the pollinator-based research comes from Europe and North America, while significant data gaps occur for Asian and African regions that are currently experiencing an intense agricultural and industrial development (Timberlake and Morgan, 2018). Specifically, in Sub-Saharan Africa, the land use intensification through urban and agricultural expansion is increasing as fast as the population growth (Eckert et al., 2017; Sulemana et al., 2019). In Sub-Saharan countries, agriculture represents the main source of family sustainment (Stein et al., 2017) with about 80% of the population relying on subsistence farming in Tanzania (Sawe, Nielsen, & Eldegard, 2020). Moreover, with 80% of farms being smaller than 2 ha, these agriculture systems are mainly repre- sented by smallholder farms (Garrity et al., 2010) that are widely diffused in urban and peri-urban landscapes (Armar-Klemesu, 2000). The spread of high commercial value pollination-dependent crops (e.g., coffee, watermelon, and beans; (Gemmill-Herren et al., 2014) also makes these agricultural systems more susceptible to fluctuations in terms of pollination service quality (Dainese et al., 2019).

Studies conducted in Ghana highlighted that urban farmlands host lower abundances of pollinating insects compared to urban greenspaces (Guenat et al., 2019). Other studies addressed how pollination efficiency and different management conditions affect yield and quality of crops (Classen et al., 2014; Sawe et al., 2020b; Stein et al., 2017). Apart from these studies, the effect of land use intensification on pollinators was poorly investigated. However, a better and exhaustive understanding of plant-pollinator insect dynamics in Sub-Saharan smallholder farming systems is necessary to promote effective farm-scale solutions focusing on the management of biological features. For example, specific policy actions directed to the enhancement of available floral resources, such as the establishment of flower strips, are of primary concern. As already demonstrated in other studies, these strategies can increase the pollinators abundance (Jönsson et al., 2015), enhance crop-flower visitation (Feltham et al., 2015) and contribute to mitigate the impact of land use intensification.

One efficient way to describe ecosystem functioning is the implementation of network theory in the context of interactions between plants and pollinators (Biella et al., 2017). Recently, the identification of pollen taxonomy has been based on DNA metabarcoding approaches to characterize the composition of the pollen foraged by pollinator insects and to evaluate variation in plant-pollinator interactions (eg. Biella et al., 2019; Macgregor et al., 2019). Although this approach could add valuable ecological details about the effects of land use change on biodiversity features (Adedoja & Kehinde, 2018), to the best of our knowledge, no similar studies were conducted employing this highly informative molecular-based method in Sub-Saharan Africa. Several case studies proved the suitability of this approach in other countries (Danner et al., 2017; Nürnberger et al., 2019) also because it requires relatively simple molecular-biology skills and allows to reduce the time spent for field observation while improving the number of observed interactions (Bell et al., 2017).

In this study, we combined a DNA metabarcoding-based approach with field monitoring and land use analysis to investigate how different features of surrounding landscape affect the plant-pollinator communities in smallholder farms of Northern Tanzania by quantifying multiple issues. Firstly, we characterized biodiversity parameters, and in particular, we evaluated how the species richness of bees and hoverflies, here selected for their importance as main representers of the pollinators guild (Hennig & Ghazoul, 2012; Ssymank et al., 2008), was affected by land use intensification. Secondly, we characterized plant-pollinator interaction networks in response to landscape features. Overall, we aimed at verifying if local scale biodiversity features, that can be actively managed and promoted by landowners, could mitigate the negative effects of land use intensification. This is expected to decrease the habitat quality within the farm surroundings, due to the loss of nesting and foraging niches, and to the higher habitat fragmentation and isolation (Kovács-Hostyánszki et al., 2017). For these reasons we hypothesized to find negative effects on plant and pollinators richness and alteration of the foraging preferences and structural properties of the interaction networks. Since these factors could imply relevant changes in the stability of the overall pollination service, with consequences at the agricultural production level, this assessment intended to provide a first baseline to drive and support reliable policies for a more sustainable development of the smallholder farming systems of Sub-Saharan Africa.

Methods

Study sites and landscape description

The study was conducted in Northern Tanzania, in the area surrounding Mt. Meru and the southern-western slopes of Mt. Kilimanjaro. Specifically, the areas of the rural and urban district of the Arusha region and the rural areas of the Moshi and Hai districts of Kilimanjaro region were investigated. Within this study area, 27 smallholder farms (c 1 ha of occupied surface) were selected as sampling sites (Fig. 1 and Appendix A, Table S1). These were representative of different levels of land use intensification. In particular, the investigated farms ranged from those located in urban areas, with a prevalence of impervious surfaces in the surrounding, to those localized in highly exploited homogeneous agricultural landscapes that were mainly surrounded by large-scale cultivated lands. Finally, farms mainly surrounded by semi-natural landscapes, such as grassland and forest, were also selected as representative of the minimum disturbance conditions induced by land use intensification in Tanzania. The distance among study sites was at least of 1 km (a distance considered higher than the usual home range of most pollinator insects (Garibaldi et al., 2014)). To demarcate the boundaries of each farm we used a Garmin eTrex Venture HC GPS device (declared accuracy, 3 m). For each farm, we manually quantified the area of different land uses by poligonizing satellite images in a 500 m radius buffer, corresponding to the expected mean foraging range of most bees and hoverflies (Fisogni et al., 2020). This assessment was conducted by using QGIS 3.4 with basemap Bing Aerial (OpenLayers QGIS plugin updated in 2018). The area of polygons that shared the same land use type was summed to calculate the total amount of impervious surfaces (e.g., houses, infrastructures and cemented roads), cultivated land, and semi-natural land (i.e., natural, unmanaged patches, meadows and lawns). These land use categories were chosen to estimate urbanization (proportion of impervious land), as well as the degree of agricultural land use intensification (ratio between cultivated and semi-natural land). Furthermore, a Shannon-Wiener index of land use was calculated to understand the effects of land use heterogeneity on plant and pollinator communities. A visual check was performed in the field, prior to sampling activities, to verify the coherence between the results of land use categorization and the landscape features of the farms' surroundings (e.g., presence of infrastructures, agricultural fields or semi-natural areas). All the selected farms were characterized by field margins hosting wild or barely managed vegetation rich in flowering species. The natural remnant that surrounded the farms ranged from small patches of ornamental trees in the more urbanized areas, to large patches of forest or grassland in the farming sites showing low land use intensification. Fruit trees, such as avocado, and hedgerows were abundant in most of the farms, either for production or demarcation purposes. The main cultivated crops at the time of sampling were maize, beans, sorghum, but also strawberry and banana or leafy vegetables such as cabbage.

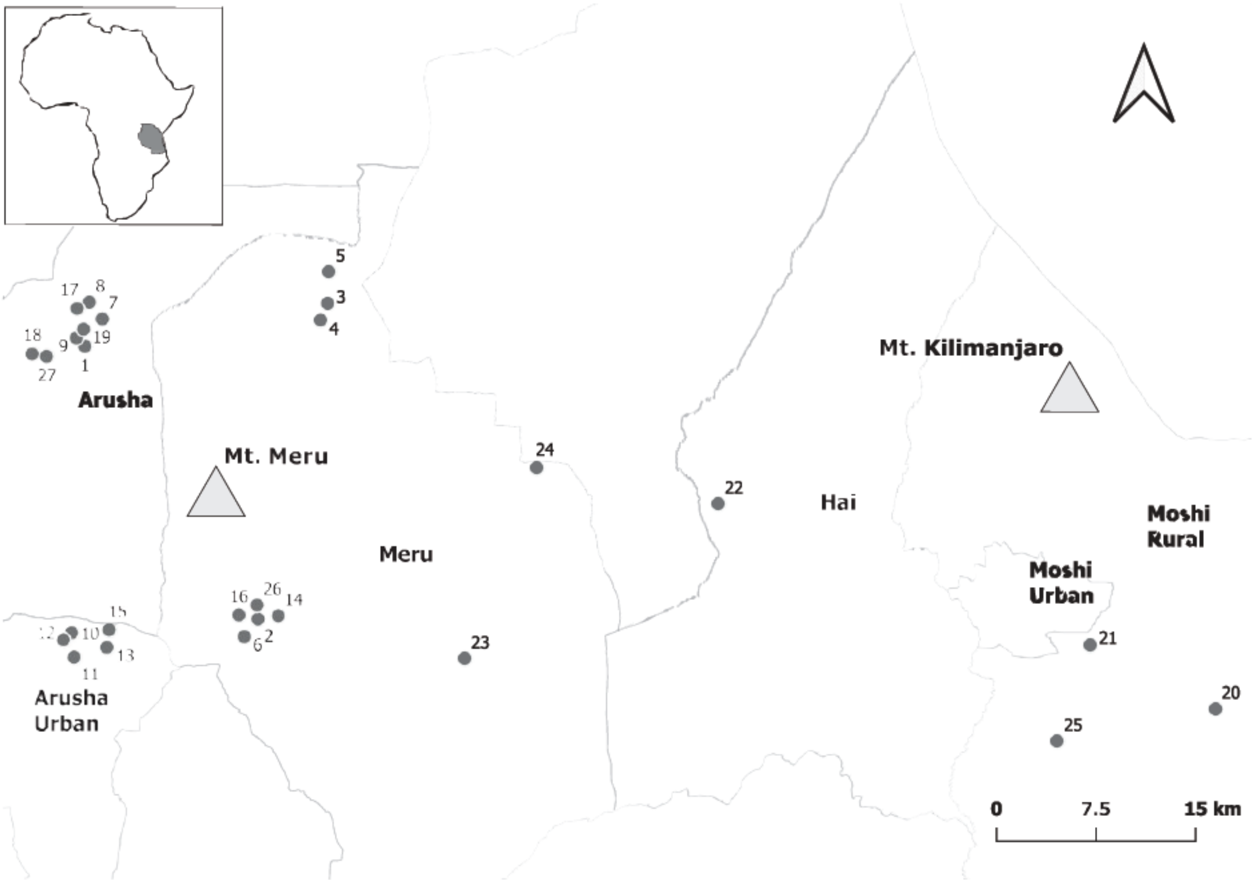


Fig. 1. Map of the study sites, further details about sampling methodology are reported in Appendix A, Table S1.

Characterization of pollinator and plant communities

Sampling activities were performed in June 2018 at the end of the wet season. This period is still favorable for agricultural production in Northern Tanzania and actually, many crops were still flowering during sampling, that was performed during sunny or moderately cloudy days. In the selected farms (see Appendix A, Table S1) insect and plant com- munities were investigated by using pan traps and net sampling (to assess the network interactions through DNA metabarcoding of pollen, see next sections) and vegetation quadrats, respectively. Six colored pan traps (2 Blue, 2 Yellow and 2 White, 25 cm diameter and 10 cm depth), filled with 200 mL of water and 1 mL of soap, were placed with alternate colours at the margin of the cultivated area. The traps were placed directly on the ground, since the vegetation was low and most of the surrounding flowers were nearly at the same level. Furthermore, we carefully checked that all the traps were clearly visible from each side of the investigated area. The inter distance between each trap was approximately 10 m and the exposure time was 24 h. After collection, we selected bees and hoverflies because of their well-known importance as flower visitors. These insects were assigned to morphospecies and used to estimate the abundance of flower visitors at each farm (i.e., the ratio between the number of flower visitor insects caught per site, and the total number of flower visitor insects at all sites).

Plant community species richness, plant cover (i.e., cm^2 of plant occupied surface), and floral abundance (i.e., the number of blooming flowers or inflorescences) were estimated at the field margins by using vegetation quadrats. Briefly, after a preliminary visual assessment of the field margins extension and heterogeneity of the flowering plant com- munity, three to six vegetation quadrats (0.5*0.5 m) were performed. Furthermore, the ratio between flower abundance and plant cover was calculated as a measure of flower density.

Plant DNA reference database

A reference database of nuclear ITS2 sequences, comprehensive of the main flowering species occurring at the study sites, was produced as in Biella et al. (2019) to overcome DNA metabarcoding identification drawbacks posed by the unavailability of a local dataset of plant DNA barcodes. Briefly, some leaves of plant species observed in vegetational squares or occurring in the study sites were collected and subjected to DNA extraction and ITS2 amplification and sequencing. These specimens were stored in the herbarium of the Department of Biotechnology and Biosciences, University of Milano-Bicocca, Milan, Italy (herbarium code MIB: ZPL). A list of the plant taxa found into the vegetational quadrats, as well as information about reference sequences produced in this study are available in Appendix A, Table S2.

Pollen DNA metabarcoding

In order to obtain information about plant-pollinator interactions, the taxonomic composition of the pollen carried by insects was assessed through ITS2 DNA metabarcoding. To do this, only insects collected through an entomological net and observed foraging on flowers were analysed. At each farm, the insect capture sessions were performed for 1 h of sampling in a ~ 50 50 m subplot (Appendix A, Table S1). Sampling was performed between 7:30 am and 5:30 pm and to prevent cross contamination a clean net was used at each farm. Each individual was stored in single plastic tubes filled with 70% ethanol.

To remove pollen grains from the collected pollinators, tubes containing ethanol 70% and the insects were vigorously vortexed for 10 s. Afterwards, insects were removed from the tubes and the preserving ethanol was centrifuged at 14,000 rpm for 10 min to allow the pollen grains deposition. Ethanol was completely removed through evaporation under a chemical hood.

Pollen DNA extraction and sequencing details are reported in Appendix A, Supplementary Text S1. Briefly, the samples were grinded, and DNA was extracted according to standard protocols. The internal transcribed spacer 2 (ITS2) region was amplified using primers S2F and S3R (Chen et al., 2010) with the addition of the Illumina overhang sequence adapters. Library preparation and sequencing were performed through the Illumina MiSeq instrument using MiSeq 600 V3 (2 300-bp paired-end sequencing). The obtained reads were paired, pre-processed and clustered in Exact Sequence Variants ESVs (Callahan et al., 2017) following a standard bioinformatic pipeline prior to taxonomic assignment (See Appendix A, Supplementary Text S1 for taxonomic assignment and further details). After this treatment, the insects were identified at the best taxonomic level and this information was also coupled with that coming from the pantrapped insects to evaluate the overall pollinator species richness at the sampling sites (further details about the identification of net collected insects involved in plant pollinator network analysis are available in Appendix A, Table S4).

Interaction networks

Matrices of interactions between pollinator individuals (single pollinator insects) and plant species were built to calculate network indices at the site (farm) level. This approach allows to describe changes in the foraging choices of pollinators (Biella et al., 2019; Tur et al., 2015) and is informative of the possible effects of land use change and other anthropogenic stressors on biodiversity (Adedoja & Kehinde, 2018). Indices of network-level complementary specialization, foraging overlap in the pollen resources carried by insects (i.e., pollinator foraging niche overlap), and network size were calculated through the R package *bipartite* (Dormann et al., 2008). Network complementary specialization is a network-level index that ranges from 0 (no specialisation) to 1 (complete specialisation). Low complementary specialization is usually related to low functional redundancy in flower visitation (Blüthgen & Klein, 2011; Kaiser-Bunbury & Blüthgen, 2015). To allow a more intuitive comparison of $H2^r$ with the pollinator foraging niche overlap, we calculated $1\text{-}H2^r$ as a measure of complementary generalization (so that zero corresponds to complete specialization and one to no specialization). This index has been shown to be robust against sampling intensity and network size, making it a useful tool for the comparison of networks across multiple habitats (Classen et al., 2020). To calculate this index, the number of DNA reads was used as a measure of the abundance of the pollen carried by an individual and then as the weight of plant pollinator interactions as in Biella et al., (2019). The pollinator foraging niche overlap was inferred as the mean similarity in interaction patterns among in- dividuals. This index was calculated as the

Jaccard similarity index among pollinators in terms of plants found on their body. Finally, the pollinator group level mean was then derived. Values tending 0 s indi- cate low or no common use of plants, while 1 s indicates perfect overlap and thus foraging choices converging on few resources. Network size was calculated as the product between the number of animal species and the number of plant species in the matrix of interactions and used as a predictor to account for the role of network size variation on the network indices as in Olesen & Jordano (2002)and as in Biella et al., (2020).

Statistical analysis

To evaluate the effects of local biotic features (i.e., flower density and abundance, plant cover and flower visitors abundance) and of land use intensification covariates, such as urbanization (i.e., proportion of impervious land), agricultural land use intensification (i.e. ratio of cultivated-to-natural land) and land use heterogeneity on the investigated response variables (i.e., pollinator and plant species richness, pollen sample species richness and proportion of crop pollen and network indices), we used a Generalized Linear Models (GLM) regression approach. To exclude correlation among the covariates included in the models, the vif function in the car R package (i.e., variance inflation factor with an exclusion threshold of 3) was used. Furthermore, a visual validation approach was employed to evaluate the use of logarithm or square root transformations on covariates to improve the goodness of fit between covariates and response variables (details about the used transformation are reported in Table 1). The few missing data were either removed or replaced with simple random imputation (Kadengye et al., 2012). The regression models were largely built on ecological expectation bases. In detail, we expected that the considered response variables would have been influenced by the covariates of land use intensification that were included in all the evaluated models. Different local biotic features were included as covariates in the models. Specifically, flower abundance and flower visitor abundance were included as covariates in the models related to i) pollen species richness, ii) pro- portion of crop pollen collected, and iii) network indices. This is because it is reasonable to expect that the availability of floral resources and the abundance of insects that compete for them are important drivers of competition between individuals. This competition should lead differences in insects' foraging preferences (pollen composition features) and strategies (network indices) (Araújo et al., 2011; Fontaine et al., 2008). The flower density was used as a covariate to predict variation in pollinator species richness. As a matter of fact, high resource density conditions are known to be highly attractive for pollinators, thus they were also expected to improve species richness (Hegland & Boeke, 2006; Vrdoljak et al., 2016). Concerning plant richness, the effect of plant cover was investigated since it could be expected that species richness increases where the cover is higher (Sanaei et al., 2018). Details on the distribution applied in regression models are reported in Table 1. The log likelihood ratio test was used to test predictor significance (P c 0.05), while the Moran test was applied to confirm the absence of spatial auto-correlation within data. This test revealed only non-significant results (P > 0.05), thus indicating that no serious spatial autocorrelation occurred in the dataset. All the analyses were performed using R (version 3.6.1; R CoreTeam 2019).

Results

Characterization of pollinator and plant communities

Overall, 141 flower visitors belonging to 27 morphospecies, with 91.5% of the individuals classified as bees, were collected through pan traps. Moreover, 264 flower visitors belonging to 56 taxa with 87.5% of the individuals classified as bees, were collected through net sampling (Appendix A, Table S4). Seventy-three plant taxa were identified from the vegetation survey (Appendix A, Table S2. Asteraceae (27.39%) and Fabaceae (9.5%) were the most represented families. About 22% of the identified plants belonged to non-native taxa, with exotic species such as *Ageratum conyzoides, Argemone mexicana, Lantana camara, Datura stra- monium* and *Parthenium hysterophorus* largely represented in almost all the visited farms.

Pollinator species richness was negatively related to the amount of impervious land (Fig. 2a) and to the ratio between cultivated and natural land (Fig. 2b) but positively related to flower density (Fig. 2c). Plant richness was positively related to land use heterogeneity (Appendix A, Fig. S1-a) and plant cover (Appendix A, Fig. S1-b). Regression model details are reported in Table1 - section Pollinator and plant communities.

Pollen DNA metabarcoding and interaction networks

The HTS sequencing yielded 18,506,952 reads (mean 41,772.87 reads per sample), after raw sequence processing 1778 ESVs were obtained, and assigned to 149 plant taxa, with 70.5% of the assignment at species level. The mean number of pollen taxa per insect was 4.2 T 2.9 (range 1–18 plant taxa).

As reported in Table 1 (section Pollen composition analysis), the species richness in pollen samples was not significantly related to landscape or local covariates. Conversely, the collection of pollen from crop species was higher in landscapes with a high proportion of cultivated land (Appendix A, Fig. S1-c).

Concerning the network metrics (Table 1), the pollinator foraging niche overlap significantly increased in the farms with higher pro- portions of impervious surface (Fig. 3a) and agricultural land use intensification expressed as cultivated-to-natural land ratio (Fig. 3b), while it was negatively affected by flower abundance (Fig. 3c). The Complementary generalization (1-H2^{r}) significantly increased with the abundance of flower visitors (Fig. 3d) and decreased with flower abundance. Finally, the network size negatively affected pollinator foraging niche overlap and positively impacted network generalization. Additional details about the calculated network indices for each investigated farm are available in Appendix A, Table S3.

Table 1: Results of the final regression models analysis of pollinator species richness, plant species richness, pollen species richness, proportion of crop pollen, pollinator foraging niche overlap and generalization (1-H2') as function of both landscape and local covariates. **β_i**: regression coefficient; **x^2**: log-likelihood ratio test; ***p***: p-values (significant value in bold).

Section	Response variables	Distribution	Covariates	β_i	χ^2_1	*p*
Pollinator - plant communities	Pollinator species richness	Quasi-Poisson	log(prop impervious land+1)	-6.96	9.43	**0.002**
			log(flower density*100)	0.34	5.40	**0.02**
			sqrt(cultivated/natural land)	-0.71	4.55	**0.03**
			log(land use heterogeneity+1)	1.97	0.39	0.19
	Plant species richness	Quasi-Poisson	log(prop impervious land+1)	-0.01	0.01	0.92
			sqrt(cultivated/natural land)	-0.07	0.24	0.61
			log(land use heterogeneity+1)	1.14	3.47	0.06
			log(plant cover+1)	0.30	5.28	**0.02**
Pollen composition analysis	Pollen species richness	Poisson	log(prop impervious land+1)	0.03	0.19	0.66
			log(cultivated/natural land+1)	-0.02	0.03	0.86
			log(flower abundance +1)	-0.05	0.09	0.76
			log(flower visitor abundance+1)	-0.48	0.13	0.71
	Proportion of crop pollen	Binomial	log(prop impervious land+1)	0.12	0.45	0.50
			log(cultivated/natural land+1)	0.59	4.01	**0.05**
			log(flower abundance +1)	0.02	0.00	0.97
			log(flower visitor abundance+1)	-5.66	0.82	0.36
Interaction network metrics	Pollinator foraging niche overlap	Quasi- Binomial	log(prop impervious land+1)	2.52	14.6	**< 0.001**
			log(cultivated/natural land+1)	1.48	6.64	**0.001**
			sqrt(flower abundance)	-2.27	4.27	**< 0.001**
			log(flower visitor abundance+1)	2.12	0.02	0.86
			network size	-5.85	45.35	**< 0.001**
	1-H2'	Quasi- Binomial	log(prop impervious land+1)	2.31	0.80	0.37
			log(cultivated/natural land+1)	-0.06	0.08	0.76
			sqrt(flower abundance)	0.08	5.66	**0.01**
			log(flower visitor abundance+1)	8.29	3.6	**0.05**
			network size	0.00061	3.9	**0.04**

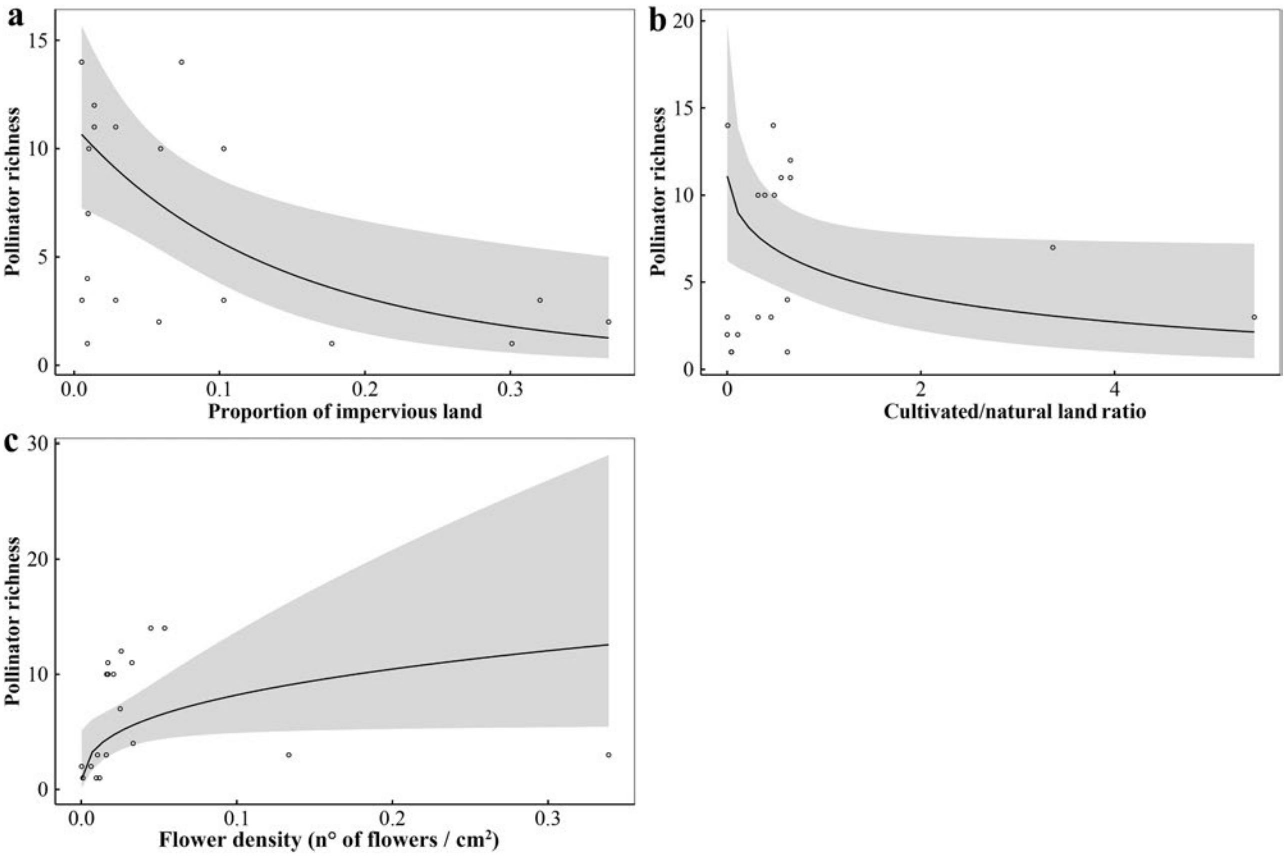


Fig. 2. Regression analysis of pollinator richness as a function of the proportion of impervious land (a), ratio between cultivated and natural land (b) and flower density (n°of flowers/cm^2) (c).

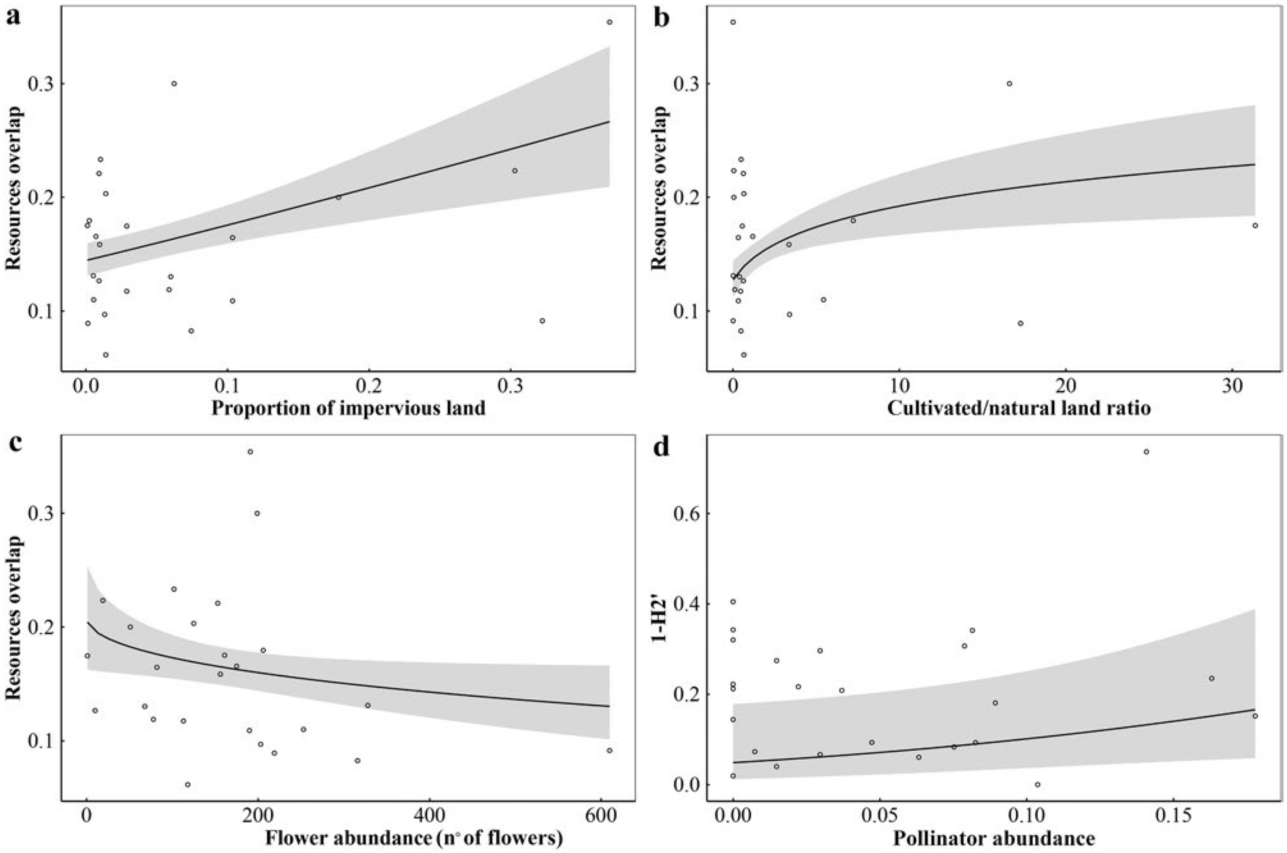


Fig. 3. Regression analysis of pollinator foraging niche overlap (resource overlap) as a function of the proportion of impervious land (a), cultivated/natural land ratio (b) and flower abundance (n° of flowers) (c). The Plot (d) represents the regression output between complementary generalization 1-H2^{1} and flower visitor abundance.

Discussion

In this study, we shed light on the ways by which plant and pollinator insect assemblages, and the interactions between them, are influenced by land use intensification and by local features of resource availability and abundance of flower visitor insects at smallholder farms in Northern Tanzania. This region represents a clear example of the intense spread of anthropogenic landscapes that urban and rural areas of several Sub- Saharan African regions are facing. Apart from conventional field investigations, we exploited the high-resolution power of DNA meta- barcoding to successfully characterize the foraging preferences of pollinators. In this context, the building of a dedicated DNA reference database, representative of the local plant biodiversity, facilitated the success rate and the reliability of taxonomic identification of pollen samples. This has also been confirmed by other studies showing that an integrated molecular-field approach is useful for expanding the amount of information from field sampling activities (Biella et al., 2019; Elliott et al., 2021). Based on our results, we also recommended the use of this approach for future studies requiring the analysis of pollen samples, especially in countries where the local biodiversity has already not been fully characterized.

In this survey, the standard field monitoring approaches highlighted that at the investigated farms, the pollinator richness was negatively affected by the amount of impervious surfaces in the surrounding landscape. This result confirms a previous research from West African farming systems (Guenat et al., 2019). Reasons for this trend could be found in the increase of impervious surface, responsible for the contraction of green spaces and for the increase of their isolation. This, in turn, leads to a landscape characterized by discontinuous and intermittent distribution of floral resources, a condition that could result into locally poor pollinator assemblages, due to resources that are difficult to access (Egerer et al., 2020). Similarly, agricultural land use intensification is expected to reduce habitat quality and leads to a simplified landscape with lower habitat diversity and availability (Deguines et al., 2014), and this could explain the reduction in pollinator richness observed in response to the increase of agricultural surfaces.

From the pollen analysis, we found that the proportion of pollen of crops increased with cultivated-to-natural land ratio. This phenomenon could be justified by considering the possible "pollinator magnet" effect of mass flowering crops occurring in rural landscapes, where the cultivated species largely overwhelm the abundance of flower resources offered by the spontaneous ones (Gilpin et al., 2019). Hence, in the context of smallholder farms, flowering crops might play an important role as food resources for pollinator insects. In heavily cultivated areas, the generalist pollinator species might be more abundant and advantaged instead of the specialist ones because of the higher propensity to change their foraging preferences for exploiting the available crop re- sources. Thus, changes in the pollinator community composition could also explain the higher collection of crop pollen in response to increased cultivated-to-natural land ratio.

A neutral relationship with agricultural land use intensification was found for plant richness. This observation disagrees with other studies indicating detrimental effects of the agricultural landscape on the composition and complexity of floral communities (Nicholls & Altieri, 2013). Conversely to what conventionally practiced in intensive agriculture, many smallholder farmers in Tanzania still manually extirpate weeds (personal observation), thus avoiding agrochemical run-off. This manual practice contributes to maintain the floral resources offered by wild plants at the field margins. Interestingly, plant species richness was higher at farms characterized by a higher plant coverage. Our result further contrasts with the expected simplification of the flowering plant community in agricultural landscapes (Hall et al., 2020) that should promote the abundance of the more competitive species, even in conditions of high plant coverage. This supports the possibility that small- holder agroecosystems could host an unexpectedly high flowering plant biodiversity with consequent benefit for pollinators (Fründ et al., 2010; Ouvrard et al., 2018). The relevance of biodiversity friendly local-scale practices on pollinator diversity was also found in other studies centred in Africa (Delaney et al., 2020). Hence, policies and management promoting farm-level plant cover will scale up to sustaining highly diverse pollinator communities, fostering the small-scale ecological intensification of smallholder farms.

Local diversity influences biotic interactions among organisms, and alterations of the environment will also alter network structures by filtering species assemblages and driving which interactions occur (Biella et al., 2020). The adoption of DNA metabarcoding to characterize such interactions, allowed us to evaluate fine changes in the foraging preference of pollinators, but also to highlight changes in the structure of plant-pollinator networks in response to land use and local resource availability. Considering individuals instead of species-level interactions allows us to consider intraspecific behavioural variation and to account for early impacts of changing foraging contexts and alterations of competitive dynamics that might otherwise be overlooked (Araújo et al., 2010; Ings et al., 2009). Positive relationships between the overlap in transported pollen resources (an indication of foraging niche overlap) and the landscape features were observed in this study for the urban and agricultural surfaces. In both cases this trend could be the results of an increased community of generalist pollinators or could reflect low diversity in plant communities of urban areas and intensified agricultural landscapes, which led pollinator individuals to converge on the avail- able floral resources. In particular, more intensified rural sites do not only means mass flowering crops, but also implies lower cover of the natural land use and hence less non-crop floral resources at the landscape-level. This condition is also supported by the higher amount of crop species found in pollen samples also by a previous study (eg., Pornon et al., 2019). The mechanism by which the amount of resources determines foraging niche convergence is evident not only at the land- scape but also at the local scale, where higher floral abundance led to a higher foraging niche complementarity (Blüthgen & Klein, 2011) and hence to a reduction in the overlap of the resources foraged by insects. This result is confirmed by the reduction of complementary generalization observed in response to flower abundance and fits well within the framework of the Optimal Foraging Theory, for which foragers are expected to converge on the available resources when plant abundance is low (Biella et al., 2019; Fontaine et al., 2008). Furthermore, the complementary generalization index was found to be significantly affected by the abundance of flower visitors, with higher generalism at the network level in conditions of high abundance of flower visitors. A possible explanation of this phenomenon is that more competitive conditions may lead to a faster depletion of floral resources. According to the optimal foraging theory (OFT), this condition could drive to a diversification and/or expansion of the pollinators' diet, possibly increasing (Araújo et al., 2011) the generalism of the foraged plants. Although specific investigations are necessary to address this issue, the observed increase of network level generalization, could reflect a higher functional redundancy and stability of interactions (Kaiser-Bunbury & Blüthgen, 2015). These considerations further support the necessity of enhancing pollinator insects abundance in Sub-Saharan farming context (e.g., by means of ecological intensification; Kovács-Hostyánszki et al., 2017)

Conclusion

Our study pointed out that increasing urbanization and agricultural cover reduces plant and pollinator biodiversity and negatively impacts the complexity of their interactions. Conversely, the local scale availability of floral resources has shown positive effects in buffering pollinator decline and mitigating all the detrimental effects induced by land use intensification phenomena in the Sub-Saharan context. Thus, our study clearly highlights the importance of policies and managements targeting small-scale measures aiding local biodiversity. Based on our first evidence, such policies should include actions aimed at improving the presence of green spaces in urban landscape to break the continuity of impervious coverage and maintaining high habitat heterogeneity and seminatural spaces in rural landscapes. Good practices in the management of both private and public greenspaces and agroforestry (e.g., reducing mowing frequency, planting flower strips, and encouraging rotation strategies by introducing pollinator forage crops), should be fostered by administrations to reduce the risks related to the loss of pollinators and thus of the pollination service. Actions to preserve pollinators is therefore pivotal in Sub-Saharan farming systems to achieve some of the United Nations SDGs and to reduce human nutritional deficits (Patel et al., 2021; Smith et al., 2015) in a framework of ‘one health’ concept, for which the health of people is closely connected to the health of biodiversity and ecosystems where they live.

Declaration of competing interest

Data Availability

The dataset generated through DNA metabarcoding in this study was submitted to the EBI metagenomics portal (https://www.ebi.ac.uk/metagenomics/). BioSamples accessions are: PRJEB41466 (ERP125246). ITS2 DNA barcode sequences are available on GeneBank with the accession number MZ489668 - MZ489808. All relevant data are within the paper or stored in a public repository (https://doi/10.6084/m9.figshare.13637576).

Supplementary materials

Table S1: Sampling details (district and geographic coordinates) of all the investigated farms and sampling methodology (pan trap, vegetation quadrats and net sampling).

Farm ID	Administrative Region	Latitude	Longitude	Net sampling	Pantrap-vegetation quadrat
1	Arusha rural district	-3.1767	36.7024	yes	yes
2	Meru district	-3.3616	36.8145	yes	yes
3	Meru district	-3.1486	36.8669	yes	-
4	Meru district	-3.1599	36.8621	yes	yes
5	Meru district	-3.1265	36.8682	yes	yes
6	Meru district	-3.3742	36.8104	yes	yes
7	Arusha rural district	-3.1584	36.7140	yes	yes
8	Arusha rural district	-3.1472	36.7054	yes	yes
9	Arusha rural district	-3.1712	36.6968	yes	yes
10	Arusha urban district	-3.3721	36.6938	yes	yes
11	Arusha urban district	-3.38858	36.69557	yes	yes
12	Arusha urban district	-3.3769	36.6884	yes	yes
13	Arusha urban district	-3.3820	36.7175	yes	yes
14	Meru district	-3.3602	36.8333	yes	yes
15	Arusha urban district	-3.3701	36.7191	yes	yes
16	Meru district	-3.3597	36.8068	yes	yes
17	Arusha rural district	-3.1514	36.6973	yes	yes
18	Arusha rural district	-3.1819	36.6671	yes	yes
19	Arusha rural district	-3.1653	36.7015	yes	yes
20	Moshi rural district	-3.4230	37.4690	yes	-
21	Moshi rural district	-3.3800	37.3840	yes	-
22	Kilimanjaro Hai district	-3.2840	37.1320	yes	-
23	Meru district	-3.3890	36.9600	yes	-
24	Meru district	-3.2500	37.0090	yes	-

25	Moshi rural district	-3.4450	37.3620	yes	-
26	Meru district	-3.3570	36.8163	-	yes
27	Arusha rural district	-3.1835	36.6767	-	yes

Table S2: List of the plant taxa identified during vegetation sampling. Plants used to produce the ITS2 DNA reference database are also indicated, as well as NCBI submitted voucher name. In the last column T indicates tree/woody species while H indicates herbs.

Family	**Genus**	**Species**	**Vegetation quadrat**	**ITS2 Sequence produced in this study**	**Voucher name**	**Tree/Herbs**
Asteraceae	*Bidens*	*Bidens pilosa*	**x**	**x**	MIB:SASS 0001	H
Commelinaceae	*Commelina sp1*	-	**x**	**x**	MIB:SASS 0002	H
Fabaceae	*Acacia sp*	-	**x**	**-**		T
Asteraceae	*Ageratum*	*Ageratum conyzoides*	**x**	**x**	MIB:SASS 0003	H
Amaranthaceae	*Amaranthus sp*	-	**x**	**x**	MIB:SASS 0004	H
Asteraceae	*Galinsoga*	*Galinsoga parviflora*	**-**	**x**	MIB:SASS 0005	H
Asteraceae	*Ageratum sp*	-	**x**	**x**	MIB:SASS 0006	H
Asteraceae sp4	-	-	**x**	**x**	MIB:SASS_0009	H
Acanthaceae	*Thunbergia*	*Thunbergia alata*	**-**	**x**	MIB:SASS 0010	H
Commelinaceae	*Commelina*	*Commelina communis*	**-**	**x**	MIB:SASS 0011	H
Fabaceae	*Aeschynomene*	*Aeschynomene schimperi*	**x**	**x**	MIB:SASS 0013	H
Convolvulaceae	*Ipomoea*	*Ipomoea obscura*	**-**	**x**	MIB:SASS 0014	H
Asteraceae	*Sonchus sp*	-	**x**	**x**	MIB:SASS 0017	H
Oxalidaceae	*Oxalis sp*	-	**x**	**x**	MIB:SASS 0020	H
Commelinaceae	*Commelina sp*	-	**x**	**-**		H
Malvaceae sp1	-	-	**-**	**x**	MIB:SASS_0022	H
Asteraceae	*Tagetes*	*Tagetes minuta*	**x**	**x**	MIB:SASS 0027	H
Verbenaceae	*Lantana*	*Lantana camara*	**x**	**x**	MIB:SASS 0028	H
Asteraceae	*Senecio*	*Senecio hadiensis*	**-**	**x**	MIB:SASS 0031	H

Acanthaceae sp1	-	-	**x**	**x**	MIB:SASS 0032	H
Solanaceae	*Datura*	*Datura stramonium* (A)	**x**	**x**	MIB:SASS 0036	H
Asteraceae	*Galinsoga sp*	-	**-**	**-**		H
Fabaceae	*Sesbania sp*	-	**-**	**x**	MIB:SASS 0037	T
Asteraceae sp5	-	-	**-**	**x**	MIB:SASS_0038	H
Acanthaceae	*Asystasia sp*	-	**x**	**x**	MIB:SASS 0040	H
Acanthaceae	*Justicia sp*	-	**x**	**x**	MIB:SASS 0042	H
Solanaceae	*Solanum*	*Solanum lycopersicum*	**x**	**x**	MIB:SASS_0046	H
Asteraceae sp6	-	-	**x**	**x**	MIB:SASS 0049	H
Asteraceae	*Hirpicium*	*Hirpicium diffusum*	**x**	**x**	MIB:SASS_0051	H
Lamiaceae	*Leucas sp*	-	**x**	**x**	MIB:SASS 0052	H
Malvaceae	*Abutilon sp 1*	-	**-**	**x**	MIB:SASS_0053	H
Malvaceae	*Sida sp*	-	**-**	**x**	MIB:SASS_0055	H
Fabaceae	*Crotalaria sp*	-	**x**	**x**	MIB:SASS_0056	H
Cucurbitaceae	*Cucumis*	*Cucumis dipsaceus*	**-**	**x**	MIB:SASS 0058	H
Brassicaceae sp1	-	-	**x**	**-**		H
Malvaceae	*Abutilon sp 2*	-	**-**	**x**	MIB:SASS 0059	H
Lamiaceae sp2	-	-	**-**	**-**		H
Asteraceae	*Spilanthes*	*Spilanthes paniculata*	**-**	**x**	MIB:SASS 0063	H
Malvaceae sp2	-	-	**-**	**x**	MIB:SASS 0065	H
Malvaceae	*Malvastrum*	*Malvastrum coromandelianum* (A)	**-**	**x**	MIB:SASS 0066	H
Fabaceae	*Calliandria sp*	-	**-**	**x**	MIB:SASS 0069	T
Fabaceae	*Phaseolus*	*Phaseolus vulgaris*	**-**	**x**	MIB:SASS 0070	H
Amaranthaceae	*Celosia*	*Celosia argentea*	**-**	**-**		H

Fabaceae	*Desmodium*	*Desmodium tortuosum*	**-**	**x**	MIB:SASS 0071	H
Lamiaceae	*Salvia sp 3*	-	**-**	**x**	MIB:SASS_0072	H
Rubiaceae	*Spermacoce*	*Spermacoce remota*	**x**	**x**	MIB:SASS 0073	H
Solanaceae	*Solanum*	*Solanum nigrum*	**-**	**x**	MIB:SASS 0074	H
Cannaceae	*Canna sp*	-	**-**	**x**	MIB:SASS 0075	H
Solanaceae	-	-	**-**	**x**	MIB:SASS_0077	H
Asteraceae	*Tagetes*	*Tagetes erecta*	**-**	**x**	MIB:SASS 0078	H
Lamiaceae	*Salvia sp 2*	-	**-**	**x**	MIB:SASS 0079	H
Lamiaceae	*Salvia sp 1*	-	**-**	**x**	MIB:SASS 0081	H
Acanthaceae sp2	-	-	**-**	**x**	MIB:SASS 0084	H
Convolvulaceae sp1	-	-	**x**	**-**		H
Cucurbitaceae	*Cucurbita sp*	-	**-**	**x**	MIB:SASS 0086	H
Asteraceae	*Emilia sp*	-	**x**	**x**	MIB:SASS_0088	H
Solanaceae	*Physalis sp*	-	**-**	**x**	MIB:SASS 0090	H
Verbenaceae	*Lantana sp*	-	**-**	**-**		H
Solanaceae	*Capsicum*	*Capsicum annuum*	**-**	**x**	MIB:SASS 0093	H
Boraginaceae	*Heliotropium*	*Heliotropium steudneri*	**x**	**x**	MIB:SASS 0094	H
Lamiaceae sp3	-	-	**-**	**x**	MIB:SASS_0096	H
Lamiaceae sp4	-	-	**-**	**x**	MIB:SASS 0098	H
Asteraceae sp7	-	-	**x**	**x**	MIB:SASS 0099	H
Malvaceae sp3	-	-	**-**	**x**	MIB:SASS_0100	H
Fabaceae	*Senna sp 1*	-	**-**	**x**	MIB:SASS 0101	T
Fabaceae	*Senna sp 2*	-	**-**	**x**	MIB:SASS 0103	T
Solanaceae	*Datura*	*Datura stramonium* (B)	**-**	**x**	MIB:SASS_0104	H
Acanthaceae sp3	-	-	**-**	**x**	MIB:SASS 0105	H
Papaveraceae	*Argemone*	*Argemone mexicana*	**x**	**x**	MIB:SASS_0108	H
Asteraceae	*Schkuhria*	*Schkuhria pinnata*	**-**	**x**	MIB:SASS 0109	H
Solanaceae	*Nicandra sp*	-	**-**	**x**	MIB:SASS 0111	H

Malvaceae	*Hibiscus sp 2*	-	**-**	**x**	MIB:SASS_0116	H
Fabaceae	*Crotalaria sp 2*	-	**x**	**x**	MIB:SASS_0117	H
Commelinaceae	*Commelina*	*Commelina benghalensis*	**-**	**x**	MIB:SASS_0118	H
Fabaceae	*Lablab*	*Lablab purpureus*	**-**	**x**	MIB:SASS_0119	H
Solanaceae	*Solanum*	*Solanum tuberosum*	**-**	**x**	MIB:SASS_0121	H
Euphorbiaceae	*Euphorbia*	*Euphorbia pulcherrima*	**-**	**x**	MIB:SASS_0122	H
Fabaceae	*Lupinus sp*	-	**-**	**x**	MIB:SASS_0126	H
Lamiaceae sp5	-	-	**-**	**-**		H
Linaceae sp	-	-	**-**	**x**	MIB:SASS_0129	H
Asteraceae	*Kleinia sp*	-	**-**	**x**	MIB:SASS_0130	H
Asteraceae	*Gutenbergia sp*	-	**x**	**-**		H
Campanulaceae	*Campanula sp*	-	**-**	**x**	MIB:SASS_0131	H
Fabaceae	*Crotalaria sp 4*	-	**-**	**x**	MIB:SASS_0135	H
Lamiaceae sp6	-	-	**-**	**-**		H
Malvaceae	*Hibiscus sp 3*	-	**-**	**-**		H
Malvaceae	*Hibiscus sp*	-	**x**	**-**		H
Lamiaceae sp7	-	-	**-**	**-**		H
Solanaceae	*Solanum sp 1*	-	**-**	**x**	MIB:SASS_0137	H
Nyctaginaceae	*Mirabilis sp*	-	**-**	**x**	MIB:SASS_0139	H
Brassicaceae	*Capsella*	*Capsella bursa-pastoris*	**-**	**x**	MIB:SASS_0142	H
Asteraceae	*Tithonia*	*Tithonia diversifolia*	**x**	**x**	MIB:SASS_0367	H
Acanthaceae sp4	-	-	**-**	**x**	MIB:SASS_0369	H
Asteraceae sp8	-	-	**-**	**x**	MIB:SASS_0370	H
Rubiaceae	*Spermacoce sp*	-	**-**	**x**	MIB:SASS_0372	H
Lamiaceae sp8	-	-	**-**	**-**		H

Brassicaceae sp2	-	-	**-**	**x**	MIB:SASS_0374	H
Fabaceae	*Vigna sp*	-	**-**	**x**	MIB:SASS_0378	H
Asteraceae	*Bidens sp*	-	**x**	**-**		H
Malvaceae	*Malvastrum*	*Malvastrum coromandelianum* (B)	**x**	**x**	MIB:SASS_0379	H
Apocynaceae	*Asclepias sp*	-	**-**	**x**	MIB:SASS_0382	H
Orobanchaceae	*Sopubia*	*Sopubia lanata*	**-**	**x**	MIB:SASS_0384	H
Caprifoliaceae	*Sambucus sp*	-	**-**	**x**	MIB:SASS_0386	H
Fabaceae	*Pseudarthria*	*Pseudarthria panii*	**-**	**x**	MIB:SASS_0387	H
Solanaceae	*Solanum sp 2*	-	**-**	**x**	MIB:SASS_0390	H
Scrophulariaceae sp	-	-	**-**	**-**		H
Verbenaceae	*Verbena*	*Verbena officinalis*	**-**	**x**	MIB:SASS_0392	H
Verbenaceae	*Duranta*	*Duranta erecta*	**-**	**x**	MIB:SASS_0393	H
Lamiaceae	*Leonotis sp*	-	**x**	**-**		H
Asteraceae sp9	-	-	**x**	**x**	MIB:SASS_0395	H
Asteraceae	*Calotis*	*Calotis scabiosifolia*	**-**	**x**	MIB:SASS_0397	H
Asteraceae sp1	-	-	**x**	**x**	MIB:SASS_0398	H
Poaceae	*Lolium sp*	-	**x**	**-**		H
Fabaceae	*Indigofera*	*Indigofera arrecta*	**x**	**x**	MIB:SASS_0399	H
Boraginaceae sp	-	-	**x**	**x**	MIB:SASS_0401	H
Convolvulaceae	*Ipomoea sp*	-	**-**	**x**	MIB:SASS_0402	H
Asteraceae	*Aster sp*	-	**-**	**x**	MIB:SASS_0405	H
Fabaceae	*Indigofera sp*	-	**-**	**x**	MIB:SASS_0406	H
Campanulaceae sp	-	-	**-**	**x**	MIB:SASS_0408	H
Caprifoliaceae	*Lonicera sp*	-	**-**	**-**		H
Acanthaceae	*Hypoestes sp*	-	**x**	**x**	MIB:SASS_0410	H

Nyctaginaceae	*Mirabilis*	*Mirabilis jalapa*	**x**	**-**		H
Oleaceae	*Jasminum*	*Jasminum elongatum*	**-**	**x**	MIB:SASS_0411	H
Cyperaceae	*Cyperus*	*Cyperus exilis*	**x**	**x**	MIB:SASS_0413	H
Malvaceae sp4	-	-	**-**	**x**	MIB:SASS_0414	H
Asteraceae sp10	-	-	**-**	**x**	MIB:SASS_0419	H
Asteraceae sp11	-	-	**-**	**x**	MIB:SASS_0420	H
Asteraceae	*Parthenium*	*Parthenium hysterophorus*	**x**	**-**		H
Euphorbiaceae	*Euphorbia sp*	-	**x**	**x**	MIB:SASS_0421	H
Orchidaceae	*Eulophia*	*Eulophia streptopetala*	**-**	**x**	MIB:SASS_0422	H
Fabaceae sp		-	**-**	**x**	MIB:SASS_0423	H
Euphorbiaceae	*Croton*	*Croton megalocarpus*	**-**	**x**	MIB:SASS_0425	T
Portulacaceae	*Portulaca sp*	-	**x**	**-**		H
Apocynaceae	*Catharanthus*	*Catharanthus roseus*	**x**	**x**	MIB:SASS_0426	H
Moraceae	*Morus sp*	-	**-**	**x**	MIB:SASS_0427	T
Acanthaceae sp5	-	-	**-**	**x**	MIB:SASS_0429	H
Asparagaceae	*Chlorophytum*	*Chlorophytum sp*	**-**	**x**	MIB:SASS_0430	H
Asphodelaceae sp1	-	-	**-**	**x**	MIB:SASS_0432	H
Araceae	*Colocasia sp*	-	**x**	**x**	MIB:SASS_0433	H
Asteraceae sp2	-	-	**x**	**x**	MIB:SASS_0434	H
Malvaceae	*Sida*	*Sida pusilla*	**x**	**x**	MIB:SASS_0436	H
Cyperaceae	*Cyperus sp*	-	**x**	**x**	MIB:SASS_0437	H
Poaceae	*Setaria sp*	-	**x**	**x**	MIB:SASS_0439	H
Lamiaceae sp9	-	-	**x**	**-**		H
Asteraceae	*Erigeron sp*	-	**x**	**x**	MIB:SASS_0442	H
Polygonaceae	*Oxygonum sp*	-	**x**	**x**	MIB:SASS_0445	H

Asteraceae sp12	-	-	**x**	**x**	MIB:SASS 0447	H
Apiaceae	*Centella*	*Centella asiatica*	**x**	**x**	MIB:SASS_0453	H
Solanaceae	*Solanum*	*Solanum incanum*	**x**	**-**		H
Cucurbitaceae	*Cuscuta sp*	-	**x**	**x**	MIB:SASS_0454	H
Poaceae	*Cenchrus sp*	-	**x**	**x**	MIB:SASS_0456	H
Lamiaceae sp1	-	-	**-**	**x**	MIB:SASS_0457	H
Poaceae sp2	-	-	**-**	**x**	MIB:SASS_0462	H
Fabaceae	*Leucaena*	*Leucaena leucocephala*	**x**	**x**	MIB:SASS 0463	T
Acanthaceae	*Dyschoriste sp*	-	**x**	**x**	MIB:SASS 0465	H
Araliaceae	*Hydrocotyle*	*Hydrocotyle nepalensis*	**x**	**x**	MIB:SASS_0467	H
Malvaceae	*Corchorus*	*Corchorus olitorius*	**x**	**x**	MIB:SASS 0470	H
Poaceae	*Cynodon*	*Cynodon dactylon*	**x**	**x**	MIB:SASS 0473	H
Asteraceae sp13	-	-	**x**	**x**	MIB:SASS_0475	H
Caryophyllaceae	*Stellaria sp*	-	**x**	**-**		H
Fabaceae	*Teramnus*	*Teramnus labialis*	**x**	**x**	MIB:SASS_0476	H
Apiaceae sp	-	-	**x**	**x**	MIB:SASS 0477	H
Poaceae	*Cenchrus*	*Cenchrus purpureus*	**x**	**x**	MIB:SASS 0478	H
Convolvulaceae	*Convolvulus sp*	-	**x**	**x**	MIB:SASS 0481	H
Convolvulaceae sp2	-	-	**-**	**x**	MIB:SASS 0483	H
Poaceae sp1	-	-	**x**	**x**	MIB:SASS 0485	H
Euphorbiaceae	*Euphorbia*	*Euphorbia heterophylla*	**-**	**x**	MIB:SASS 0486	H

Table S3: List of the calculated network indices values for each of the investigated farms. Farm's identification number is the same as reported in Table S1. The network level index H2' is reported in the second column while the Foraging niche overlap, calculated as individual pollinator level index, is reported in the third column.

FARM ID	H2'	Foraging niche overlap
1	1.0000	0.2333
2	0.8561	0.1302
3	0.9336	0.1099
4	0.7038	0.1584
5	0.7650	0.1310
6	0.9602	0.1646
7	0.7835	0.2209
8	0.2635	0.1746
9	0.8483	0.2032
10	0.7881	0.1173
11	0.7916	0.0914
12	0.9272	0.3542
13	0.9807	0.2000
14	0.7780	0.1188
15	0.5953	0.2234
16	0.6575	0.1090
17	0.6799	0.1265
18	0.7257	0.0824
19	0.6588	0.0614
20	0.9168	0.0891
21	0.9396	0.1795
22	0.8193	0.1751
23	0.6934	0.3000
24	0.9072	0.1656
25	0.9069	0.0969

TABLE S4: List of the insects collected through entomological net and used to build and analyse plant pollinator interaction networks. The first columns report to sample name, the second report the identification number of the farm where samples were collected. The last column reports the results of morphological identification, bee specimens were identified by the co-author Paolo Biella.

Sample ID	Farm ID	insect ID
B9N5	19	*Amegilla fallax*
B9N7	19	*Amegilla fallax*
B9N8	19	*Amegilla fallax*
S113	20	*Amegilla sp1*
S117	20	*Amegilla sp1*
S119	20	*Amegilla sp1*
S122	20	*Amegilla sp1*
S127	21	*Amegilla sp1*
S142	21	*Amegilla sp1*
S164	20	*Amegilla sp1*
S221	22	*Amegilla sp1*
S239	22	*Amegilla sp1*
S71	25	*Amegilla sp1*
S211	4	*Amegilla sp8*
S65	24	*Amegilla sp8*
9N2	9	*Anthophora cf. vestita*
10N1	1	*Apis mellifera*
2N7	3	*Apis mellifera*
3N7	4	*Apis mellifera*
4N2	5	*Apis mellifera*
4N4	5	*Apis mellifera*
6N1	7	*Apis mellifera*
6N2	7	*Apis mellifera*
6N5	7	*Apis mellifera*
6N8	7	*Apis mellifera*
9N4	9	*Apis mellifera*
B11N10	10	*Apis mellifera*
B11N11	10	*Apis mellifera*
B11N12	10	*Apis mellifera*
B11N14	10	*Apis mellifera*
B11N2	10	*Apis mellifera*
B11N5	10	*Apis mellifera*
B11N8	10	*Apis mellifera*
B12N1	11	*Apis mellifera*
B12N10	11	*Apis mellifera*

B12N11	11	*Apis mellifera*
B12N16	11	*Apis mellifera*
B12N17	11	*Apis mellifera*
B12N2	11	*Apis mellifera*
B12N3	11	*Apis mellifera*
B12N4	11	*Apis mellifera*
B12N5	11	*Apis mellifera*
B12N6	11	*Apis mellifera*
B12N8	11	*Apis mellifera*
B12N9	11	*Apis mellifera*
B13N2	12	*Apis mellifera*
B13N3	12	*Apis mellifera*
B13N4	12	*Apis mellifera*
B13N5	12	*Apis mellifera*
B13N6	12	*Apis mellifera*
B14N3	13	*Apis mellifera*
B15N1	14	*Apis mellifera*
B15N6	14	*Apis mellifera*
B16N10	15	*Apis mellifera*
B16N11	15	*Apis mellifera*
B16N13	15	*Apis mellifera*
B16N14	15	*Apis mellifera*
B16N2	15	*Apis mellifera*
B16N7	15	*Apis mellifera*
B5N1	16	*Apis mellifera*
B5N10	16	*Apis mellifera*
B5N14	16	*Apis mellifera*
B5N2	16	*Apis mellifera*
B6N1	17	*Apis mellifera*
B6N10	17	*Apis mellifera*
B6N11	17	*Apis mellifera*
B6N12	17	*Apis mellifera*
B6N13	17	*Apis mellifera*
B6N14	17	*Apis mellifera*
B6N15	17	*Apis mellifera*
B6N2	17	*Apis mellifera*
B6N3	17	*Apis mellifera*
B6N4	17	*Apis mellifera*
B6N5	17	*Apis mellifera*
B6N6	17	*Apis mellifera*
B6N7	17	*Apis mellifera*

B6N8	17	*Apis mellifera*
B6N9	17	*Apis mellifera*
B7N1	18	*Apis mellifera*
B9N14	19	*Apis mellifera*
B9N15	19	*Apis mellifera*
B9N16	19	*Apis mellifera*
S108	20	*Apis mellifera*
S109	20	*Apis mellifera*
S114	20	*Apis mellifera*
S118	20	*Apis mellifera*
S124	20	*Apis mellifera*
S128	21	*Apis mellifera*
S129	21	*Apis mellifera*
S133	21	*Apis mellifera*
S137	21	*Apis mellifera*
S144	21	*Apis mellifera*
S167	20	*Apis mellifera*
S168	20	*Apis mellifera*
S222	22	*Apis mellifera*
S230	22	*Apis mellifera*
S28	23	*Apis mellifera*
S60	24	*Apis mellifera*
S68	24	*Apis mellifera*
S72	25	*Apis mellifera*
S76	25	*Apis mellifera*
S77	25	*Apis mellifera*
S78	25	*Apis mellifera*
S82	25	*Apis mellifera*
S84	25	*Apis mellifera*
S85	25	*Apis mellifera*
S88	25	*Apis mellifera*
S98	23	*Apis mellifera*
1AN5	2	*Apis mellifera*
2N1	3	*Apis mellifera*
3N3	4	*Apis mellifera*
B12N7	11	*Apis mellifera*
B16N9	16	*Apis mellifera*
B9N11	19	*Apis mellifera*
B9N13	19	*Apis mellifera*
B9N2	19	*Apis mellifera*
B9N9	19	*Apis mellifera*

1AN3	2	*Apis mellifera scutellata*
1AN4	2	*Apis mellifera scutellata*
1BN4	2	*Apis mellifera scutellata*
2N2	3	*Apis mellifera scutellata*
2N3	3	*Apis mellifera scutellata*
2N4	3	*Apis mellifera scutellata*
3N1	4	*Apis mellifera scutellata*
3N2	4	*Apis mellifera scutellata*
3N4	4	*Apis mellifera scutellata*
3N5	4	*Apis mellifera scutellata*
3N6	4	*Apis mellifera scutellata*
4N3	5	*Apis mellifera scutellata*
6N7	7	*Apis mellifera scutellata*
8N1	8	*Apis mellifera scutellata*
8N2	8	*Apis mellifera scutellata*
B11N13	10	*Apis mellifera scutellata*
B11N15	10	*Apis mellifera scutellata*
B11N16	10	*Apis mellifera scutellata*
B11N4	10	*Apis mellifera scutellata*
B11N6	10	*Apis mellifera scutellata*
B11N7	10	*Apis mellifera scutellata*
B11N9	10	*Apis mellifera scutellata*
B12N12	11	*Apis mellifera scutellata*
B12N13	11	*Apis mellifera scutellata*
B12N14	11	*Apis mellifera scutellata*
B12N15	11	*Apis mellifera scutellata*
B14N1	13	*Apis mellifera scutellata*
B14N2	13	*Apis mellifera scutellata*
B14N4	13	*Apis mellifera scutellata*
B14N5	13	*Apis mellifera scutellata*
B14N6	13	*Apis mellifera scutellata*
B15N10	14	*Apis mellifera scutellata*
B15N11	14	*Apis mellifera scutellata*
B15N12	14	*Apis mellifera scutellata*
B15N13	14	*Apis mellifera scutellata*
B15N15	14	*Apis mellifera scutellata*
B15N2	14	*Apis mellifera scutellata*
B15N3	14	*Apis mellifera scutellata*
B15N4	14	*Apis mellifera scutellata*
B15N5	14	*Apis mellifera scutellata*
B15N7	14	*Apis mellifera scutellata*

B15N8	14	*Apis mellifera scutellata*
B15N9	14	*Apis mellifera scutellata*
B16N1	15	*Apis mellifera scutellata*
B16N15	15	*Apis mellifera scutellata*
B16N3	15	*Apis mellifera scutellata*
B16N4	15	*Apis mellifera scutellata*
B16N6	15	*Apis mellifera scutellata*
B5N11	16	*Apis mellifera scutellata*
B5N12	16	*Apis mellifera scutellata*
B5N13	16	*Apis mellifera scutellata*
B5N15	16	*Apis mellifera scutellata*
B5N3	16	*Apis mellifera scutellata*
B5N4	16	*Apis mellifera scutellata*
B5N6	16	*Apis mellifera scutellata*
B5N7	16	*Apis mellifera scutellata*
B5N9	17	*Apis mellifera scutellata*
B7N14	18	*Apis mellifera scutellata*
B9N1	19	*Apis mellifera scutellata*
B9N10	19	*Apis mellifera scutellata*
B9N4	19	*Apis mellifera scutellata*
B9N6	19	*Apis mellifera scutellata*
4N5	5	*Bembix sp1*
4N6	5	*Betasyrphus aff. adligatus "A"*
8N4	8	*Betasyrphus aff. adligatus "A"*
6N4	7	*Ceratina moerenhouti*
B7N3	18	*Ceratina moerenhouti*
9N3	9	*Ceratina sp. 2*
9N7	9	*Ceratina sp. 2*
9N6	9	*Ceratina sp.1*
9N5	9	*Cerceris sp.1*
S234	22	Compsomerinae, Genus sp1
S92	23	Compsomerinae, Genus sp1
S235	22	Compsomerinae, Genus sp10
B11N3	10	*Episyrphus trisectus*
4N1	5	*Eristalinus cf. fuscicornis*
5N8	6	*Eristalinus myathropinus*
B9N12	19	*Eristalinus taeniops*
B9N3	19	*Eristalinus taeniops*
S244	4	*Heriades sp1*
10N7	1	Hymenoptera B
4N7	5	Hymenoptera D

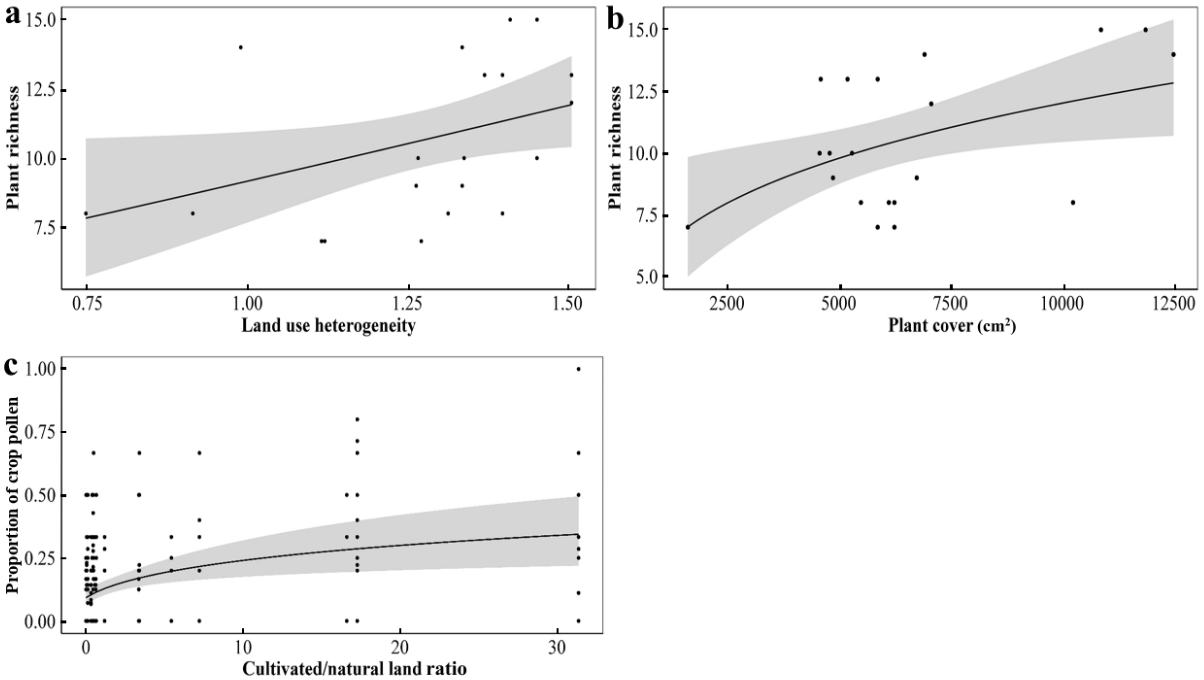
4N9	5	Hymenoptera E
6N3	7	Hymenoptera F
8N6	8	Hymenoptera G
B7N13	18	Hymenoptera N
B7N7	18	Hymenoptera X
S209	22	*Lasioglossum bellulum*
10N2	1	*Lasioglossum sp.1*
B11N1	10	*Lipotriches hylaeoides*
B7N8	18	*Megachile aff ungulata*
B7N12	18	*Megachile aff. Frontalis*
B7N2	18	*Megachile aff. Frontalis*
B7N5	18	*Megachile aff. Frontalis*
B7N6	18	*Megachile aff. Frontalis*
B15N14	14	*Megachile bituberculata*
2N8	3	*Megachile felina*
B7N4	18	*Megachile sp. 2*
S115	20	*Megachile sp16*
S215	22	*Megachile sp16*
S22	23	*Megachile sp16*
S238	22	*Megachile sp16*
S240	4	*Megachile sp16*
S74	25	*Megachile sp16*
S79	25	*Megachile sp16*
S89	25	*Megachile sp16*
S48	24	*Megachile sp16 / Brounsapis sp3*
S120	20	*Megachile sp3*
S83	25	*Megachile sp9*
B7N11	18	*Megachile venusta*
5N9	6	*Melanostoma bituberculatum*
9N8	9	*Paragus haemorrous*
5N7	6	*Paragus minutus*
1AN7	2	*Phytomia bulligera*
1BN2	2	*Phytomia bulligera*
1BN6	2	*Phytomia bulligera*
5N3	6	*Phytomia bulligera*
B5N5	16	*Phytomia bulligera*
1BN3	2	*Phytomia incisa*
2N6	3	*Phytomia incisa*
5N4	6	*Phytomia incisa*
1AN2	2	*Plebeina armata*
S75	25	*Schwaizia emmae*

8N3	8	*Seladonia foana*
B7N10	18	*Seladonia foana*
S229	22	*Seladonia foana*
B5N8	16	*Seladonia jucunda*
S37	23	*Steganomos junodi*
8N7	8	*Tetraloniella cf. alboscopacea*
8N8	8	*Tetraloniella cf. alboscopacea*
9N1	9	*Tetraloniella cf. alboscopacea*
S112	20	*Thyreus sp3*
S223	22	*Thyreus sp4*
S70	24	*Thyreus sp4*
1AN6	2	*Toxomerus floralis*
1BN1	2	*Toxomerus floralis*
1BN5	2	*Toxomerus floralis*
5N1	6	*Toxomerus floralis*
5N2	6	*Toxomerus floralis*
5N5	6	*Toxomerus floralis*
5N6	6	*Toxomerus floralis*
S111	20	*Xylocopa flavicollis*
S131	21	*Xylocopa inconstans*
S163	20	*Xylocopa inconstans*
S165	21	*Xylocopa inconstans*
S206	22	*Xylocopa inconstans*
S62	24	*Xylocopa somalica*

Supplementary Text S1: Details on sample preparation, DNA extraction, sequencing, bioinformatics analysis and taxonomic assignment.

After the isolation of pollen grains samples were grinded with a Tissue Lyser® II (Qiagen©, Hilden, Germany) prior to freezing in liquid nitrogen. DNA was extracted under a laminar flow cabinet using the Qiagen© DNeasy® Plant Mini Kit (Qiagen, Hilden, Germany) following the manufacturer's instruction, with a final elution volume of 50 µl. The nuclear internal transcribed spacer 2 region (ITS2) was selected as the DNA barcode region given the high resolution shown in other studies (Chen et al., 2010; Biella et al., 2019; Frigerio et al., 2020). The selected locus was amplified using primers S2F and S3R with the addition of the Illumina overhang adapter sequences, primer sequence and sample preparation protocol prior to sequencing are extensively explained in Biella et al. (2019). Library preparation and sequencing were performed through the Illumina MiSeq instrument using MiSeq 600 V3 (2 × 300-bp paired-end sequencing). The library preparation and the sequencing process were conducted at the Center for Translational Genomics and Bioinformatics (San Raffaele Scientific Institute, Milan, Italy). Before proceeding with the taxonomic assignment of pollen ITS2 reads, raw sequences were paired and pre-processed with QIIME2 (ver. 2019.4; https://qiime2.org/) (Bolyen et al., 2018). Primers were trimmed and ASVs sequences (or features) were obtained using the DADA2 algorithm (Callahan et al., 2016), performing a quality filter with an expected error of 2.0 and removing chimeras. Features outside the bounds of 200 and 550 bp were removed. The taxonomic assignment was carried out using the BLAST algorithm (Camacho et al., 2009) against our local DNA reference dataset and, in case of no reliable match, on the entire NCBI nucleotide database. After checking for the presence of unlikely matches (i.e., plants found not to be present in the study area), only assignments with a max identity and a query coverage ≥ 98% were accepted. The identified species were also categorized in wild or horticultural species. The dataset generated for this study was submitted to the EBI metagenomics portal (https://www.ebi.ac.uk/metagenomics/). BioSamples accessions are: PRJEB41466 (ERP125246)

Figure S1: Plots (a) and (b) depict the relationship between plant species and land use heterogeneity and plant cover (cm^2), respectively. Plot (c) shows the result of the regression analysis of proportion of pollen from horticultural species carried by pollinators as a function of the cultivated - natural land ratio.



Chapter V

A synopsis of the bee occurrence data of northern Tanzania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Summary

Background

Bees (Hymenoptera: Apoidea: Anthophila) are the most important group of pollinators with about 20,507 known species worldwide. Despite the critical role of bees in providing pollination services, studies aiming at understanding which species are present across disturbance gradients are scarce. Limited taxonomic information for the existing and unidentified bee species in Tanzania make their conservation haphazard. Here, we present a dataset of bee species records obtained from a survey in northern Tanzania i.e. Kilimanjaro, Arusha and Manyara regions. Our findings serve as baseline data necessary for understanding the diversity and distribution of bees in the northern parts of the country, which is a critical step in devising robust conservation and monitoring strategies for their populations.

New information

In this paper, we present information on 45 bee species belonging to 20 genera and four families sampled using a combination of sweep-netting and pan trap methods. Most species (27, ~ 60%) belong to the family Halictidae followed by 16 species (35.5%) from the family Apidae. Megachilidae and Andrenidae were the least represented, each with only one species (2.2%). Additional species of Apidae and Megachilidae sampled during this survey are not yet published on Global Biodiversity Information Facility (GBIF), once they will be available on GBIF, they will be published in a subsequent paper. From a total of 953 occurrences, highest numbers were recorded in Kilimanjaro Region (n = 511), followed by Arusha (n = 410) and Manyara (n = 32), but this pattern reflects the sampling efforts of the research project rather than real bias in the distributions of bee species in northern Tanzania.

Keywords: agriculture; bee pollinator; distribution; disturbance gradient; grazing; species diversity Tanzania

Introduction

Bees (Hymenoptera: Apoidea: Anthophila) play an important ecological role in ecosystem. They serve a pollination role through mutualistic interactions with plants that in turn maintain the functionality of natural ecosystem, enhancing crop production and hence promoting human well-being (Potts et al., 2016). Improved pollination service is essential for biodiversity conservation because plants act as primary producers in ecosystem. Nonetheless, they provide a vast array of ecosystem services: carbon sequestration, soil erosion prevention, nitrification and maintaining water tables, just to name a few. About 94% flowering plants reproduction depend on animal pollination in particular bee pollinators (Ollerton et al., 2011). Therefore, bees are considered as the most important pollinator of crops and wild plants as they can visit more than 90% of the leading 107 global crop types (Klein, Vaissière, et al., 2007).

Taxonomic information of bee species in many parts of the world is poorly understood (Eardley et., 2016; Williams et al., 2001; Winfree, 2010) and Tanzania is no exception. The distribution and diversity of wild bee species in Tanzania is equivocal, given the lack of a countrywide bee catalogue and limited scientific studies. Tanzania is renowned for its unique biodiversity and high endemism (URT 2014). With a mainland area of 945,087 km^2, lack of information on distribution and diversity of bee species poses a risky scenario, as unknown bee species may disappear even before they are discovered and documented. On the other hand, decline of bee populations are increasingly becoming a global concern, a situation which jeopardizes provision of pollination sevices to both natural and agro- ecosystems (Cameron et al., 2011; Koh et al., 2016; Potts et al., 2016; Tommasi et al., 2021; Westphal et al., 2008) Nonetheless, knowledge of local bee fauna, including species present and their distribution, is worthy understanding and should be a conservation concern regardless of their importance in the agriculture sector. Research shows that land- use intensification, climate change, introduction of alien invasive species and pathogens are amongst the major driving factors for bee populations declines (Bartomeus & Dicks, 2019; Potts et al., 2016). There is also lack of empirical data on synergistic interaction of such factors owing to their interconnection and complexity which impedes the management and conservation of wild bee pollinators (Gemmill-Herren et al., 2014; Potts et al., 2016; Westphal et al., 2008).

In recent years, a few studies have provided partial information on the ecology of bees in Tanzania (Classen et al., 2015, 2017, 2020). However, these studies focused on bee diversity using morphospecies, plant-bee interactions and body size trait along elevation gradients of Mt.Kilimanjaro. Additionally, some studies on bee species conducted in the country were confined to a specific taxon, for example, in the genus *Apis* (Mumbi et al., 2014) and tribe Meliponini (Hamisi, 2016). To date, no studies have comprehensively compiled occurrence of bee species in Tanzania to understand their diversity and distribution. In 2017, the College of African Wildlife Management, Mweka (CAWM), in collaboration with local and international partners, developed a three-year Bee Pollinator Monitoring Project to bridge this information gap. On this account, this paper presents bee occurrence data of northern Tanzania (Kilimanjaro, Arusha and Manyara administrative regions) with reference to an online dataset shared to the wider scientific community through https://doi.org/10.15468/hdcdf3 (Lasway et al., 2021a). The result is a qualitative improvement in the availability of primary data on the bee species of this country.

Project description

Title: Bee – Pollinator Monitoring Project, Tanzania

Personnel: The project is hosted at CAWM, Mweka Tanzania and is being implemented in collaboration with local and international partner institutions. Local institutions include Sokoine

University of Agriculture (SUA), Tanzania Wildlife Research Institute (TAWIRI), Tanzania Commission for Science and Technology (COSTECH), Ministry of Agriculture - Tanzania, Tropical Pesticide Research Institute (TPRI) and National Museum of Tanzania (NMT). Partner institutions from outside Tanzania include the University of Würzburg (Germany), Agricultural Research Council ARC (South Africa), Royal Belgian Institute of Natural Sciences RBINS (Belgium), and the University of Kansas (USA).

Goals: The project's main goal was to determine the current distribution and status of bee pollinators in Tanzania. Other project objectives were:

- To strengthen the capacity of Tanzanians in the aspects of biodiversity informatics; plant-bee interactions; DNA-based and morphological identification techniques; and collection management;
- To develop and implement a standardized bee pollinator monitoring programme;
- To share data on bee species, abundance and their interactions with plants via dedicated databases, such as Global Biodiversity Information Facility (GBIF), Tanzania Biodiversity Information Facility (TanBIF) and African Pollinator Initiative (API);
- To disseminate results to the scientific community through peer-reviewed publications and conference presentations; and
- To raise awareness of the general public on the importance of bee pollinators through various media.

Funding: The project is financed by the JRS Biodiversity Foundation, USA.

Methods

Study extent: The study was carried out in a set of study sites established in agricultural (transformed), grazing (degraded) and natural savannah (conserved) lands to represent different land-use categories as presented in Table 1. Agriculture intensity was measured, based on magnitude of land use intensification, i.e. moderately intensive agriculture habitat was mainly characterized by smallholder farms with field sizes of less than 1 ha with mixed crops, such as maize, beans and sunflower. It is also characterized by moderate use of agricultural machines and agrochemicals, while intensive agriculture was characterized by monoculture farms. In this habitat, there is a high use of heavy agricultural machines and agricultural inputs (i.e. pesticides and chemical fertilizers). Nonetheless, grazing intensity was measured, based on the visual inspection of on-site signs of obvious grazing like shortened tufts of grass, presence or absence of livestock footprints and by calculating the distance between study sites to bomas (livestock enclosures and living grounds of families holding large herds of livestock) using remote sensing and GIS techniques. Study sites with signs of intensive grazing activity were very near to bomas (average distance 0.09 ± 0.05 (SD) km while study sites with moderate livestock grazing intensity were at a far distance to bomas (i.e. average distance 25.3 ± 27.6 km (SD).

Table 1.

The regional study sites location

Study site	**Study site ID**	**Latitude**	**Longitude**	**Elevation (m.a.s.l.)**	**Region**
Miwaleni	IA1	-3.4233	37.4604	702	Kilimanjaro
Mjohoroni	IA2	-3.3813	37.3836	764	Kilimanjaro
Kahe	IA3	-3.4451	37.3564	741	Kilimanjaro
Lambo estate	IA4	-3.3095	37.2436	1007	Kilimanjaro
Bomang'ombe	IA5	-3.2834	37.1292	1036	Kilimanjaro
West Kilimanjaro	IA6	-3.0205	37.0488	1497	Kilimanjaro
West Kilimanjaro	IA7	-2.9461	37.0597	1708	Kilimanjaro
Kikatiti	IA8	-3.3892	36.9592	1047	Arusha
NARCO	IG1	-3.098	36.9852	1359	Kilimanjaro
Lekrumuni	IG2	-3.1378	36.9434	1404	Kilimanjaro
Lekrumuni	IG3	-3.1508	36.9115	1391	Kilimanjaro
KIA	IG4	-3.4504	37.0394	890	Kilimanjaro
Meserani	IG5	-3.4079	36.4956	1330	Arusha
Arkatani	IG6	-3.418	36.3967	1327	Arusha
Bwawani	IG7	-3.4531	36.1923	1314	Arusha
Makuyuni juu	IG8	-3.5081	36.1431	1227	Arusha
Njia panda	MIA1	-3.3932	37.5191	847	Kilimanjaro
Njia panda	MIA2	-3.4375	37.5334	759	Kilimanjaro
Kibo estate	MIA3	-3.3044	37.2078	1025	Kilimanjaro
Donyo Moru	MIA4	-3.2526	37.0964	1101	Kilimanjaro
New Molomo farm	MIA5	-3.1602	37.0356	1376	Kilimanjaro
King'ori	MIA6	-3.3058	36.9875	1167	Arusha
Kisongo	MIA7	-3.3809	36.5465	1368	Arusha
Nanja	MIA8	-3.3981	36.2493	1478	Arusha
Challa	MIG1	-3.3162	37.6383	1137	Kilimanjaro
Challa	MIG2	-3.3475	37.6357	1023	Kilimanjaro
Holili	MIG3	-3.3682	37.5968	940	Kilimanjaro
Dachkona	MIG4	-3.1259	37.0264	1380	Kilimanjaro

Mwangaza	MIG5	-3.0544	37.0575	1532	Kilimanjaro
KIA	MIG6	-3.4187	37.0668	900	Kilimanjaro
Nelson Mandela	MIG7	-3.4002	36.7848	1216	Arusha
UN	MIG8	-3.3562	36.5838	1441	Arusha
Challa	SAV1	-3.3091	37.685	945	Kilimanjaro
Challa	SAV2	-3.2957	37.6817	954	Kilimanjaro
ANAPA	SAV3	-3.2372	36.8663	1406	Arusha
ANAPA	SAV4	-3.309	36.8803	1576	Arusha
Manyara ranch	SAV5	-3.5657	36.0478	1065	Manyara
TANAPA	SAV6	-3.7476	41.9738	1031	Manyara
TANAPA	SAV7	-3.7944	36.0406	1071	Manyara
TANAPA	SAV8	-3.846	36.0525	1073	Manyara

Sampling description: Data were collected in 40 study sites distributed along savannah, grazing and agriculture gradients in the three regions. A paired patch study design (i.e. sampling plots were positioned in two contrasting habitats within each study site) was used to minimize spatial autocorrelation. In each study site, two 50 x 50 m sampling plots were positioned and spaced at least 150 m apart. The coordinates of the plots were recorded at the mid-point between the paired plots. Bee data collection involved a combination of standardized pan trapping and random walk methods. These techniques have successfully been used for sampling bee species in northern Tanzania (Classen et al., 2015, 2017, 2020) and in other parts of the world (e.g. Noyes, 1989; Spafford & Lortie, 2013; Stephen & Rao, 2007; Westphal et al., 2008; Yi et al., 2012). In each plot, four clusters of UV-Reflecting pan traps (each with yellow, white and blue) were installed and left in the field to collect bees for 48 hours. Two of the clusters were installed using a 120 cm pole to increase the chances of collecting bees foraging on shrubs and the other two were installed using a 35 cm pole to capture bees foraging on herbaceous plants. In each of three quota water-filled pan traps, a drop of scentless colorless liquid soap was added to break the surface tension and prevent bees from escaping. The total sampling effort for this technique summed to 1,152 hours per site. For the standardized random walk, two researchers actively collected bees for two hours within each sampling plot using sweep nets. This method summed to a sampling effort of four man-hours per study site.

Quality control: Controlling data: For each of the study sites, we recorded the habitat type, GPS coordinates and elevation (metres above sea level, m a.s.l.). The coordinate and elevation of localities were derived from a hand-held Garmin GPS (Model: GPSMAP64s; resolution ± 3 m; Garmin Ltd, Taiwan). In addition, for each study site, information on weather parameters (temperature and precipitation) and forage resources were recorded. The specimens collected were preserved in 70% ethanol before being mounted and identified by afro-tropical bee taxonomists (Alain Pauly and Connal Eardley). Bees were identified following the nomenclatural system of Michener (2007) "The Bees of the World, Second Edition" with the exception of the family Halictidae that followed Pauly (1990) and Pauly (1999). Both Michener (2007) and Halictidae taxonomic publications contain keys, diagnosis and descriptions of bees. The reference collections for identified bee species are available at the CAWM, Mweka.

Geographic coverage

Description: The study was conducted in the northern part of Tanzania i.e., Kilimanjaro, Arusha and Manyara regions (Fig. 1). The study regions are located between latitude 3°30’ S and 4°45’ S and longitude 4°30' E and 5°45’ E. The study regions have two rainy seasons: a long rainy season from March to May and a short rainy season in November and December. Average annual rainfall ranges geographically between 1300 mm and 2400 mm. Annual mean maximum temperature (hottest season) is 25.4°C between July and September and minimum temperature (cold season) is 12.8°C between May and June.

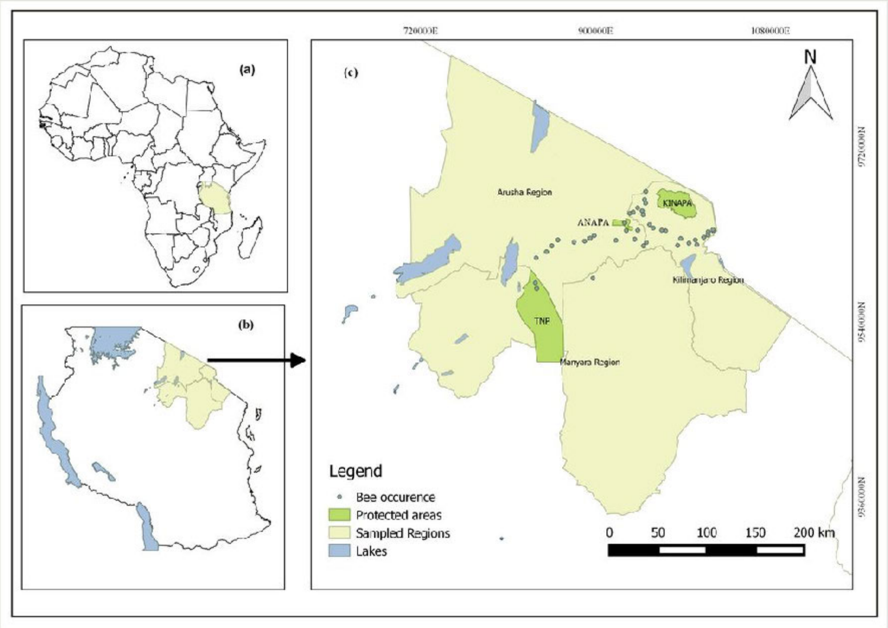

Figure 1. Map of the study area showing study sites. **(a)** Location of Tanzania (pale yellow background) on the map of Africa; **(b)** Location of the study area (pale yellow background) in Tanzania; **(c)** Enlarged map of the study area showing sampling sites (grey dots) in northern Tanzania i.e Kilimanjaro, Arusha and Manyara regions. **Coordinates:** 3°30’ S and 4°45’ S Latitude and; 4°30' E and 5°45’ E Longitude.

Taxonomic coverage

Description: This data paper describes a total of 953 occurrences for bee species representing four families, 20 genera and 45 species (Table 2), amongst 20,507 species that have been described worldwide (Ascher and Pickering 2020). Seven families of bee species (Andrenidae, Halictidae, Apidae, Melittidae, Colletidae, Megachilidae and Stenotridae) are currently recognized globally (Michener, 2007), though only four (Andrenidae, Apidae, Halictidae and Megachilidae) have been recorded in this study. In this sample, seven species (*Apis mellifera* (Linnaeus, 1758), *Macrogalea* *candida* (Smith, 1879), *Lasioglossum bowkeri* (Cockerell, 1920), *L. rubritarse* (Cockerell, 1937), *L. transvaalense* (Cameron & Cockerell, 1937), *Seladonia foana* (Vachal, 1899) and *S. hotoni* (Vachal, 1903) are reported to occur across all land-use types: agricultural (transformation), grazing (degradation) and natural savannah (conservation), whereas other species are found in a subset of land-use types (Table 3).

Table 2.
Summary of bee occurrence records from northern Tanzania by family.

Class	**Order**	**No. of genera recorded**		**No. of species recorded**	**No. of individuals recorded**
Insecta	Hymenoptera	Andrenidae	1	1	1
		Apidae	9	16	570
		Halictidae	9	27	352
		Megachilidae	1	1	30
Total			20	45	953

Table 3.
Species list of bee data records from northen Tanzania.

Family	**Genera**	**Scientific name and authorship**	**Land-use type**
Andrenidae	*Andrena*	*Andrena notophila.* (Cockerell, 1933)	Savannah habitat in Arusha region.
Apidae	*Apis*	*Apis mellifera* (Linnaeus, 1758)	Savannah, intensive agriculture, intensive grazing, mid-intensive agriculture and mid-intensive grazing habitat in Arusha and Kilimanjaro regions.
Apidae	*Eucara*	*Eucara macrognatha* (Gerstaecker, 1870)	Mid-intensive agriculture and mid-intensive grazing habitat in Kilimanjaro region.
Apidae	*Hypotrigona*	*Hypotrigona gribodoi (Magretti, 1884)*	Mid-intensive agriculture and mid-intensive grazing habitat in Kilimanjaro

Apidae	*Liotrigona*	*Liotrigona bottegoi* (Magretti, 1895)	Savannah habitat in Kilimanjaro region.
Apidae	*Macrogalea*	*Macrogalea candida* (Smith, 1879)	Savannah, intensive agriculture, intensive grazing, mid-intensive agriculture and mid-intensive grazing habitat in Arusha and Kilimanjaro regions.
Apidae	*Meliponula*	*Meliponula ferruginea* (Lepeletier, 1836)	Intensive agriculture habitat in Arusha region.
Apidae	*Meliponula*	*Meliponula togoensis* (Stadelmann)	Savannah and mid-intensive grazing habitat in Arusha and Kilimanjaro regions.
Apidae	*Pleibena*	*Plebeina armata* (Magretti, 1895)	Mid-intensive grazing habitat in Kilimanjaro region.
Apidae	*Schwarzia*	*Schwarzia emmae* (Eardley, 2009)	Intensive agriculture habitat in Kilimanjaro region.
Apidae	*Xylocopa*	*Xylocopa caffra* (Linnaeus, 1767)	Intensive agriculture and mid-intensive grazing habitat in Kilimanjaro region.
Apidae	*Xylocopa*	*Xylocopa erythrina* (Gribodo, 1894)	Intensive grazing habitat in Kilimanjaro region.
Apidae	*Xylocopa*	*Xylocopa flavicollis* (DeGeer, 1778)	Intensive agriculture, mid-intensive agriculture and mid-intensive grazing habitat in Arusha and Kilimanjaro regions.
Apidae	*Xylocopa*	*Xylocopa flavorufa* (DeGeer, 1778)	Intensive agriculture habitat in Kilimanjaro region.
Apidae	*Xylocopa*	*Xylocopa inconstans* (Smith, 1874)	Intensive agriculture, intensive grazing, mid- intensive agriculture habitat in Arusha and Kilimanjaro regions.
Apidae	*Xylocopa*	*Xylocopa nigrita* (Fabricius, 1775)	Intensive agriculture habitat in Kilimanjaro region.
Apidae	*Xylocopa*	*Xylocopa somalica* (Magretti, 1895)	Intensive agriculture, intensive grazing, mid- intensive agriculture habitat in Arusha and Kilimanjaro regions.
Halictidae	*Acunomia*	*Acunomia theryi* (Gribodo, 1894)	Intensive agriculture, mid-intensive agriculture habitat in Arusha and Kilimanjaro regions.
Halictidae	*Crocisaspidia*	*Crocisaspidia chandleri* (Ashmead,1899)	Mid-intensive agriculture habitat in Kilimanjaro region.
Halictidae	*Crocisaspidia*	*Crocisaspidia forbesii* (Kirby, 1900)	Intensive grazing habitat in Kilimanjaro region.

Halictidae	*Lasioglossum*	*Lasioglossum acuiferum* (Cockerell, 1935)	Savannah, intensive grazing, mid-intensive agriculture and mid-intensive grazing habitat in Manyara, Arusha and Kilimanjaro regions.
Halictidae	*Lasioglossum*	*Lasioglossum atricrum* (Vachal, 1903)	Intensive agriculture, mid-intensive grazing habitat in Arusha and Kilimanjaro regions.
Halictidae	*Lasioglossum*	*Lasioglossum bellulum* (Vachal, 1910)	Intensive agriculture, intensive grazing, mid- intensive agriculture and mid-intensive grazing habitat in Arusha and Kilimanjaro regions.
Halictidae	*Lasioglossum*	*Lasioglossum bowkeri* (Cockerell, 1920)	Savannah, intensive agriculture, intensive grazing, mid-intensive agriculture and mid-intensive grazing habitat in Arusha and Kilimanjaro regions.
Halictidae	*Lasioglossum*	*Lasioglossum deceptum* (Smith, 1853)	Intensive agriculture, mid-intensive agriculture habitat in Arusha and Kilimanjaro regions.
Halictidae	*Lasioglossum*	*Lasioglossum hancocki* (Cockerell, 1945)	Intensive agriculture, intensive grazing, mid- intensive agriculture and mid-intensive grazing habitat in Arusha and Kilimanjaro regions.
Halictidae	*Lasioglossum*	*Lasioglossum matopiense* (Cockerell, 1940)	Savannah, intensive grazing, mid-intensive agriculture and mid-intensive grazing habitat in Manyara, Arusha and Kilimanjaro regions.
Halictidae	*Lasioglossum*	*Lasioglossum rubritarse* (Cockerell, 1937)	Savannah, intensive agriculture, intensive grazing, mid-intensive agriculture and mid-intensive grazing habitat in Arusha and Kilimanjaro regions.
Halictidae	*Lasioglossum*	*Lasioglossum scobe* (Vachal, 1903)	Intensive agriculture, mid-intensive agriculture habitat in Arusha and Kilimanjaro regions.
Halictidae	*Lasioglossum*	*Lasioglossum transvaalense* (Cameron&Cockerell, 1937)	Savannah, intensive agriculture, intensive grazing, mid-intensive agriculture and mid-intensive grazing habitat in Manyara, Arusha and Kilimanjaro regions.
Halictidae	*Macronomia*	*Macronomia armatula* (Dalla Torre, 1896)	Savannah habitat in Manyara region.
Halictidae	*Nubenomia*	*Nubenomia reichardia* (Strand, 1911)	Savannah, intensive agriculture, mid-intensive agriculture habitat in Manyara and Kilimanjaro regions.
Halictidae	*Pachynomia*	*Pachynomia flavicarpa* (Vachal, 1903)	Mid-intensive grazing habitat in Kilimanjaro region.

Halictidae	*Patellapis*	*Patellapis itigiensis* (Kuhlmann & Pauly, 2010)	Intensive agriculture habitat in Kilimanjaro region.
Halictidae	*Pseudapis*	*Pseudapis pandeana* (Strand, 1914)	Mid-intensive agriculture and mid-intensive grazing habitat in Arusha and Kilimanjaro regions.
Halictidae	*Pseudapis*	*Pseudapis usambarae* (Pauly, 1990)	Mid-intensive agriculture in Kilimanjaro region.
Halictidae	*Seladonia*	*Seladonia africana* (Friese, 1909)	Intensive agriculture, mid-intensive agriculture habitat in Kilimanjaro region.
Halictidae	*Seladonia*	*Seladonia foana* (Vachal, 1899)	Savannah, intensive agriculture, intensive grazing, mid-intensive agriculture and mid-intensive grazing habitat in Arusha and Kilimanjaro regions.
Halictidae	*Seladonia*	*Seladonia hotoni* (Vachal, 1903)	Savannah, intensive agriculture, intensive grazing, mid-intensive agriculture and mid-intensive grazing habitat in Manyara, Arusha and Kilimanjaro regions.
Halictidae	*Seladonia*	*Seladonia lucidipennis* (Smith, 1853)	Mid-intensive agriculture habitat in Kilimanjaro region.
Halictidae	*Steganomus*	*Steganomus junodi* (Gribodo, 1895)	Savannah, mid-intensive agriculture and mid- intensive grazing habitat in Manyara, Arusha and Kilimanjaro regions.
Halictidae	*Trinomia*	*Trinomia cirrita* (Vachal, 1903)	Savannah, intensive agriculture, mid-intensive grazing habitat in Manyara and Arusha regions.
Halictidae	*Zonalictus*	*Zonalictus kabetensis* (Cockerell, 1937)	Savannah, intensive agriculture habitat in Arusha and Kilimanjaro regions.
Halictidae	*Zonalictus*	*Zonalictus kivuicola* (Cockerell, 1937)	Savannah, mid-intensive agriculture habitat in Arusha and Kilimanjaro regions.
Megachilidae	*Lithurgus*	*Lithurgus pullatus* (Vachal, 1903)	Savannah, intensive agriculture, mid-intensive agriculture and mid-intensive grazing habitat in Arusha and Kilimanjaro regions.

The Halictidae was richest in species, with 27 species, followed by Apidae with 16 species. Two families (Andrenidae and Megachilidae) were represented by single species: *Andrena notophila* (Cockerell, 1933) and *Lithurgus pullatus* (Vachal, 1903), respectively (Table 3). Greater numbers of records from Kilimanjaro (511 occurrences), compared to Arusha (410 occurrences) and

Manyara (32 occurrences) is attributed to more sample plots in the region and not fewer bee species in Arusha or Manyara regions.

Temporal coverage

Data range: 2018-8-06 - 2018-12-21.

Notes: Bees were collected intermittently between August and December 2018. Two study sites were visited per day for data collection using pan trap and sweep-net methods. Pan traps were left in the field to collect bees for 48 hours before they were emptied and moved to the next study site. Additionally, sweep-netting was used to collect bee species actively for two hours per study site, excluding handling and processing time. Data collection by hand net was conducted when bees were most active in the morning between 9:00 and 11:00 am.

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Data resources

Data package title: Occurrence of bees along grazing and agricultural gradients in northern Tanzania

Resource link: https://doi.org/10.15468/hdcdf3

Number of data sets: 1

Data set name: Occurrence of bees along grazing and agricultural gradients in northern Tanzania

Download URL: https://bit.ly/32tklEA

Data format: Darwin Core Archive

Description The data were prepared following DARWIN CORE format

Column label	Column description
The acronym in use by the institution having custody of the information referred in the record.	
basisOfRecord	The specific nature of the data record.
occurrenceID	The Globally Unique Identifier number for the record.
individualCount	The number of individuals that were recorded
habitat	A category or description of the habitat in which the Event occurred.
countryCode	The standard code for the country in which the Location occurs
decimalLatitude	The verbatim original latitude of the Location.
decimalLongitude	The verbatim original longitude of the Location.
scientificName	The full scientific name including the genus name and the lowest level of taxonomic rank with the authority.
Kingdom	The full scientific name of the kingdom in which the taxon is classified
eventDate	The date or date interval during which the occurrence record was collected.
geodeticDatum	The coordinate system and set of reference points upon which the geographic coordinates are based.
coordinateUncertaintyInMetres	The horizontal distance from the given decimalLatitude and decimalLongitude in metres, describing the smallest circle

	containing the whole of the location.
organismQuantity	A number or enumeration value for the quantity of organisms.
organismQuantityType	The type of quantification system used for the quantity of organisms
samplingProtocol	The description of the method used during sampling
taxonRank	The taxonomic rank of the most specific name in the scientificName.
scientificNameAuthorship	The authorship information for the scientificName formatted according to the conventions of the applicable nomenclaturalCode.
ScientificName	The full scientific name of a taxon.
acceptedNameUsage.	The full name, with authorship and date information, if known, of the currently valid or accepted taxon.
taxonomicStatus	The status of the use of the scientificName as a label for a taxon

Part VI

General discussion


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This thesis aimed to investigate the impact of anthropogenic activities (in this case, livestock grazing and agriculture intensification) on bee assemblages and floral resources used by bee pollinators. This one has come into mind because the human population and land use changes in Africa are increasing at a very high rate (Fig. 5) with largely unknown consequences on pollinator diversity. Moreover, the impact of ambient temperature and its interaction with livestock grazing and agriculture is largely unknown. Therefore, to ensure ecosystem health and function in the globe, there is a high demand for understanding the consequences of land-use changes and their interaction with increasing temperature resulting from global change.

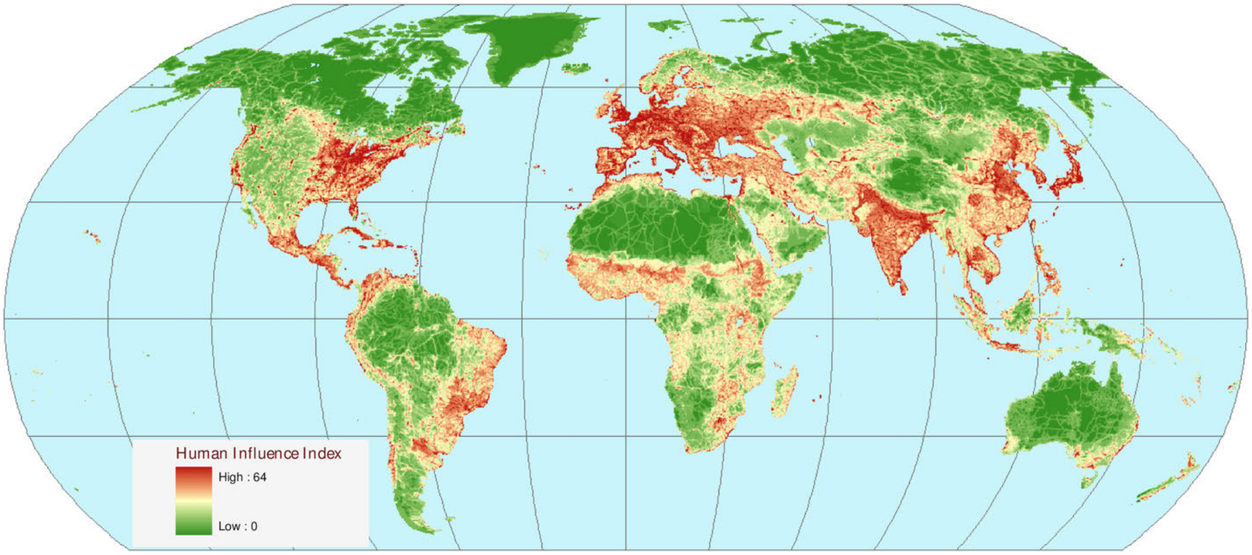

Fig. 5 | The human influence index map shows a measure of direct human influence on terrestrial ecosystems using the best available data sets on human settlement (population density, built-up areas), infrastructure (roads network, railways, and electric power), and landscape transformation (land use/land cover). The small key in the left-bottom corner show values ranging from 0 to 64. Zero value represent no human influence, and 64 represent maximum human influence possible. *Figure adapted from the Trustees of Columbia University in the City of New York, 2008.*

Influence of livestock grazing on East African bee assemblages

Study shows that bee species richness slightly increased with moderate livestock grazing intensity. However, high levels of livestock grazing intensity was associated with a strong decline in bee species richness and abundance. Meaning that in the grazing systems, moderate livestock grazing intensity could probably decrease the population size of the dominant grass species that would allow recruitment of high diverse flowering plant communities that attract high bee diversity (Lazaro et al., 2016; Lázaro et al., 2016). Again, low grazing intensity sites could have dominant matured grasses that prevent the recruitment of diverse plant community, resulting in low bee species richness. Findings also show that higher intensity of livestock grazing was associated with loss of flowering plant species, effecting a decline in both bee abundance and richness. This could be driven by a general reduction in food resource availability for polylectic bees (bees that collect pollen from a wide range of floral resources/generalist bees) or a loss of certain food plant species of oligolectic bees (bees that visit a limited variety of plant species/specialist bees) (Elwell et al., 2016; Hoiss et al., 2013) since bees feed exclusively on nectar and pollen, the availability of floral resources is a major driver of bee communities (Vulliamy et al., 2006).

Impact of local agriculture intensification on East African bee diversity

Contrary to our expectations, findings show that agriculture intensification in the tropical dryland of East Africa was associated with an increase in bee diversity. This observation is inconsistent with most studies conducted along agricultural intensification gradients in temperate Europe and America (Coutinho et al., 2018; Ekroos et al., 2020; Le Féon et al., 2010; Steffan-Dewenter & Westphal, 2008). However, a similar pattern was reported by Classen et al. (2015) on the foothill of Mt. Kilimanjaro and Vogel et al. (2021) in Mzimba district, Northern Malawi. These findings suggest that effects of agricultural intensification on bees and other pollinators are diverse, and differ between taxonomic groups, landscape types, climatic regions, and specificities of agriculture systems (Tscharntke et al., 2005; Winfree et al., 2011). Crop cultivation in the study area is practiced mainly during the long rainy season when water is available for crop growth and development since most parts of Tanzania consist of drought-prone ecosystems (Gebrechorkos et al., 2019b). Following crop harvesting, the land is left fallow for several months until the next annual rain season (Abass et al., 2014). Over this time, fallow fields are dominated by annual herbs and grass cover (Verhulst et al., 2004; Massante et al., 2019), which can flourish even with small amounts of rainfall, thus providing forage resources and nesting sites for bee pollinators (Tucker & Rehan, 2017). Therefore, abandoned agriculture fields increase bee nesting substrate and offer higher spatial-temporal stability of food resources from which bees could benefit (Nicholls & Altieri, 2013; Requier & Leonhardt, 2020; Steffan-Dewenter & Tscharntke, 2001). This long period of fallow land with climate fostering bee activity strongly contrasts with the conditions of intensified agriculture in many temperate regions. In these regions, crops are cultivated from spring to summer, at the time of the year when the temperature is high enough for crop production (Sloat et al., 2020). Before and after the harvesting period, low temperatures do not support the activity of ectothermic bees and the growth of their floral resources (Borghi et al., 2019). This can lead to severe low bee species richness and abundance in intensified agriculture systems in temperate Europe and America. Moreover, in these areas, they use a relatively high amount of agrochemicals (chemical fertilizers and herbicides) that sometimes lead to the direct intoxication of bee pollinators.

Impact of mean annual temperature, MAT on bee assemblages in livestock and agricultural gradients

Studies found that mean bee species richness and abundance show the unimodal distribution pattern with mean annual temperature in the grazing gradient. That means temperature had a strong influence on bee species richness and abundance. The observed unimodal relationship between bee richness and temperature in grazing gradient may suggest that current temperatures in parts of the study region have already exceeded optimum temperatures for bees. Therefore, future increases in temperature through climate change will likely lead to a further decrease in species richness and abundance with potential consequences for pollination services. However, this pattern is probably due to the lack of vegetation cover in highly grazing intensity sites that fail to absorb the sunlight leading to a direct impact on bee pollinators.

Apart from that, the agriculture gradient showed a monotonic increase of bee species richness with ambient temperature. Meaning that temperature had a positive influence on bee species richness. Increases in bee species richness with temperature in agriculture gradient was expected, because, under warm temperatures, bee foraging activities and net energy gain are higher than in cold temperatures (Classen et al., 2015). Additionally, biological processes that shape species richness such as species interactions and evolutionary rates in ectotherms depend on temperature (Puurtinen et al., 2016). In that regard, temperature-mediated speciation rates or enhanced negative density-dependent mortality at higher temperatures may increase the pool of coexisting species at warm habitats.

Impacts of agriculture intensification and landscape composition on plants and pollinators in smallholder farms

The study found that pollinator richness was negatively affected by the amount of impervious surfaces in the surrounding landscape. This finding confirms previous research from West African farming systems (Guenat et al., 2019). Reasons for this trend could be because the increase of impervious surfaces may lead to contraction of green spaces and therefore lead to an increase in isolation. This, in turn, leads to a landscape characterized by the discontinuous and intermittent distribution of floral resources a condition that could result in locally poor pollinator assemblages due to resources that are difficult to access (Egerer et al., 2020). Similarly, agricultural land use intensification is expected to reduce habitat quality and leads to a simplified landscape with lower habitat diversity and availability (Deguines et al., 2014), and this could explain the reduction in pollinator richness observed in response to the increase of agricultural surfaces.

The study also found that the proportion of pollen of crops increased with cultivated-to-natural land ratio. This phenomenon could be justified by considering the possible "pollinator magnet" effect of mass flowering crops occurring in rural landscapes, where the cultivated species largely overwhelm the abundance of flower resources offered by the spontaneous ones (Gilpin et al., 2019). Hence, in the context of smallholder farms, flowering crops might play an important role as food resources for pollinator insects. In intensively cultivated areas, the generalist pollinator species might be more abundant and advantaged instead of the specialist ones because of the higher propensity to change their foraging preferences for exploiting the available crop resources. Thus, changes in the pollinator community composition could also explain the higher collection of crop pollen in response to increased cultivated-to-natural land ratio.

Bee diversity of northern Tanzania

Our study gave the first-ever checklist of bee species of Tanzania and among the first checklists in East Africa. However, out of all 5429 sampled bees across all studies that represent 249 species belonging to 63 genera and six families (Andrenidae, Halictidae, Apidae, Melittidae, Colletidae, and Megachilidae). We have published only 45 species with 943 occurrences in Biodiversity Data Journal. Additional bee species sampled during this survey will be published in a subsequent paper to encourage understanding the distribution of species which is a critical step in devising robust conservation and monitoring strategies. Besides, data sharing (through publications) facilitates collaboration among researchers that could result in new findings.

General conclusion

Findings conclude that livestock grazing at moderate levels may be important in preserving diverse flowering plant assemblages that consequently attract more bee species richness. The study therefore strongly speaks for setting upper limits to livestock grazing in the drylands of tropical East Africa as an insect conservation strategy since most areas of the region are heavily degraded; thus, active restoration through reduction in livestock number will be necessary. While the study did not find support for an interaction between temperature and livestock grazing on species richness, the unimodal relationship between temperature and the richness of both floral resources and bees underscores the fragility of current bee and plant assemblages to further climatic warming. Further warming may push species assemblages in many dryland areas of East Africa beyond the peak of the unimodal distribution, which will probably contribute to a further decline of tropical bee pollinators. The study also concludes that current agricultural intensification practice with long periods of seasonal fallow land is crucial in preserving diverse flowering plant communities and bee species richness with varying body sizes in the tropical drylands of East Africa. Further, the findings of this study suggest that understanding the interplay of the multiple anthropogenic drivers is necessary for mitigating their potential consequences on bee communities and the provision of pollination services. In addition to that, findings also pointed out that increasing urbanization and agricultural cover reduces plant and pollinator biodiversity and negatively impacts the complexity of their interactions. Conversely, the local-scale availability of floral resources has shown positive effects in buffering pollinator decline and mitigating all the detrimental effects induced by land-use intensification phenomena in the Sub-Saharan context.

References

Abass, A. B., Ndunguru, G., Mamiro, P., Alenkhe, B., Mlingi, N., & Bekunda, M. (2014). Post-harvest food losses in a maize-based farming system of semi-arid savannah area of Tanzania. *Journal of Stored Products Research*, *57*, 49–57. https://doi.org/10.1016/j.jspr.2013.12.004

Abel, C., Horion, S., Tagesson, T., De Keersmaecker, W., Seddon, A. W. R., Abdi, A. M., & Fensholt, R. (2021). The human–environment nexus and vegetation–rainfall sensitivity in tropical drylands. *Nature Sustainability*, *4*(1), 25–32. https://doi.org/10.1038/s41893-020-00597-z

Abrahamczyk, S., Gottleuber, P., Matauschek, C., & Kessler, M. (2011). Diversity and community composition of euglossine bee assemblages (Hymenoptera: Apidae) in western Amazonia. *Biodiversity and Conservation*, *20*(13), 2981–3001. https://doi.org/10.1007/s10531-011-0105-1

Adedoja, O., & Kehinde, T. (2018). Changes in interaction network topology and species composition of flower-visiting insects across three land use types. *African Journal of Ecology*, *56*(4), 964–971. https://doi.org/10.1111/aje.12527

Almusaed, A. (2016). *Landscape Ecology: The Influences of Land Use and Anthropogenic Impacts of Landscape Creation*. BoD – Books on Demand.

Araújo, M. S., Bolnick, D. I., & Layman, C. A. (2011). The ecological causes of individual specialisation. *Ecology Letters*, *14*(9), 948–958. https://doi.org/10.1111/j.1461-0248.2011.01662.x

Araújo, M. S., Martins, E. G., Cruz, L. D., Fernandes, F. R., Linhares, A. X., Dos Reis, S. F., & Guimarães Jr, P. R. (2010). Nested diets: A novel pattern of individual-level resource use. *Oikos*, *119*(1), 81–88. https://doi.org/10.1111/j.1600-0706.2009.17624.x

Bartomeus, I., Ascher, J. S., Gibbs, J., Danforth, B. N., Wagner, D. L., Hedtke, S. M., & Winfree, R. (2013). Historical changes in northeastern US bee pollinators related to shared ecological traits. *Proceedings of the National Academy of Sciences*, *110*(12), 4656–4660. https://doi.org/10.1073/pnas.1218503110

Bartomeus, I., & Dicks, L. V. (2019). *The need for coordinated transdisciplinary research infrastructures for pollinator conservation and crop pollination resilience*. *14*(4), 045017. https://doi.org/10.1088/1748-9326/ab0cb5

Basu, P., Parui, A. K., Chatterjee, S., Dutta, A., Chakraborty, P., Roberts, S., & Smith, B. (2016). Scale dependent drivers of wild bee diversity in tropical heterogeneous agricultural landscapes. *Ecology and Evolution*, *6*(19), 6983–6992. https://doi.org/10.1002/ece3.2360

Bell, K. L., Fowler, J., Burgess, K. S., Dobbs, E. K., Gruenewald, D., Lawley, B., Morozumi, C., & Brosi, B. J. (2017). Applying pollen DNA metabarcoding to the study of plant–pollinator interactions. *Applications in Plant Sciences*, *5*(6), 1600124. https://doi.org/10.3732/apps.1600124

Bennett, A. B., & Lovell, S. (2019). Landscape and local site variables differentially influence pollinators and pollination services in urban agricultural sites. *PLOS ONE*, *14*(2), e0212034. https://doi.org/10.1371/journal.pone.0212034

Biella, P., Akter, A., Ollerton, J., Nielsen, A., & Klecka, J. (2020). An empirical attack tolerance test alters the structure and species richness of plant–pollinator networks. *Functional Ecology*, *34*(11), 2246–2258. https://doi.org/10.1111/1365-2435.13642

Biella, P., Ollerton, J., Barcella, M., & Assini, S. (2017). Network analysis of phenological units to detect important species in plant-pollinator assemblages: Can it inform conservation strategies? *Community Ecology*, *18*(1), 1–10. https://doi.org/10.1556/168.2017.18.1.1

Biella, P., Tommasi, N., Akter, A., Guzzetti, L., Klecka, J., Sandionigi, A., Labra, M., & Galimberti, A. (2019). Foraging strategies are maintained despite workforce reduction: A multidisciplinary survey on the pollen collected by a social pollinator. *PLOS ONE*, *14*(11), e0224037. https://doi.org/10.1371/journal.pone.0224037

Blüthgen, N., & Klein, A.-M. (2011). Functional complementarity and specialisation: The role of biodiversity in plant–pollinator interactions. *Basic and Applied Ecology*, *12*(4), 282–291. https://doi.org/10.1016/j.baae.2010.11.001

Borghi, M., Souza, L. P. de, Yoshida, T., & Fernie, A. R. (2019). Flowers and climate change: A metabolic perspective. *New Phytologist*, *224*(4), 1425–1441. https://doi.org/10.1111/nph.16031

Brown, M. J., & Paxton, R. J. (2009). The conservation of bees: A global perspective. *Apidologie*, *40*(3), 410–416. https://doi.org/10.1051/apido/2009019

Broxton, P. D., Zeng, X., Sulla-Menashe, D., & Troch, P. A. (2014). A Global Land Cover Climatology Using MODIS Data. *Journal of Applied Meteorology and Climatology*, *53*(6), 1593–1605. https://doi.org/10.1175/JAMC-D-13-0270.1

Burnham, K. P., & Anderson, D. R. (2004). Multi model Inference: Understanding AIC and BIC in Model Selection. *Sociological Methods & Research*, *33*(2), 261–304. https://doi.org/10.1177/0049124104268644

Bystriakova, N., Griswold, T., Ascher, J. S., & Kuhlmann, M. (2018). Key environmental determinants of global and regional richness and endemism patterns for a wild bee subfamily. *Biodiversity and Conservation*, *27*(2), 287–309.

Callahan, B. J., McMurdie, P. J., & Holmes, S. P. (2017). Exact sequence variants should replace operational taxonomic units in marker-gene data analysis. *The ISME Journal*, *11*(12), 2639–2643. https://doi.org/10.1038/ismej.2017.119

Cameron, S. A., Lozier, J. D., Strange, J. P., Koch, J. B., Cordes, N., Solter, L. F., & Griswold, T. L. (2011). Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences*, *108*(2), 662–667. https://doi.org/10.1073/pnas.1014743108

Carman, K., & Jenkins, D. G. (2016). Comparing diversity to flower-bee interaction networks reveals unsuccessful foraging of native bees in disturbed habitats. *Biological Conservation*, *202*, 110–118. https://doi.org/10.1016/j.biocon.2016.08.030

Chen, S., Yao, H., Han, J., Liu, C., Song, J., Shi, L., Zhu, Y., Ma, X., Gao, T., Pang, X., Luo, K., Li, Y., Li, X., Jia, X., Lin, Y., & Leon, C. (2010). Validation of the ITS2 Region as a Novel DNA Barcode for Identifying Medicinal Plant Species. *PLOS ONE*, *5*(1), e8613. https://doi.org/10.1371/journal.pone.0008613

Classen, A., Eardley, C. D., Hemp, A., Peters, M. K., Peters, R. S., Ssymank, A., & Steffan-Dewenter, I. (2020). Specialization of plant–pollinator interactions increases with temperature at Mt. Kilimanjaro. *Ecology and Evolution*, *10*(4), 2182–2195. https://doi.org/10.1002/ece3.6056

Classen, A., Peters, M. K., Ferger, S. W., Helbig-Bonitz, M., Schmack, J. M., Maassen, G., Schleuning, M., Kalko, E. K. V., Böhning-Gaese, K., & Steffan-Dewenter, I. (2014).

Complementary ecosystem services provided by pest predators and pollinators increase quantity and quality of coffee yields. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1779), 20133148. https://doi.org/10.1098/rspb.2013.3148

Classen, A., Peters, M. K., Kindeketa, W. J., Appelhans, T., Eardley, C. D., Gikungu, M. W., Hemp, A., Nauss, T., & Steffan-Dewenter, I. (2015). Temperature versus resource constraints: Which factors determine bee diversity on M ount K ilimanjaro, T anzania? *Global Ecology and Biogeography*, *24*(6), 642–652. https://doi.org/10.1111/geb.12286

Classen, A., Steffan-Dewenter, I., Kindeketa, W. J., & Peters, M. K. (2017). Integrating intraspecific variation in community ecology unifies theories on body size shifts along climatic gradients. *Functional Ecology*, *31*(3), 768–777. https://doi.org/10.1111/1365-2435.12786

Coutinho, J. G. da E., Garibaldi, L. A., & Viana, B. F. (2018). The influence of local and landscape scale on single response traits in bees: A meta-analysis. *Agriculture, Ecosystems & Environment*, *256*, 61–73. https://doi.org/10.1016/j.agee.2017.12.025

Dainese, M., Martin, E. A., Aizen, M. A., Albrecht, M., Bartomeus, I., Bommarco, R., Carvalheiro, L. G., Chaplin-Kramer, R., Gagic, V., Garibaldi, L. A., Ghazoul, J., Grab, H., Jonsson, M., Karp, D. S., Kennedy, C. M., Kleijn, D., Kremen, C., Landis, D. A., Letourneau, D. K., … Steffan-Dewenter, I. (2019). A global synthesis reveals biodiversity-mediated benefits for crop production. *Science Advances*, *5*(10), eaax0121. https://doi.org/10.1126/sciadv.aax0121

Danner, N., Keller, A., Härtel, S., & Steffan-Dewenter, I. (2017). Honey bee foraging ecology: Season but not landscape diversity shapes the amount and diversity of collected pollen. *PLOS ONE*, *12*(8), e0183716. https://doi.org/10.1371/journal.pone.0183716

Davidson, K. E., Fowler, M. S., Skov, M. W., Forman, D., Alison, J., Botham, M., Beaumont, N., & Griffin, J. N. (2020). Grazing reduces bee abundance and diversity in saltmarshes by suppressing flowering of key plant species. *Agriculture, Ecosystems & Environment*, *291*, 106760. https://doi.org/10.1016/j.agee.2019.106760

Deguines, N., Jono, C., Baude, M., Henry, M., Julliard, R., & Fontaine, C. (2014). Large-scale trade-off between agricultural intensification and crop pollination services. *Frontiers in Ecology and the Environment*, *12*(4), 212–217. https://doi.org/10.1890/130054

Delaney, A., Dembele, A., Nombré, I., Gnane Lirasse, F., Marshall, E., Nana, A., Vickery, J., Tayleur, C., & Stout, J. C. (2020). Local-scale tree and shrub diversity improves pollination services to shea trees in tropical West African parklands. *Journal of Applied Ecology*, *57*(8), 1504–1513. https://doi.org/10.1111/1365-2664.13640

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences*, *105*(18), 6668–6672. https://doi.org/10.1073/pnas.0709472105

Dicks, L. V., Breeze, T. D., Ngo, H. T., Senapathi, D., An, J., Aizen, M. A., Basu, P., Buchori, D., Galetto, L., Garibaldi, L. A., Gemmill-Herren, B., Howlett, B. G., Imperatriz-Fonseca, V. L., Johnson, S. D., Kovács-Hostyánszki, A., Kwon, Y. J., Lattorff, H. M. G., Lungharwo, T., Seymour, C. L., … Potts, S. G. (2021). A global-scale expert assessment of drivers and risks associated with pollinator decline. *Nature Ecology & Evolution*, 1–9. https://doi.org/10.1038/s41559-021-01534-9

Dormann, C. F., Gruber, B., & Fründ, J. (2008). *Introducing the bipartite Package: Analysing Ecological Networks*. *8*, 4.

Dorrough, J., Ash, J., & McIntyre, S. (2004). Plant responses to livestock grazing frequency in an Australian temperate grassland. *Ecography*, *27*(6), 798–810. https://doi.org/10.1111/j.0906-7590.2004.04004.x

Eardley *C,* Freitas BM, Kevan PG, Rader R, Gikungu M, Klein AM, Maus C, Melndez Ramrez V, Singh Palni LM, Vergara CH, Wiantoro S (2016) Background to pollinators, pollination and food production. In: Potts SG, Imperatriz-Fonseca VL, Ngo HT (Eds) The assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production. Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn, Germany, 1-25 pp. [ISBN 978-92-807-3567-3]. https://doi.org/10.5281/zenodo.3402857

Eckert, S., Kiteme, B., Njuguna, E., & Zaehringer, J. G. (2017). Agricultural Expansion and Intensification in the Foothills of Mount Kenya: A Landscape Perspective. *Remote Sensing*, *9*(8), 784. https://doi.org/10.3390/rs9080784

Egerer, M., Cecala, J. M., & Cohen, H. (2020). Wild Bee Conservation within Urban Gardens and Nurseries: Effects of Local and Landscape Management. *Sustainability*, *12*(1), 293. https://doi.org/10.3390/su12010293

Elisante, F., Ndakidemi, P., Arnold, S. E. J., Belmain, S. R., Gurr, G. M., Darbyshire, I., Xie, G., & Stevenson, P. C. (2020). Insect pollination is important in a smallholder bean farming system. *PeerJ*, *8*, e10102. https://doi.org/10.7717/peerj.10102

Elliott, B., Wilson, R., Shapcott, A., Keller, A., Newis, R., Cannizzaro, C., Burwell, C., Smith, T., Leonhardt, S. D., Kämper, W., & Wallace, H. M. (2021). Pollen diets and niche overlap of honey bees and native bees in protected areas. *Basic and Applied Ecology*, *50*, 169–180. https://doi.org/10.1016/j.baae.2020.12.002

Ellis, K. E., & Barbercheck, M. E. (2015). Management of Overwintering Cover Crops Influences Floral Resources and Visitation by Native Bees. *Environmental Entomology*, *44*(4), 999–1010. https://doi.org/10.1093/ee/nvv086

Elwell, S. L., Griswold, T., & Elle, E. (2016). Habitat type plays a greater role than livestock grazing in structuring shrubsteppe plant–pollinator communities. *Journal of Insect Conservation*, *20*(3), 515–525. https://doi.org/10.1007/s10841-016-9884-8

Elzay, S. D., & Baum, K. A. (2021). Landscape characteristics predict body sizes in wild bees: Implications for pollination services and foraging range. *Journal of Insect Conservation*. https://doi.org/10.1007/s10841-021-00294-y

Feltham, H., Park, K., Minderman, J., & Goulson, D. (2015). Experimental evidence that wildflower strips increase pollinator visits to crops. *Ecology and Evolution*, *5*(16), 3523–3530. https://doi.org/10.1002/ece3.1444

Filipiak, M. (2018). A Better Understanding of Bee Nutritional Ecology Is Needed to Optimize Conservation Strategies for Wild Bees—The Application of Ecological Stoichiometry. *Insects*, *9*(3), 85. https://doi.org/10.3390/insects9030085

Fisogni, A., Hautekèete, N., Piquot, Y., Brun, M., Vanappelghem, C., Michez, D., & Massol, F. (2020). Urbanization drives an early spring for plants but not for pollinators. *Oikos*, *129*(11), 1681–1691. https://doi.org/10.1111/oik.07274

Foley, C. A., & Faust, L. J. (2010). Rapid population growth in an elephant Loxodonta africana population recovering from poaching in Tarangire National Park, Tanzania. *Oryx*, *44*(2), 205–212. https://doi.org/10.1017/S0030605309990706

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., Gibbs, H. K., Helkowski, J. H., Holloway, T., Howard, E. A., Kucharik, C. J., Monfreda, C., Patz, J. A., Prentice, I. C., Ramankutty, N., & Snyder, P. K. (2005). Global Consequences of Land Use. *Science*, *309*(5734), 570–574. https://doi.org/10.1126/science.1111772

Fontaine, C., Collin, C. L., & Dajoz, I. (2008). Generalist foraging of pollinators: Diet expansion at high density. *Journal of Ecology*, *96*(5), 1002–1010. https://doi.org/10.1111/j.1365-2745.2008.01405.x

Fründ, J., Linsenmair, K. E., & Blüthgen, N. (2010). Pollinator diversity and specialization in relation to flower diversity. *Oikos*, *119*(10), 1581–1590. https://doi.org/10.1111/j.1600-0706.2010.18450.x

Garibaldi, L. A., Carvalheiro, L. G., Leonhardt, S. D., Aizen, M. A., Blaauw, B. R., Isaacs, R., Kuhlmann, M., Kleijn, D., Klein, A. M., Kremen, C., Morandin, L., Scheper, J., & Winfree, R. (2014). From research to action: Enhancing crop yield through wild pollinators. *Frontiers in Ecology and the Environment*, *12*(8), 439–447. https://doi.org/10.1890/130330

Garrity, D. P., Akinnifesi, F. K., Ajayi, O. C., Weldesemayat, S. G., Mowo, J. G., Kalinganire, A., Larwanou, M., & Bayala, J. (2010). Evergreen Agriculture: A robust approach to sustainable food security in Africa. *Food Security*, *2*(3), 197–214. https://doi.org/10.1007/s12571-010-0070-7

Gebrechorkos, S. H., Hülsmann, S., & Bernhofer, C. (2019a). Changes in temperature and precipitation extremes in Ethiopia, Kenya, and Tanzania. *International Journal of Climatology*, *39*(1), 18–30. https://doi.org/10.1002/joc.5777

Gebrechorkos, S. H., Hülsmann, S., & Bernhofer, C. (2019b). Long-term trends in rainfall and temperature using high-resolution climate datasets in East Africa. *Scientific Reports*, *9*. https://doi.org/10.1038/s41598-019-47933-8

Gemmill-Herren, B., Aidoo, K., Kwapong, P., Martins, D., Kinuthia, W., & Eardley, C. (2014). Priorities for research and development in the management of pollination services for agriculture in Africa. 12.

Gilpin, A.-M., Denham, A. J., & Ayre, D. J. (2019). Are there magnet plants in Australian ecosystems: Pollinator visits to neighbouring plants are not affected by proximity to mass flowering plants. *Basic and Applied Ecology*, *35*, 34–44. https://doi.org/10.1016/j.baae.2018.12.003

Goulson, D. (2010). *Bumblebees: Behaviour, Ecology, and Conservation*. OUP Oxford.

Goulson, D., Nicholls, E., Botías, C., & Rotheray, E. L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, *347*(6229). https://doi.org/10.1126/science.1255957

Graitson, E., Ursenbacher, S., & Lourdais, O. (2020). Snake conservation in anthropized landscapes: Considering artificial habitats and questioning management of semi-natural habitats. *European Journal of Wildlife Research*, *66*(3), 39. https://doi.org/10.1007/s10344-020-01373-2

Greenleaf, S. S., Williams, N. M., Winfree, R., & Kremen, C. (2007). Bee foraging ranges and their relationship to body size. *Oecologia*, *153*(3), 589–596. https://doi.org/10.1007/s00442-007-0752-9

Grime, J. P. (1973). Competitive Exclusion in Herbaceous Vegetation. *Nature*, *242*(5396), 344–347. https://doi.org/10.1038/242344a0

Guenat, S., Kunin, W. E., Dougill, A. J., & Dallimer, M. (2019). Effects of urbanisation and management practices on pollinators in tropical Africa. *Journal of Applied Ecology*, *56*(1), 214–224. https://doi.org/10.1111/1365-2664.13270

Hall, R. M., Penke, N., Kriechbaum, M., Kratschmer, S., Jung, V., Chollet, S., Guernion, M., Nicolai, A., Burel, F., Fertil, A., Lora, Á., Sánchez-Cuesta, R., Guzmán, G., Gómez, J., Popescu, D., Hoble, A., Bunea, C.-I., Zaller, J. G., & Winter, S. (2020). Vegetation management intensity and landscape diversity alter plant species richness, functional traits and community composition across European vineyards. *Agricultural Systems*, *177*, 102706. https://doi.org/10.1016/j.agsy.2019.102706

Hamblin, A. L., Youngsteadt, E., & Frank, S. D. (2018). Wild bee abundance declines with urban warming, regardless of floral density. *Urban Ecosystems*, *21*(3), 419–428. https://doi.org/10.1007/s11252-018-0731-4

Hamisi, I. (2016). *Diversity, status and threats to stingless bees (Apidae: Meliponini) of Ipembampazi Forest Reserve, Tabora - Tanzania* [Thesis, Sokoine University of Agriculture]. http://www.suaire.sua.ac.tz/handle/123456789/1533

Hanley, N., Breeze, T. D., Ellis, C., & Goulson, D. (2015). Measuring the economic value of pollination services: Principles, evidence and knowledge gaps. *Ecosystem Services*, *14*, 124–132. https://doi.org/10.1016/j.ecoser.2014.09.013

Hegland, S. J., & Boeke, L. (2006). Relationships between the density and diversity of floral resources and flower visitor activity in a temperate grassland community. *Ecological Entomology*, *31*(5), 532–538. https://doi.org/10.1111/j.1365-2311.2006.00812.x

Hennig, E. I., & Ghazoul, J. (2012). Pollinating animals in the urban environment. *Urban Ecosystems*, *15*(1), 149–166. https://doi.org/10.1007/s11252-011-0202-7

Herrero-Jáuregui, C., & Oesterheld, M. (2018). Effects of grazing intensity on plant richness and diversity: A meta-analysis. *Oikos*, *127*(6), 757–766. https://doi.org/10.1111/oik.04893

Hoiss, B., Gaviria, J., Leingärtner, A., Krauss, J., & Steffan-Dewenter, I. (2013). Combined effects of climate and management on plant diversity and pollination type in alpine grasslands. *Diversity and Distributions*, *19*(4), 386–395. https://doi.org/10.1111/j.1472-4642.2012.00941.x

Hopfenmüller, S., Holzschuh, A., & Steffan-Dewenter, I. (2020). Effects of grazing intensity, habitat area and connectivity on snail-shell nesting bees. *Biological Conservation*, *242*, 108406. https://doi.org/10.1016/j.biocon.2020.108406

H.J. de Blij and P.O. Miller. 1996. Physical Geography of the Global Environment. John Wiley, New York. Pp. 290.

Identification guides and checklists of plants and animals—Discover Life. Retrieved November 4, 2021, from https://www.discoverlife.org/mp/20q?%20guide=Apoidea_species&flags=HAS:

Ings, T. C., Montoya, J. M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C. F., Edwards, F., Figueroa, D., Jacob, U., Jones, J. I., Lauridsen, R. B., Ledger, M. E., Lewis, H. M., Olesen, J. M., Van Veen, F. J. F., Warren, P. H., & Woodward, G. (2009). Review: Ecological networks – beyond food webs. *Journal of Animal Ecology*, *78*(1), 253–269. https://doi.org/10.1111/j.1365-2656.2008.01460.x

Jönsson, A. M., Ekroos, J., Dänhardt, J., Andersson, G. K. S., Olsson, O., & Smith, H. G. (2015). Sown flower strips in southern Sweden increase abundances of wild bees and hoverflies in the wider landscape. *Biological Conservation*, *184*, 51–58. https://doi.org/10.1016/j.biocon.2014.12.027

Kadengye, D. T., Cools, W., Ceulemans, E., & Van den Noortgate, W. (2012). Simple imputation methods versus direct likelihood analysis for missing item scores in multilevel educational data. *Behavior Research Methods*, *44*(2), 516–531. https://doi.org/10.3758/s13428-011-0157-x

Kaiser-Bunbury, C. N., & Blüthgen, N. (2015). Integrating network ecology with applied conservation: A synthesis and guide to implementation. *AoB PLANTS*, *7*(plv076). https://doi.org/10.1093/aobpla/plv076

Kammerer, M., Goslee, S. C., Douglas, M. R., Tooker, J. F., & Grozinger, C. M. (2021). Wild bees as winners and losers: Relative impacts of landscape composition, quality, and climate. *Global Change Biology*, *27*(6), 1250–1265. https://doi.org/10.1111/gcb.15485

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth’s land surface areas. *Scientific Data*, *4*(1), 170122. https://doi.org/10.1038/sdata.2017.122

Kearns, C. A., & Oliveras, D. M. (2009). Environmental factors affecting bee diversity in urban and remote grassland plots in Boulder, Colorado. *Journal of Insect Conservation*, *13*(6), 655–665. https://doi.org/10.1007/s10841-009-9215-4

Kershaw, H. M., & Mallik, A. U. (2013). Predicting plant diversity response to disturbance: Applicability of the intermediate disturbance hypothesis and mass ratio hypothesis. *Critical Reviews in Plant Sciences*, *32*(6), 383–395. https://doi.org/10.1080/07352689.2013.791501

Kijne, J. W., Barker, R., & Molden, D. J. (2003). *Water Productivity in Agriculture: Limits and Opportunities for Improvement*. CABI.

Kim, J., Williams, N., & Kremen, C. (2006). Effects of Cultivation and Proximity to Natural Habitat on Ground-nesting Native Bees in California Sunflower Fields. *Journal of the Kansas Entomological Society*, *79*(4), 309–320. https://doi.org/10.2317/0507.11.1

Kimoto, C., DeBano, S. J., Thorp, R. W., Taylor, R. V., Schmalz, H., DelCurto, T., Johnson, T., Kennedy, P. L., & Rao, S. (2012). Short-term responses of native bees to livestock and implications for managing ecosystem services in grasslands. *Ecosphere*, *3*(10), 1–19. https://doi.org/10.1890/ES12-00118.1

Klein, A.-M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1608), 303–313. https://doi.org/10.1098/rspb.2006.3721

Koh, I., Lonsdorf, E. V., Williams, N. M., Brittain, C., Isaacs, R., Gibbs, J., & Ricketts, T. H. (2016). Modeling the status, trends, and impacts of wild bee abundance in the United States. *Proceedings of the National Academy of Sciences*, *113*(1), 140–145. https://doi.org/10.1073/pnas.1517685113

Kovács-Hostyánszki, A., Espíndola, A., Vanbergen, A. J., Settele, J., Kremen, C., & Dicks, L. V. (2017). Ecological intensification to mitigate impacts of conventional intensive land use on pollinators and pollination. *Ecology Letters*, *20*(5), 673–689. https://doi.org/10.1111/ele.12762

Lasway, J., Kinabo, N., Mremi, R., Martin, E., Nyakunga, O., Sanya, J., Pauly, A., Eardly, C., Rwegasira, G., Lesio, N., Peters, M., Stefan-Dewenter, I., & Njovu, H. (2021a). *Occurrence of Bee Pollinator species along agricultural and grazing gradient in Northern Tanzania*. https://doi.org/10.15468/hdcdf3

Lasway, J. V., Kinabo, N. R., Mremi, R. F., Martin, E. H., Nyakunga, O. C., Sanya, J. J., Rwegasira, G. M., Lesio, N., Gideon, H., Pauly, A., Eardley, C., Peters, M. K., Peterson, A. T., Steffan-Dewenter, I., & Njovu, H. K. (2021b). A synopsis of the Bee occurrence data of northern Tanzania. *Biodiversity Data Journal*, *9*, e68190. https://doi.org/10.3897/BDJ.9.e68190

Laurance, W. F., Sayer, J., & Cassman, K. G. (2014). Agricultural expansion and its impacts on tropical nature. *Trends in Ecology & Evolution*, *29*(2), 107–116. https://doi.org/10.1016/j.tree.2013.12.001

Lazaro, A., Tscheulin, T., Devalez, J., Nakas, G., & Petanidou, T. (2016). Effects of grazing intensity on pollinator abundance and diversity, and on pollination services. *Ecological Entomology*, *41*(4), 400–412. https://doi.org/10.1111/een.12310

Lázaro, A., Tscheulin, T., Devalez, J., Nakas, G., Stefanaki, A., Hanlidou, E., & Petanidou, T. (2016). Moderation is best: Effects of grazing intensity on plant–flower visitor networks in Mediterranean communities. *Ecological Applications*, *26*(3), 796–807. https://doi.org/10.5061/dryad.p3c75

Le Féon, V., Schermann-Legionnet, A., Delettre, Y., Aviron, S., Billeter, R., Bugter, R., Hendrickx, F., & Burel, F. (2010). Intensification of agriculture, landscape composition and wild bee communities: A large scale study in four European countries. *Agriculture, Ecosystems & Environment*, *137*(1), 143–150. https://doi.org/10.1016/j.agee.2010.01.015

Ma, Q., Chai, L., Hou, F., Chang, S., Ma, Y., Tsunekawa, A., & Cheng, Y. (2019). Quantifying grazing intensity using remote sensing in alpine meadows on Qinghai-Tibetan Plateau. *Sustainability (Switzerland)*, *11*(2), 1–14. https://doi.org/10.3390/su11020417

Macgregor, C. J., Kitson, J. J. N., Fox, R., Hahn, C., Lunt, D. H., Pocock, M. J. O., & Evans, D. M. (2019). Construction, validation, and application of nocturnal pollen transport networks in an agro-ecosystem: A comparison using light microscopy and DNA metabarcoding. *Ecological Entomology*, *44*(1), 17–29. https://doi.org/10.1111/een.12674

Mayr, A. V., Peters, M. K., Eardley, C. D., Renner, M. E., Röder, J., & Steffan-Dewenter, I. (2020). Climate and food resources shape species richness and trophic interactions of cavity-nesting Hymenoptera. *Journal of Biogeography*, *47*(4), 854–865. https://doi.org/10.1111/jbi.13753

Michener, C. D. (2007). The Bees of the World (Second., Vol. 1). *Baltimore: The Johns Hopkins University Press. Doi*, *10*.

Millard, J., Outhwaite, C. L., Kinnersley, R., Freeman, R., Gregory, R. D., Adedoja, O., Gavini, S., Kioko, E., Kuhlmann, M., Ollerton, J., Ren, Z.-X., & Newbold, T. (2021). Global effects of land-use intensity on local pollinator biodiversity. *Nature Communications*, *12*(1), 2902. https://doi.org/10.1038/s41467-021-23228-3

Müller, A., Diener, S., Schnyder, S., Stutz, K., Sedivy, C., & Dorn, S. (2006). Quantitative pollen requirements of solitary bees: Implications for bee conservation and the evolution of bee–flower relationships. *Biological Conservation*, *130*(4), 604–615. https://doi.org/10.1016/j.biocon.2006.01.023

Mumbi, C., Mwakatobe, A., Issa, H., Mpinga, Richard, A., Machumu, R., Cassian, T., Mumbi, A., Mwakatobe, Mpinga, A., Richard, R., & Machumu. (2014). Parasitic mite, Varroa species (Parasitiformes: Varroidae) infesting the colonies of African honeybees, Apis mellifera scutellata (Hymenoptera: Apididae) in Tanzania. *Journal of Entomology and Zoology Studies*, *188*, 188–196.

Murray, T. E., Fitzpatrick, Ú., Byrne, A., Fealy, R., Brown, M. J. F., & Paxton, R. J. (2012). Local-scale factors structure wild bee communities in protected areas. *Journal of Applied Ecology*, *49*(5), 998–1008. https://doi.org/10.1111/j.1365-2664.2012.02175.x

Newbold, T., Boakes, E. H., Hill, S. L. L., Harfoot, M. B. J., & Collen, B. (2017). The present and future effects of land use on ecological assemblages in tropical grasslands and savannas in Africa. *Oikos*, *126*(12), 1760–1769. https://doi.org/10.1111/oik.04338

Nicholls, C. I., & Altieri, M. A. (2013). Plant biodiversity enhances bees and other insect pollinators in agroecosystems. A review. *Agronomy for Sustainable Development*, *33*(2), 257–274. https://doi.org/10.1007/s13593-012-0092-y

Njovu, H. K., Peters, M. K., Schellenberger Costa, D., Brandl, R., Kleyer, M., & Steffan-Dewenter, I. (2019). Leaf traits mediate changes in invertebrate herbivory along broad environmental gradients on Mt. Kilimanjaro, Tanzania. *Journal of Animal Ecology*, *88*(11), 1777–1788. https://doi.org/10.1111/1365-2656.13058

Noyes, J. S. (1989). A study of five methods of sampling Hymenoptera (Insecta) in a tropical rainforest, with special reference to the Parasitica. *Journal of Natural History*, *23*(2), 285–298. https://doi.org/10.1080/00222938900770181

Nürnberger, F., Keller, A., Härtel, S., & Steffan-Dewenter, I. (2019). Honey bee waggle dance communication increases diversity of pollen diets in intensively managed agricultural landscapes. *Molecular Ecology*, *28*(15), 3602–3611. https://doi.org/10.1111/mec.15156

Odanaka, K. A., & Rehan, S. M. (2019). Impact indicators: Effects of land use management on functional trait and phylogenetic diversity of wild bees. *Agriculture, Ecosystems & Environment*, *286*, 106663. https://doi.org/10.1016/j.agee.2019.106663

Olesen, J. M., & Jordano, P. (2002). Geographic Patterns in Plant–Pollinator Mutualistic Networks. *Ecology*, *83*(9), 2416–2424. https://doi.org/10.1890/0012-9658(2002)083[2416:GPIPPM]2.0.CO;2

Oliver, T. H., & Morecroft, M. D. (2014). Interactions between climate change and land use change on biodiversity: Attribution problems, risks, and opportunities. *WIREs Climate Change*, *5*(3), 317–335. https://doi.org/10.1002/wcc.271

Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, *120*(3), 321–326. https://doi.org/10.1111/j.1600-0706.2010.18644.x

Orr, M. C., Hughes, A. C., Chesters, D., Pickering, J., Zhu, C.-D., & Ascher, J. S. (2021). Global Patterns and Drivers of Bee Distribution. *Current Biology*, *31*(3), 451-458.e4. https://doi.org/10.1016/j.cub.2020.10.053

Osborne, C. P., Charles-Dominique, T., Stevens, N., Bond, W. J., Midgley, G., & Lehmann, C. E. R. (2018). Human impacts in African savannas are mediated by plant functional traits. *New Phytologist*, *220*(1), 10–24. https://doi.org/10.1111/nph.15236

Otieno, M., Sidhu, C. S., Woodcock, B. A., Wilby, A., Vogiatzakis, I. N., Mauchline, A. L., Gikungu, M. W., & Potts, S. G. (2015). Local and landscape effects on bee functional guilds in pigeon pea crops in Kenya. *Journal of Insect Conservation*, *19*(4), 647–658. https://doi.org/10.1007/s10841-015-9788-z

Ouvrard, P., Transon, J., & Jacquemart, A.-L. (2018). Flower-strip agri-environment schemes provide diverse and valuable summer flower resources for pollinating insects. *Biodiversity and Conservation*, *27*(9), 2193–2216. https://doi.org/10.1007/s10531-018-1531-0

Palma, A. D., Kuhlmann, M., Roberts, S. P. M., Potts, S. G., Börger, L., Hudson, L. N., Lysenko, I., Newbold, T., & Purvis, A. (2015). Ecological traits affect the sensitivity of bees to land-use pressures in European agricultural landscapes. *Journal of Applied Ecology*, *52*(6), 1567–1577. https://doi.org/10.1111/1365-2664.12524

Papanikolaou, A. D., Kühn, I., Frenzel, M., & Schweiger, O. (2017a). Semi-natural habitats mitigate the effects of temperature rise on wild bees. *Journal of Applied Ecology*, *54*(2), 527–536. https://doi.org/10.1111/1365-2664.12763

Papanikolaou, A. D., Kühn, I., Frenzel, M., & Schweiger, O. (2017b). Landscape heterogeneity enhances stability of wild bee abundance under highly varying temperature, but not under highly varying precipitation. *Landscape Ecology*, *32*(3), 581–593. https://doi.org/10.1007/s10980-016-0471-x

Patel, V., Pauli, N., Biggs, E., Barbour, L., & Boruff, B. (2021). Why bees are critical for achieving sustainable development. *Ambio*, *50*(1), 49–59. https://doi.org/10.1007/s13280-020-01333-9

Pauly, A. (1990). Classification of the African Nomiinae (Hymenoptera Apoidea Halictidae). Annales - Musee Royal de l'Afrique Centrale. Sciences Zoologiques (Belgium) *Tervuren*,261 :206 pp., 542 figs.

Pauly, A. (1999). Classification des Halictini de la région afrotropicale (Hymenoptera Apoidea Halictidae). *Bulletin de l'Institut Royal Des Sciences Naturelles de Belgique, Entomologie*, *69*, 137–196.

Peper, J., Jansen, F., Pietzsch, D., & Manthey, M. (2011). Patterns of plant species turnover along grazing gradients. *Journal of Vegetation Science*, *22*(3), 457–466. https://doi.org/10.1111/j.1654-1103.2011.01260.x

Petanidou, T., & Ellis, W. N. (1996). Interdependence of native bee faunas and floras in changing Mediterranean communities. *Linnean Society. Symposia Series*, *18*, 201–226.

Peters, M. K., Hemp, A., Appelhans, T., Becker, J. N., Behler, C., Classen, A., Detsch, F., Ensslin, A., Ferger, S. W., Frederiksen, S. B., Gebert, F., Gerschlauer, F., Gütlein, A., Helbig-Bonitz, M., Hemp, C., Kindeketa, W. J., Kühnel, A., Mayr, A. V., Mwangomo, E., … Steffan-Dewenter, I. (2019). Climate–land-use interactions shape tropical mountain biodiversity and ecosystem functions. *Nature*, *568*(7750), 88–92. https://doi.org/10.1038/s41586-019-1048-z

Pornon, A., Baksay, S., Escaravage, N., Burrus, M., & Andalo, C. (2019). Pollinator specialization increases with a decrease in a mass-flowering plant in networks inferred from DNA metabarcoding. *Ecology and Evolution*, *9*(24), 13650–13662. https://doi.org/10.1002/ece3.5531

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology & Evolution*, *25*(6), 345–353. https://doi.org/10.1016/j.tree.2010.01.007

Potts, S. G., Imperatriz-Fonseca, V., Ngo, H. T., Aizen, M. A., Biesmeijer, J. C., Breeze, T. D., Dicks, L. V., Garibaldi, L. A., Hill, R., Settele, J., & Vanbergen, A. J. (2016). Safeguarding pollinators and their values to human well-being. *Nature*, *540*(7632), 220–229. https://doi.org/10.1038/nature20588

Potts, S. G., Vulliamy, B., Dafni, A., Ne'eman, G., & Willmer, P. (2003). Linking Bees and Flowers: How Do Floral Communities Structure Pollinator Communities? *Ecology*, *84*(10), 2628–2642. https://doi.org/10.1890/02-0136

Potts, S. G., Woodcock, B. A., Roberts, S. P. M., Tscheulin, T., Pilgrim, E. S., Brown, V. K., & Tallowin, J. R. (2009). Enhancing pollinator biodiversity in intensive grasslands. *Journal of Applied Ecology*, *46*(2), 369–379. https://doi.org/10.1111/j.1365-2664.2009.01609.x

Prado, S. G., Ngo, H. T., Florez, J. A., & Collazo, J. A. (2017). Sampling bees in tropical forests and agroecosystems: A review. *Journal of Insect Conservation*, *21*(5–6), 753–770.

Prendergast, K. S., Menz, M. H. M., Dixon, K. W., & Bateman, P. W. (2020). The relative performance of sampling methods for native bees: An empirical test and review of the literature. *Ecosphere*, *11*(5), e03076. https://doi.org/10.1002/ecs2.3076

Puurtinen, M., Elo, M., Jalasvuori, M., Kahilainen, A., Ketola, T., Kotiaho, J. S., Mönkkönen, M., & Pentikäinen, O. T. (2016). Temperature-dependent mutational robustness can explain faster molecular evolution at warm temperatures, affecting speciation rate and global patterns of species diversity. *Ecography*, *39*(11), 1025–1033. https://doi.org/10.1111/ecog.01948

Rader, R., Edwards, W., Westcott, D. A., Cunningham, S. A., & Howlett, B. G. (2011). Pollen transport differs among bees and flies in a human-modified landscape. *Diversity and Distributions*, *17*(3), 519–529. https://doi.org/10.1111/j.1472-4642.2011.00757.x

Ramankutty, N., Mehrabi, Z., Waha, K., Jarvis, L., Kremen, C., Herrero, M., & Rieseberg, L. H. (2018). Trends in Global Agricultural Land Use: Implications for Environmental Health and Food Security. *Annual Review of Plant Biology*, *69*(1), 789–815. https://doi.org/10.1146/annurev-arplant-042817-040256

Ratnam, J., Bond, W. J., Fensham, R. J., Hoffmann, W. A., Archibald, S., Lehmann, C. E. R., Anderson, M. T., Higgins, S. I., & Sankaran, M. (2011). When is a 'forest' a savanna, and why does it matter? *Global Ecology and Biogeography*, *20*(5), 653–660. https://doi.org/10.1111/j.1466-8238.2010.00634.x

Requier, F., & Leonhardt, S. D. (2020). Beyond flowers: Including non-floral resources in bee conservation schemes. *Journal of Insect Conservation*, *24*(1), 5–16. https://doi.org/10.1007/s10841-019-00206-1

Rojas-Downing, M. M., Nejadhashemi, A. P., Harrigan, T., & Woznicki, S. A. (2017). Climate change and livestock: Impacts, adaptation, and mitigation. *Climate Risk Management*, *16*, 145–163. https://doi.org/10.1016/j.crm.2017.02.001

Rollin, O., Pérez-Méndez, N., Bretagnolle, V., & Henry, M. (2019). Preserving habitat quality at local and landscape scales increases wild bee diversity in intensive farming systems. *Agriculture, Ecosystems & Environment*, *275*, 73–80. https://doi.org/10.1016/j.agee.2019.01.012

Rota, C., Manzano, P., Carmona, C. P., Malo, J. E., & Peco, B. (2017). Plant community assembly in Mediterranean grasslands: Understanding the interplay between grazing and spatio-temporal water availability. *Journal of Vegetation Science*, *28*(1), 149–159. https://doi.org/10.1111/jvs.12470

Roulston, T. H., & Goodell, K. (2011). The Role of Resources and Risks in Regulating Wild Bee Populations. *Annual Review of Entomology*, *56*(1), 293–312. https://doi.org/10.1146/annurev-ento-120709-144802

Rowhani, P., Lobell, D. B., Linderman, M., & Ramankutty, N. (2011). Climate variability and crop production in Tanzania. *Agricultural and Forest Meteorology*, *151*(4), 449–460. https://doi.org/10.1016/j.agrformet.2010.12.002

Sanaei, A., Ali, A., & Chahouki, M. A. Z. (2018). The positive relationships between plant coverage, species richness, and aboveground biomass are ubiquitous across plant growth forms in semi-steppe rangelands. *Journal of Environmental Management*, *205*, 308–318. https://doi.org/10.1016/j.jenvman.2017.09.079

Sanchez-Bayo, F., & Goka, K. (2014). Pesticide Residues and Bees – A Risk Assessment. *PLOS ONE*, *9*(4), e94482. https://doi.org/10.1371/journal.pone.0094482

Saunders, M. E., Janes, J. K., & O'Hanlon, J. C. (2020). Moving On from the Insect Apocalypse Narrative: Engaging with Evidence-Based Insect Conservation. *BioScience*, *70*(1), 80–89. https://doi.org/10.1093/biosci/biz143

Sawe, T., Nielsen, A., & Eldegard, K. (2020). Crop Pollination in Small-Scale Agriculture in Tanzania: Household Dependence, Awareness and Conservation. *Sustainability*, *12*(6), 2228. https://doi.org/10.3390/su12062228

Sawe, T., Nielsen, A., Totland, Ø., Macrice, S., & Eldegard, K. (2020). Inadequate pollination services limit watermelon yields in northern Tanzania. *Basic and Applied Ecology*, *44*, 35–45. https://doi.org/10.1016/j.baae.2020.02.004

Shapira, T., Henkin, Z., Dag, A., & Mandelik, Y. (2020). Rangeland sharing by cattle and bees: Moderate grazing does not impair bee communities and resource availability. *Ecological Applications*, *30*(3), e02066. https://doi.org/10.1002/eap.2066

Shipley, B. (2016). *Cause and correlation in biology: A user's guide to path analysis, structural equations and causal inference with R*. Cambridge University Press.

Skarpe, C. (1996). Plant functional types and climate in a southern African savanna. *Journal of Vegetation Science*, *7*(3), 397–404. https://doi.org/10.2307/3236283

Sloat, L. L., Davis, S. J., Gerber, J. S., Moore, F. C., Ray, D. K., West, P. C., & Mueller, N. D. (2020). Climate adaptation by crop migration. *Nature Communications*, *11*(1), 1243. https://doi.org/10.1038/s41467-020-15076-4

Smith, M. R., Singh, G. M., Mozaffarian, D., & Myers, S. S. (2015). Effects of decreases of animal pollinators on human nutrition and global health: A modelling analysis. *The Lancet*, *386*(10007), 1964–1972. https://doi.org/10.1016/S0140-6736(15)61085-6

Soroye, P., Newbold, T., & Kerr, J. (2020). Climate change contributes to widespread declines among bumble bees across continents. *Science*, *367*(6478), 685–688. https://doi.org/10.1126/science.aax8591

Spafford, R. D., & Lortie, C. J. (2013). Sweeping beauty: Is grassland arthropod community composition effectively estimated by sweep netting? *Ecology and Evolution*, *3*(10), 3347–3358. https://doi.org/10.1002/ece3.688

Ssymank, A., Kearns, C. A., Pape, T., & Thompson, F. C. (2008). Pollinating Flies (Diptera): A major contribution to plant diversity and agricultural production. *Biodiversity*, *9*(1–2), 86–89. https://doi.org/10.1080/14888386.2008.9712892

Steffan-Dewenter, I., & Tscharntke, T. (2001). Succession of bee communities on fallows. *Ecography*, *24*(1), 83–93. https://doi.org/10.1034/j.1600-0587.2001.240110.x

Steffan-Dewenter, I., & Westphal, C. (2008). The interplay of pollinator diversity, pollination services and landscape change. *Journal of Applied Ecology*, *45*(3), 737–741. https://doi.org/10.1111/j.1365-2664.2008.01483.x

Stein, K., Coulibaly, D., Stenchly, K., Goetze, D., Porembski, S., Lindner, A., Konaté, S., & Linsenmair, E. K. (2017). Bee pollination increases yield quantity and quality of cash crops in Burkina Faso, West Africa. *Scientific Reports*, *7*(1), 17691. https://doi.org/10.1038/s41598-017-17970-2

Stein, K., Stenchly, K., Coulibaly, D., Pauly, A., Dimobe, K., Steffan-Dewenter, I., Konaté, S., Goetze, D., Porembski, S., & Linsenmair, K. E. (2018). Impact of human disturbance on bee pollinator communities in savanna and agricultural sites in Burkina Faso, West Africa. *Ecology and Evolution*, *8*(13), 6827–6838. https://doi.org/10.1002/ece3.4197

Stephen, W. P., & Rao, S. (2007). Sampling Native Bees in Proximity to a Highly Competitive Food Resource (Hymenoptera: Apiformes). *Journal of the Kansas Entomological Society*, *80*(4), 369–376. https://doi.org/10.2317/0022-8567(2007)80[369:SNBIPT]2.0.CO;2

Sulemana, I., Nketiah-Amponsah, E., Codjoe, E. A., & Andoh, J. A. N. (2019). Urbanization and income inequality in Sub-Saharan Africa. *Sustainable Cities and Society*, *48*, 101544. https://doi.org/10.1016/j.scs.2019.101544

Sunday, J. M., Bates, A. E., Kearney, M. R., Colwell, R. K., Dulvy, N. K., Longino, J. T., & Huey, R. B. (2014). Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the National Academy of Sciences*, *111*(15), 5610–5615. https://doi.org/10.1073/pnas.1316145111

Sutter, L., Jeanneret, P., Bartual, A. M., Bocci, G., & Albrecht, M. (2017). Enhancing plant diversity in agricultural landscapes promotes both rare bees and dominant crop-pollinating bees through complementary increase in key floral resources. *Journal of Applied Ecology*, *54*(6), 1856–1864. https://doi.org/10.1111/1365-2664.12907

Svensson, J. R., Lindegarth, M., Jonsson, P. R., & Pavia, H. (2012). Disturbance–diversity models: What do they really predict and how are they tested? *Proceedings of the Royal*

Society B: Biological Sciences, *279*(1736), 2163–2170. https://doi.org/10.1098/rspb.2011.2620

Tadey, M. (2015). Indirect effects of grazing intensity on pollinators and floral visitation. *Ecological Entomology*, *40*(4), 451–460. https://doi.org/10.1111/een.12209

Theodorou, P., Baltz, L. M., Paxton, R. J., & Soro, A. (2021). Urbanization is associated with shifts in bumblebee body size, with cascading effects on pollination. *Evolutionary Applications*, *14*(1), 53–68. https://doi.org/10.1111/eva.13087

Tommasi, N., Biella, P., Guzzetti, L., Lasway, J. V., Njovu, H. K., Tapparo, A., Agostinetto, G., Peters, M. K., Steffan-Dewenter, I., Labra, M., & Galimberti, A. (2021). Impact of land use intensification and local features on plants and pollinators in Sub-Saharan smallholder farms. *Agriculture, Ecosystems & Environment*, *319*, 107560. https://doi.org/10.1016/j.agee.2021.107560

Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters*, *8*(8), 857–874. https://doi.org/10.1111/j.1461-0248.2005.00782.x

Tucker, E. M., & Rehan, S. M. (2017). Wild Bee Community Assemblages Across Agricultural Landscapes1. *Journal of Agricultural and Urban Entomology*, *33*(1), 77–104. https://doi.org/10.3954/1523-5475-33.1.77

Tur, C., Olesen, J. M., & Traveset, A. (2015). Increasing modularity when downscaling networks from species to individuals. *Oikos*, *124*(5), 581–592. https://doi.org/10.1111/oik.01668

Verhulst, J., Báldi, A., & Kleijn, D. (2004). Relationship between land-use intensity and species richness and abundance of birds in Hungary. *Agriculture, Ecosystems & Environment*, *104*(3), 465–473. https://doi.org/10.1016/j.agee.2004.01.043

Vesk, P. A., & Westoby, M. (2001). Predicting plant species' responses to grazing. *Journal of Applied Ecology*, *38*(5), 897–909. https://doi.org/10.1046/j.1365-2664.2001.00646.x

Vrdoljak, S. M., Samways, M. J., & Simaika, J. P. (2016). Pollinator conservation at the local scale: Flower density, diversity and community structure increase flower visiting insect activity to mixed floral stands. *Journal of Insect Conservation*, *20*(4), 711–721. https://doi.org/10.1007/s10841-016-9904-8

Vulliamy, B., G. Potts, S., & G. Willmer, P. (2006). The effects of cattle grazing on plant-pollinator communities in a fragmented Mediterranean landscape. *Oikos*, *114*(3), 529–543. https://doi.org/10.1111/j.2006.0030-1299.14004.x

Weiner, C. N., Werner, M., Linsenmair, K. E., & Blüthgen, N. (2011). Land use intensity in grasslands: Changes in biodiversity, species composition and specialisation in flower visitor networks. *Basic and Applied Ecology*, *12*(4), 292–299. https://doi.org/10.1016/j.baae.2010.08.006

Westphal, C., Bommarco, R., Carré, G., Lamborn, E., Morison, N., Petanidou, T., Potts, S. G., Roberts, S. P. M., Szentgyörgyi, H., Tscheulin, T., Vaissière, B. E., Woyciechowski, M., Biesmeijer, J. C., Kunin, W. E., Settele, J., & Steffan-Dewenter, I. (2008). Measuring Bee Diversity in Different European Habitats and Biogeographical Regions. *Ecological Monographs*, *78*(4), 653–671. https://doi.org/10.1890/07-1292.1

Williams, N. M., Crone, E. E., Roulston, T. H., Minckley, R. L., Packer, L., & Potts, S. G. (2010). Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation*, *143*(10), 2280–2291. https://doi.org/10.1016/j.biocon.2010.03.024

Williams, N., Minckley, R., & Silveira, F. (2001). Variation in Native Bee Faunas and its Implications for Detecting Community Changes. *Conservation Ecology*, *5*(1). https://doi.org/10.5751/ES-00259-050107

Winfree, R. (2010). The conservation and restoration of wild bees: Wild bee conservation. *Annals of the New York Academy of Sciences*, *1195*(1), 169–197. https://doi.org/10.1111/j.1749-6632.2010.05449.x

Winfree, R., Aguilar, R., Vázquez, D. P., LeBuhn, G., & Aizen, M. A. (2009). A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology*, *90*(8), 2068–2076. https://doi.org/10.1890/08-1245.1

Winfree, R., Bartomeus, I., & Cariveau, D. P. (2011). Native Pollinators in Anthropogenic Habitats. *Annual Review of Ecology, Evolution, and Systematics*, *42*(1), 1–22. https://doi.org/10.1146/annurev-ecolsys-102710-145042

Wright, I. R., Roberts, S. P. M., & Collins, B. E. (2015). Evidence of forage distance limitations for small bees (Hymenoptera: Apidae). *European Journal of Entomology*, *112*(2), 303–310. https://doi.org/10.14411/eje.2015.028

Yi, Z., Jinchao, F., Dayuan, X., Weiguo, S., & Axmacher, J. C. (2012). A Comparison of Terrestrial Arthropod Sampling Methods. *Journal of Resources and Ecology*, *3*(2), 174–182. https://doi.org/10.5814/j.issn.1674-764x.2012.02.010

Yoshihara, Y., Chimeddorj, B., Buuveibaatar, B., Lhagvasuren, B., & Takatsuki, S. (2008). Effects of livestock grazing on pollination on a steppe in eastern Mongolia. *Biological Conservation*, *141*(9), 2376–2386. https://doi.org/10.1016/j.biocon.2008.07.004

Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S., & Dorn, S. (2010). Maximum foraging ranges in solitary bees: Only few individuals have the capability to cover long foraging distances. *Biological Conservation*, *143*(3), 669–676. https://doi.org/10.1016/j.biocon.2009.12.003

Authors' contribution

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Authors' contribution: Ingolf Steffan-Dewenter, **Marcell K. Peters**, and **Henry K. Njovu** conceived the ideas and design methodology; **Julius Vincent Lasway** collected the data; **Alain Pauly** identify the collected bee specimens; **Julius V. Lasway, Neema R. Kinabo** and **Rudolf F. Mremi** organized the data; **Julius V. Lasway** led the writing of the manuscript with input from **Neema R. Kinabo**, **Rudolf F. Mremi**, **Emanuel H. Martin**, **Oliver C. Nyakunga**, **John J. Sanya**, **Gration M. Rwegasira**, **Nicephor Lesio**, **Hulda Gideon**, **Alain Pauly**, **Connal Eardley**, and **Andrew T. Peterson**. All authors contributed critically to the drafts and gave final approval for the publication.

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Publication List

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Julius V. Lasway*, Neema R. Kinabo, Rudolf F. Mremi, Emmanuel H. Martin, Oliver C. Nyakunga, John Sanya, Gration M. Rwegasira, Nicephor Lesio, Hulda Gideon, Alain Pauly, Connal Eardley, Marcell K. Peters, Andrew T. Peterson, Ingolf Steffan-Dewenter, Henry K Njovu., (2021). **A synopsis of the Bee occurrence data of Northern Tanzania**. ***Biodiversity Data Journal*** https://doi.org/10.3897/BDJ.9.e68190

Other publications

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Julius V. Lasway*, Henry H. Njovu, Marcell K. Peters, Oliver O. Nyakunga, Emmanuel H. Martin, Neema R. Kinabo, John S. Julius, Rudolf F. Mremi, Alain Pauly, Connal Eardley and Ingolf Steffan-Dewenter., (2021). **Bees of Northern Tanzania**. **GBIF**, DOI: https://doi.org/10.15468/o3tmyw

Julius V. Lasway*, Henry K. Njovu, Neema R. Kinabo, Abraham Eustace, Karen Marie Mathisen, Christina Skarpe, and Marcell K. Peters., (2021). **Species richness, Vegetation structure and floristic composition of woody plants along the elevation gradient of Mt. Meru, Tanzania**. ***Submitted to African Journal of Ecology***, (Reference Number: AFJE-20-426.R1) (Under review).

Wilfred Kalumuna*, **Julius V. Lasway**, Gideon A. Mseja**,** and Henry K. Njovu. **Effects of farming systems on the foliar herbivory of *Coffea arabica* on the slopes of Mt. Kilimanjaro, Tanzania**. ***In preparation for submission to Agroecology and Sustainable food systems Journal.***

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