

2023-07-17

Insect visitation and pollination networks across traditional rangeland management categories in a Northern Tanzanian rangeland

Mpondo, Faith

Elsevier B.V.

<https://doi.org/10.1016/j.gecco.2023.e02581>

Provided with love from The Nelson Mandela African Institution of Science and Technology

Contents lists available at [ScienceDirect](https://www.sciencedirect.com)

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Insect visitation and pollination networks across traditional rangeland management categories in a Northern Tanzanian rangeland

Faith T. Mpondo^{a,b,*}, Patrick A. Ndakidemi^b, Shelard C. Mukama^c,
Anna C. Treydte^{b,d,e}

^a Department of Biology, College of Natural and Mathematical Sciences, University of Dodoma, P.O. Box 338, Dodoma, Tanzania

^b Department of Sustainable Agriculture, Biodiversity Conservation and Ecosystem Management, School of Life Sciences and Bioengineering, The Nelson Mandela African Institution of Science and Technology, (NM-AIST), P.O. Box 447, Arusha, Tanzania

^c Department of Environmental Studies, The Open University of Tanzania, P.O. Box 1944 Dar es Salaam, Tanzania

^d Department of Ecology of Tropical Agricultural Systems, Hans-Ruthenberg Institute, University of Hohenheim, Garbenstr. 13, 70599 Stuttgart, Germany

^e Department of Physical Geography, Stockholm University, Svante Arrhenius väg 8, 106 91 Stockholm, Sweden

ARTICLE INFO

Keywords:

Flower visitors
Semi-arid
Insect conservation
Pollinator networks
Plant interaction
Ecosystem service
Eastern Africa

ABSTRACT

The structure of pollination networks is critical to ecosystem stability and functioning. We investigated pollinator-plant interactions to understand the foraging preference and develop pollination networks in a semi-arid rangeland of different grazing management categories in Tanzania. Along three line transects, each measuring 100 m, in each of the four grazing management categories (private and communal enclosures, wet and dry season grazing areas), we laid out three quadrats measuring 5 m x 5 m (25 m²) located 30 m apart. We recorded insects visiting flowering plants for two consecutive days in each quadrat every week at each site from April to May, in 2019 and 2020. *Aspilota mossambicensis* received the most significant proportion of insect visitors (28%), followed by *Justicia debile* (21%). The mean protein concentration in sampled pollen varied significantly between plant species ($\chi^2 = 25.9$, $P = 0.001$), with *Solanum incanum* containing the highest concentration (299.3 ± 0.68 g/100 g). We did not notice any correlation between honey bee visitation and protein concentration in pollen ($r = -0.471$, $P = 0.239$) nor with fatty acids concentration ($r = 0.253$, $P = 0.546$). When comparing pollinator-plant network properties including connectance, nestedness, robustness, number of links, modularity, network diversity and linkage density across rangeland management, we found that the private enclosure contained significantly larger networks than the communal enclosure, the dry and the wet season grazing sites. We conclude that particularly private enclosures are vital to promote pollination networks in our studied rangeland system as they include important pollinator forage plants.

* Corresponding author at: Department of Biology, College of Natural and Mathematical Sciences, University of Dodoma, P.O. Box 338, Dodoma, Tanzania.

E-mail address: chypo08@gmail.com (F.T. Mpondo).

<https://doi.org/10.1016/j.gecco.2023.e02581>

Received 31 December 2022; Received in revised form 3 July 2023; Accepted 16 July 2023

Available online 17 July 2023

2351-9894/© 2023 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

Pollination is an essential mutualistic interaction necessary for the reproduction of many cultivated crops, native forbs and an array of other flowering plants (Kelly and Elle, 2020; Ratto et al., 2018; Ollerton et al., 2011). Interactions between pollinators and flowering plants in a community are represented by network graphs that allow the visualization of interaction patterns that can be measured, predicted, and compared (Bascompte and Jordano, 2014). These graphs may therefore be used to predict what might happen to a community if the conditions change (Dormann et al., 2009); therefore, the structure of a pollination network is a crucial predictor of ecosystem stability and functioning (Lázaro et al., 2016). Furthermore, understanding pollinator networks is vital due to the growing evidence that many pollinator populations worldwide are declining (Potts et al., 2010; Tylianakis et al., 2010; Vanbergen and Initiative, 2013).

Pollinator networks possess conservative properties which are patterns that remain relatively constant or stable within a single network across time and geography; including low connectance, asymmetric distribution of interactions, nestedness and modularity (Oleques et al., 2019). Hence, networks provide more detailed information compared with traditional analyses, which focus only on quantifying species abundances (Bascompte and Jordano, 2007). Plant-pollinator network analyses provide a more functional perspective by identifying the number of plant and animal species that interact within a community, the frequency of their interaction, and how these interactions are structured. The structure of pollinator networks depend on visitations by insects, which relies on pollen availability and nutrition content as the most crucial food source for both consumption and collection by flower-visiting insects (Nicholls, de Ibarra, N, 2017). Proteins, lipids, carbohydrates, starch, sterols, vitamins and minerals are the nutritional contents of pollen, with the quality of pollen nutrition usually determined by its protein (Cook et al., 2003). However, pollinators' assessment of pollen rewards and how they shape pollinator–plant interactions are not fully understood (Nicholls & Hempel de Ibarra, 2017).

Studies have shown that pollinator network structure can be influenced by anthropogenic disturbances, including grazing, even when species richness within a community is unaffected (Aizen et al., 2008; Yoshihara et al., 2008). In addition, livestock grazing indirectly affects the pollination process due to changes in the abundance and diversity of flowers (Mayer et al., 2020). A comparison between grazed and ungrazed sites in Scotland reported grazing to increase the size, diversity, and generalization of networks (Vanbergen et al., 2014, Yoshihara et al., 2008). Understanding the influence of grazing disturbances on pollinator networks in

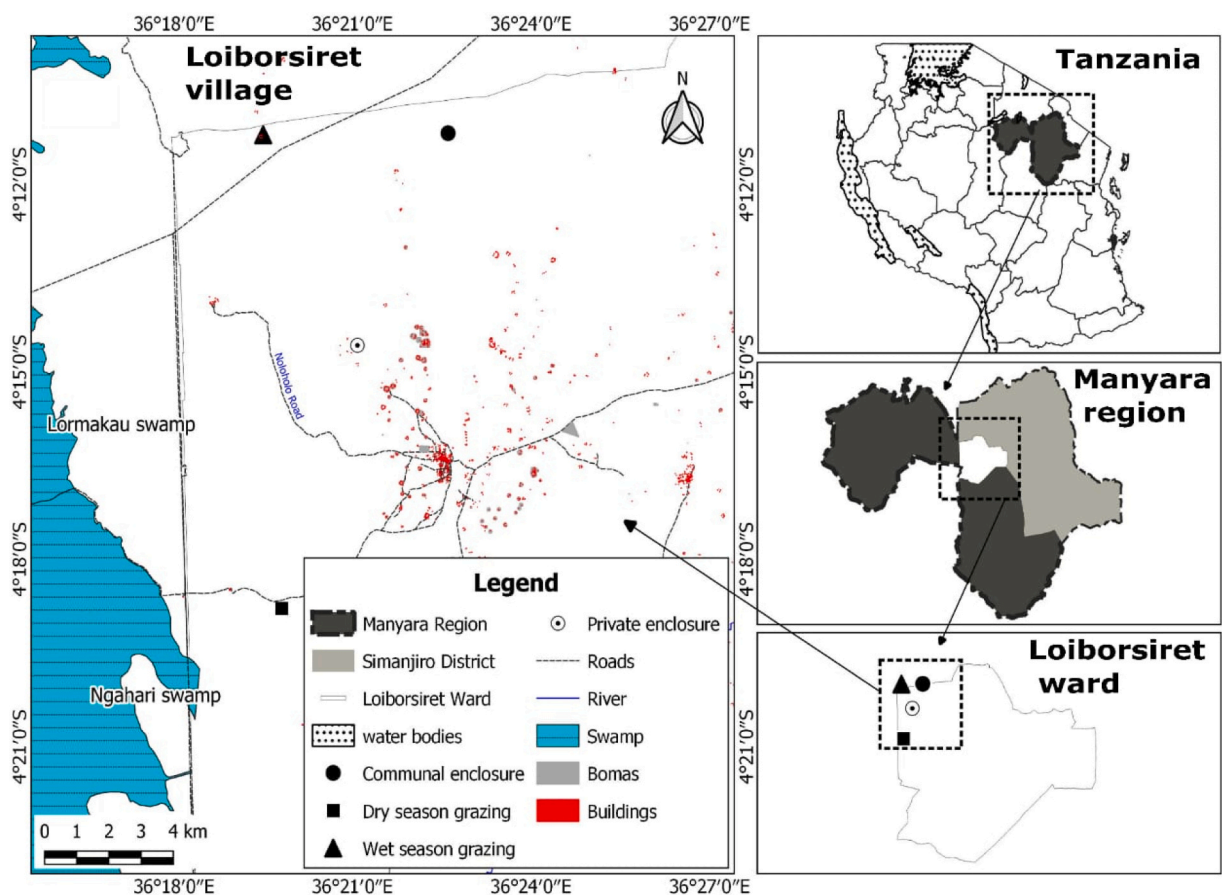


Fig. 1. : Map of study sites showing the location of the four rangeland management categories, including a private enclosure, communal enclosure, wet and dry season grazing areas in Loiborsiret, Simanjiro. For grazing categories see also Table 1.

rangelands is essential for conserving pollinators as grazing forms dominant land uses (Yoshihara et al., 2008).

The Simanjiro rangelands are a major pastoral ecosystem in northern Tanzania, a significant portion of which has been exposed to rapid population increase, overgrazing, and reduced vegetation cover that leads to degradation and fragmentation (Msoffe et al., 2011). There is an increasing use of range enclosures, a traditional management system that may promote rangeland restoration in areas with heavily grazed rangelands, has been reported to allow the herbaceous vegetation diversity to recover (Angassa et al., 2010; Haftay et al., 2013). Enclosures are fenced-off grazing lands that only allow low-density grazing of weak or young livestock, while most livestock individuals graze neighboring open rangelands (Angassa et al., 2010). The use of enclosures in grazing management promotes insect pollinator abundance, diversity and species composition in semi-arid areas of rangelands (Mpondo et al., 2021).

Despite an increase in the use of traditional enclosures in the area to promote vegetation recovery, responses of the pollinator visitations and their networks remain poorly understood. It is unclear whether enclosures promote pollinator networks, foraging visitation and sustainable pollination in Simanjiro rangelands. We explored how traditional rangeland management influences insect flower visitation. In addition, we investigated whether traditional grazing management influences plant-pollinator network properties, including connectance, nestedness, stability, richness and diversity. Furthermore, we explored how variation in pollen nutrients, specifically protein and fatty acids, affect bee visitation to flowering plants in our study area. We hypothesized that areas of low grazing pressure would render more flowering plants, and, thus, host more insect visitors compared to areas of higher grazing pressure. In addition, we expected a positive correlation between pollen nutrient concentration and pollinator visitation. We also expected more connected, nested and stable networks in areas of lower compared to higher grazing pressure. Our study findings will guide conservation authorities, policy makers and the local pastoral community in sustainable management and utilization of rangelands in semi-arid areas.

2. Material and Methods

2.1. Study area

We conducted our study in Loiborsiret village, Simanjiro district, northern Tanzania (3° 33' 42.55" S and 36° 58' 44.22" E) (Fig. 1). The average annual rainfall is between 575 and 650 mm, with sparse and unreliable short rains between October and December, followed by long rains between March and April (Msoffe et al., 2011). The average daily maximum temperature ranges between 18 and 30 °C, as the district is semi-arid area (Mbinile et al., 2020). Our study sites were distributed across four grazing categories, including private (04.24250°E and 036.35167°S) and communal enclosures (04.22847°E and 036.37111°S). In these enclosures, access by livestock (low numbers of goats, sheep, and young or sick cattle) is temporarily allowed during the dry season with a maximum herd size of thirty animals per boma (Angassa et al., 2010). Boma refers to Maasai homestead that typically consists of several mud huts with a livestock enclosure. The number of the huts depends on the family size as Maasai are polygamous and every woman builds her hut within a husband boma (Kissui, 2008). Our study also investigated communal wet (04.18724°E and 036.3229°S) and communal dry season grazing lands (04.31187°E and 036.32961°S), which are used for large livestock herds during the wet and dry seasons, respectively (Mpondo et al., 2021). Details regarding sampling sites is further provided in Table 1. Maasai pastoralists are the primary residents, with livestock keeping as the primary source of income (Woodhouse and McCabe, 2018). Other livelihood activities include agriculture, beekeeping and trading. Crops cultivated include maize (*Zea mize*), hyacinth beans (*Dolichos lablab*) and sesame (*Sesame indicum*). Grazing areas in Simanjiro are still communal; however, individuals are recently assigned private holdings (McCabe et al., 2010) as most Maasai are settled in permanent villages (Msoffe et al., 2011; Woodhouse and McCabe, 2018).

Table 1

Characteristics of the four grazing categories in the Simanjiro district, comprising private and communal enclosures, wet and dry season grazing areas. Grazing intensity was computed by dividing livestock animal abundance over a sampled area in each site during data collection from April to May 2019.

Management category	Area (ha)	Access and use	Mean livestock abundance	Mean Grazing intensity (animals/ha)
Private enclosure	200	<ul style="list-style-type: none"> • Accessed by owner only • Grazing of goats, sheep, calves and a maximum of 30 sick/weak cows 	7.8 ± 3.7	0.02
Communal enclosure	1200	<ul style="list-style-type: none"> • Accessible in dry season only • Accessed by entire village • Grazing of goats, sheep, calves and a maximum of 30 sick/weak cows per boma • Accessible in dry season only 	133.3 ± 78.1	0.33
Open communal wet season grazing	1032	<ul style="list-style-type: none"> • Accessed by entire village • Used by large livestock herds during the wet (growing) season • No limitation in herd size • Open in the wet season 	102.2 ± 42.2	0.26
Open communal dry season grazing	700	<ul style="list-style-type: none"> • Accessed by entire village • Used by large livestock herds during the dryseason (no vegetation growth) • No limitation in herd size • Open during the dry season 	166.7 ± 50.0	0.42

3. Data collection

3.1. Sampling design

Our study used stratified random sampling technique to collect data from four different grazing areas categorized based on different management categories (Table 1). The sites included private and communal enclosures, wet and dry season grazing areas. All sampled sites were located in areas with similar soil conditions (Appendix 2). In each grazing management category, we systematically laid out three line transects, each with a length of 100 m, located 400 m away from each other. We established three 5×5 m (25 m^2) plots along each transect systematically that were located 30 m apart (Westphal et al., 2008).

4. Insect flower visitor survey and identification

Insect flower visitors were recorded through direct observations for two consecutive days within the established 5×5 m (25 m^2) plots along the transects in each grazing management category between April to May in the year 2019 and 2020. The sampling period was selected because it was within the peak of flowering in our study area because flowering starts in late March following rainy season and continues until end of June (Mpondo et al., 2021). We selected simultaneously flowering forbs, herbaceous plants and grass species during our observations within the 5×5 m plots and excluded trees as our sites were composed of scattered *Vachellia* trees species which bloom during the dry season. The observed plants were selected based on their availability and abundance during the sampling period. Direct observations for pollinator activities were made twice a day, in the morning between 09:00 – 11:00 a.m. and afternoon from 02:00 – 04:00 p.m., to accommodate pollinators with different diurnal activity patterns based on preliminary surveys in 2018 to determine pollinator activity which showed to be between 09:00 – 11:00 a.m. and afternoon from 02:00 – 04:00 p.m., therefore all subsequent observations were limited to that time (Manincor et al., 2020). Two surveyors accompanied by one assistant each walked along the transects, recording insects visiting open flowers within the 5×5 m plots. The study was designed such that two transects were surveyed simultaneous during each round with one surveyor and assistant for each transect. As the sites are in semi-arid grasslands, flowering plants were not clustered, allowing easy navigation of observers within the plots without vegetation trampling. The observation time allocated for each plot was 15 min, making a total of 135 min for the three transects in each grazing category (Lázaro et al., 2019) and a total of 96 observational hours equivalent to 5760 min for the entire data collection. All observations were made in similar weather conditions with clear sunlight and without strong winds (Classen et al., 2020). The minimum temperature was 21°C , suitable for maximum insect activities (Potts et al., 2004). Flower visitors are termed as “pollinators” here; however, their contribution to pollination success was not measured. All visiting insects were identified immediately in the field with the assistance of field guides, photographed, or captured using a sweep net and preserved in 70% alcohol for later identification in the laboratory (Stein et al., 2018). Insect visitors were assigned to respective taxonomic groups, including honey bees, solitary bees, butterflies, beetles, hoverflies, bee flies and other flies.

5. Pollinator resources and flower survey

We determined flowering plant species abundances and the number of floral units within the four different grazing management categories, in each of the three 20×20 m plots established along each transect. We counted the number of open flower units or inflorescence during pollinator visitation observations in April to May, 2019. The three 20×20 m plots were laid along the transects in each grazing category, adjacent to the 5×5 m plots used for insect observations. We did not estimate tree flower abundance due to observation limitation in height and seasonality (see above). We identified plant species in the field using a field guide to common trees and shrubs of East Africa (Dharani, 2011). Plants that could not be identified in the field were taken to the National Herbarium of Tanzania (NHT) for proper identification.

6. Pollen sampling and laboratory analysis

To determine whether pollen nutritional content such as protein and fatty acids quantity influence bee foraging behaviour, pollen samples were hand collected from selected blooming plant species that had been visited by insects during our study. Only flowering species were considered here. We collected the pollen samples randomly from three individuals of each of those selected plant species, and the sampled plant individuals were located within the quadrats across each grazing management. The pollen samples were then stored in vials filled with 70% alcohol and later taken to the laboratory at Arusha Technical College (ATC), where they were refrigerated at -50°C . Pollen protein was determined using the Kjeldahl method as described by Vanderplanck et al. (2014) with 1 g of protein sample added in the test tube. Total fatty acids were determined using the titrimetric method in a similar way as described in Trout et al. (1960) with 10 g of pollen sample from each species.

7. Data analysis

Data were analyzed using R software version 3.6.2 (R Core Development team, 2019). We used Vegan, MASS, iNext, car and Bipartite packages during our analysis. The homogeneity of variance and the normality of data were checked using Levene's and Shapiro-Wilk's tests, respectively. Insect visitation data recorded in the 5×5 m plots were pooled together to compute the average for each transect. Analysis of variance (ANOVA) was used to compare variation between mean flower visitor abundance across grazing

categories. In addition, we computed flower visitors species abundance, richness and Shannon diversity across the management categories. Since our insect visitation data were count data, we determined variables that explained variation in the total insect visitation using a Generalized Linear Model with a Poisson error distribution using MASS package. When we observed overdispersion in the fitted variables, we used a Generalized Linear Model with negative error distribution. In our model, insect visitation was specified as a response variable, while flower abundance, grazing intensity, and area of grazing categories were specified as predictor variables. If variables were highly correlated, we took the variable that was integral to our hypothesis, i.e., grazing intensity. To analyze the variation of pollinator networks between management categories, we pooled data from each 5 m x 5 m plot to get the average of every transect in each grazing category. A quantitative matrix of interactions was constructed, with pollinator species in rows and plant species in columns, as described in Oleques et al. (2019). Later, pollinator networks were constructed for each management category; network metrics, including connectance, nestedness, robustness, number of links, modularity, network diversity and linkage density, were extracted from each transect in grazing categories. Connectance (C) refers to the proportion of realized/observed links over the number of all possible connections (Manincor et al., 2020; Oleques et al., 2019). Nestedness of a network is measured as weighted Nestedness based on Overlap and Decreasing Fill (NODF) which refers to a situation where species that interact with specialists are a proper subset of the species interacting with generalists in a network (Bascompte and Jordano, 2007; Tylianakis et al., 2010; Dalsgaard et al., 2013; Oleques et al., 2019), where high values indicate more nestedness (Lázaro et al., 2019). Linkage density explains generalization when networks differ in size (Tylianakis et al., 2010). Pearson correlation was computed between honey bee visitation and protein and fatty acids concentration in pollens to determine whether there is correlation because honey bee visitation depends on pollen quality and quantity (Roulston et al., 2000). The mean protein and fatty acid concentration between plant species was compared using a Kruskal-Wallis test as the data were not normally distributed. Tukey-Kramer's HSD was used to confirm significant differences in the mean number of insect visitor abundances, mean pollen nutrient parameters and variation in network matrix. Significant values were accepted at $P \leq 0.05$.

8. Results

8.1. Flower visitor abundances, richness and diversity across grazing management

A total of 1896 floral visitors of all pollinator groups were recorded during the entire data collection period across all grazing management categories (Table 3). We found a significant variation in visitor abundance across management categories ($F=2.8$, $P = 0.049$) whereby private enclosure contained highest visitor abundance compared to other grazing categories (Fig. 2a). In addition, private enclosure site showed highest visitor richness (17 species) while wet season grazing had with 14 species the lowest richness but differences were not significant (Fig. 2b). The results further showed diverse flower visitor composition whereby Hymenoptera, especially bees, significantly contributed most of the flower visitors (45%), with honey bees, *A. mellifera* dominating as the most prevalent species among all visitor group (28%) while Diptera were least frequent (Table 3). Our model showed that variation in insect visitation was most strongly influenced by grazing intensity ($\chi^2 = 7.23$, $P < 0.007$), with most visitors found in the private enclosure (Table 2, Fig. 2a).

9. Pollinator resources and flower survey

Our survey of pollinator resources revealed variation in floral abundances and diversity across the management categories. Overall, we recorded a total of 7364 floral units during the entire sampling period. The private enclosure had the highest floral abundance compared to other grazing categories while floral diversity was highest in the communal enclosure compared to other grazing categories (Table 4).

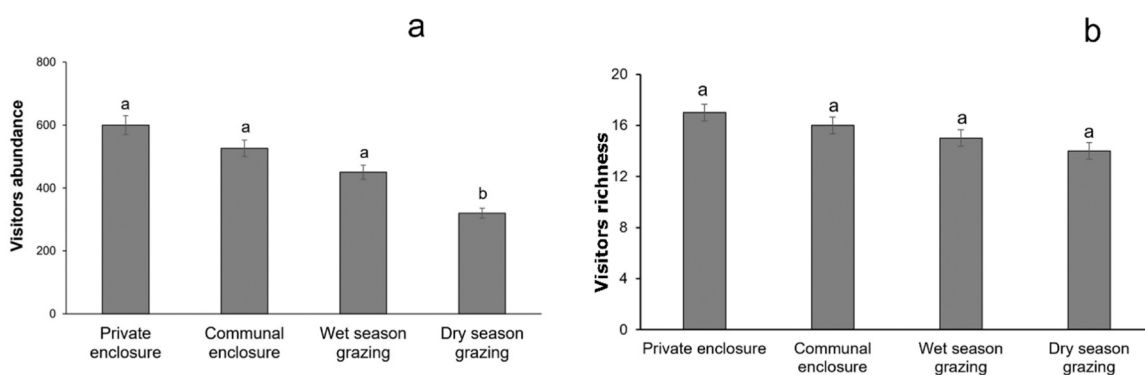


Fig. 2. : Insect flower visitor abundance (a) and richness (b) from observations across four grazing management categories of private and communal enclosures, wet and dry season grazing sites in Simanjiro, as sampled between April to May 2019 and 2020. For description of grazing management categories see also Table 1.

Table 2

Output of the Generalized Linear Model (negative binomial) to select the variables that best explained the variation in the total insect visitation across grazing sites in Simanjiro.

Predictor variables	Response variables		
	Total visitation		
	df	χ^2	p-value
Grazing intensity	1	7.23	0.007
Area of grazing category	1	0.95	0.33

Table 3

Composition of different groups of flower visitors from our observations across four management categories of private and communal enclosures, wet and dry season grazing sites in Simanjiro, sampled between April and May 2019 and 2020. For description of grazing management categories see also Table 1.

Order	Common name	Number (n)	% of all visitors
Hymenoptera	Honey bees	538	28.38
	Solitary bees	270	14.24
	Ants	124	6.54
	Lasioglossum bees	26	1.37
	Wasp	22	1.16
	Xylocopa bees	20	1.05
Lepidoptera	Yellow butterflies	226	11.92
	B. aurota	92	4.85
	Orange butterflies	80	4.22
	White butterflies	30	1.58
	Flower moth	8	0.42
Coleoptera	Chaffer beetle	116	6.12
	Blister beetles	90	4.75
	Lady beetle	54	2.85
	Other beetles	44	2.32
	Flower beetle	16	0.84
Diptera	Other Flies	24	1.27
	Bee flies	16	0.84
	Hoverflies	16	0.84
	Blowfly	4	0.21
Hemiptera	Bugs	80	4.22

Table 4

Mean flower species abundance and diversity across grazing management categories collected during sampling from April to May 2019 in Loiborsiret, Simanjiro. For description of grazing management categories see also Table 1.

	Grazing management				SD	F	P
	Private enclosure	Communal enclosure	Wet season grazing	Dry season grazing			
Flower abundance	827 ^b	627 ^{ab}	517 ^{ab}	484 ^a	154.75	362.5	0.001
Flower diversity	1.99 ^{ab}	2.13 ^b	1.84 ^a	1.88 ^{ab}	0.13	4.2	0.047

Means with different letters are significantly different according to Tukey Kramer's HSD post hoc test at $P < 0.05$.

10. Network metrics and grazing management

Our quantitative pollinator-plant networks for the four grazing areas management show that the private enclosure had the largest networks with significantly more (57 interactions) and more linkages per species as well as higher linkage density (4.48) compared to other grazing categories (Fig. 3). There was also a difference in nestedness (N) between pollinator networks across the four grazing management categories, with communal enclosures and wet season grazing having higher N compared to private enclosure and dry season grazing sites (Table 5).

Networks in the dry season grazing site were least robust (0.68) compared to other management categories (Table 5). However, only connectance was significantly different across management categories.

The upper-level black boxes indicate insect species, while the lower-level black boxes indicate plant species. The width of the black box indicates the number of visits, while the grey lines indicate the interactions. The abbreviations of insects are B.A.: B. aurota, B.B.: Blister beetle, B.G.: Bug, H.B.: Honey bee, S.B.: Solitary bee, Y.B.: Yellow butterfly, C.B.: Chaffer beetle, OBT: Orange butterfly, O.B.:

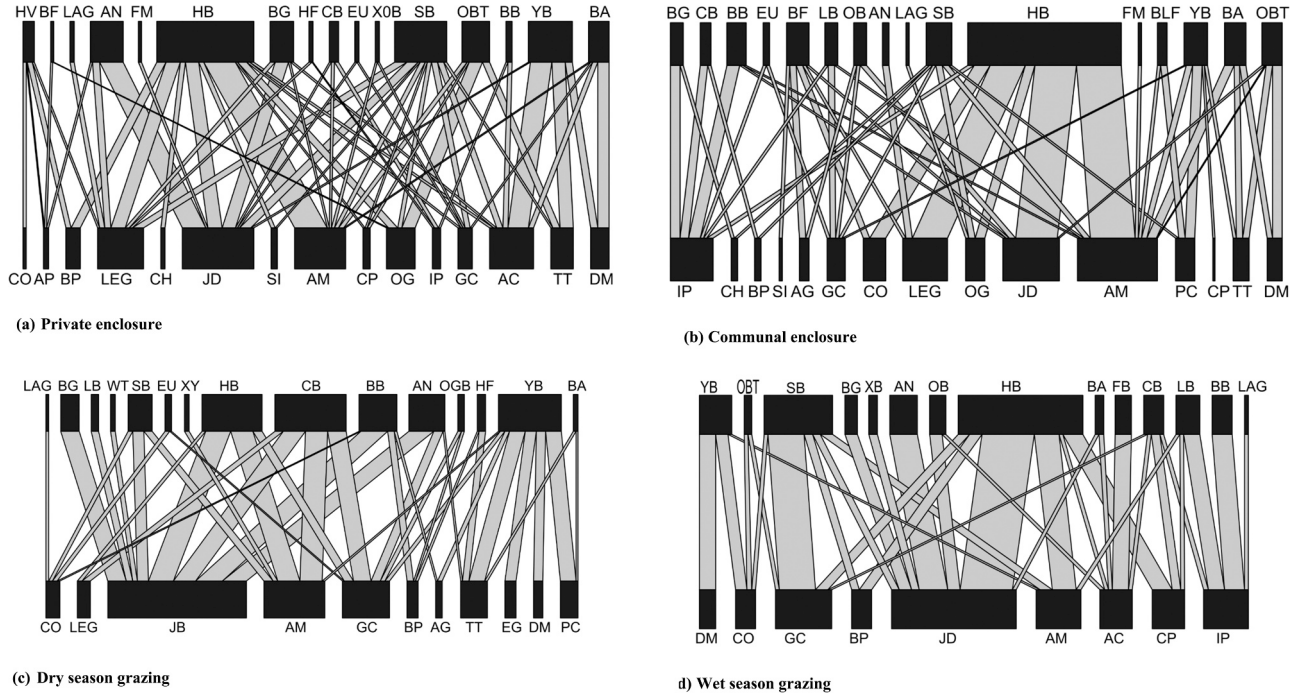


Fig. 3. : A network showing plant-pollinator interaction in grazing areas management in Loiborsiret, Simanjiro. (a) Private enclosure (b) Communal enclosure (c) Dry season grazing (d) Wet season grazing. For description of grazing management categories see also [Table 1](#).

Table 5

Network properties across four grazing management categories of the private and communal enclosure, wet and dry season grazing land in the Simanjiro rangelands, based on pollinator visitation in April to May, 2019 and 2020. For description of grazing management categories see also Table 1.

Network-Level Metrics	Grazing Category				SD
	Private enclosure	Communal enclosure	Wet season grazing	Dry season grazing	
Nestedness	22.65	29.77	29.16	20.26	4.73
Shannon diversity	3.68	3.45	3.18	3.13	0.26
Connectance	0.24	0.20	0.26	0.22	0.03
Robustness	0.76	0.74	0.78	0.68	0.04
Specialization degree H2'	-0.01	0.08	-0.09	-0.17	0.11
Generality	4.76	3.95	3.08	2.73	0.91
Linkage per species	1.84	1.58	1.44	1.38	0.21
Linkage density	4.48	3.62	3.01	3.81	0.61

Other beetles, B.F.: Bee fly, AN: Ants, H.V.: Hoverfly, E.U.: Wasps, H.F.: Housefly, FM: Flower moth, LAG: Lasioglossum bee. On the other hand, plants species are abbreviated as A.C.: *Ageratum conyzoides*, AM: *Aspilia mossambicensis*, A.P.: *Aspilia plurisetata*, B.P.: *Bidens Pilosa*, CH: *Chasccanum hildebrandtii*, CP: *Commicarpus plumbagineus*, CO: *Cyathula orthacantha*, D.M.: *Digitaria macroblephara*, G.C.: *Gutenbergia cordifolia*, I.P.: *Ipomoea sp.*, J.D.: *Justicia debile*, LEG: *Leucas glabrata*, O.G.: *Ocimum gratissimum*, P.C.: *Panicum coloratum*, SI: *Solanum incanum*, T.T.: *Themeda trianda*.

11. Protein, fatty acids content and visitation by bees

Our results showed that mean protein concentration in sampled pollen varied significantly between plant species ($\chi^2 = 25.9$, $P = 0.001$; Table 6). Overall, pollen of *Solanum incanum* contained the highest concentration of total protein (299.3 ± 0.68), and *Ocimum gratissimum* had the lowest concentration (Table 6). On the contrary, average fatty acids concentration ranged between 1.7 mol/kg to 3.3 mol/kg; *Justicia debile* contained the highest fatty acids concentration (3.3 ± 0.17), followed by *Gutenbergia cordifolia* (2.8 ± 0.19) as compared with other sampled plants. We further found a significant variation in fatty acid contents between the sampled plant species ($\chi^2 = 25.9$, $P = 0.04$). However, we did not notice any correlation between honey bee visitation and protein concentration in pollen ($r = -0.471$, $P = 0.239$) nor with fatty acids concentration ($r = 0.253$, $P = 0.546$).

12. Discussion

12.1. Flower visitation, pollinator networks and grazing management

The high level of generalization in private, communal enclosures and wet season grazing sites increased the robustness of pollinator networks as it also promotes the connectance of networks (Oleques et al., 2019) and the stability of networks (Dormann et al., 2009). Plant pollinator communities with high generalization may further be less vulnerable to disruption due to increased network resilience and interaction redundancy (Aizen et al., 2002). In general, if a plant or pollinator species possesses many interaction partners, it is less likely that losing an interaction partner will result in secondary population extinctions (Elle et al., 2012). In addition, specialized plants and pollinators have long been thought to be more vulnerable to disturbances, such as habitat alteration or fragmentation, than more generalized species (Memmmott et al., 2004).

Our results regarding the higher number of links per species in enclosures are similar to that of Lázaro et al. (2019), who also reported a higher number of links and generalization in sites with moderate grazing in a study conducted in the Mediterranean phrygana shrubs. The higher number of links in enclosures might have been enabled by the low grazing intensity recorded in our enclosures, similar to results reported by Lázaro et al. (2016) from a study in Lesvos Island, Greece. However, Lázaro et al. (2019)

Table 6

Mean (\pm SE) protein and fatty acid concentration in pollen of selected bee forage plants, collected across the four grazing categories of the private enclosure, communal enclosure, wet season grazing and dry season grazing in Loiborsiret Simanjiro from data collection in Simanjiro between April and May 2020.

Plant species	Family	Protein concentration (g/100 g)	Fatty acid concentration (mol/kg)
<i>Solanum incanum</i>	<i>Solanaceae</i>	47.9 ± 0.68	2.2 ± 0.09
<i>Cyathanula orthacantha</i>	<i>Amaranthaceae</i>	41.5 ± 1.44	2.8 ± 0.10
<i>Leucas glabrata</i>	<i>Lamiaceae</i>	34.6 ± 1.61	1.7 ± 0.08
<i>Gutenbergia cordifolia</i>	<i>Asteraceae</i>	33.8 ± 0.91	2.8 ± 0.19
<i>Bidens pilosa</i>	<i>Asteraceae</i>	33.3 ± 0.83	2.8 ± 0.17
<i>Justicia debile</i>	<i>Acanthaceae</i>	33.2 ± 2.10	3.3 ± 0.17
<i>Aspilia mosambicensis</i>	<i>Asteraceae</i>	30.3 ± 0.95	2.3 ± 0.15
<i>Ocimum gratissimum</i>	<i>Lamiaceae</i>	30.0 ± 1.16	1.7 ± 0.09

results relating to higher species diversity in moderately grazed areas are contrary to our study, as we found that all grazing categories contained a rather high visitor species diversity.

Our findings regarding the high diversity of floral visitors in networks of moderate and high grazing are similar to that of [Vulliamy et al. \(2006\)](#) in northern Scotland. The finding might have been contributed by the higher floral abundance we recorded in enclosures compared to wet and dry season grazing sites. In general, the effects of grazing on flower visitors vary across different ecosystems, making generalization difficult ([Oleques et al., 2019](#)). We found only slight variation in connectance across grazing management, contradicting strong variations found across grazing intensities that were reported by [Oleques et al. \(2019\)](#). The NODF values reported in our study coincide with a range of 20 – 60 observed by other studies ([Elwell, 2012](#)), regardless of the lower values we found in the dry season grazing area. The dominance of *A. mossambicensis* (*Asteraceae*) and *J. debile* (*Acanthaceae*) we found in floral visitation for honey bees and other pollinators including Xylocopa, butterflies and beetles we attributed to their abundance in the ecosystem. Furthermore, *Aspilia* is a member of *Asteraceae*, an observation, which agrees with findings from other studies in South America, whereby members of the family *Asteraceae* frequently receive a large number of visitors because they usually offer good resources to pollinators ([Oleques et al., 2019](#)).

12.2. Pollen quality and flower visitation

We found that pollen protein and fatty acids concentrations varied significantly between species, similar to results by [Russo et al. \(2019\)](#), [Rowe et al. \(2020\)](#) and [Vaudo et al. \(2020\)](#). In general, pollen serves as the primary protein and lipid source for developing offspring in most bee species (Michener, 2000; [Vaudo et al., 2020](#)). The pollen concentration range for our studied plants in Simanjiro (30.0–47.9%) was within the reported range of 2.5–61% from various plant species elsewhere ([Radev, 2018](#); [Roulston and Cane, 2002](#); [Roulston et al., 2000](#)). Furthermore, our recorded protein content for *Solanum* was in line with that of [Buchmann and Cane \(1989\)](#) and [Roulston et al. \(2000\)](#), which ranged between 40% and 56%.

Our findings regarding the lack of correlation between pollen protein concentrations and honey bee visitation correspond with that of [Roulston et al. \(2000\)](#), whereby zoophilous plant species were not statistically richer in pollen protein than anemophilous species and, therefore, did not influence visitation. Furthermore, the need for growing pollen tubes likely plays an essential role in determining pollen protein content rather than rewarding pollinators ([Roulston et al., 2000](#)). While [Russo et al. \(2019\)](#) reported, in contrast to our study, a significant correlation between bee visitation and protein content in thistle (*C. acanthoides*), these authors did not find a correlation with lipid contents either, similar to our study findings.

Surprisingly, despite high protein content of *S. incanum* pollen, we found low honey bee visitation rates. Generally, the *Solanaceae* family have protein-rich pollen while members of the *Asteraceae* family, such as *Aspilia* spp, have rather poor quality pollen ([Praz et al., 2008](#)). Yet, in our study, the latter received higher visitor numbers, probably due to their higher floral abundances. We propose that the low pollinator visitation to *Solanum* might be attributed to flower morphology and abundance as mentioned by [Somme et al. \(2015\)](#). According to [Buchmann and Cane \(1989\)](#), *Solanum* attracts fewer pollinators even though their pollen is abundant and nutritious because it is hidden from direct visual and chemosensory inspection by pollen-collecting insects. In addition to our study, we suggest that other pollen qualities, such as carbohydrates, could be measured.

13. Conclusion and recommendations

Our study showed that private traditional enclosures in rangeland systems might have the potential to maintain the largest pollinator networks with significantly more interactions and higher linkages per species. As plant and insect species with more linkages are less vulnerable to ecosystem disturbances, including species loss, we highlight the importance of pasture resting time in rangeland systems. We further found that pollen nutrition does not influence pollinator foraging in our study area, which is a crucial aspect to consider in conserving and maintaining pollinator foraging networks, especially in rangelands under constant grazing pressure. The plants preferred by bees, such as *A. mossambicensis* and *J. debile*, did not contain higher protein compared to less frequently visited plants in our study. Communities should be well informed on protecting these preferred bee forage plants, which have also proven to be resistant to grazing, as highlighted by their abundance and pollinator network patterns in our study sites. Our study is limited by multiplication of sample sites as data were collected on one site per grazing management category. However, we found similar plant species distribution and plant structures in other sites of the same grazing category in Simanjiro (unpublished), which makes us believe that our selected sites are representative for the area. We recommend more intensive studies that will involve more sampling sites and cover more years as well as more pollen characteristics. However, we highlight that our study was one of the first in eastern Africa that related rangeland management categories with pollinator networks, which is an important step towards savanna system conservation in times of human and climatic pressure.

Ethics statement

The permit to conduct this study was granted by The Tanzania Commission for Science and Technology (COSTECH) through the Tanzania Wildlife Research Institute (TAWIRI). We later presented the permits to respective district, ward and village leaders.

Funding

The Centre for Research, Agricultural Advancement, Teaching Excellence and Sustainability (CREATES – Tanzania) provided

funding for this research as part of a Ph.D. Scholarship. We appreciate CEBioS for funding capacity building in taxonomy through Global Taxonomy Initiative (GTI). Finally, we acknowledge additional research funding from the Eva Crane Trust (ECT) based in the U.K., intending to protect bees and promote beekeeping grant Number ECTA_20190903_Mpondo.

Declaration of Competing Interest

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

Data Availability

Data will be made available on request.

Acknowledgement

We express our sincere gratitude to the district authority of Simanjiro, the Ward and Village Executive Officers, and the Loiborsiret village chairman. We are also grateful to Mr Emmanuel Mboya for assistance in plant taxonomy and our research assistants for their work. We appreciate the Maasai community of Loiborsiret for allowing the research.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2023.e02581](https://doi.org/10.1016/j.gecco.2023.e02581).

References

- Aizen, M.A., Ashworth, L., Galetto, L., 2002. Éxito Reproductivo En Hábitats Fragmentados: ¿Importan Los Sistemas De Compatibilidad Y La Especialización En Polinización? *Rev. De Cienc. De La Veg.* 6, 885–892.
- Aizen, M.A., Morales, C.L., Morales, J.M., 2008. Invasive mutualists erode native pollination webs. *PLoS Biol.* 6 (2), 0396–0403. <https://doi.org/10.1371/journal.pbio.0060031>.
- Angassa, A., Oba, G., Treydte, A.C., Weladji, R.B., 2010. Role of traditional enclosures on the diversity of herbaceous vegetation in a semi-arid rangeland, southern Ethiopia. *Livest. Res. Rural Dev.* 22, 9.
- Bascompte, J., Jordano, P., 2007. Plant-animal mutualistic networks: the architecture of biodiversity. *Annu. Rev. Ecol. Evol. Syst.* 38, 567–593. <https://doi.org/10.1146/annurev.ecolsys.38.091206.095818>.
- Classen, A., Eardley, C.D., Hemp, A., Peters, M.K., Peters, R.S., & Szymank, A. (2020). Specialization of plant – pollinator interactions increases with temperature at Mt. Kilimanjaro. July 2019, 2182–2195. <https://doi.org/10.1002/ece3.6056>.
- Cook, S.M., Awmack, C.S., Murray, D.A., Williams, I.H., 2003. Are honey bees' foraging preferences affected by pollen amino acid composition? *Ecol. Entomol.* 28 (5), 622–627. <https://doi.org/10.1046/j.1365-2311.2003.00548.x>.
- Dalsgaard, B., Trøjelsgaard, K., Martín González, A.M., Nogués-Bravo, D., Ollerton, J., Petanidou, T., Sandel, B., Schleuning, M., Wang, Z., Rahbek, C., Sutherland, W. J., Svenning, J.C., Olesen, J.M., 2013. Historical climate-change influences modularity and nestedness of pollination networks. *Ecography* 36 (12), 1331–1340. <https://doi.org/10.1111/j.1600-0587.2013.00201.x>.
- Dormann, C.F., Frund, J., Bluthgen, N., Gruber, B., 2009. Indices, graphs and null models: analyzing bipartite ecological networks. *Open Ecol. J.* 2 (1), 7–24. <https://doi.org/10.2174/1874213000902010007>.
- Elle, E., Elwell, S.L., Gielens, G.A., 2012. The use of pollination networks in conservation. *Botany* Vol. 90 (7), 525–534. <https://doi.org/10.1139/B11-111>.
- Elwell, S.L. (2012). The Effects of Livestock Grazing and Habitat Type on Plant-Pollinator Communities of British Columbia 's Endangered Shrubsteppe by.
- Kelly, T., Elle, E., 2020. Effects of community composition on plant–pollinator interaction networks across a spatial gradient of oak-savanna habitats. *Oecologia* 193 (1), 211–223. <https://doi.org/10.1007/s00442-020-04661-5>.
- Kissui, B.M., 2008. Livestock predation by lions, leopards, spotted hyenas, and their vulnerability to retaliatory killing in the Maasai steppe, Tanzania. *Anim. Conserv.* 11 (5), 422–432. <https://doi.org/10.1111/j.1469-1795.2008.00199.x>.
- Lázaro, A., Tscheulin, T., Devalez, J., Nakas, G., Petanidou, T., 2016. Effects of grazing intensity on pollinator abundance and diversity, and on pollination services. *Ecol. Entomol.* 41 (4), 400–412. <https://doi.org/10.1111/een.12310>.
- Lázaro, A., Tscheulin, T., Devalez, J., Nakas, G., Hanlidou, E., Petanidou, T., Lázaro, A., Tscheulin, T., Devalez, J., Nakas, G., & Stefanaki, A. (2019). *Moderation is best: effects of grazing intensity on plant – flower visitor networks in Mediterranean communities Stefanaki, Effie Hanlidou and Theodora Petanidou Published by: Wiley on behalf of the Ecological Society of America Stable URL : (https://www). 26(3), 796–807.*
- Manincor, N.De, Hautekete, N., Mazoyer, C., Moreau, P., Piquot, Y., 2020. How biased is our perception of plant-pollinator networks? A comparison of visit- and pollen-based representations of the same networks *Acta Oecologica* How biased is our perception of plant-pollinator networks? A comparison of visit- and pollen-based re. *Acta Oecol.* 105 (May), 103551 <https://doi.org/10.1016/j.actao.2020.103551>.
- Mbinile, S.D., Munishi, L.K., Ngondya, I.B., Ndakidemi, P.A., 2020. Spatial distribution and anthropogenic threats facing medicinal plant *Zanthoxylum chalybeum* in Simanjiro Area, Northern Tanzania. *Sci. Afr.* 10, e00562 <https://doi.org/10.1016/j.sciaf.2020.e00562>.
- Mccabe, J.T., Leslie, P.W., & Deluca, L. (2010). Adopting Cultivation to Remain Pastoralists: The Diversification of Maasai Livelihoods in Northern Tanzania. 321–334. <https://doi.org/10.1007/s10745-010-9312-8>.
- Memmot, J., Waser, N.M., Price, M.V., 2004. Tolerance of pollination networks to species extinctions. *Proc. R. Soc. B: Biol. Sci.* 271 (1557), 2605–2611. <https://doi.org/10.1098/rspb.2004.2909>.
- Mpondo, F.T., Ndakidemi, P.A., Pauly, A., Treydte, A.C., 2021. Acta Oecologica Traditional rangeland management can conserve insect pollinators in a. *Acta Oecol.* 113 (April), 103790 <https://doi.org/10.1016/j.actao.2021.103790>.
- Msoffe, F.U., Kifugo, S.C., Said, M.Y., Neselle, M.O., van Gardingen, P., Reid, R.S., Ogutu, J.O., Herero, M., de Leeuw, J., 2011. Drivers and impacts of land-use change in the Maasai Steppe of northern Tanzania: an ecological, social and political analysis. *J. Land Use Sci.* 6 (4), 261–281. <https://doi.org/10.1080/1747423X.2010.511682>.
- Nicholls, E., de Ibarra, N., Hempel, 2017. Assessment of pollen rewards by foraging bees. *Funct. Ecol.* 31 (1), 76–87. <https://doi.org/10.1111/1365-2435.12778>.

- Oleques, S.S., Vizentin-Bugoni, J., Overbeck, G.E., 2019. Influence of grazing intensity on patterns and structuring processes in plant–pollinator networks in a subtropical grassland. *Arthropod-Plant Interact.* 13 (5), 757–770. <https://doi.org/10.1007/s11829-019-09699-8>.
- Potts, S.G., Vulliamy, B., Roberts, S., Toole, C.O., Dafni, A., Ne, G., & Willmer, P.G. (2004). Nectar resource diversity organises flower-visitor community structure. 103–107.
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* 25 (6), 345–353. <https://doi.org/10.1016/j.tree.2010.01.007>.
- Praz, C.J., Müller, A., Dorn, S., 2008. Specialized bees fail to develop on non-host pollen: Do plants chemically protect their pollen? *Ecology* 89 (3), 795–804. <https://doi.org/10.1890/07-0751.1>.
- Radev, Z., 2018. Variety in protein content of pollen from 50 plants from Bulgaria. *Bee World* 95 (3), 81–83. <https://doi.org/10.1080/0005772x.2018.1486276>.
- Roulston, T.H., Cane, J.H., 2002. The effect of pollen protein concentration on body size in the sweat bee *Lasioglossum zephyrum* (Hymenoptera: Apiformes). *Evolut. Ecol.* 16 (1), 49–65. <https://doi.org/10.1023/A:1016048526475>.
- Rowe, L., Gibson, D., Bahlai, C.A., Gibbs, J., Landis, D.A., Isaacs, R., 2020. Flower traits associated with the visitation patterns of bees. *Oecologia* 193 (2), 511–522. <https://doi.org/10.1007/s00442-020-04674-0>.
- Russo, L., Vaudo, A.D., Fisher, C.J., Grozinger, C.M., Shea, K., 2019. Bee community preference for an invasive thistle associated with higher pollen protein content. *Oecologia* 190 (4), 901–912. <https://doi.org/10.1007/s00442-019-04462-5>.
- Somme, L., Vanderplanck, M., Michez, D., Lombaerde, I., Moerman, R., Wathelet, B., Wattiez, R., Lognay, G., Jacquemart, A.L., 2015. Pollen and nectar quality drive the major and minor floral choices of bumble bees. *Apidologie* 46 (1), 92–106. <https://doi.org/10.1007/s13592-014-0307-0>.
- 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. *Ecol. Evol.* 8 (13), 6827–6838. <https://doi.org/10.1002/ece3.4197>.
- Tylianakis, J.M., Laliberté, E., Nielsen, A., Bascompte, J., 2010. Conservation of species interaction networks. *Biol. Conserv.* 143 (10), 2270–2279. <https://doi.org/10.1016/j.biocon.2009.12.004>.
- Vanbergen, A.J., & Initiative, P. (2013). Threats to an ecosystem service: pressures on pollinators. <https://doi.org/10.1890/120126>.
- Vaudo, A.D., Tooker, J.F., Patch, H.M., Biddinger, D.J., Coccia, M., Crone, M.K., Fiely, M., Francis, J.S., Hines, H.M., Hodges, M., Jackson, S.W., Michez, D., Mu, J., Russo, L., Safari, M., Treanore, E.D., Vanderplanck, M., Yip, E., Leonard, A.S., Grozinger, C.M., 2020. Pollen protein: Lipid macronutrient ratios may guide broad patterns of bee species floral preferences. *Insects* 11 (2). <https://doi.org/10.3390/insects11020132>.
- Vulliamy, B., Potts, S.G., Willmer, P.G., 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>.
- 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., Biesmeier, J.C., Kunin, W.E., Settele, J., Steffan-Dewenter, I., 2008. Measuring bee diversity in different European habitats and biogeographical regions. *Ecol. Monogr.* 78 (4), 653–671. <https://doi.org/10.1890/07-1292.1>.
- Woodhouse, E., McCabe, J.T., 2018. Well-being and conservation: Diversity and change in visions of a good life among the maasai of northern Tanzania. *Ecol. Soc.* 23 (1) <https://doi.org/10.5751/ES-09986-230143>.
- Yoshihara, Y., Chimeddorj, B., & Buuveibaatar, B. (2008). Effects of livestock grazing on pollination on a steppe in eastern Mongolia. 1. <https://doi.org/10.1016/j.biocon.2008.07.004>.