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

Nicola Tommasi[a], Paolo Biella[a], Lorenzo Guzzetti[a], Julius Vincent Lasway[b,c], Henry Kenneth Njovu[d], Andrea Tapparo[a], Giulia Agostinetto[a], Marcell Karl Peters[b], Ingolf Steffan-Dewenter[b], Massimo Labra[a], Andrea Galimberti[a,*]

[a] *ZooplantLab, Department of Biotechnology and Biosciences, University of Milano-Bicocca, Milano, Italy*
[b] *Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Am Hubland, Würzburg 97074, Germany*
[c] *College of African Wildlife Management, Mweka, P.O. Box 3031, Moshi, Tanzania*
[d] *Wildlife Conservation Society of Tanzania, P.O. Box 70919, Dar Es Salaam, Tanzania*

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ABSTRACT

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′), 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.

1. Introduction

Anthropogenic land use conversion and intensification are among the major drivers of landscape changes and habitat loss in natural and semi-natural contexts (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; Smith et al., 2015; Stein et al., 2017; Elisante et al., 2020). 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., 2020). 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

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* Correspondence to: P.za Della Scienza, 2, 20126-I Milan, Italy.
E-mail address: andrea.galimberti@unimib.it (A. Galimberti).

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decline in agricultural sites that are surrounded by progressively higher built-up surfaces (Bennett and 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 et al., 2020a). Moreover, with 80% of farms being smaller than 2 ha, these agriculture systems are mainly represented 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; Stein et al., 2017; Sawe et al., 2020b). 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 (e.g. 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 and 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 and 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.

2. Materials and methods

2.1. 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 (< 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.

2.2. Characterization of pollinator and plant communities

Sampling activities were performed in June 2018 at the end of the wet season. This period is still favourable for agricultural production in

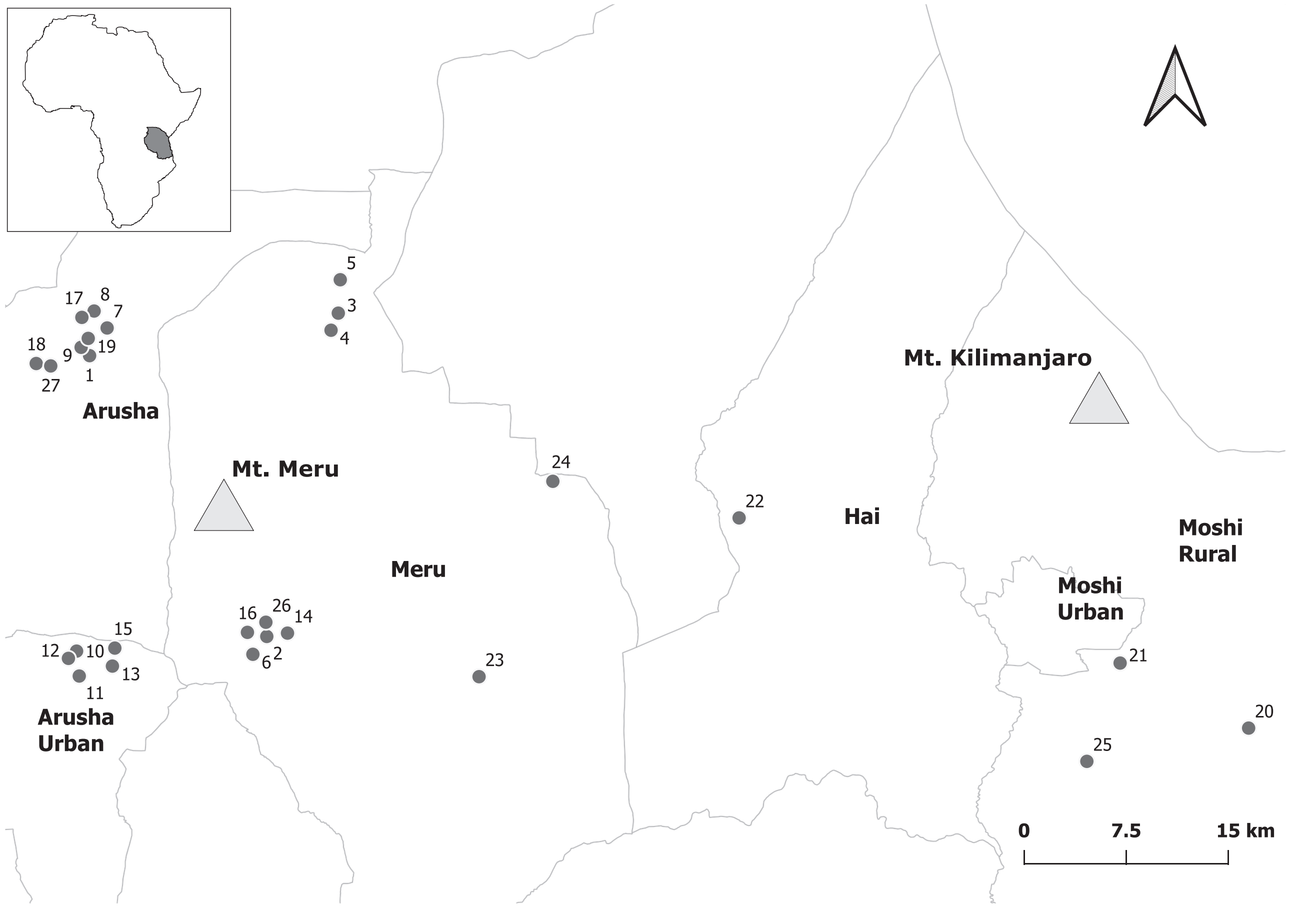

Fig. 1. Map of the study sites, further details about sampling methodology are reported in Appendix A, Table S1.

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 communities 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 coloured 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 community, 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.

2.3. *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.

2.4. *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).

2.5. *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 (Tur et al., 2015; Biella et al., 2019) and is informative of the possible effects of land use change and other anthropogenic stressors on biodiversity (Adedoja and 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 (Kaiser-Bunbury and Blüthgen, 2015). To allow a more intuitive comparison of H2′ with the pollinator foraging niche overlap, we calculated 1-H2′ 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 individuals. 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 indicate 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 and Jordano (2002) and as in Biella et al. (2020).

2.6. *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) proportion 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 and 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 ($P < 0.05$), 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).

3. Results

3.1. *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 stramonium* 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.

3.2. *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 ± 2.9

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; **χ^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**

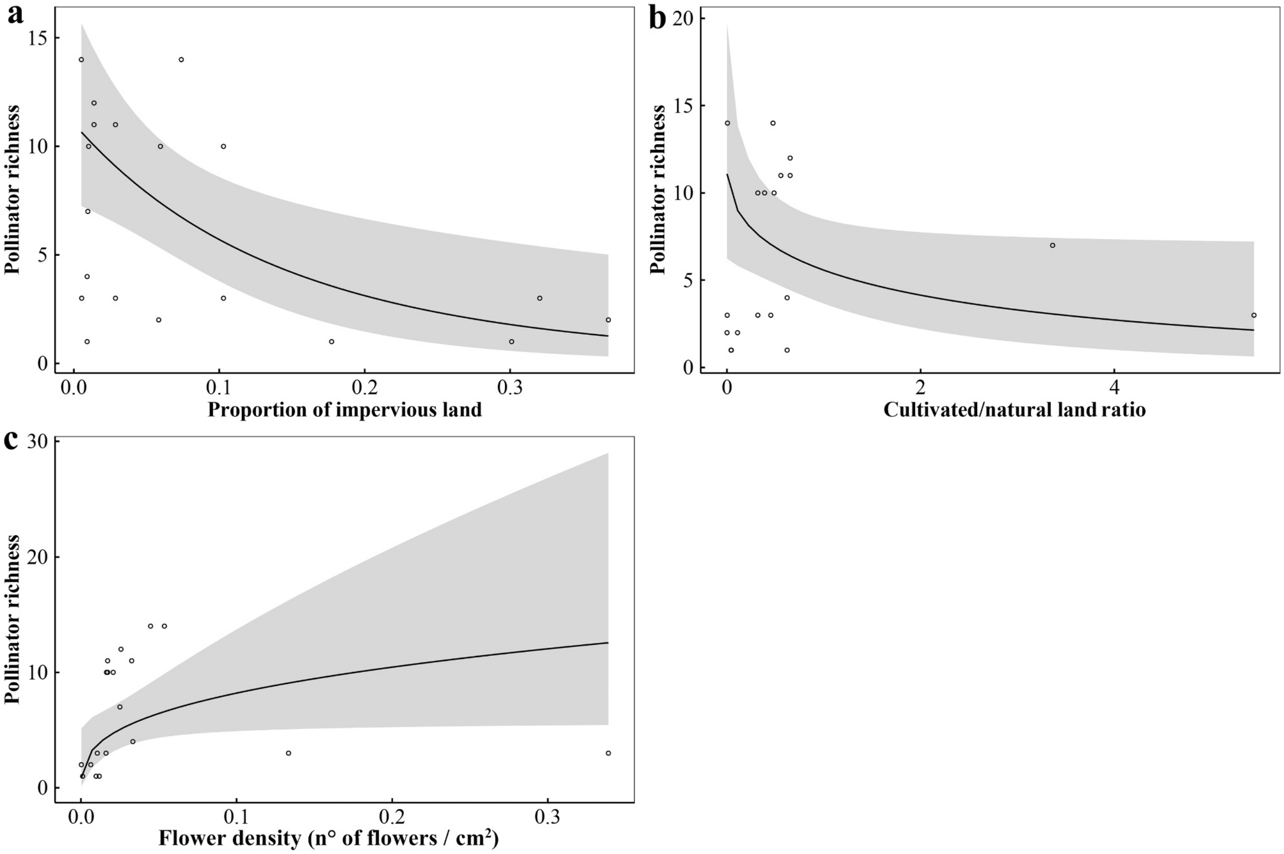

Fig. 2. Regression analysis of pollinator richness as a function of the proportion of impervious land (a), ratio between cultivated and natural land (b) and flower density (n°of flowers/cm^2) (c).

(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 proportions 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′) 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.

4. 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 metabarcoding 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., 2020). 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

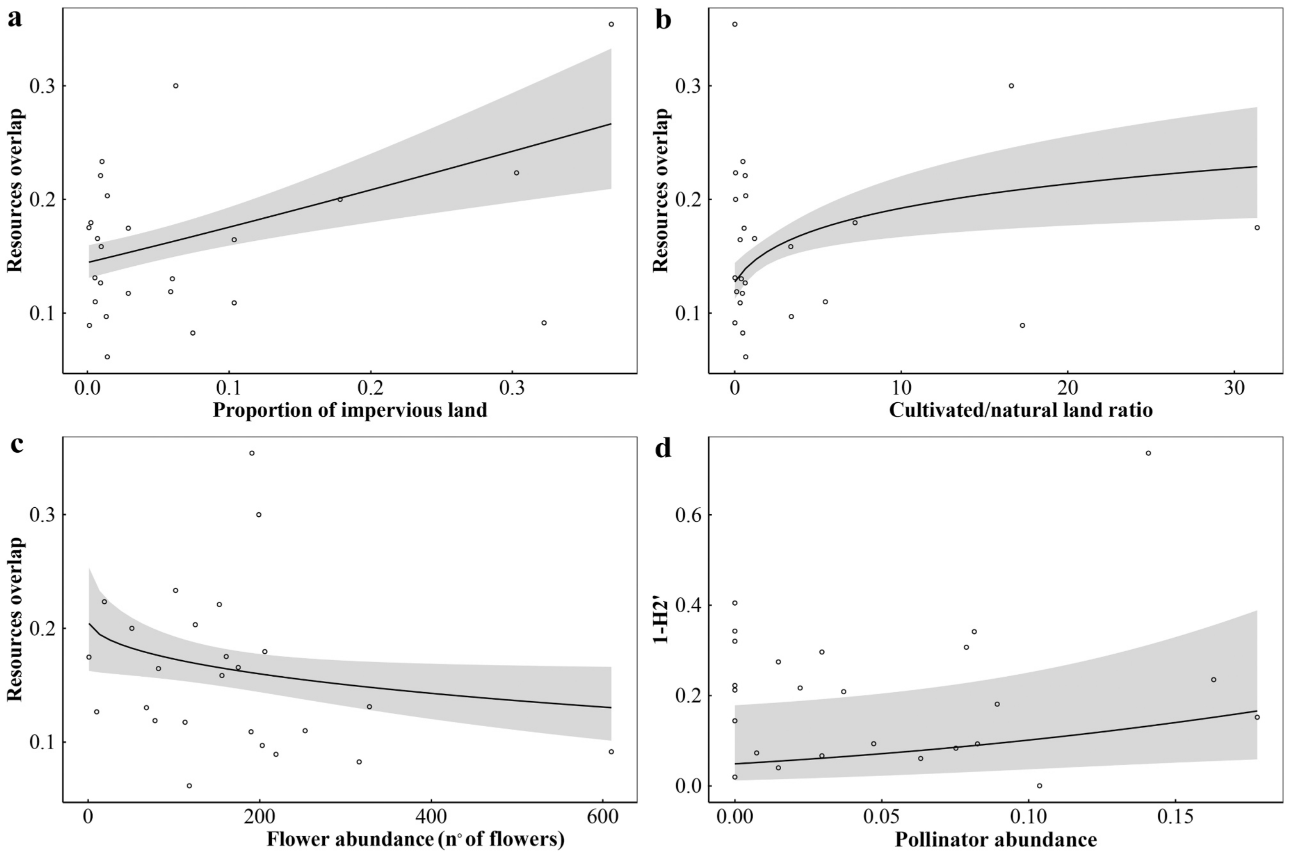

Fig. 3. Regression analysis of pollinator foraging niche overlap (resource overlap) as a function of the proportion of impervious land (a), cultivated/natural land ratio (b) and flower abundance (n° of flowers) (c). The Plot (d) represents the regression output between complementary generalization 1-H2′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

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 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.

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 and 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 smallholder 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 (Ings et al., 2009; Araújo et al., 2010). 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 available 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 (e.g., Pornon et al., 2019). The mechanism by which the amount of resources determines foraging niche convergence is evident not only at the landscape but also at the local scale, where higher floral abundance led to a higher foraging niche complementarity (Blüthgen and 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 (Fontaine et al., 2008; Biella et al., 2019). 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 and Blüthgen, 2015). These considerations further support the necessity of enhancing pollinator insects abundance in Sub-Saharan farming contexts (e.g., by means of ecological intensification; Kovács-Hostyánszki et al., 2017).

5. Conclusions

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 (Smith et al., 2015; Patel et al., 2020) 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.

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CRediT authorship contribution statement

Nicola Tommasi: Methodology, Investigation, Formal analysis, Writing - original draft, Writing - review & editing. **Paolo Biella:** Methodology, Investigation, Formal analysis, Writing - review & editing. **Lorenzo Guzzetti:** Methodology, Investigation, Formal analysis. **Julius Vincent Lasway:** Investigation, Writing - review & editing. **Henry Kenneth Njovu:** Investigation, Writing - review & editing. **Andrea Tapparo:** Investigation. **Giulia Agostinetto:** Software, Visualization. **Marcell Karl Peters:** Writing - review & editing. **Ingolf Steffan-Dewenter:** Writing - review & editing. **Massimo Labra:** Funding acquisition, Conceptualization, Writing - review & editing. **Andrea Galimberti:** Funding acquisition, Conceptualization, Writing - review & editing.

Declaration of Competing Interest

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

Data Availability

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 GenBank with the accession number MZ489668 - MZ489808. All relevant data are within the paper or stored in a public repository (http://doi/10.6084/m9.figshare.13637576).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2021.107560.

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