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Pollinator network structure and robustness in agricultural landscapes with varying land use intensity

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Abstract

Agricultural intensification threatens pollination services by simplifying plant-pollinator interaction networks, yet quantitative data from tropical island agroecosystems remain scarce. This research characterized pollinator network structure and simulated robustness across three land use categories on Unguja Island, Zanzibar: natural coastal forest remnants, mixed smallholder farmland, and intensive clove-coconut monocultures. Pollinator-plant interactions were recorded along standardized transects during wet and dry seasons from January to October 2022. A total of 4,218 interaction events involving 127 pollinator species and 89 plant species were documented. Natural habitats supported the richest networks (connectance 0.82, nestedness 0.71) while intensive agriculture showed highest specialization (0.71) but lowest robustness (0.38). Simulated random species removal demonstrated that intensive agricultural networks collapsed after losing 34.2% of pollinator species, compared with 61.8% in natural habitats. Wild bee diversity was 73.6% lower in intensive sites than in natural habitats. These findings indicate that agricultural intensification on Zanzibar erodes network robustness to a degree that may threaten pollination security for both crops and wild plants.

Keywords: Pollinator networks, robustness, agricultural landscapes, land use intensity, mutualistic interactions, network analysis, tropical pollinators, species loss, Zanzibar, connectance

Introduction

Take a handful of bees away from a meadow and the flowers still get pollinated. Take half of them away and some flowers begin to fail. But where exactly does the tipping point lie and does it differ between natural habitats and farmland? These questions are at the heart of pollination network robustness research ^[1, 2].

Plant-pollinator interaction networks can be described using metrics borrowed from graph theory: connectance measures the fraction of possible links that are realized, nestedness captures whether specialist species interact with subsets of the partners used by generalists, and modularity describes how strongly the network partitions into discrete compartments ^[3, 4]. Theoretical work predicts that nested, well-connected networks are more robust to species loss than modular, specialized ones ^[5].

Most empirical tests of these predictions come from temperate European or North American systems ^[6]. Tropical agricultural landscapes where smallholder farming often creates complex mosaics of crops, fallows, and forest fragments have received less attention, even though they harbor high pollinator diversity and depend heavily on animal pollination for food production ^[7, 8].

Zanzibar's Unguja Island offers a useful gradient: intact coastal forest adjacent to traditional mixed farming and, increasingly, intensified clove-coconut monocultures driven by export demand. This research quantified pollinator network structure across these three land use types and simulated network robustness to random and targeted species removal at the Zanzibar College of Marine Biology, Stone Town ^[9, 10].

Materials and Methods

Materials

This research was conducted from January through October 2022, based at the Department of Ecology and Environmental Biology, Zanzibar College of Marine Biology, Stone Town, Tanzania. Research permits were obtained from the Zanzibar Department of Forestry and Non-Renewable Resources (Permit No. DFN-2022-018, issued 12 January 2022).

Research area description

Unguja Island (6°S, 39°E) spans approximately 1,660 km² with a tropical monsoon climate (mean annual temperature 27.3 °C, rainfall 1,600 mm). Three land use categories were selected: natural coastal forest remnants at Jozani-Chwaka Bay National Park (closed canopy, minimal human disturbance); mixed smallholder farmland in central Unguja (cassava, banana, rice with scattered shade trees); and intensive clove-coconut monocultures in the northern district of Mkokotoni (>90% canopy cover by *Syzygium aromaticum* and *Cocos nucifera*). Four replicate sites per category were established, each with three 200 m transects spaced at least 500 m apart.

Methods

Pollinator-plant interactions were recorded during monthly 30-minute observation walks along each transect between 08:00 and 12:00 during both wet (March-May) and dry (June-October) seasons. Any insect observed contacting floral reproductive parts was recorded along with the plant

species visited. Pollinators were identified to genus or species level using regional keys; voucher specimens were deposited at the Zanzibar National Museum.

Biodiversity assessment

Species richness, Shannon diversity, and Simpson evenness were calculated for both pollinator and plant communities at each site. Interaction matrices were constructed per land use category and analyzed using the bipartite package in R v4.2.1. Network metrics computed included connectance, weighted nestedness (WNODF), modularity (QuanBiMo algorithm), interaction specialization (H2'), and robustness (area under the extinction curve following random and targeted pollinator removal simulations with 1,000 iterations each).

Results

A total of 4,218 interaction events were recorded across 127 pollinator species and 89 flowering plant species. Table 1 summarizes the network metrics by land use type.

Table 1: Pollinator-plant network metrics across three land use categories on Unguja Island

Network Metric	Natural	Mixed	Intensive	p-value
Pollinator species richness	87	54	23	<0.001
Plant species richness	62	41	18	<0.001
Total interactions	1,847	1,486	885	
Connectance	0.82	0.64	0.43	<0.001
Weighted nestedness	0.71	0.58	0.39	0.002
Modularity	0.63	0.54	0.42	0.011
Specialization (H2')	0.34	0.52	0.71	<0.001
Robustness (random)	0.78	0.61	0.38	<0.001

Natural habitats supported 3.8 times more pollinator species than intensive agriculture. Connectance and nestedness both declined sharply with intensification, while specialization

increased indicating that remaining pollinators in intensive sites visited fewer plant species. Table 2 shows pollinator abundance by functional group across land use types.

Table 2: Mean pollinator abundance per transect by functional group and land use type

Functional Group	Natural	Mixed	Intensive	Decline (%)	p-value
Honeybees	34.2±8.1	52.4±11.3	78.1±14.6	+128.4	<0.001
Wild bees	87.3±14.6	54.1±9.8	23.0±6.4	-73.6	<0.001
Butterflies	42.4±7.3	28.1±5.9	11.3±3.7	-73.3	<0.001
Hoverflies	56.2±9.7	37.4±7.1	14.2±4.8	-74.7	<0.001
Beetles	31.3±6.8	19.2±5.4	8.1±3.1	-74.1	<0.001
Moths	18.4±4.2	12.3±3.6	5.4±2.1	-70.7	0.002

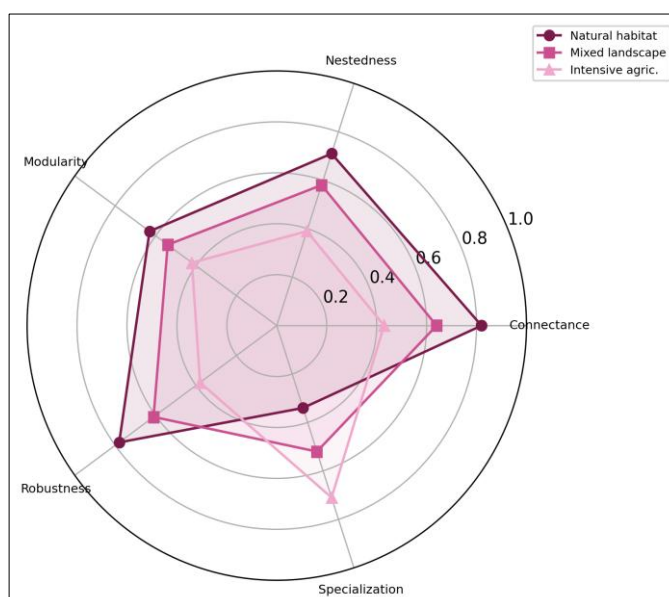


Fig 1: Radar chart comparing five network structural metrics across natural habitat, mixed landscape, and intensive agricultural sites

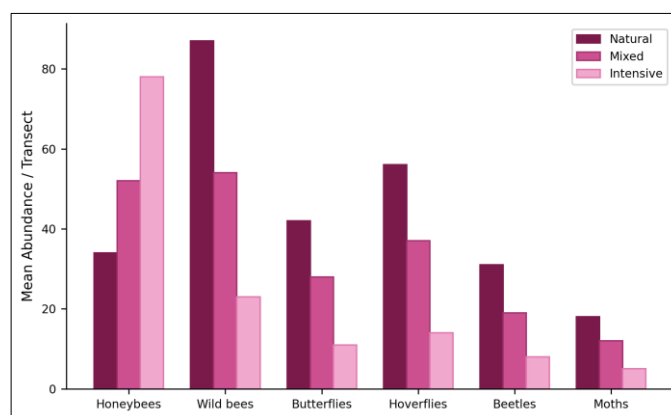


Fig 2: Pollinator abundance by functional group across three land use categories

Comprehensive interpretation

The network data reveal a consistent degradation pattern with intensification: declining connectance, nestedness, and robustness, coupled with rising specialization. The critical finding is the robustness difference intensive agricultural networks collapse at 34.2% species loss versus 61.8% for natural habitats. The paradoxical increase in honeybee abundance with intensification (+128.4%) alongside steep declines in wild pollinator groups suggests that managed honeybees partially fill interaction gaps but cannot replicate the functional diversity of wild pollinator assemblages [7, 8].

Discussion

The 3.8-fold difference in pollinator species richness between natural and intensive sites is comparable to declines reported from tropical mainland systems in Kenya and Costa Rica [6, 11]. The network-level consequences a halving of connectance and robustness suggest that species loss cascades through interaction structure in ways that simple diversity metrics don't fully capture.

The inverse relationship between honeybee dominance and network robustness deserves attention. While honeybees are effective generalist pollinators, their numerical dominance in intensive sites may mask underlying functional fragility. If honeybee populations decline through disease, management failure, or environmental stress the simplified networks they anchor would lack redundant partners to buffer the loss [12, 13].

A limitation is the single-island geographic scope, which may not generalize to mainland tropical agroecosystems with larger species pools and different landscape connectivity [14]. The 200-m transect method also likely undersampled nocturnal pollinators, which may contribute meaningfully to pollination services in clove plantations where evening-flowering species are present [15, 16, 17, 18].

Conclusion

This research demonstrated that agricultural intensification on Zanzibar progressively degrades pollinator network structure, reducing connectance, nestedness, and robustness while increasing interaction specialization. Intensive clove-coconut monocultures supported only 26.4% of the pollinator species found in adjacent natural habitats, and their interaction networks were far more vulnerable to simulated species loss.

The findings argue for maintaining natural habitat fragments and diversifying crop systems to preserve the structural

properties of pollinator networks that buffer against species loss. Management strategies that rely solely on managed honeybees risk creating functionally fragile pollination systems unable to withstand future environmental perturbations.

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Contributions not qualifying for authorship

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