

Article

Plant-Pollinator Networks in Savannas of Burkina Faso, West Africa

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Abstract: West African savannas are severely threatened with intensified land use and increasing degradation. Bees are important for terrestrial biodiversity as they provide native plant species with pollination services. However, little information is available regarding their mutualistic interactions with woody plant species. In the first network study from sub-Saharan West Africa, we investigated the effects of land-use intensity and climatic seasonality on plant–bee communities and their interaction networks. In total, we recorded 5686 interactions between 53 flowering woody plant species and 100 bee species. Bee-species richness and the number of interactions were higher in the low compared to medium and high land-use intensity sites. Bee- and plant-species richness and the number of interactions were higher in the dry compared to the rainy season. Plant–bee visitation networks were not strongly affected by land-use intensity; however, climatic seasonality had a strong effect on network architecture. Null-model corrected connectance and nestedness were higher in the dry compared to the rainy season. In addition, network specialization and null-model corrected modularity were lower in the dry compared to the rainy season. Our results suggest that in our study region, seasonal effects on mutualistic network architecture are more pronounced compared to land-use change effects. Nonetheless, the decrease in bee-species richness and the number of plant–bee interactions with an increase in land-use intensity highlights the importance of savanna conservation for maintaining bee diversity and the concomitant provision of ecosystem services.

Keywords: bees; community composition; connectance; land-use intensity; modularity; mutualism; number of interactions; seasonality; woody plant richness



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1. Introduction

Insect pollination is a key ecosystem service as the reproduction of many wild flowering plants depends on pollinating insects, especially bees [1,2]. Due to current environmental challenges (i.e., habitat loss and degradation, agriculture intensification, non-native species, diseases, and climate change), pollinators and consequently pollination are considered to be under threat [3–5]. In the past decades, numerous studies have focused on

the effects of global-change pressures and especially land use on pollinators and their host flowering plants [6,7]. However, the effects of land-use intensity on flowering-plant and insect-pollinator communities may also influence their interaction patterns, and thus the architecture of their mutualistic networks [8,9]. In addition to land-use change, climate seasonality in tropical regions may affect plant and bee diversity and further influence their mutualistic network architecture [10]. The structure of mutualistic networks is considered to be important for community stability and functioning [11]. Network thinking has been integrated into conservation, restoration, and management [12,13]. This integration offers promising tools to cope with the urgent challenge to understand and mitigate the effects of environmental change and species loss on crucial ecological processes such as pollination [14–17]. Furthermore, a review by Vizentin-Bugoni et al. [18] highlights an uneven global distribution of plant–pollinator network studies biased towards nontropical areas. Moreover, within the tropics, there is a bias towards the neotropical region where partial networks represent 70.1% of the published studies. Only 11 network studies have been carried out in tropical Africa (e.g., Seychelles and Cameroon) vs. 137 neotropical network studies; out of these only one study by Trøjelsgaard et al. [19] investigated plant–pollinator networks on the Canary Islands comprising one location on the African mainland in Western Sahara (26.1610° N, 14.4222° W).

Savannas are a major component of the world’s vegetation, covering one-sixth of the land surface and accounting for ca. 30% of the primary production of all terrestrial ecosystems. Africa contains by far the largest area of savanna, covering as much as about 50% of the African territory [20]. Savanna habitats provide fundamental resources that allow for continued ecosystem functioning. Regulating ecosystem services (ESS) concern sequestration of considerable amounts of carbon [21], soil retention, and purification of water and air, as well as pollination, seed dispersal, and natural pest control. Central ESS providers in agro-ecological savanna systems are the savanna trees along with associated animal species, which are socio-economically and ecologically important, such as wild bees and natural pest predators [22].

The Sudanian and Guinean savannas of West Africa comprise a vast mosaic of woodland, near natural and utilized savanna, and cultivated areas, the latter replacing original ecosystems rich in woody species and fauna [23–26]. The population in these rural areas with widespread poverty heavily depends on local ecosystem services for their livelihood [27,28]. As in the developing world, human populations spread and agriculture intensifies with uncontrolled usage of pesticides; 120 million hectares of natural habitats are expected to be converted to farmland by 2050 [29,30]. West African savannas have been progressively converted into cultivation areas for decades, leading to widespread and rapid disappearance of native species being large-scale providers of provisioning, regulating, and cultural ESS that local populations traditionally and essentially rely on. Furthermore, habitat destruction and degradation comprise serious threats to bee diversity in these regions, which is important for both agriculture and maintaining indigenous ecosystems [31–33]. This will most likely increase pollination deficits, particularly in areas of high and increasing pollination demand [34,35]. Lack of plant regeneration and pollination services will soon have severe consequences on ESS provision, resulting in loss of income, food security, and weakened livelihood of rural populations, being detrimental to societies and economies [36].

Our plant–pollinator network study is the first of its kind from sub-Saharan West Africa. By addressing this knowledge gap and in the framework of potential conservation measures, we aimed to investigate the effects of climate seasonality and land-use intensity on (i) bee and flowering-plant community structure, and (ii) the plant–bee visitation network architecture.

We found that climate seasonality affected plant- and bee-species richness and their mutualistic network architecture. Bee- and plant-species richness, the number of interactions, and network connectance were higher during the dry season. Land-use intensity did not affect network architecture per se; however, we documented a decrease in bee-

species richness and the number of plant–bee interactions with increasing land-use intensity. Our study highlights the importance of savanna conservation to maintain wild-bee diversity and concomitantly the provision of ecosystem services.

2. Materials and Methods

2.1. Study Areas and Study Design

This study was carried out in the Sudanian zone of Burkina Faso, West Africa. This zone is characterized by two pronounced seasons per year: a rainy season from June to October and a dry season from November to May, with October being a transition month [37]. Mean annual rainfall varies between 800 and 1000 mm, while mean annual temperature ranges from 27 to 28 °C [38]. Phytogeographically, the study areas belong to the Sudanian Regional Centre of Endemism [39]. The vegetation is dominated by a mosaic of various savanna types, including shrub and tree savannas. Our sampling took place in three areas: the Dano basin (11°08'56.566"N, 003°03'36.446"W), the Wildlife Reserve of Bontioli (10°48'26.393"N, 003°04'39.564"W) and the Nazinga Game Ranch (11°06'34.998"N, 001°29'07.181"W) (Figure 1). The elevations range between 271 and 448 m a.s.l. Sampling areas were chosen along a gradient of land-use intensity and were classified as areas with low, medium and high land-use intensity based on land-use/land-cover data via multitemporal Landsat images [26,40].

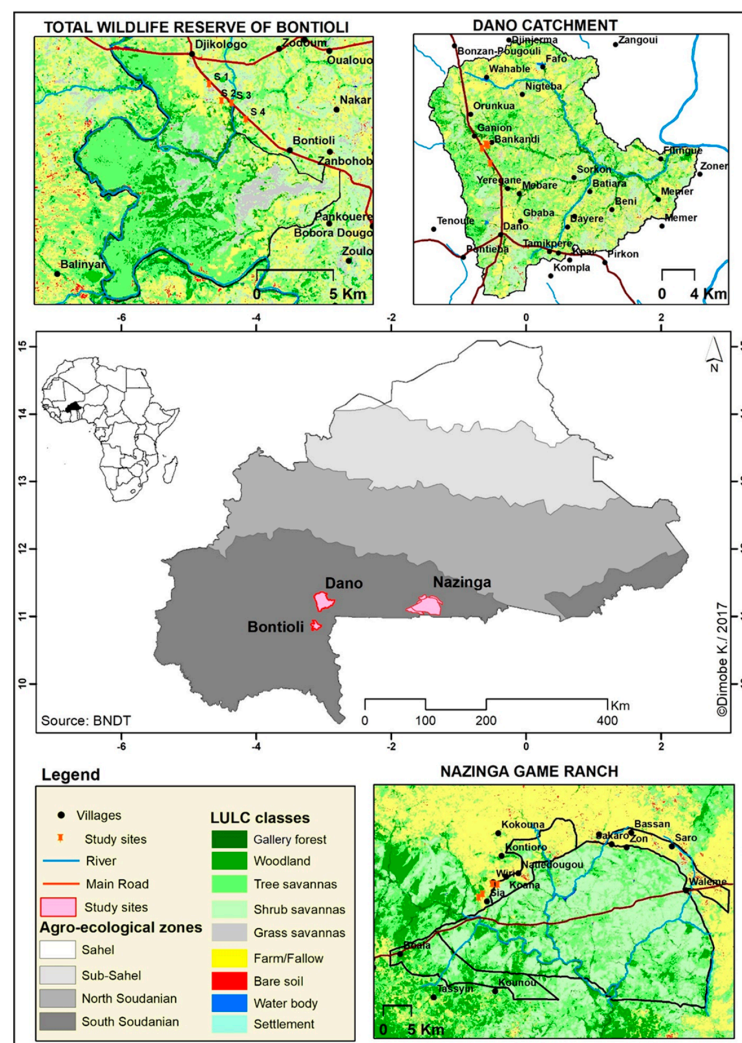


Figure 1. Map with land-use and land-cover (LULC) data of 2014 of the three study areas: Nazinga (low land-use intensity), Bontioli (medium land-use intensity), and Dano (high land-use intensity) and their location within Burkina Faso, West Africa.

The Nazinga Game Ranch is a “Wildlife Reserve” and belongs to category VI of the world database of protected areas of the IUCN. Its area amounts to 97,536 ha [38] and is characterized by woody species typical of pristine tree and shrub savanna, such as *Terminalia macroptera* Guill. & Perr., *Detarium microcarpum* Guill. & Perr., and *Prosopis africana* (Guill. & Perr.) Taub. At the beginning of the dry season there are regular, managed fires, and only small settlements with agricultural fields are to be found at the margin of the reserve. The forest cover (grass, shrub, and tree savannas included) amounts to 88.2%, crop land (farm and fallows) to 0.8% [40]. We considered land-use intensity in this area as “low”. The Bontioli Wildlife Reserve is a protected “Nature Reserve” according to Burkina Faso’s legislation (IUCN categories I and IV as both partial and total faunal reserve). The area of the Bontioli Nature Reserve amounts to 25,000 ha and is dominated by woody species such as *Terminalia laxiflora* Engl. & Diels and *Vitellaria paradoxa* C.F. Gaertn. The reserve is surrounded by several villages and a wide agricultural landscape. Human activities include crop production, livestock grazing, fire, traditional mining, uncontrolled logging, and timber extraction; some of these activities were registered even inside the reserve. Forest cover amounts to 77.85%, crop land to 12.59% [26]. Land-use intensity in this area was considered as “medium”. The study area of Dano consists of a small city of about 50,000 inhabitants with a fast-growing population, where mostly farmers spread their settlements more and more to the surrounding savanna. As a result, only a few very limited “near-natural” savanna ecosystems exist, and only commercially important tree species such as Karité (*Vitellaria paradoxa*) and Neré (*Parkia biglobosa* (Jacq.) R.Br. ex G.Don) have been left, forming the so-called parkland landscape. The land of the Dano savanna is used intensively for agricultural production and is characterized by degraded soils and intensive grazing, regular fire events, and deforestation. Forest cover amounts to 52.9%, crop land to 37.2% (Dimobe, unpublished data). We therefore considered the land-use intensity in the Dano region as “high”.

2.2. Sampling Flowering Plants, Bees and Their Interactions

In each study area, four plots measuring 1 ha were established randomly. Within each plot, four subplots of 500 m² (20 m × 25 m) were laid out in the four corners, giving a total of 48 subplots (3 areas × 4 plots in each area × 4 subplots in each plot). Inventories of woody plant species were carried out on the 48 subplots during the rainy season. Melliferous trees and shrubs were identified through regular observation of bees’ presence and foraging on the inflorescences from January to December 2015. Once bees were observed visiting the flowers, the respective plant species were classified as “melliferous”. Plant species flowered at different times of a year and were grouped according to the seasons: dry season (November to May) and rainy season (June to October) [41]. Each flowering plant species (i.e., a plant species that was in flower) within the subplots was monitored for 10 days during alternating hours (6 a.m. to 12 p.m., or 12 p.m. to 6 p.m.) to assess the number of bee visitors, resulting in a total of 3180 hours of observation. When leaving a flower, the bee visitor was caught, etherized and stored in 70% ethanol. Each bee specimen was numbered according to the identity of the visited flower, and then pinned and identified to genus or species level (voucher specimens are held at the Université Félix Houphouët-Boigny, Abidjan and at the Université Peleforo Gon Coulibaly, Korhogo, Côte d’Ivoire).

2.3. Flower Visitation Networks

Pooled flower-visitation data from all of our 48 subplots and across the 10 days of sampling per plant species in both seasons were combined and used for flowering plant–bee network analysis. A quantitative network for each study area (Nazinga = low land-use intensity; Bontioli = medium land-use intensity; Dano = high land-use intensity) and season (dry season and rainy season) was represented as a matrix in which each cell contained the number of interactions between flowering plant species in n rows and bee species in m columns. In addition to the traditional biodiversity measures, indices that describe the architecture of mutualistic plant–pollinator networks are further important

metrics to improve our understanding about the ability of these communities to cope with increasing pressure on land use and habitat fragmentation [42,43]. The degree of nestedness, modularity, and connectance of ecological interactions—the way the interactions among species are organized—is expected to play a key role in the robustness of ecological assemblages [44–46]. To examine flowering plant–bee mutualistic network architecture, we generated network metrics using the R package bipartite v.2.15 [47]. For each plant–flower visitor network, we estimated five commonly used network metrics that are potentially relevant for biodiversity conservation [18,48–50]: connectance, nestedness (NODF), modularity, complementary specialization (H_2'), and bee specialization (d'). Connectance is calculated as the sum of links divided by the number of cells in the matrix and describes the proportion of realized interactions in a network. Nestedness (NODF) evaluates whether species with fewer partners (specialized species) tend to interact with subsets of species that more-connected species (generalist species) interact with [51]. To calculate modularity we used the QuanBiMo algorithm [52]. QuanBiMo detects modules in quantitative networks based on a hierarchical random graph [53]. Species within a module are more linked with each other than they are with species in other modules. Complementary specialization (H_2') reflects the degree of niche divergence among species and ranges between 0 (highly generalized) to 1 (highly specialized). Bee specialization (d') reflects how specialized a bee species is with respect to the available flowering plant resources, and it ranges from 0 (little specialization) to 1 (high specialization) [54]. Overall bee specialization (d') was estimated by averaging the d' value for each bee species per network.

Due to the dependence of network metrics, i.e., connectance, nestedness, and modularity, on network size [47], we used Patefield's algorithm [55] and simulated 1000 random interaction networks for each site and season and then Δ -transformed all of our network metrics [49,56,57]. The Δ -transformed metrics were calculated as $N - \bar{N}_r$, where N is the observed value of a network metric and \bar{N}_r is the mean value for the 1000 randomized networks and reflects the degree to which a network metric deviates from a random expectation. Raw network metrics are shown in Table S1.

2.4. Statistical Analyses

To test for differences in flowering-plant richness, bee richness, and number of interactions between low, medium and high land-use intensity sites, we used generalized linear mixed models (GLMMs) with negative binomial error structure with site and season as random effect factors. We used GLMMs with negative binomial error structure and site as a random effect, to test for differences in flowering-plant richness, bee richness, and number of interactions between seasons (dry vs. rainy). Number of interactions was used as a covariate for all the GLMMs of flowering plant and bee richness.

We used an adonis analysis to test for differences in bee- and plant-community composition among low, medium and high land-use intensity sites. For this analysis, we used the Bray-Curtis distance matrix of bee-species composition and, due to presence/absence data, the Jaccard distance matrix of plant-species composition as response variables and land use as a predictor. The strata argument was set to "season". In order to determine the effect of climatic seasonality on bee- and plant-community composition, we performed an adonis analysis and specified strata = site such that randomizations only occurred within each sampling site and not across all sampling sites. The adonis analysis was run with 1000 randomizations and implemented using the R package vegan.

We calculated Δ -transformed network indices that reflect the degree to which a metric deviates from random expectation. To test for differences in the null-model corrected Δ -transformed network metrics between low, medium and high land-use intensity areas, we used linear mixed models (LMMs) with site and season as random effects. We used LMMs and site as a random effect to test for differences in the null-model Δ -transformed network metrics between seasons (dry vs. rainy).

All mixed model analyses were performed using the R package lme4 [58]. Further Tukey HSD posthoc tests were performed using the R package multcomp [59].

3. Results

3.1. Plant and Bee Richness in Relation to Land-Use Intensity and Climatic Seasonality

The low land-use intensity area supported higher bee-species richness (57.5 ± 33.2 SD) compared to medium (18 ± 12.7 SD) and high (9 ± 5.7 SD) land-use intensity areas (GLMM; low vs. medium, $Z = 4.654$, $p < 0.001$; low vs. high, $Z = 4.038$, $p < 0.001$; Figure 2a). Bee-species richness did not differ significantly between medium (18.0 ± 12.7 SD) and high (9 ± 5.7 SD) land-use intensity areas (GLMM; medium vs. high, $Z = 0.819$, $p = 0.413$; Figure 2a). Flowering-plant species richness did not differ among low (23.5 ± 13.4 SD), medium (16.5 ± 10.6 SD), and high (14.5 ± 10.6 SD) land-use intensity areas (GLMM; low vs. medium, $Z = 0.193$, $p = 0.847$; low vs. high, $Z = 1.003$, $p = 0.316$; medium vs. high, $Z = 1.234$, $p = 0.217$; Figure 2b). Community composition of bees and flowering plants did not differ between land-use intensity sites (adonis; $F = 0.520$, $p > 0.05$; $F = 0.412$, $p > 0.05$, respectively).

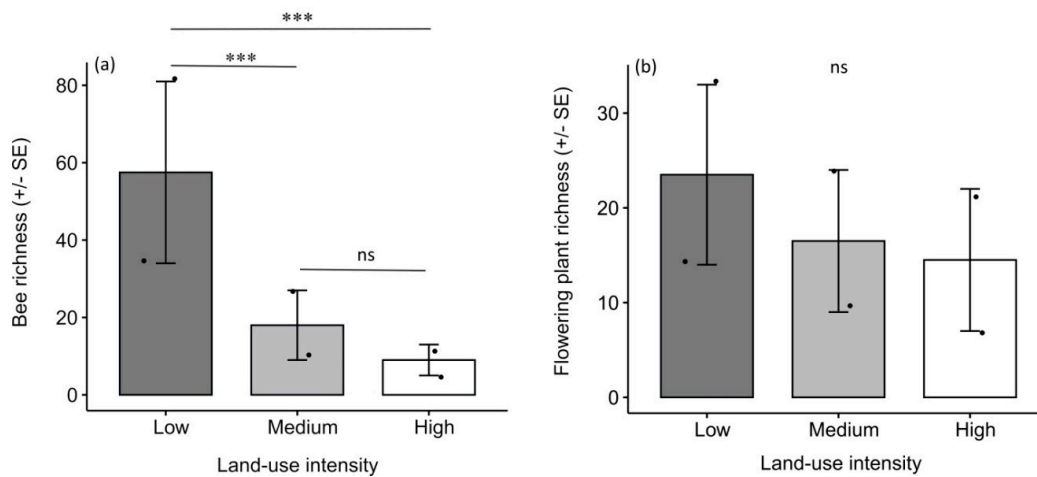


Figure 2. Mean (a) bee richness and (b) flowering-plant richness (i.e., number of plant species in flower) in low, medium and high land-use intensity areas; means \pm SE are shown; ns not significant, *** $p < 0.001$.

Bee species richness was higher in the dry (40.3 ± 35.9 SD) compared to the rainy (16 ± 15.8 SD) season (GLMM; $Z = 2.822$, $p = 0.004$; Figure 3a). Flowering-plant species richness was higher in the dry (26.3 ± 5.9 SD) compared to the rainy (10 ± 3.6 SD) season (GLMM; $Z = 4.66$, $p < 0.001$; Figure 3b). Community composition of bees and flowering plants did not differ between seasons (adonis; $F = 4.852$, $p > 0.05$, $F = 5.635$, $p > 0.05$, respectively).

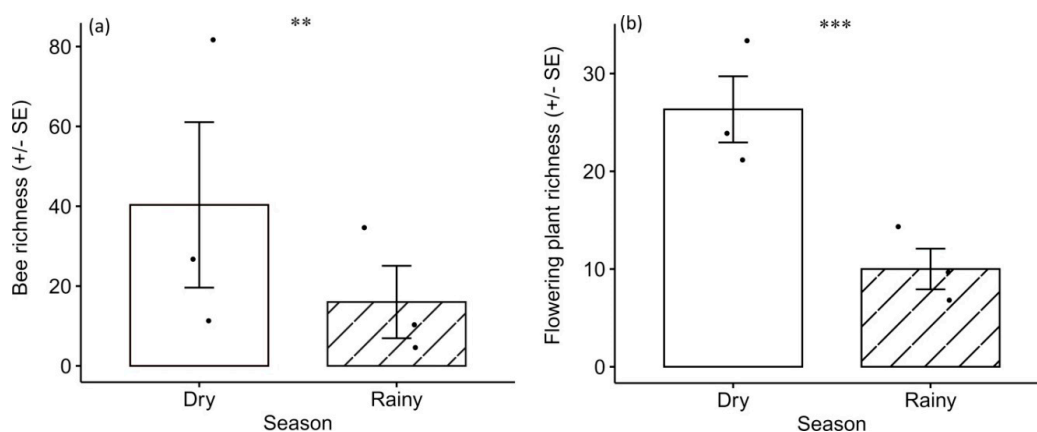


Figure 3. Mean (a) bee richness and (b) flowering-plant richness (i.e., number of plant species in flower) in the dry and rainy season; means \pm SE are shown; ** $p < 0.01$, *** $p < 0.001$.

3.2. Plant-Bee Network Architecture in Relation to Land-Use Intensity and Climatic Seasonality

Overall, we observed a total of 5686 interactions between bees and flowering plants. Low land-use intensity areas had higher numbers of interactions (1388 ± 888.1 SD) compared to medium (971 ± 968.7 SD) and high (484 ± 509.1 SD) land-use intensity areas (GLMM; low vs. medium, $Z = 2.119$, $p = 0.034$; low vs. high, $Z = 3.766$, $p < 0.001$; medium vs. high, $Z = 1.647$, $p = 0.099$; Figures 4 and 5a). Our network metrics (Δ -transformed connectance, network-level specialization (H_2'), Δ -transformed nestedness (NODF), Δ -transformed modularity, Δ -transformed bee-species specialization) did not differ among low vs. medium vs. high land-use intensity areas (LMM; $p > 0.05$; Figure 6 and Figure S1, Table S2). Honey bees (*Apis mellifera* Linnaeus) and the stingless bee *Hypotrigona gribodoi* Magretti were the most abundant flower visitors, and *Combretum glutinosum* Perr. ex DC. (Combretaceae) the most visited plant species at all locations and seasons.

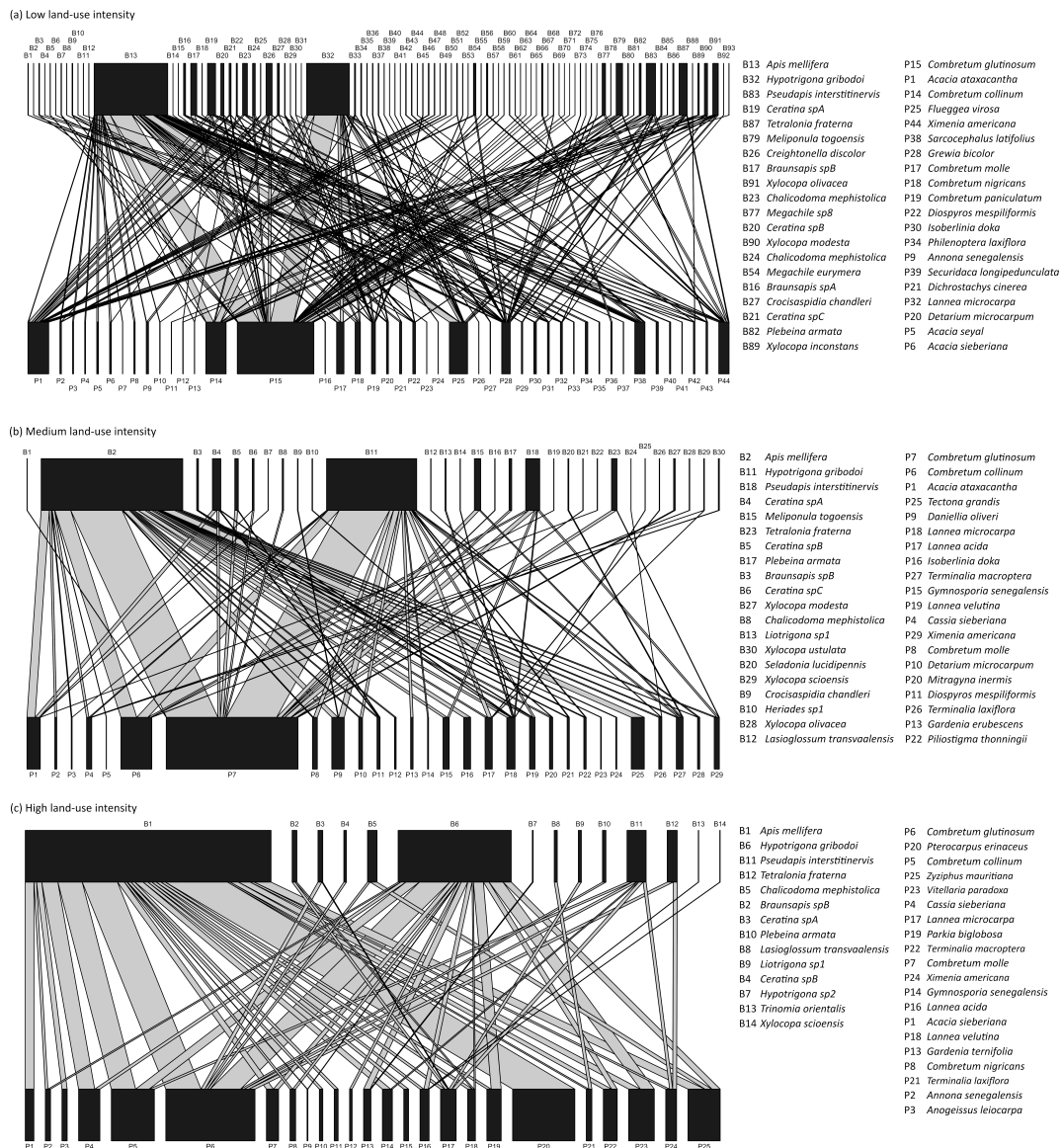


Figure 4. A bipartite graph of flowering-plant and bee interactions in the areas of (a) low, (b) medium, and (c) high land-use intensity, constructed using the R package ‘bipartite’v.2.15 [47]. Bee–flower visitors are displayed as rectangles at the top, and the plants are shown as rectangles at the bottom of each bipartite graph. The width of the rectangles represents the relative frequency of interactions of each species. The number added to each rectangle refers to the flower visitor and plants’ identity. The top 20 most frequent flower visitors and visited flowering plants are listed on the right. In the area of high land-use intensity (c) only 14 bee species were observed.

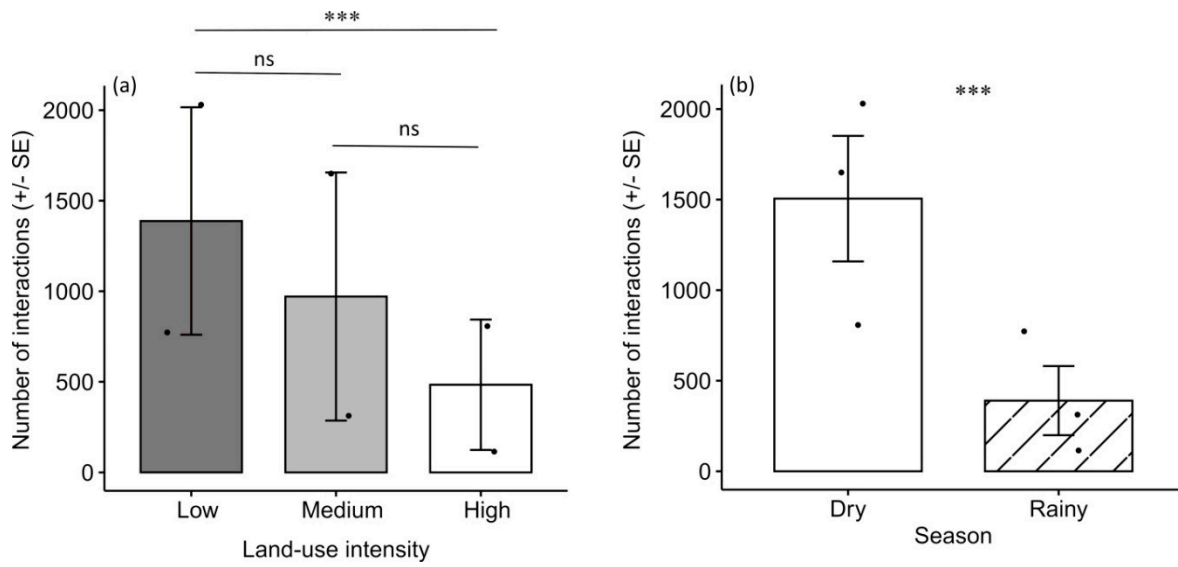


Figure 5. Mean number of interactions in (a) low, medium and high land-use intensity areas and (b) in the dry and rainy season; means \pm SE are shown; ns not significant, *** $p < 0.001$.

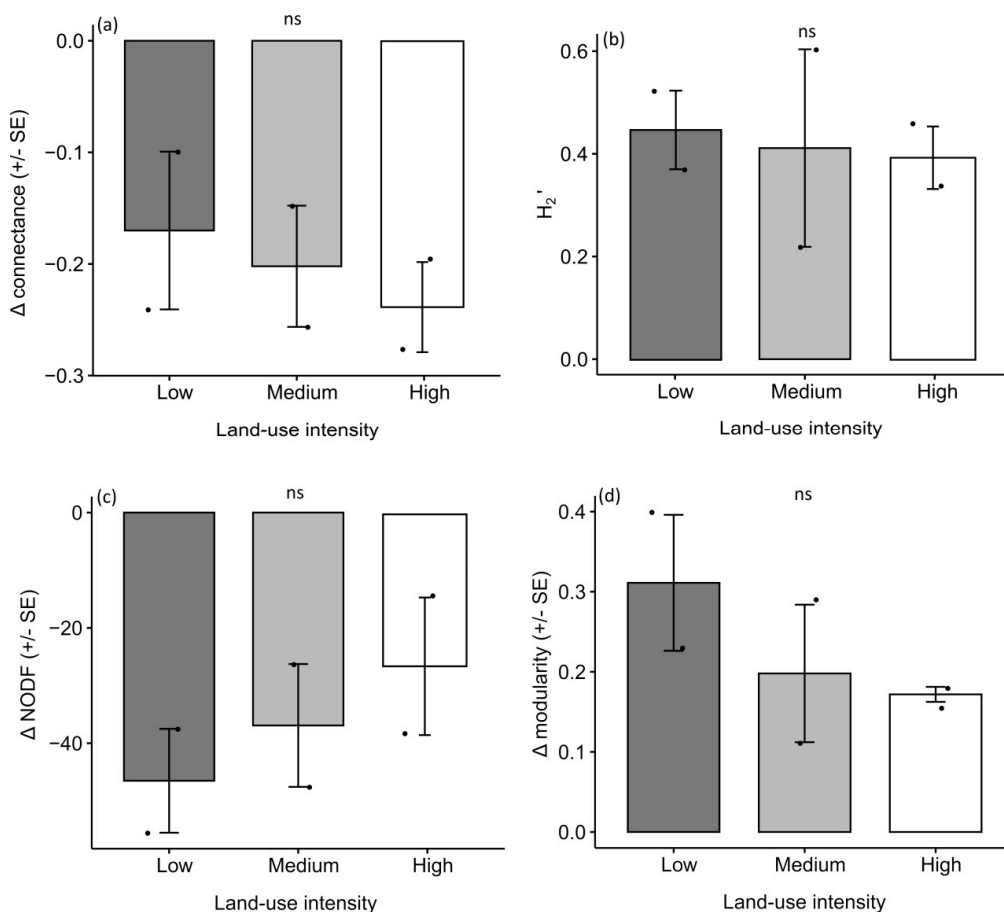


Figure 6. Mean network metrics and land-use intensity (low, medium, high); (a) Δ -transformed connectance, (b) network-level specialization (H_2'), (c) Δ -transformed nestedness (NODF), and (d) Δ -transformed modularity; means \pm SE are shown; ns not significant.

The number of interactions was higher in the dry (1505.3 ± 600.4 SD) compared to the rainy (390 ± 330.5 SD) season (GLMM; $Z = 6.354$, $p < 0.001$; Figure 5b). The Δ -transformed

connectance was higher in the dry season compared to the rainy season (LMM; $Z = 6.545$, $p < 0.001$; Figure 7a). Network specialization (H_2') was higher in the rainy season compared to the dry season (LMM; $Z = 3.569$, $p < 0.001$; Figure 7b). The Δ -transformed nestedness (NODF) was higher in the dry season compared to the rainy season (LMM; $Z = 11.320$, $p < 0.001$; Figure 7c). The Δ -transformed network modularity was lower in the dry season compared to the rainy season (LMM; $Z = 2.369$, $p = 0.017$; Figure 7d). Relative bee-species specialization (d') did not differ between seasons (Figure S2).

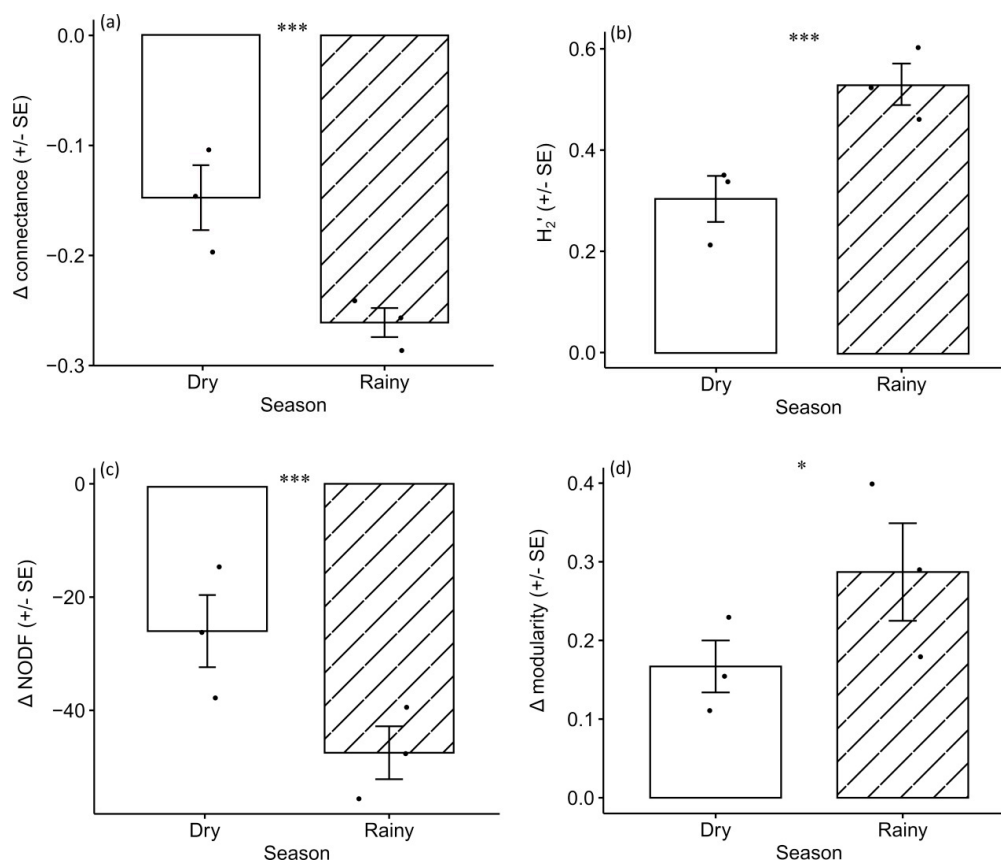


Figure 7. Mean network metrics in the dry and rainy season; (a) Δ -transformed connectance, (b) network-level specialization (H_2'), (c) Δ -transformed nestedness (NODF), and (d) Δ -transformed modularity; means \pm SE are shown; ns not significant, * $p < 0.05$, *** $p < 0.001$.

4. Discussion

4.1. Bee and Flowering Plant Richness, Land-Use Intensity and Climatic Seasonality

In contrast to flowering-plant richness not showing any differences among land-use intensities (LUI), bee-species richness significantly decreased with increasing LUI. A meta-analysis of 54 published studies documenting bee abundance and/or species richness as a function of destructive human-related activities explicitly found that habitat loss contributed to a significant decline in unmanaged bee-species richness [6]. Similar results were reported from a study in Burkina Faso based on pan-trap records revealing that with increasing disturbance, bee diversity decreased and bee communities became more and more differentiated [32]. In the region of high LUI, much of the savanna areas have been converted into agricultural land, leaving only small fragments of near-natural savanna. Another reason for the decrease of bee-species richness in our study might be a loss of specialized species with particular traits and nesting requirements or specialized diets [60] that could not be provided any longer by the disturbed and fragmented savannas of medium and high LUI. In general, specialist species with narrower niches are predicted

to be more sensitive to land-use than generalists [61,62]. However, a study in forested ecosystems in New Jersey (USA) did not provide evidence for a strong negative effect of land-use intensity on specialist bee species [63].

The honey bee (*Apis mellifera*) and the stingless bee *Hypotrigona gribodoi* were the most abundant flower visitors in all locations and seasons. *Hypotrigona gribodoi* is a generalist in terms of food and nesting resources. It seems to benefit from agriculture-bound landscapes with a heterogeneous small-scale matrix of arable fields, savanna patches, and home gardens in the vicinity of villages, which also offer abundant and diverse floral resources [63]. The resources available at the more disturbed sites appear to be sufficient for bee nutrition and not to limit certain bee populations. No effects of varying LUI could be observed in *Apis mellifera*. This is likely due to its diverse diet, broader ranges of foraging relative to other solitary bees, and its ability to find and use discrete patches of resources in the wider landscape, as it efficiently uses scouting [64,65]. Our study revealed that *Combretum glutinosum* (Combretaceae) was the most visited plant species in all locations and seasons. This is in line with a study from the same area in Burkina Faso where species of the Combretaceae family were the most visited by bees in comparison to all other observed woody plants. According to the authors, the choice of Combretaceae species by many bees could also be due to the long flowering time of these species. In addition to being one of the most dominant families in the areas, Combretaceae may offer a more significant amount of nectar and pollen compared to the other families [41].

Our study did not reveal significant differences of flowering-plant richness as a function of LUI. In terms of plant family diversity, the predominance of legumes, Rubiaceae and especially Combretaceae is a main characteristic of natural plant formations in Sudano-Guinean and Sudanian areas [66]. The savanna areas in our study host similar numbers of flowering plant species belonging to these dominant plant families.

In terms of seasonality, both bee-species richness and flowering-plant richness were higher in the dry compared to the rainy season. The majority of the melittophilous savanna plants in Burkina Faso are in flower during the dry season or at the very beginning of the rainy season [41,66]. Hence, savanna systems appear to provide bees with sufficient resources in the dry season when fields lay fallow, whereas crop fields and home gardens offer pollen and nectar during the rainy season. The observed higher bee-species richness in the savanna areas during the dry season is in line with a study from Burkina Faso that revealed an across-habitat spillover of bees (mostly abundant social bee species) from savanna into crop fields during the rainy season when crops are mass-flowering, whereas most savanna plants are not in bloom [32].

4.2. Plant-Bee Network Architecture, Land-Use Intensity and Climatic Seasonality

The number of interactions between bee and plant species decreased significantly with increasing LUI. When visualizing the interaction network of flower visitors and visited plants (bipartite graph, Figure 4) it is obvious that most interactions were detected in the area of low LUI. In the area of high LUI, only 14 bee species were observed in total. The three most frequent flower visitors in all areas were *Apis mellifera*, *Hypotrigona gribodoi* and *Pseudapis interstitinervis* Strand. As for the first two species, *P. interstitinervis* is polylectic. It visits the flowers of plants—for example of several *Acacia* species and *Cassia siberiana* [67]—that are among the top 20 most frequently visited plant species in our study. All three bee species extend their frequency range with increasing LUI (larger width of the rectangles) and almost dominate the network in the area of high LUI. Other frequent flower visitors were carpenter bees (*Ceratina* sp.). Some of these mostly polylectic bees are partially oligolectic and visit flowers of certain plant families such as Fabaceae, Malvaceae, Rubiaceae, and Asteraceae [68]. While we recorded three *Ceratina* species in the areas of low and medium LUI, only one species was observed in the area of high LUI. The latter area might comprise fewer species of these plant families and thus offer fewer food resources.

All of our Δ -transformed network metrics were consistently different from zero, relative connectance and nestedness were lower than zero, and relative modularity were

larger than zero, revealing the existence of isolated groups of interacting bee and flower-plant species. We documented that climatic seasonality was a stronger determinant of change in the flower–bee network architecture compared to land-use intensity. The number of flowering savanna plants differed significantly between both seasons, having a peak during the dry season and leading to a three times more frequent interaction between plants and pollinators (Figure 5). As the larger number of interactions was obviously distributed over an equal number of plants and with it the overlap in identity of the mutualistic partners of pollinators increased [69], the networks' connectance was significantly higher and network specialization was lower in the dry season than in the rainy season. If connectance increases, the size of the core of links between generalized species also increases, which in our case reduced the level of modularity and increased the level of nestedness [9,70,71]. Greater connectance and nestedness could increase network stability and robustness via reducing interspecific competition [70]. Modularity implies some subsets (modules) of species being more linked to each other than to species on other modules [72], and as such are expected to be an essential ingredient of network complexity and thus of the robustness of communities [42–44,73]. A flower-visitation study considering season and land-use intensity carried out in the highlands of Guatemala [49] also revealed that seasonality did not only affect species diversity, but also the way species were interacting in the community and, similar to our study, reported higher nestedness and lower modularity in the dry season.

Although we could not detect a statistically significant effect of LUI on the architecture of plant–pollinator networks, our data revealed that networks' modular structure decreases with increasing land-use intensity. Here, changes in modularity may already reflect reduced habitat heterogeneity of savannas underlying high land-use intensity that in turn has already led to a significant decrease in bee-species richness (Figure 2). As both modularity [44] and nestedness [70] capture different aspects of network architecture [43] and are thought to provide strong benefits for ecological communities' robustness to perturbation [69,74], our results highlight the importance of savanna conservation and surrounding habitat in maintaining wild-bee diversity. The small sample size of only three land-use intensity areas might explain the low statistical power when testing the effect of LUI. Alternatively, the lack of an effect of LUI on network architecture might reflect the stability of network properties to habitat degradation [75]. Further studies should consider more sample areas per disturbance class to enhance statistical model power.

5. Conclusions

In this paper, we have extended studies of biodiversity from merely looking at species numbers to also including their mutualistic interactions. We have investigated detailed network structures by focusing on the number of species interactions and network specialization level, connectance, and modularity considering a land-use intensity gradient and seasonality.

There is a complex interplay of patterns and processes related to the variation and influence of spatial, temporal, and biotic drivers in an ecological network, still limiting our current knowledge about the effects of environmental change (i.e., land use, climate) on such systems [42]. This work is a step toward a better understanding of the impact of land-use change and climatic seasonality on bees, flowering plants, and their mutualistic network architecture in West African savannas.

Supplementary Materials: The following are available online at <https://www.mdpi.com/1424-2818/13/1/1/s1>, Figure S1: Relative bee species specialization (d') in low, medium, and high land-use intensity areas, Figure S2: Relative bee species specialization (d') in dry and rainy season, Table S1: Raw network metrics of all three areas (Dano, Bontioli, Nazinga, Burkina Faso) in the dry and rainy season, Table S2: Δ -transformed network metrics of all three areas (Dano, Bontioli, Nazinga, Burkina Faso) in the dry and rainy season.

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