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Cattle pasture management filters functional traits and alters trait–role relationships in plant–butterfly interaction networks

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Abstract

Grazing intensity and tree cover has potential repercussions for plant–butterfly interactions. Here, we evaluated how three cattle management types—open pastures (OP), woody pastures (WP), and pastures adjacent to forest remnants (FAP)—are associated with species roles within plant–butterfly networks in a deforested tropical dry forest (TDF) region of northern Colombia. Across 24 pastures, we quantified butterfly and plant traits, constructed interaction networks, and estimated species roles using centrality-based indices from a principal component analysis.

Our results show that cattle management filtered both plant and butterfly traits, modifying the identity of interacting species even though overall centrality did not differ among management types. Trait–role relationships shifted across management regimes: corolla width influenced plant centrality in FAP ($\beta = 0.036$, $p < 0.03$) and WP ($\beta = 0.041$, $p < 0.03$), whereas butterfly wing length ($\beta = -0.028$, $p = 0.049$) and body length ($\beta = -0.073$, $p = 0.011$) were the main traits associated with their interactive roles only in WP. These patterns indicate that environmental filtering reorganizes trait distributions and the mechanisms by which traits shape species importance within plant–butterfly networks.

Overall, we show that cattle management does not directly modify species' interactive roles, but instead acts primarily as a trait-based filter, indirectly shaping plant–butterfly networks by altering trait distributions and trait–role relationships rather than the overall network structure. Promoting tree cover and maintaining forest adjacency within cattle landscapes may enhance the ecological functionality of mutualistic networks in TDF ecosystems.

Introduction

Tropical dry forests (TDF) are among the most threatened terrestrial biomes, characterized by marked seasonality, high levels of endemism, and long historical exposure to human transformation (Powers et al. 2018; Tabarelli et al. 2024; Teixeira et al. 2025). Across the Neotropics, extensive conversion of TDF to agricultural systems—especially cattle production—has resulted in highly fragmented landscapes where remnant forest patches persist within a matrix of pastures (Dupin et al. 2018; Rocha-Filho et al. 2025). These changes influence ecological processes at multiple scales, including the dynamics of plant–pollinator interactions that underpin ecosystem functioning (Bustamante-Castillo, Hernández-Baños, and Arizmendi 2020). Understanding how mutualistic interactions persist or reconfigure under land-use change is therefore critical for conserving biodiversity and sustaining ecosystem services in these degraded yet ecologically valuable regions (Proesmans et al. 2024; Buono et al. 2023).

Within modified landscapes, species interactions often respond more strongly to trait-based mechanisms than to species identity alone (Zakharova, Meyer, and Seifan 2019; Litchman, Edwards, and Boyd 2021). Functional traits modulate how species perceive, exploit, and contribute to ecological networks. In pollination systems, traits such as floral morphology or pollinator body size shape partner accessibility, interaction frequency, and specialization (Gómez, Perfectti, and Klingenberg 2014; Muchhala 2007). Because traits determine how species cope with habitat alteration, management

practices that restructure vegetation can induce non-random filtering of traits (Liu, Liu, and Zheng 2015; Gilhaus et al. 2017; Swift and Bell 2011), ultimately affecting the distribution of interactive roles within mutualistic networks (Dáttilo, Guimarães, and Izzo 2013; Guimarães et al. 2017; Fuzessy and Pizo 2025). Empirical research has identified species that play a highly interactive role, characterized by significant network importance and a major influence on co-occurring species. This framework has proven useful for understanding responses of plant–pollinator systems to disturbance yet remains understudied for plant–butterfly assemblages in highly transformed TDF landscapes.

Livestock systems provide a valuable context for investigating trait-mediated mechanisms, as pasture management strongly modify vegetation structure and floral resource availability (Vanbergen et al. 2014; Lázaro and Santamaría 2016). Forest-adjacent pastures (FAP) and Woody pastures (WP) retain higher greater structural complexity and microhabitat heterogeneity than open pastures (OP), potentially influencing both plant assemblages and butterfly communities. Such differences can influence both the abundance of weed plants and the assemblage of butterfly species visiting flowers (de Araújo Silva et al. 2025; Neff, Fettig, and VanOverbeke 2007; Marini et al. 2009; Mitja and Miranda 2010). Importantly, weedy plants exhibit phenological asynchrony relative to TDF trees. While forest species reproduce around rainfall cues, pasture weeds often flower opportunistically, extending resource availability into periods when the surrounding matrix offers limited or no floral resources (Cortés-Flores et al. 2017; McLaren and McDonald 2005). These asynchronous blooms may help sustain pollinator activity and thereby maintain interaction flow across the broader landscape (Shrotri et al. 2025; Genini et al. 2021).

Because vegetation structure and the phenology of resource-providing plants differ among management regimes, livestock systems in TDF landscapes have the potential to filter functional traits of both plants and butterflies. In such systems, floral traits strongly influence the accessibility of nectar resources and subsequently determine whether plant species become central or peripheral within plant–butterfly networks. Floral size, density, and corolla morphology affect interaction frequency and can increase the likelihood that certain species act as local hubs (Xiang et al. 2023), while morphological matching between corolla architecture and pollinator morphology further shapes the emergence of modular structures and interaction clusters (Maglianesi et al. 2024; Izquierdo-Palma et al. 2021). The integration of floral traits has been shown to drive network roles in multiple systems (Lázaro and Santamaría 2016), underscoring the importance of trait-mediated filters in determining the functional contributions of plant species within mutualistic assemblages.

Similarly, butterfly traits influence their position as key connectors or peripheral elements in mutualistic networks. Morphological and phenological characteristics often determine interaction frequency, with trait-matching between pollinator morphology and floral architecture being a primary predictor of interaction probability (Guo et al. 2022; Mertens et al. 2021). In particular, body size and wing dimensions are closely linked to mobility, energetic demands, and foraging range, thereby constraining the number and diversity of potential interaction partners. Larger-bodied butterflies, often characterized by broader wings and higher flight capacity, tend to forage over wider spatial scales but may interact less frequently with individual plant species due to higher energetic costs and lower maneuverability in

structurally complex habitats (Hagen et al. 2012; Dehling et al. 2016). Conversely, smaller butterflies with reduced wing spans often exhibit higher visitation rates and tighter coupling with specific floral resources, which can promote more frequent but spatially constrained interactions (Bartomeus et al. 2016; Junker et al. 2013). Species with extended activity periods tend to accrue more connections across modules (Guzman, Chamberlain, and Elle 2021), whereas generalist foraging strategies often lead to more central network roles (Coux et al. 2016; Pires et al. 2022). Environmental variation and microclimatic conditions can further shape butterfly centrality (Álamo et al. 2025), suggesting that both internal (trait-based) and external (environmental) filters govern the functional contributions of butterflies in plant–pollinator systems.

Cattle management introduces an additional environmental filtering in TDF landscapes. Grazing, browsing, and trampling modify microhabitats and plant assemblages (Maza-Villalobos et al. 2022), influencing the functional traits of ground-layer vegetation, which in turn structures the foraging opportunities available to butterflies. These management-driven shifts can cascade through local interaction networks by altering which traits are favored (Maza-Villalobos et al. 2022). Exclusion of cattle has been shown to increase woody plant density and species richness (Quisehuatl-Medina et al. 2020), yet working pastoral landscapes—such as those characteristics of northern Colombia—must balance conservation objectives and the realities of food production. Given that trait distributions shape partner availability and interaction patterns (Santos and Ribeiro 2023), understanding how cattle management regimes filter traits are fundamental for interpreting functional variation in butterfly–plant networks. These dynamics unfold within multifunctional landscapes, where biodiversity conservation must coexist with productive activities such as cattle ranching. Multifunctional systems emphasize reconciling agricultural production with ecological processes by maintaining heterogeneous landscapes, enhancing ecosystem multifunctionality, and supporting services such as pollination (McGranahan 2014; Leroy et al. 2025). Trade-offs are unavoidable—biodiversity-friendly practices may reduce short-term production (Burian et al. 2023) or generate complex landscape responses (van der Plas et al. 2019)—yet adaptive management frameworks and collaborative stewardship can facilitate sustainable outcomes (Chirwa et al. 2024; Garibaldi et al. 2023; Cockburn et al. 2019). In TDF regions of northern Colombia, where cattle ranching dominates land use, developing management strategies that support pollinator communities and maintain interaction networks is essential for sustaining both biodiversity and agricultural resilience.

Against this backdrop, WP, FAP, and OP represent distinct management regimes that may impose different environmental filters on plants and butterflies, potentially altering trait distributions and, consequently, the interactive roles species assume. Nevertheless, despite growing evidence that functional traits structure mutualistic networks under land-use change, we still lack empirical tests of how cattle management regimes influence trait–role relationships in plant–butterfly networks in TDF. Addressing this gap is essential for understanding how biodiversity persists and how pollination processes can be enhanced in multifunctional tropical landscapes. Specifically, we ask: (1) *Do different pasture management types influence the interactive roles of plants and butterflies? and (2) To what extent do functional traits explain variation in these roles?* We hypothesize that (i) management indirectly shapes interactive roles by filtering traits of both plants and butterflies; (ii) plants with wider corollas attain

higher centrality due to enhanced accessibility; and (iii) butterfly morphological traits—particularly wing size and overall body size—predict interactive roles. Specifically, smaller butterflies are expected to interact with a greater diversity of plant species and to exhibit higher centrality, reflecting enhanced mobility, broader resource use, and reduced energetic constraints under simplified pasture conditions. Collectively, these hypotheses reflect the expectation that trait-based mechanisms, rather than management per se, are the primary drivers of functional positioning within plant–butterfly networks in livestock-dominated TDF landscapes.

Methods

Study area

We conducted this study in the highly transformed landscape of the Sinú medio and San Jorge subregions (< 200 m asl), in the Córdoba department on the northern Caribbean coast of Colombia. The Caribbean region is characterized by some of the highest human footprint values in the country and a low proportion of remaining natural áreas (Correa Ayram et al. 2020). Córdoba was originally dominated by TDF; however, agricultural expansion and extensive cattle ranching have resulted in the loss of approximately 85% of its original forest cover (Ramos et al. 2016). The current landscape is a mosaic dominated by cattle pastures, interspersed with agricultural fields, remnant forest patches, and human settlements (Ruiz 2022).

The climate is characterized by a marked dry season between December and March, and a rainy season from May to November which strongly constrains plant phenology and floral resources for pollinators. Relative humidity above 80%, mean annual temperature ranges from 26.9°C to 27.8°C, and annual precipitation ranges from 1500 to 2000 mm (Meisel and Pérez 2006; Galvis 2009; IAvH 1998).

We conducted fieldwork during the peak flowering season of pasture herbaceous plants, from October to December 2024, which corresponds to the regional rainy season (IGAC 2009; Meisel and Pérez 2006). We studied three common pasture management types in Córdoba's cattle ranches: (1) FAP: forest-adjacent pastures, (2) WP: woody pastures (high tree density), and (3) OP: open pastures (low tree density).

We selected 24 cattle pastures representing three management types (eight per type) within the same biogeographic region to minimize climatic and historical variation. Pasture size ranged from 5 to 35 ha. To ensure spatial independence between sampling sites, we maintained a minimum separation distance of 2 km between pastures; where possible, we selected one pasture of each type within the same farm (Fig. 1).

The herbaceous layer in FAP was dominated by *Bothriochloa pertusa*, *Brachiaria brizantha* cv. Toledo, *Echinochloa polystachya*, and *Brachiaria humidicola*. WP featured *Dichanthium aristatum*, *Megathyrsus maximus* cv Mombasa, *Brachiaria humidicola*, and *Bothriochloa pertusa*, while OP were dominated by *Brachiaria humidicola*, *Brachiaria mutica*, and *Bothriochloa pertusa*. The woody component of WP

pastures showed high native tree diversity, including *Pachira quinata*, *Simarouba amara*, *Cavanillesia platanifolia*, *Bursera simaruba*, *Samanea saman*, *Lecythis minor*, *Pterocarpus acapulcensis*, *Ficus carica*, and *Tabebuia rosea*. FAP and OP shared common trees such as *Tabebuia rosea*, *Samanea saman*, *Gliricidia sepium*, *Guazuma ulmifolia*, *Crescentia cujete*, and *Pachira quinata*.

Poor soil drainage—a characteristic feature of the alluvial soils with high clay and silt content in the Sinú River valley (IGAC 2009)—was observed in 37.5% (3/8) of FAP sites and 62.5% (5/8) of WP and OP sites. All farms had over 50 years of cattle production history. Farm size varied from 79.5 to 2,380 ha, with herd sizes ranging from 130 to 4,200 head. Pasture covered 50–98% of the land area across farms, with stocking rates of 0.87–8.5 animals/ha under rotational grazing management.

Sampling plant-butterfly interaction

To record plant-butterfly interactions, we employed linear transects within each of the 24 selected cattle pastures. In each pasture, we established three 300 m long by 5 m wide linear transects (recording area: 2.5 m on each side of the observer). We surveyed each transect for 30 minutes per day over four consecutive days, resulting in a total sampling effort of six hours per pasture.

On each sampling day, we visited at least three different pastures. We conducted all sampling between 7:30 am and 3:30 pm on days with favorable weather conditions (sunny or partly cloudy with minimal wind). To control potential time-of-day effects on butterfly activity and flower visitation, we randomized the order in which we visited the pastures each day.

We recorded a flower’s visitation event only upon observing a butterfly's proboscis making direct contact with the reproductive structures of a flower. Butterflies were identified either by sight (for species that could be reliably recognized in flight or perched) or by capture with an entomological net for closer examination. We used visitation frequency as a metric for pollinator functional performance (Vázquez, Morris, and Jordano 2005). For captured specimens, following standard entomological practices and minimizing specimen removal to the extent possible we sacrificed a voucher series of 5–10 individuals per species; all others were photographed and released on site. Sacrificed specimens were stored in plastic containers for transport.

Butterfly identification was completed by comparing collected vouchers and photographs to authoritative illustrated guides for Colombian species (Garwood 2017). For plant identification, we photographed the habit, leaves (including their arrangement), flowers, and fruits (when available). We provisionally identified plants in the field using common names provided by local farm workers. Subsequently, we assigned scientific names by comparing photographs to specimens in digital herbarium collections (STRI 2025; WFO 2025; Vibrans 2012).

All butterfly vouchers were deposited in the entomological collection of the Pontificia Universidad Javeriana in Bogotá. Specimen collection was conducted under the permit for collection and

mobilization of biological specimens, Resolution ANLA No. 1255 (June 24, 2024), and was certified by the Vice-Rectory for Research of the Pontificia Universidad Javeriana-Bogotá (Official Communication VI-0472).

Plant and butterfly traits

For butterfly species, we measured three morphological traits: proboscis length, body length, and forewing length (Table S1). Proboscis length was estimated for one to ten specimens per species (typically five). Heads were separated from the body, antennae removed and subsequently softened in 70% ethanol for 20 minutes. Each head was pinned onto a polystyrene surface, and labial palps were removed to expose the proboscis insertion. To measure the proboscis, it was then fully extended and fixed using entomological pins. A segmented reference scale (1-mm precision) was placed beside each preparation, and the structures were photographed, following (Lehnert et al. (2016) and Bauder et al. (2015).

Body and forewing lengths were obtained from scaled photographs taken with a 1-mm precision reference. Body length was defined as the distance from the most distal point of the head to the abdomen, and forewing length as the distance from the anterior wing insertion to the wing apex. Forewing length was averaged from one to seven specimens, and body length from one to five (Table S1). When only one specimen was available, its measurement served as the species-level estimate. Because specimen collection was limited to avoid disturbing plant–butterfly interactions, some traits were measured from regional museum specimens or from calibrated images available through Butterflies of America (Warren et al. 2024). For each species and trait, we calculated a mean and its standard deviation (Table S2).

For plant species, we compiled six traits, including five floral attributes: corolla width, corolla length, corolla shape (achlamydeous; bell-shaped; bell- to urn-shaped; obovate; papilionaceous; petaloid calyx; rotate; salverform; spatulate; tubular; two-lipped or zygomorphic), corolla type (dialipetalous, gamopetalous, or achlamydeous), and corolla color (blue, green, lilac, orange, pink, purple, red, white, yellow). We additionally recorded species' geographic origin (native/exotic). Quantitative floral traits were measured from field photographs taken with a 1-mm precision scale, using measurements from 2–17 flowers collected per species across multiple sites when available. Categorical traits were assigned using botanical literature and digital herbaria, including World Flora Online (WFO 2025), the STRI Research Portal (STRI 2025), and *Fichas de Malezas de México* (Vibrans 2012). When field specimens were unavailable, trait measurements were extracted from literature or from scaled photographs of herbarium specimens in these digital repositories (Table S3).

All butterfly and plant trait measurements were extracted from scaled images using ImageJ (Schneider, Rasband, and Eliceiri 2012).

Interactive role of plants and butterflies

To quantify the importance of plant and butterfly species within interaction networks, we estimated the interactive role of every species occurring in each network constructed for each of the three pasture management types (FAP, WP and OP). For each management type, we built a plant–butterfly meta-network by pooling all interactions recorded across the eight pastures belonging to that category (Table S4; Fig S1). This approach was adopted to characterize regime-level interaction patterns and emergent species roles associated with each management type, rather than site-specific network variation, thereby emphasizing the structural and functional properties that consistently arise under shared management conditions and reducing the influence of local stochasticity in species interactions. Each meta-network was weighted, where $a_{(i,j)}$ represents the number of interactions between plant *i* and butterfly *j*, and zero indicates absence of interaction. Weighted networks that combine interaction frequencies and abundances are appropriate for estimating species roles in ecological interaction systems (Miranda et al. 2019).

For each meta-network, we quantified the interactive role of plant and butterfly species using three complementary centrality metrics: degree centrality, betweenness centrality, and closeness centrality (Martín González, Dalsgaard, and Olesen 2010; Cagua, Wootton, and Stouffer 2019). Degree centrality reflects a species' importance based on the number of interaction partners— with generalist species exhibiting high degree values and specialists exhibiting low values (Bascompte and Jordano 2013). Betweenness centrality identifies species that act as connectors between otherwise separated portions of the network; species with BC > 0 bridge structural gaps (Freeman 1979; Martín González, Dalsgaard, and Olesen 2010). Closeness centrality measures the overall proximity of each species to all others in the network, meaning that species with high closeness can influence, and be influenced by, other species more rapidly (Sazima et al. 2010). All centrality metrics were computed using the *bipartite* package in R (Dormann 2025).

Because centrality metrics tend to be moderately to strongly correlated (Sazima et al. 2010; Estrada 2007), we summarized them into a single generalized centrality index using principal component analysis (PCA). This PCA was conducted separately for plants and butterflies within each meta-network to account for taxon-specific differences in interaction patterns. In all taxon–management combinations (n = 6), the first principal component (PC1) captured the largest proportion of variation (≥ 68.3%; Table S5), confirming that the three centrality descriptors carry complementary information and supporting the use of PC1 as an integrative measure of species centrality (Sazima et al. 2010; Dáttilo et al. 2022; Cruz et al. 2024; Ratoni et al. 2025). We added the minimum negative value among the PC1 data to obtain positive interactive role values, a linear transformation that does not alter the structure of the data but improves numerical handling and interpretability of the composite index. Given the positive correlations between PC1 and the original centrality metrics, high PC1 scores indicate species with high interactive roles (i.e. generalists), whereas low PC1 scores correspond to species with lower interactive roles (i.e. specialists).

Statistical analysis

Comparing interactive roles across management types

To assess whether species' interactive roles differed among pasture management types (FAP, WP, OP), we first estimated a centrality index. Because only one meta-network was available per management type, classical inferential procedures requiring replicated networks could not be applied. To address this limitation and obtain inference on mean interactive roles for each management category, we implemented a non-parametric bootstrap procedure (Efron and Tibshirani 1986).

For butterflies and plants separately, we generated 1000 bootstrap resamples from the empirical distribution of PC1 scores within each management type, calculating mean values and 95% confidence intervals for each resample set. This approach provides robust distribution-free estimates of uncertainty and allows comparisons across management types based on the degree of overlap among confidence intervals. Overlapping intervals indicate that differences among management categories are not reliably distinguishable given the available data structure. All bootstrap procedures were implemented using the boot() function from the *boot* package (Canty A and Ripley B 2025).

Functional traits on species interactive roles

We evaluated whether interspecific variation in traits predicted species' interactive roles within each management type. Analyses were conducted separately for butterflies and plants. For butterflies, explanatory variables included wing length, body length, and proboscis length. For plants, we considered corolla width, corolla length, corolla type, corolla shape, corolla color, and geographic origin (native/exotic). For each meta-network (i.e. taxon × management combination), we fitted separate generalized linear models (GLMs) using PC1 scores as the response variable.

Error distributions and link functions were selected according to the nature of the response variable and predictors. Models with continuous predictors were fitted using Gaussian distributions with identity link functions, whereas models with categorical floral traits employed appropriate error structures ensuring correct residual behavior. All models were fitted using the glm() function from base R.

Before model fitting, we evaluated normality and homoscedasticity of residuals using Shapiro–Wilk and Breusch–Pagan tests, respectively, and assessed overdispersion for non-Gaussian models. Residual diagnostics were conducted using simulation-based procedures with the DHARMa package (Hartig F 2024), allowing detection of non-uniformity, dispersion issues, and potential outliers. Multicollinearity among predictors was evaluated through Variance Inflation Factors (VIF) computed with the vif() function from the *car* package (Fox J and Weisberg S 2019).

We initially explored an information-theoretic model selection approach; however, due to sample size constraints and model singularities, this approach did not yield stable model subsets across all taxon × management combinations. Therefore, we adopted a stepwise model simplification strategy using the step() function from base R, applying both backward and forward selection based on AIC. For each retained model, we extracted coefficients, standard errors, confidence intervals, and significance values, and computed marginal R^2 using the r.squaredGLM() function from *MuMIn*.

All analyses were conducted in R version 4.3.1. (R Core Team 2023).

Results

Across the 24 surveyed pastures, we recorded 33 butterfly species and 67 plant species. Because networks from individual pastures were pooled by management type, we constructed three plant–butterfly meta-networks corresponding to FAP, WP and OP (Table S4). A total of 3,617 interaction events were documented across the study, ranging from 816 (FAP) to 1,706 (OP).

In FAP, we recorded 816 interactions involving 43 plant species and 27 butterfly species. *Sida acuta* (Malvaceae) was the most frequently visited plant (200 visits; 24.5%), whereas *Hedone vibex* was the butterfly species interacting for the highest number of plants (228 visits; 27.9%).

In WP, we documented 1,095 interactions, comprising 38 plant species and 24 butterfly species. *Malachra alceifolia* (Malvaceae) was the most frequently visited plant (295 visits; 27%), while *Spicauda procne* accounted for the highest number of butterfly interactions (382 visits; 35%).

In OP, 1,706 interactions were recorded. *Lippia dulcis* (Verbenaceae) received the highest visitation frequency (421 visits; 24.7%), and *Spicauda procne* again emerged as the butterfly accounting for the highest number of interaction events (467 visits; 27.4%).

Regarding floral traits, dialipetalous (66.5%), yellow (37%), rotaceous (41.3%) and native (92.9%) flowers were the most frequently visited across the entire study. Corolla width ranged from 1.5 mm in *Cissus* sp. to 50 mm in *Limnocharis flava*. Corolla length varied between 0.4 mm in *Murdannia keisak* and 27.9 ± 2.79 mm in *Isertia haenkeana*. Trait–visitation patterns remained generally consistent across management types, with the exception of OP, where white flowers received comparatively more visits (Table S6).

Across the entire dataset, butterfly traits exhibited substantial interspecific variation. Wing length ranged from 8.53 ± 0.09 mm in *Hemiargus hanno* to 48.52 ± 1.28 mm in *Heraclides thoas*. Body size varied between 7.05 ± 0.34 mm (*H. hanno*) and 27.15 ± 2.23 mm (*Dryadula phaetusa*). Proboscis length spanned a wide gradient, from 4.42 ± 0.22 mm in *Hermeuptychia hermes* to *27.04 ± 4.10 mm* in *Phoebis sennae*. These trait ranges were largely consistent across management types, although the species contributing to the extremes varied (Table S2).

Effect of pasture management on the interactive role of butterflies and plants

Bootstrap estimates showed largely overlapping 95% confidence intervals among management categories for both taxa (Table S7), indicating that variation in interactive roles across management types was not strong enough to be statistically distinguished. Although WP butterflies exhibited the highest mean centrality (1.606), their 95% CI overlapped extensively with those from FAP (0.942–1.639) and OP (1.037–1.691). A similar pattern emerged for plants: despite OP plants having the highest mean (1.394), their confidence interval overlapped broadly with those of FAP (1.013–1.590) and WP (0.806–1.518) (Fig. 2).

Functional traits on species interactive roles

When evaluating whether functional traits predicted the interactive roles of plants and butterflies within the meta-networks for each pasture management type, we found that species' interactive roles were partially explained by their traits, indicating trait-dependent mechanisms influencing species roles within interaction networks. In tree-rich pastures (WP), butterfly wing length ($\beta = -0.028$, $p = 0.049$) and body length ($\beta = -0.073$, $p = 0.011$) were negatively related to centrality ($R^2 = 0.16–0.26$; Fig. 3; Table S8). In contrast, plant traits showed a consistent positive association with their interactive role. In both forest-adjacent (FAP) and tree-rich (WP) pastures, corolla width was positively related to centrality ($\beta = 0.036–0.041$, $p < 0.03$; $R^2 = 0.13–0.15$; Fig. 3; Table S8).

Discussion

Understanding how livestock management filters species' functional roles within mutualistic networks is essential in TDF landscapes, where habitat transformation is extensive, and biodiversity must operate under strong climatic seasonality. In this study, we evaluated how pasture management types in a cattle-production region of northern Colombia influence the interactive roles of butterfly and plant species within plant–butterfly networks, and whether functional traits predict these roles. In contrast to studies showing that landscape configuration and management intensity often alter pollinator assemblages and interaction patterns (Proesmans et al. 2024; Cano et al. 2025), we found no evidence that management type (woody pasture, pastures adjacent to forest, or open pasture) significantly influenced species' interactive roles. Instead, variation in interaction roles was primarily associated with functional traits, suggesting trait-based filtering rather than direct management-driven effects.

The absence of management-driven differences likely reflects the ecological characteristics of TDF pastures in the region. First, despite differing in tree cover, the studied pasture types share a similar herbaceous layer dominated by weedy plants capable of thriving under grazing pressure. These herbaceous communities may buffer potential management effects by providing relatively uniform nectar availability across sites—particularly relevant in TDF, where rainfall seasonality produces strong environmental filters (Le Bagousse-Pinguet et al. 2017; Oloumane et al. 2025). Additionally, the moderate

spatial scale of our sampling, combined with the limited functional differentiation of the herb layer across management types, may constrain the degree to which management practices translate into contrasting interaction patterns. In similar livestock landscapes, structural vegetation differences influence interaction roles only when management produces clear contrasts in resource availability, vegetation architecture, or disturbance regimes (Adedoja and Mallinger 2024; Peralta et al. 2023). Our findings suggest that, in this TDF region, such contrasts were insufficient to generate detectable differences in species-level interaction roles.

Functional traits emerged as the primary predictors of interaction roles. For plants, corolla width was positively associated with the number of butterfly partners, consistent with trait-matching mechanisms frequently reported in pollination networks (Xiang et al. 2023; de Sousa Perugini et al. 2025; Maglianesi et al. 2024). Wider corollas often facilitate access for a broader range of visitors, thereby enhancing opportunities for interactions largely independent of management type. In our TDF landscape, this trait effect must also be interpreted through the lens of phenological dynamics in herbaceous weeds.

Unlike canopy trees in TDF, which exhibit highly synchronized flowering tied to rainfall pulses (Astegiano et al. 2024; Günter et al. 2008; Silveira, Martins, and Araújo 2013), herbaceous weeds display asynchronous and flexible flowering, responding opportunistically to micro-environmental conditions (Cortés-Flores et al. 2017; McLaren and McDonald 2005). This asynchrony may produce sustained nectar availability across extended portions of the year, including periods in which forest trees are not flowering (Cortés-Flores et al. 2023). Such off-season floral resources may help sustain butterfly populations during phenological gaps, enabling their persistence within livestock systems and facilitating spillover to nearby habitats—including remnant TDF patches and fruit crop plantations that depend on pollination services (Rocha et al. 2018). Under this scenario, plants with wider and more accessible corollas may play a disproportionate role in maintaining interaction flow throughout the year, thereby stabilizing butterfly presence in an otherwise strongly seasonal environment.

For butterflies, body size and wingspan were negatively associated with interactive role: larger butterflies interacted with fewer plant species, while smaller species were more generalized. This pattern contrasts with classical expectations linking larger pollinators to higher generalization (Peralta et al. 2023), yet it aligns with ecological mechanisms expected in herbaceous, disturbance-prone systems. Smaller butterflies are better suited to exploit fine-grained floral resources, maneuver efficiently within dense low vegetation, and maintain lower energetic requirements, all of which may confer broader realized diets in weedy pastures. The absence of an effect of proboscis length further supports the idea that morphological matching played a secondary role in this system, consistent with findings from other simplified or disturbed Neotropical habitats (Sõber et al. 2024). Instead, mobility- and size-related traits appear to mediate access to heterogeneous nectar resources in TDF pastures.

Our findings align with broader evidence that functional traits mediate species responses and interaction roles under land-use change (Le Bagousse-Pinguet et al. 2017; Adedoja and Mallinger 2024; Cano et al. 2025). Land-use intensification often imposes strong environmental filters that disproportionately affect

species with particular traits, altering interaction patterns and functional overlap. However, when local resource conditions are homogeneous—as in the herb-dominated pastures we studied—trait-based processes may override management effects, generating comparable interactive roles across pasture types. Woody pastures, despite offering shade and structural heterogeneity, did not modify interactive roles, highlighting the resilience of these weedy plant–butterfly interaction networks under the tested gradients.

In heavily transformed TDF regions, where > 90% of native cover has been lost, understanding how functional traits shape interaction roles is essential for conservation planning. Our results indicate that trait-based mechanisms, rather than management type, determine the degree to which butterflies and plants contribute to interaction networks in livestock landscapes. This suggests that conservation strategies should prioritize (i) maintaining diverse herbaceous communities that provide continuous nectar resources, (ii) preserving or restoring plant species with accessible floral architectures, and (iii) safeguarding butterfly species with traits that promote broad interaction potential.

Moreover, by providing continuous or complementary resources within highly modified landscapes, well-managed livestock pastures may contribute to sustaining pollinator communities beyond their boundaries. When structural and compositional heterogeneity is maintained, these systems can function as supplementary habitats that enhance landscape-level connectivity and support pollination services across the broader tropical dry forest matrix, including remnant forest patches and surrounding agroecosystems.

Conclusion

This study shows that livestock management regimes in TDF landscapes do not have a strong direct effect on the overall centrality of species within plant–butterfly networks. Instead, management appears to act primarily as a trait-based filter, influencing which plant and butterfly species attain more influential interactive roles. Larger-bodied butterflies tended to exhibit lower centrality, whereas plant species with broader corollas consistently acted as interaction hubs. These patterns reveal that functional traits, rather than management per se, are the main determinants of species' positions within networks.

A second key mechanism emerges from the phenology of the weed species common in grazed pastures. Unlike the strongly seasonal flowering of dry forest trees, these weedy species display asynchronous and prolonged flowering, providing floral resources during periods when the surrounding forest matrix offers few or none. Such temporally decoupled resource availability may help maintain pollinator activity across seasonal bottlenecks, thereby supporting butterfly populations that later interact with both forest plant communities and pollinator-dependent fruit crops cultivated in the region.

Together, these findings underscore that biodiversity-friendly pasture management can contribute to sustaining mutualistic processes not by altering network structure directly, but by conserving trait diversity and maintaining continuous floral resource availability. Protecting woody elements and diverse ruderal assemblages within livestock systems may thus enhance functional linkages among agricultural

lands, pollinator communities, and tropical dry forest remnants, strengthening ecosystem resilience in one of the world’s most threatened biomes.

Declarations

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Competing intereses

The first author received logistical support from Agropecuaria Tabaidá S.A.S. during fieldwork on their properties. The remaining authors have no relevant financial or non-financial interests to disclose.

Author contributions

Study conception, design, material preparation and data collection were performed by R-AB and C-CA. Analysis were performed by R-AB and W-D. The first draft of the manuscript was written by R-AB and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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Figures

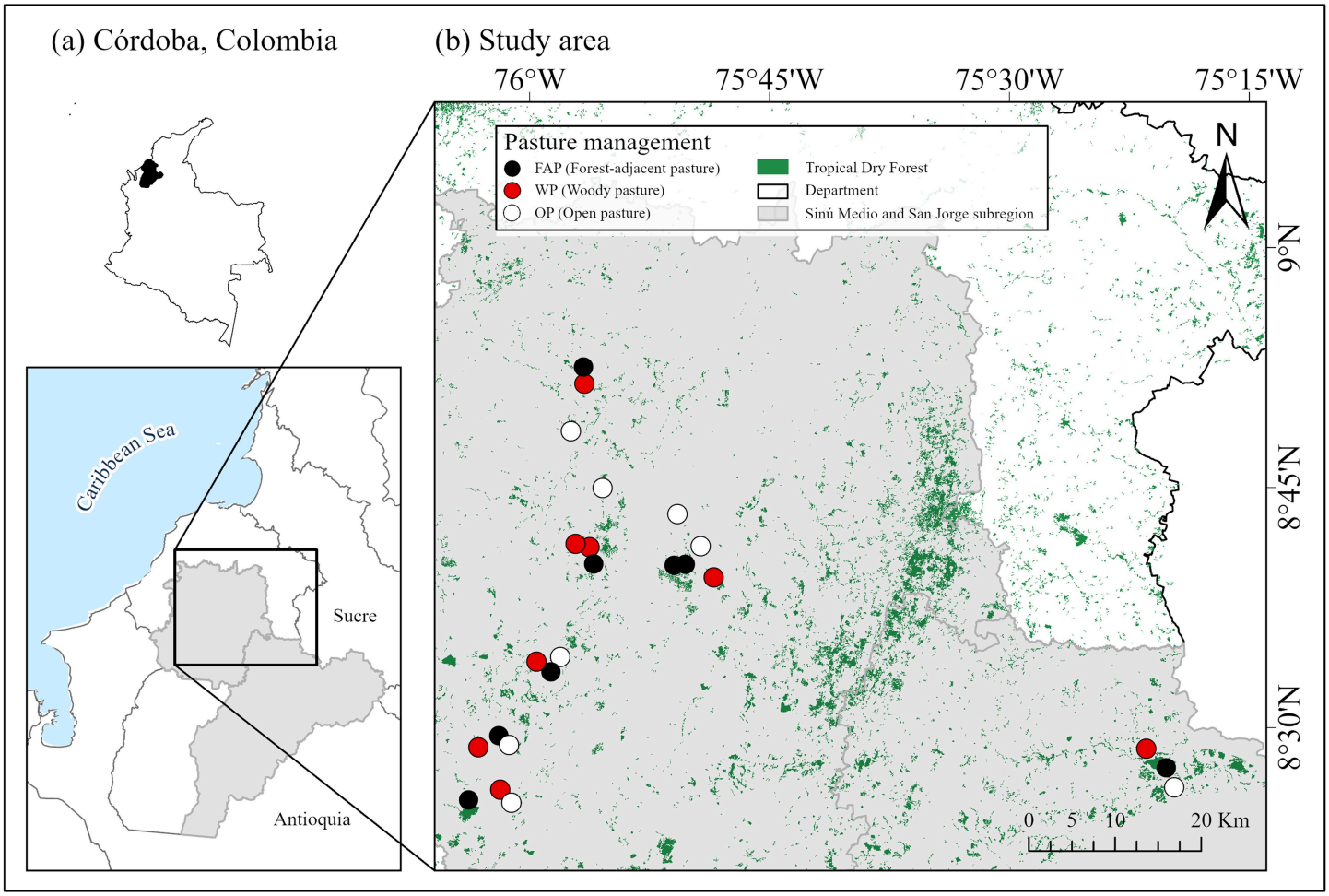


Figure 1

Geographic distribution of the 24 sampled cattle pastures within the TDF landscape of Córdoba (Colombia). Three pasture management types: forest-adjacent pastures (FAP), wooded pastures (WP), and open pastures (OP) (n = 8 per type), where ecological interaction data were compiled to build plant–butterfly networks

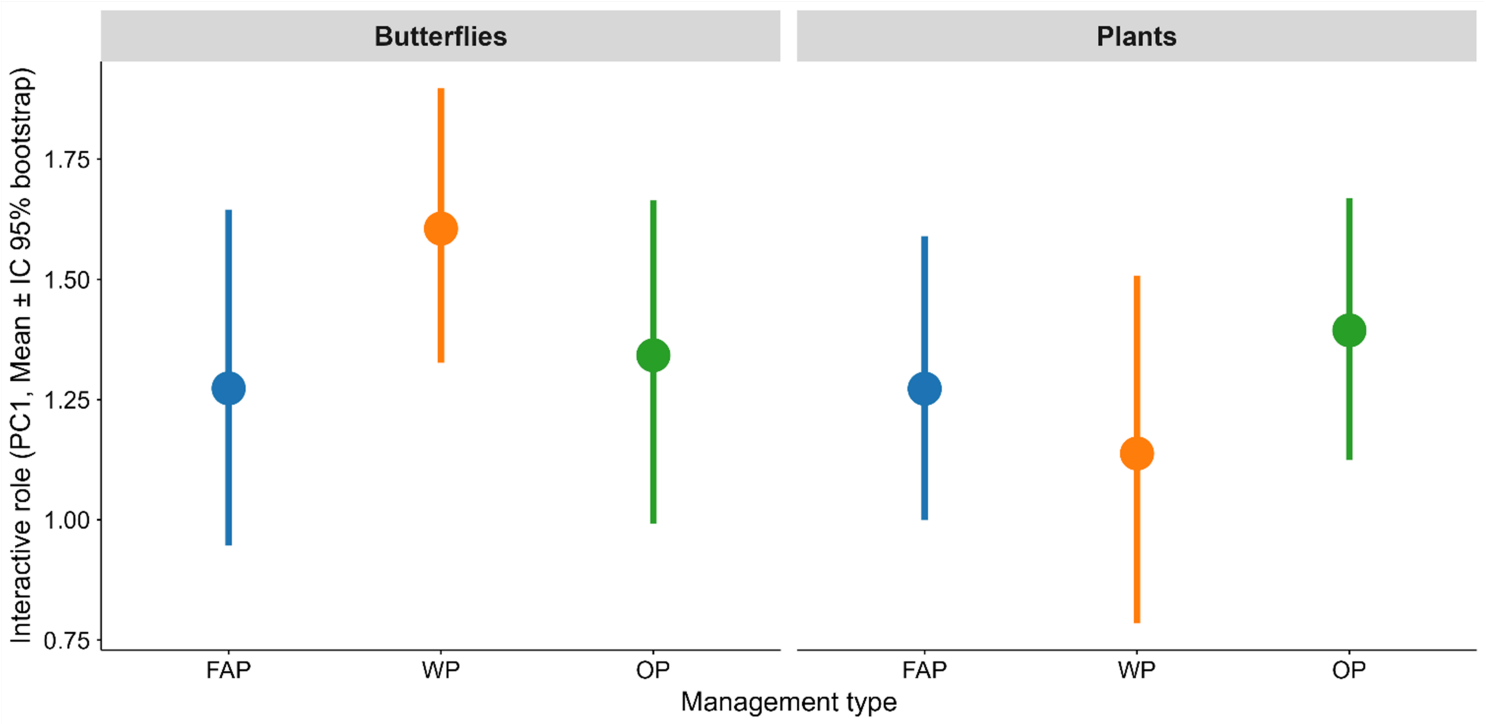


Figure 2

Mean interactive role (PC1) of butterfly and plant species across the three pasture management types—forest-adjacent pastures (FAP), wooded pastures (WP), and open pastures (OP). Points represent bootstrap means and vertical lines indicate 95% bootstrap confidence intervals for each management x taxon combination

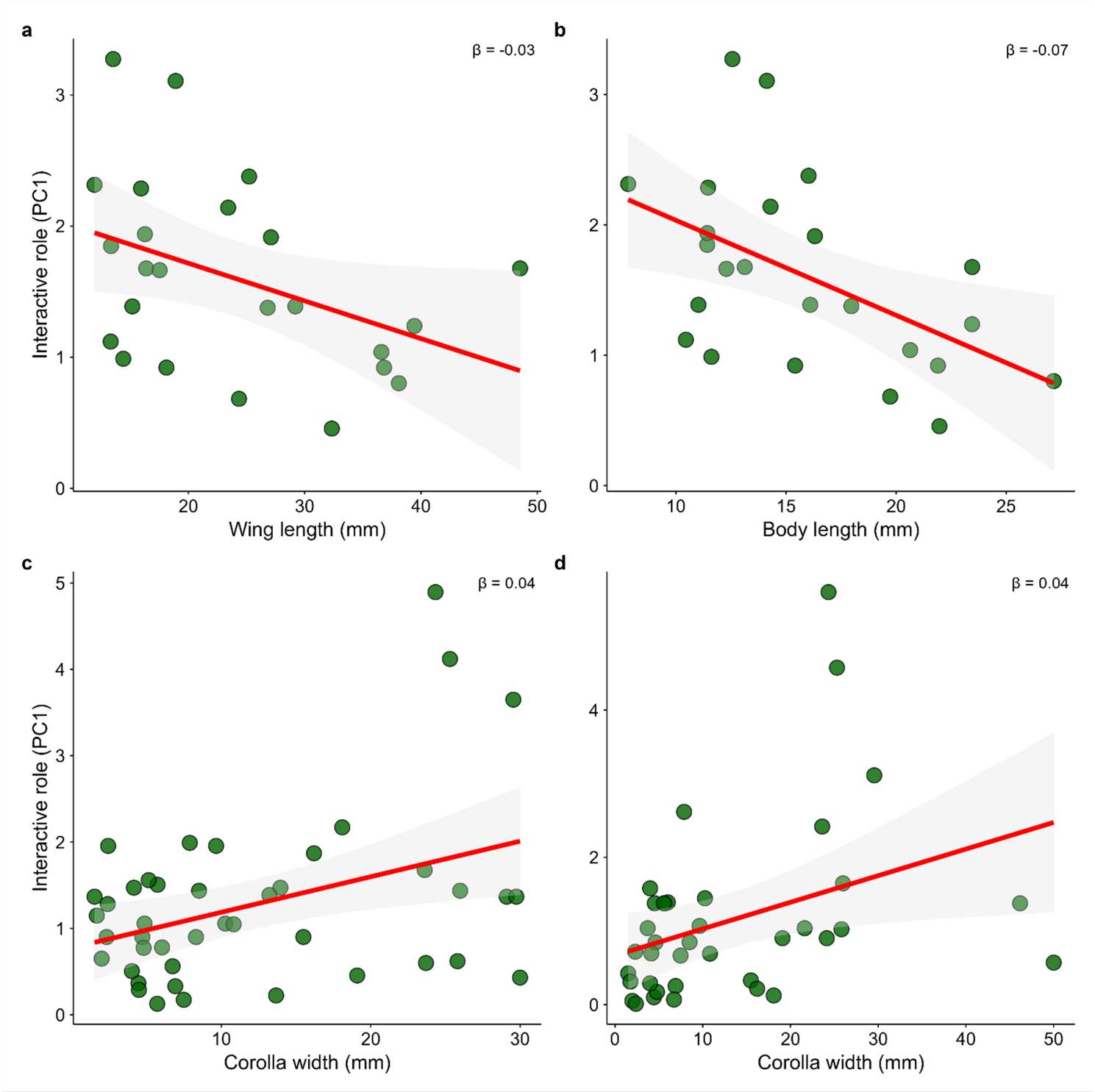


Figure 3

Species' interactive roles (PC1) and functional traits of butterflies and plants across pasture management types. Panels a and b show butterfly traits in wooded pastures (WP): (a) wing length and (b) body length. Panels c and d show plant traits, with (c) corolla width in forest-adjacent pastures (FAP) and (d) corolla width in wooded pastures (WP). Red lines represent fitted regression slopes (β), with shaded areas indicating 95% confidence intervals

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