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Abundance-driven processes best predict plant-butterfly network structure across a forest-to-agriculture gradient

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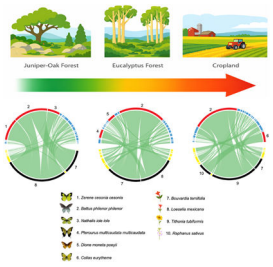
HIGHLIGHTS

- Abundance-driven processes best predict butterfly-plant networks across disturbance levels
- Phenology becomes important in croplands with concentrated floral resources
- Generalist butterflies maintain consistent roles despite habitat modification
- Network nestedness persists but weighted interactions show different patterns
- Network structure persists while underlying assembly mechanisms shift with land-use

GRAPHICAL ABSTRACT



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ABSTRACT

Land-use change threatens pollination services globally, yet interaction networks may persist through ecological processes that buffer habitat modification. We studied plant-butterfly nectar-feeding interaction networks across a forest-to-agriculture gradient in temperate Mexican forests, comparing juniper-oak forests, eucalyptus forests, and croplands over one year. We evaluated network structure and used probabilistic models to assess the relative predictive power of neutral processes (species abundance), phenological overlap, and morphological matching in explaining observed interaction patterns. We recorded 3,229 interactions among 76 species (34 plants, 42 butterflies) with moderate specialization. Networks showed significant nestedness and modularity across habitats, though weighted nestedness was lower than expected. Model selection revealed that species abundance primarily predicted network structure, with phenology becoming important in croplands where floral resources are temporally concentrated. Generalist butterflies, particularly *Battus philenor philenor*, maintained consistent structural roles across habitats, demonstrating functional stability. Pieridae and Papilionidae contributed positively to nestedness through generalist interactions, while Hesperiidae and Lycaenidae reduced it through specialized associations. Our findings suggest that abundance-driven processes best predict nectar-feeding interaction patterns in modified landscapes, though we emphasize that structural persistence does not guarantee pollination effectiveness. Conservation strategies could prioritize abundant native flowering plants and

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habitat heterogeneity that may support generalist populations, while recognizing that network topology may not fully capture functional aspects of pollination such as pollen transfer efficiency and plant reproductive success.

Introduction

Human activities have become a primary driver of global environmental change in recent decades, leading to unprecedented impacts on biodiversity and ecosystem functioning (Ceballos et al., 2017), with current extinction rates estimated to be 100 to 1,000 times higher than natural background rates (Pimm et al., 2014). Among the most pervasive forms of anthropogenic disturbance, land-use change profoundly alters ecological communities by modifying species composition, abundance, and species interactions (Valiente-Banuet et al., 2015).

Plant-pollinator networks are particularly vulnerable to anthropogenic disturbances (Ferreira et al., 2013). These networks encompass approximately 87.5% of flowering plant species worldwide (Ollerton et al., 2011) and support over 35% of global crop production (Klein et al., 2007), while playing crucial roles in maintaining ecosystem resilience (Bascompte and Jordano, 2007). Understanding how these networks respond to disturbance is critical, as habitat modification can trigger network disassembly processes that progressively erode interaction diversity and functional complexity (Bascompte and Stouffer, 2009; Aizen et al., 2012). Network disassembly does not occur randomly; instead, it follows predictable patterns where specialists and their interactions are disproportionately lost, while generalist species and their connections tend to persist (Burkle et al., 2013; Winfree et al., 2014). However, our understanding of how disturbances affect the underlying mechanisms structuring these networks remains limited, particularly regarding the relative importance of neutral versus biological processes in network structure and whether structuring rules differ between natural and anthropogenically modified systems.

The structure and dynamics of plant-pollinator networks emerge from a complex interplay of ecological and evolutionary processes. Neutral processes suggest that interactions are primarily determined by probabilistic encounters, with interaction frequencies proportional to species abundances (Vázquez et al., 2007; Krishna et al., 2008).

In contrast, biological processes involve selection mechanisms and evolutionary constraints that filter potential interactions based on species-specific traits (Olesen et al., 2011; Peralta et al., 2020). We focus on two key processes: phenological synchrony, where temporal overlap between flowering and pollinator activity determines possible interactions (CaraDonna et al., 2017), and morphological complementarity, where proboscis-corolla matching constrains resource access (Stang et al., 2009).

The relative importance of neutral versus biological processes in structuring ecological networks has profound implications for understanding network stability, resilience, and responses to environmental change (Bascompte and Jordano, 2007; Krishna et al., 2008). Networks structured primarily by neutral processes may be more resilient to random species loss through functional redundancy (Blüthgen and Klein, 2011), yet they may also be less capable of maintaining highly specialized functions that depend on specific trait matching and co-evolved relationships (Olesen et al., 2011; Valiente-Banuet et al., 2015). Moreover, if network structure shifts from trait-based to abundance-driven processes along disturbance gradients, this could represent a fundamental change in how ecological communities are organized, with cascading effects on ecosystem functioning and restoration potential (Bascompte and Stouffer, 2009).

Understanding which of these mechanisms predominate across different levels of anthropogenic disturbance is crucial for predicting network responses to environmental change. Several studies have examined how disturbance gradients affect plant-pollinator networks and the processes structuring them. For example, Burkle and Alarcon (2011) found that historical plant-pollinator networks in disturbed environments showed greater dependence on abundance patterns than on specialized morphological matching. Weiner et al. (2014) demonstrated that land-use intensification in European agricultural landscapes increases the relative importance of neutral processes over trait-based interactions. Additionally, He et al. (2025) demonstrated that both neutral processes (driven by plant and pollinator abundances) and niche-based processes (morphological matching and phenological overlap) jointly predict interaction patterns, with the relative importance varying among pollinator functional groups. However, most of these studies have examined network structure at single time points or focused primarily on describing changes in network properties (such as connectance, nestedness, or modularity) rather than explicitly testing competing structuring mechanisms across well-defined disturbance gradients (Burkle and Alarcon, 2011).

Land-use change, such as the conversion of natural habitats to agricultural areas or induced forests (e.g., Eucalyptus plantations), often leads to the loss of native plant species, homogenization of vegetation structure, and alteration of resource availability for pollinators (Moreira et al., 2015; Dainese et al., 2019). These changes can shift the relative importance of neutral versus biological processes in network structuring. Understanding these shifts is particularly important for predicting whether networks in modified landscapes retain their functional capacity or undergo progressive functional erosion even if structural properties appear stable (Winfree et al., 2014).

Butterflies represent an ideal study system for investigating these mechanisms, as they are diverse and important pollinators whose communities are highly sensitive to changes in vegetation structure and composition (Öckinger and Smith, 2006). Adult butterflies depend on floral nectar for energy and reproduction, while their larvae often have specific host plant requirements, creating multi-trophic dependencies that can be disrupted by habitat modification (Dennis et al., 2003). While multi-trophic dependencies also characterize other pollinator functional groups such as hoverflies and moths, and the coexistence of generalist and specialist species is common across most pollination systems, butterflies offer several practical advantages for field-based network studies. Butterfly-plant interactions often exhibit both generalist and specialist patterns within the same community (Forister et al., 2004). Furthermore, butterflies are highly mobile organisms that can respond rapidly to environmental changes (Thomas et al., 2004). Their flight behavior and foraging patterns can be directly observed and quantified, allowing for detailed characterization of interaction networks (Pollard and Yates, 1993). The relatively short generation times of many butterfly species mean that short-term ecological responses to environmental change can be detected within realistic study timeframes.

Despite growing recognition of the importance of plant-pollinator networks and the threats they face, relatively few studies have explicitly examined the mechanisms underlying network structure across disturbance gradients using probabilistic modeling approaches that partition variance among abundance, morphology, and phenology (e.g. Vizentin-Bugoni et al., 2014). Most research has focused on describing changes in network properties (such as connectance, nestedness, or modularity) rather than identifying the processes responsible for these changes (Burkle and Alarcon, 2011). Moreover, most studies have focused on single time points or short sampling periods, overlooking the temporal dynamics that are fundamental to understanding phenological processes in network assembly (CaraDonna et al., 2017). Additionally, few studies have examined how the functional roles of individual species change across disturbance gradients, instead focusing primarily on species composition and network-level properties.

In this study, we investigate how the transformation of original

vegetation to agricultural areas and induced forests affects plant-butterfly nectar-feeding interaction networks in Ixtacuixtla, Tlaxcala, Mexico. We focus exclusively on butterfly-plant nectar-feeding interactions and do not claim that butterflies are the sole or dominant pollinators in this temperate system. Other pollinator groups (bees, flies, etc.) are present but were not sampled in this study. Therefore, our results pertain to a taxonomically restricted subnetwork rather than the complete pollination network, and conclusions about neutral versus biological processes apply specifically to butterfly-plant interactions. We acknowledge that focusing on a single pollinator functional group may influence the observed relative importance of different structuring mechanisms, as morphological constraints and phenological factors may vary in strength across pollinator guilds (He et al., 2025). By conducting monthly sampling over a full year, we explicitly account for temporal variation in species composition and phenological overlap—factors that are often overlooked in network studies but may be critical for understanding assembly mechanisms, particularly in seasonal environments (CaraDonna et al., 2017). Additionally, by examining individual species' functional roles across habitats through network motif analysis, we assess whether key species maintain consistent structural positions or undergo role shifts as networks are assembled or disassembled along the disturbance gradient (Bascompte and Stouffer, 2009).

We address three main hypotheses: (1) species richness, connectance, nestedness, and modularity will decrease along the disturbance gradient from original vegetation to anthropized sites, reflecting the loss of specialized species and interactions consistent with network disassembly theory (Aizen et al., 2012); (2) species turnover will occur along the gradient, with communities shifting in taxonomic composition such that specialist-associated butterfly families are progressively replaced by generalist-associated families, leading to shifts in the taxonomic and functional composition of networks as predicted by models of non-random interaction loss (Winfree et al., 2014); and (3) the relative importance of neutral versus biological processes will shift along the disturbance gradient, with biological processes (phenology and morphology) being more important in structuring networks in original vegetation and neutral processes (abundances) dominating in disturbed sites as encounter probability increasingly determines interaction patterns in modified landscapes (Burkle and Alarcon, 2011; Weiner et al., 2014).

To test these hypotheses, we quantify species abundances, phenological patterns (monthly presence-absence monitoring over a full year), and phenotypic complementarity (proboscis and corolla lengths) across three vegetation types representing different disturbance levels. Using null model approaches and model selection frameworks, we explicitly disentangle the relative contributions of neutral processes (species abundances) and biological processes (phenological synchrony and morphological matching) in predicting interaction patterns. Additionally, we examine how the functional role of key species changes across the disturbance gradient using network motif analysis.

Materials and methods

Study area

This study was conducted along a disturbance gradient in an area where the natural temperate forest habitat has been modified in the municipality of Ixtacuixtla, Tlaxcala, central Mexico (Fig. 1). The site is located 14.1 km west of Tlaxcala city (19°19'68"N to 19°22'30"N, 98°20'64"W to 98°23'40"W), at an altitude between 2,200 and 2,500 m above sea level. The climate is temperate subhumid (Köppen-Geiger: Cwb), with a rainy season from May to September and the warmest months from March to May; mean annual precipitation ranges from 800−1,000 mm.

The original vegetation consisted of juniper (*Juniperus deppeana*) and oak (*Quercus* spp.) forests, of which some relicts persist (Fig. 1). However, most of this vegetation has been replaced by *Eucalyptus* spp. plantations or modified to seasonal crop areas with scattered trees around their perimeter.

Sampling design and butterfly collection

Between February 2023 and January 2024, monthly samplings (n = 12) were conducted to record nectar-feeding interactions between plants and diurnal butterflies. We established three independent study sites per vegetation type (juniper-oak forest, eucalyptus forest, and cropland), with sites separated by at least 500 m to ensure spatial independence. Sites were selected to be representative of their respective vegetation types in terms of structure, dominant species composition, and disturbance history. At each site, three 100-m long transects were established, separated from each other by at least 100 m. These transects within each site were treated as subsamples and pooled for site-level analyses. Observations were made within a 10-m strip on each side of the transect. An interaction was considered when a butterfly species was observed feeding on nectar from a flower of a particular plant species. Samplings were conducted between 10:30 and 13:30 h, the period of highest butterfly activity in the area. To avoid temporal biases, the order and direction of surveys were randomized throughout the study.

Observations were made with binoculars (Eagle Optics 10 × 42). Butterflies were photographed in situ and subsequently captured with entomological nets for identification according to Warren et al. (2024). For each interaction, the number of flowers visited was recorded as a quantitative measure of interaction intensity. For visited plants, voucher specimens (n = 5 per species) were collected and deposited in the MEXU Herbarium. Identification was performed following Rzedowski and Rzedowski (2001) and verified by specialists.

Floral abundance was estimated by counting all open flowers/inflorescences in 10 randomly selected individuals of each visited species. To quantify morphological complementarity, the following traits were measured in the field: (1) proboscis length measured from the head to the tip when fully extended using digital calipers (±0.01 mm) and (2) forewing length in butterflies (n = 10 individuals per species), and (3) corolla length measured from the base of the corolla tube to the opening, (4) corolla width measured at the widest point of the corolla opening, and (5) corolla color in plants (n = 10 flowers per species) using digital calipers (±0.01 mm) (Stang et al., 2009; Peralta et al., 2020).

Plant-butterfly interaction networks

Plant-butterfly interaction networks were constructed and analyzed using the "bipartite" package (version 2.18) in R (version 4.2.1; R Core Team, 2022). We calculated four key network metrics: nestedness, which quantifies the degree to which specialist interactions form subsets of generalist interactions (Almeida-Neto et al., 2008); modularity, which identifies compartmentalized subgroups within the network (Dormann and Strauss, 2014); specialization (H_2'), which measures the selectiveness of interactions beyond what would be expected from species abundances alone (Blüthgen et al., 2006); and species strength, which quantifies the relative importance of each species for its interaction partners (Bascompte and Jordano, 2007).

Network nestedness was analyzed using both the binary NODF metric (Nestedness metric based on Overlap and Decreasing Fill; Almeida-Neto et al., 2008) and its quantitative version WNODF (Weighted NODF; Almeida-Neto and Ulrich, 2011). For null model comparisons, we used the Patefield algorithm (Patefield, 1981), which maintains constant the total number of species (richness) and the number of interactions per species (degree distribution) while randomizing which species interact. Statistical significance was assessed using P-values derived from 1,000 null model iterations, with $P < 0.05$ indicating significant departure from random expectations.

The nestedness contribution (Nc) of each butterfly and plant family was calculated using the nestedcontribution function of the bipartite package (Dormann et al., 2008), following Saavedra et al., 2011. We

analyzed nestedness contribution at the family level rather than species level because feeding ecology and interaction patterns are evolutionarily conserved within butterfly families (Janz et al., 2006), and this approach provides sufficient statistical power while avoiding low sample size issues associated with rare species. This analysis identifies which taxonomic groups increase or decrease the global nestedness of the network. Positive Nc values indicate that the family contributes more to the nested structure than expected by chance, while negative values reflect a lesser contribution.

The modular structure of interaction networks was evaluated with the QuanBiMo algorithm (Quantitative Bipartite Modularity; Dormann and Strauss, 2014), implemented in the bipartite package of R. This algorithm uses a simulated annealing approach to optimize the modularity index Q, which measures the degree to which the network is divided into modules. Q values range from 0 (no modular structure) to 1 (perfectly compartmentalized modules), with values >0.3 generally considered indicative of meaningful modular organization (Newman, 2006). The likelihood value (M) of the observed network was calculated. To evaluate the statistical significance of modularity, the observed value was compared with distributions obtained from null networks generated under the Patefield algorithm. Significance was evaluated against null networks generated under the Patefield algorithm ($P < 0.05$).

For each pair of plant and butterfly species that interacted, two mutual dependencies were estimated (Bascompte and Jordano, 2007): (i) the dependence dP of plant *i* on butterfly *j*, defined as the fraction of visits from that butterfly with respect to the total butterfly visits to the plant, and (ii) the dependence dA of butterfly *j* on plant *i*, corresponding to the fraction of all its visits directed to that particular plant. Based on these dependencies, species strength was calculated, defined as the sum of dependencies of each species with all its interactants, which quantifies its relative importance for the set of species at the opposite trophic level. Strength was estimated for both butterflies and plants separately.

Interaction probability matrices

Probabilistic models were used to estimate the relative contribution of different factors in plant-butterfly network structure (Vizentin-Bugoni et al., 2014). We evaluated biological processes such as morphological complementarity (corolla-proboscis) and phenology of interactants, as well as neutral processes related to abundance.

For each vegetation type, we constructed probability matrices representing different structuring mechanisms. The observed matrix (O) contained empirical interaction frequencies, where each cell Oij represents the number of observed interactions between plant species i and butterfly species j.

We then generated four single-factor prediction matrices. The abundance matrix (A) calculated interaction probabilities based solely on species abundances, where for each plant-butterfly pair: $Pij(A) = (Ni \times Nj) / \Sigma(Ni \times Nj)$, with Ni representing plant abundance (total flowers counted) and Nj representing butterfly abundance (total individuals observed). This represents the neutral expectation based on encounter probability. The morphological matching matrix (M) quantified interaction probabilities based on complementarity between butterfly proboscis length and plant corolla length, calculated as: $Pij(M) = 1 - |z(\text{proboscisj}) - z(\text{corollai})|$, where $z(\cdot)$ represents z-score standardization, with higher values indicating better morphological match. The phenological overlap matrix (F) assessed temporal co-occurrence, where Pij(F) = (months of overlap) / 12. The null model matrix (N) assumed equal probabilities for all possible interactions: Pij(N) = 1 / (nplants × nbutterflies). All matrices were normalized to sum to 1.

We also constructed combined matrices by multiplying probability values from multiple factors: AF (Abundance × Phenology), AM (Abundance × Morphology), MF (Morphology × Phenology), and AMF (Abundance × Morphology × Phenology), with re-normalization after multiplication.

The predictive capacity of each model was evaluated by calculating the log-likelihood of observing the empirical interaction frequencies given the predicted probabilities. Assuming interactions follow a multinomial distribution, the log-likelihood was calculated as: $LL = \Sigma(Oij \times \log(Pij))$; where Oij is the observed number of interactions and Pij is the predicted probability from each model.

The Akaike Information Criterion (AIC) was then calculated as: $AIC = -2 \times LL + 2 \times k$; where k is the number of free parameters in each model. For single-factor models (A, M, F, N), $k = 1$, representing the single scaling parameter. For combined models, k equals the number of factors combined (e.g., $k = 2$ for AF, $k = 3$ for AMF).

Model comparison was performed using ΔAIC, defined as the difference between each model's AIC and the lowest AIC obtained, with lower ΔAIC values indicating better fit to observed interactions. Following conventional interpretation, models with $\Delta AIC < 2$ were considered to have substantial support, $\Delta AIC = 4–7$ considerably less support, and $\Delta AIC > 10$ essentially no support (Burnham and Anderson, 2002).

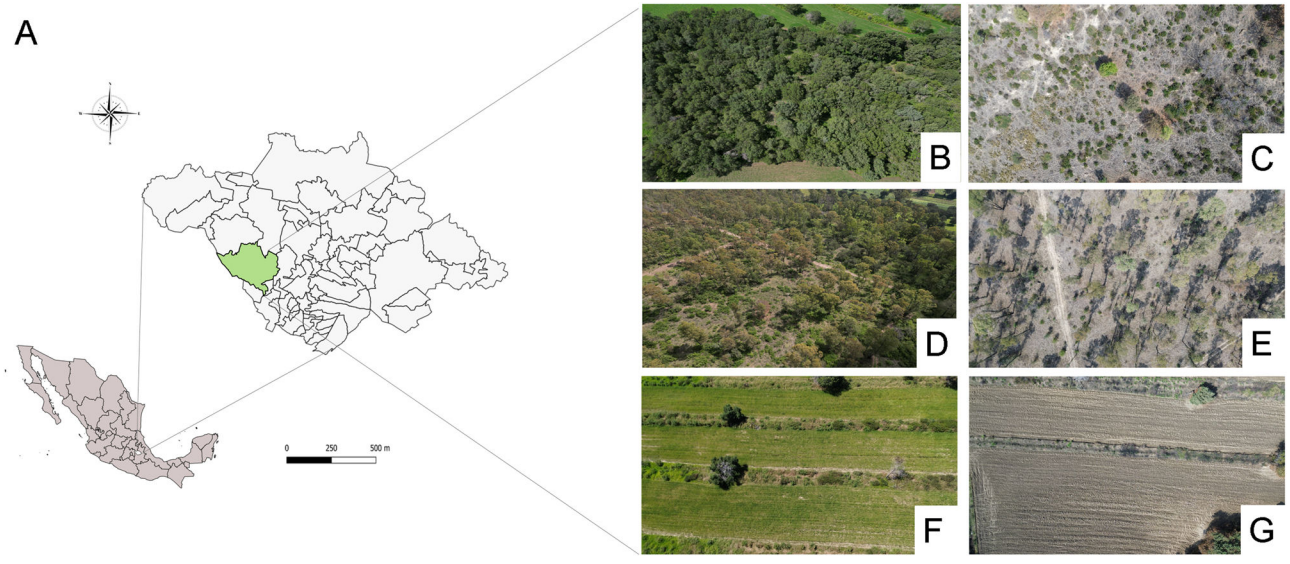

Fig. 1. Study site location and vegetation types. (A) Location of Ixtacuixtla de Mariano Matamoros municipality in Tlaxcala state, Mexico. Aerial photographs showing the three vegetation types during wet season (B, D, F) and dry season (C, E, G): juniper-oak forest (B, C), eucalyptus forest (D, E), and cropland (F, G).

Motif analysis

To analyze whether key butterfly species maintain consistent structural roles across the disturbance gradient, we performed motif analysis using the "bmotif" package (Simmons et al., 2019) in R. Position-weighted motifs quantify how frequently each species participates in different types of interaction configurations (e.g., visiting plants that are also visited by many other butterflies, or visiting plants with few other butterfly visitors). We focused on *Battus philenor philenor*, the only butterfly species present across all three vegetation types, allowing direct comparison of its functional role among habitats. We calculated the frequency distribution of motif positions for this species in each network and tested whether motif composition differed among vegetation types using PERMANOVA (adonis2 function, vegan package; 999 permutations; Oksanen et al., 2022).

Results

Community composition showed moderate turnover across the disturbance gradient (Table S1 and S2; see Appendix for supplementary information). Butterfly species richness was nearly identical between juniper-oak and cropland (25 species each), with only slightly higher richness in eucalyptus (27 species), though composition varied moderately to highly (Jaccard indices ranging from 0.421 to 0.529). Thirteen butterfly species (31%) occurred in all three habitats, while 22 species (52%) were habitat-restricted. Plant communities showed stronger differentiation, with clearer differences in richness (12, 18, and 16 species in juniper-oak, eucalyptus, and cropland, respectively) and lower compositional similarity (Jaccard indices from 0.120 to 0.304). Only three plant species (9%), *Bouvardia ternifolia*, *Dahlia coccinea*, and *Mimosa aculeaticarpa*, occurred across all three habitats, indicating stronger habitat specialization in plants than in butterflies (Table S2).

General structure of interaction networks

The full interaction network included 76 species (34 plants and 42 butterflies) with a total of 3,229 recorded interactions and moderate specialization ($H_2' = 0.50$, $P < 0.001$ based on comparison with 1,000 null model replicates; Fig. 2).

Networks showed both temporal and spatial variation along the disturbance gradient (Table S3). The rainy season network presented greater richness (62 species) and number of interactions (2,203) than the dry season (36 species, 1,000 interactions), with differing specialization levels ($H_2' = 0.51$, $P < 0.001$ and $H_2' = 0.79$, $P < 0.001$, respectively; Fig. 3A, B). Among vegetation types, the juniper-oak network showed the lowest richness (37 species, 1,267 interactions), followed by eucalyptus (45 species, 1,435 interactions) and cropland (41 species, 756 interactions), with specialization values of $H_2' = 0.49$, $P < 0.001$ for juniper-oak, and $H_2' = 0.66$, $P < 0.001$ for eucalyptus and cropland (Fig. 4A, B, C).

Network structure and nestedness patterns

Network properties across all analyzed systems are summarized in Table S4. The qualitative nestedness analysis (NODF) showed observed values significantly higher than expected by chance in all evaluated scenarios, indicating that specialist interactions tend to form subsets of generalist interactions. In the general network, nestedness obtained a value of 23.49 (null model mean value = 8.20 ± 0.61; Z = 25.15; P < 0.001). During the dry season, qualitative nestedness reached a NODF value = 18.54 (null model mean value = 10.21 ± 1.37; Z = 6.05; P < 0.001), while in the rainy season the value was NODF = 28.55 (null model mean value = 9.50 ± 0.82; Z = 23.13; P < 0.001).

In different vegetation types, NODF values were also significantly elevated compared to the null model: juniper-oak (NODF = 32.64; null model mean value = 14.77 ± 1.78; Z = 10; P < 0.001), eucalyptus (NODF = 23.65; null model mean value = 11.01 ± 1.25; Z = 10.05; P < 0.001), and cropland (NODF = 25.31; null model mean value = 9.73 ± 1.30; Z = 11.94; P < 0.001). We emphasize that these significance tests indicate that each network departs from its respective null expectation, but do not support formal statistical comparisons of nestedness magnitude among seasons or vegetation types, as NODF values are influenced by network size and sampling effort.

In contrast, the weighted nestedness analysis (WNODF) showed that in all cases, observed values were significantly lower than expected under the null model (P < 0.001; negative z-scores). For example, in the general network: 12.65 (z = −16.13). During the dry season, observed WNODF was 12.44 (z = −13.85), in the rainy season 15.84 (z = −13.70), in juniper-oak 20.54 (z = −10.85), in eucalyptus 8.52 (z = −14.73), and in cropland 9.77 (z = −12.71).

On the other hand, modularity analysis (Q) with the QuanBiMo algorithm revealed values significantly greater than those obtained in null simulations (P < 0.001; positive z-scores > 2), confirming module structuring in the networks. In the general network, modularity reached Q = 0.38 (z = 80.25), indicating moderate modular organization in the complete assemblage (Newman, 2006). During the dry season, a value of Q = 0.35 (z = 49.50) was obtained, while in the rainy season it was Q = 0.39 (z = 70.16). For vegetation types, values were similarly significant: juniper-oak (Q = 0.31; z = 35.89), eucalyptus (Q = 0.38; z = 55.92), and cropland (Q = 0.43; z = 33.47).

The nestedness contribution (Nc) analysis, performed at the family level, revealed taxonomic patterns in how different groups structure the network (Table 1). The butterfly families Pieridae and Papilionidae (with positive contributions) are associated with plant families that also have positive contributions, such as Papaveraceae, Phytolaccaceae, Orchidaceae, and Anacardiaceae. Nymphalidae, although with a slight contribution, also associates with plant families with positive contributions like Orchidaceae and Anacardiaceae, reinforcing that nested core. Conversely, Onagraceae and Rubiaceae, which have negative contributions, are strongly associated with Papilionidae and Nymphalidae. Hesperiidae and Lycaenidae have very negative values and are associated with few plant families (e.g., Lamiaceae, Fabaceae, Brassicaceae).

Key species

Key species in the interaction networks exhibited varying degrees of specialization. The most generalist butterfly species were *Battus philenor philenor*, *Dione moneta poeyii*, and *Zerene cesonia cesonia*, as evidenced by their high number of plant partners. In contrast, *Adelpha paroeca* and *Eurema salome jamapa* were among the most specialist, showing more restricted plant associations. Among plant species, *Bouvardia ternifolia* and *Loeselia mexicana* demonstrated the highest generalist behavior, attracting diverse butterfly visitors. Conversely, *Clinopodium multiflorum* and *Zephyranthes brevipes* were among the most specialist, with limited butterfly interactions (Fig. 2).

The identity of species with the highest interaction intensity varied among vegetation types descriptively. *N. iole iole* showed high interaction frequency in both cropland and juniper-oak forest environments, while *B. philenor philenor* had the highest interaction frequency in cropland areas. Regarding plant species, *L. mexicana* had high interaction frequency in both juniper-oak and eucalyptus forest areas, whereas *Tithonia tubaeformis* presented the highest number of interactions within cropland areas (Fig. 4).

Processes structuring plant-butterfly interaction networks

We compared the fit of different probabilistic models based on neutral (abundance) and biological factors (morphological and phenological matching) to determine which ecological processes better predict plant-butterfly network structure. ΔAIC values showed that abundance-based models presented the lowest AIC in most networks (general

network, rainy and dry seasons), suggesting that interaction structure is consistent with neutral encounter expectations (Fig. 5; Table S5).

The cropland environment represented a notable exception. Here, the model that combined abundance and phenology presented the best fit (ΔAIC = 0, with the abundance-only model having ΔAIC = 3.2), suggesting that in crop sites characterized by temporal and synchronized floral resources, temporal coincidence between flowering and butterfly activity may be important for interaction determination. In juniper-oak and eucalyptus habitats, abundance-based models showed the best fit, though models including morphology and phenology had moderately low ΔAIC values (2–7 units), suggesting some contribution of trait-based processes.

Motif analysis

Motif composition of *Battus philenor philenor* did not differ significantly among vegetation types (PERMANOVA: $F = 1.32$, $R^2 = 0.399$, $P = 0.198$), indicating that this generalist species maintains a consistent structural role in interaction networks across the disturbance gradient.

Discussion

Our study provides evidence that anthropogenic disturbance alters not only the composition of plant–butterfly interaction networks, but also the processes that best predict their structural patterns. It is important to note that our model selection approach identifies which factors—neutral (abundance) or biological (phenology, morphology)—best predict observed interaction patterns. While these predictions are informative about likely structuring mechanisms, they do not constitute direct proof of the underlying processes. True mechanistic understanding would require experimental manipulations or temporal assembly/disassembly observations (Bascompte and Stouffer, 2009). Nonetheless, the model selection approach revealed clear shifts in the relative predictive power of neutral and biological processes across the disturbance gradient, offering insight into how mutualistic networks likely respond to environmental change.

Support for our first hypothesis, which predicted declines in species richness and network complexity with increasing disturbance, was partial. Total species richness varied moderately among vegetation types (35, 45, and 41 species in juniper-oak, eucalyptus, and cropland, respectively), though this pattern was driven primarily by plants rather than butterflies. Plant richness showed clear habitat differentiation (12, 18, and 16 species), whereas butterfly richness remained virtually constant, with identical richness in juniper-oak and cropland (25 species each) and only marginally higher richness in eucalyptus (27 species). Despite this near-identical butterfly richness, species composition varied substantially across vegetation types for both taxonomic groups (Table S1 and S2), with Jaccard indices ranging from 0.12 to 0.53. These patterns indicate that species turnover, rather than simple richness gradients, characterized community responses to disturbance. The unexpectedly high species richness in eucalyptus forest, which exceeded that of native juniper-oak forest, likely reflects structural heterogeneity rather than habitat quality per se. Eucalyptus forest in our study area maintain diverse understory vegetation with native flowering plants, creating a mosaic of floral resources that may attract diverse butterfly assemblages. Additionally, eucalyptus sites may benefit from edge effects and proximity to multiple habitat types, facilitating species movement across the landscape matrix (Harvey et al., 2017). However, higher species richness does not necessarily indicate higher conservation value, as eucalyptus networks showed increased specialization ($H_2' = 0.66$) compared to juniper-oak forest ($H_2' = 0.49$), potentially reflecting reduced functional redundancy.

At the network level, both nestedness and modularity were consistently detected across habitats (NODF = 23.49, Q = 0.38), indicating that fundamental structural properties can persist despite disturbance (Sabatino et al., 2010). However, weighted nestedness was consistently

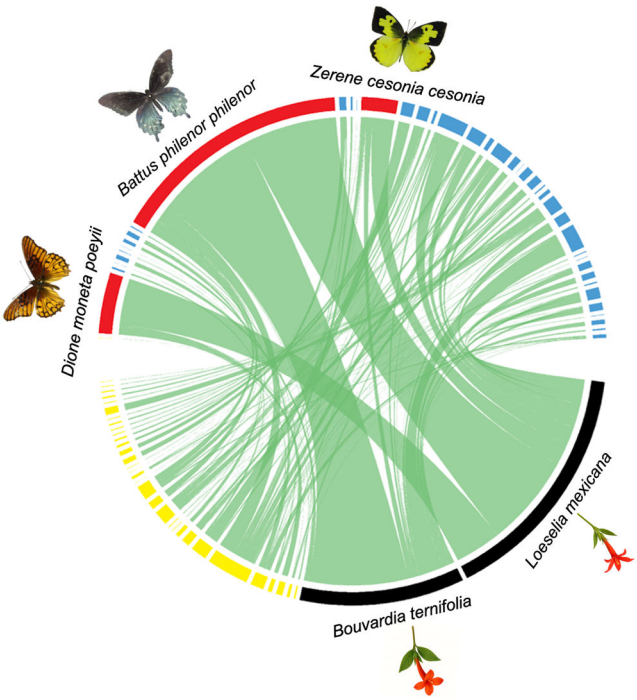

Fig. 2. Full plant-butterfly interaction network. Blue nodes represent peripheral butterfly species and red nodes represent core butterfly species. Yellow nodes represent peripheral plant species and black nodes represent core plant species. Node size is proportional to species interaction frequency (degree). Link width (green lines) indicates pairwise interaction frequency (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

lower than binary nestedness (WNODF = 12.65), suggesting that interaction strengths were unevenly distributed, with frequent interactions concentrated within specific modules (Magrach et al., 2022). The persistence of modularity across habitats further suggests that specialized subnetworks may remain even in disturbed environments, potentially buffering specialized interactions (Traveset et al., 2022). These structural patterns align with observations from network disassembly studies showing that core properties can persist even as species composition changes (Aizen et al., 2012). However, the maintenance of structural properties does not guarantee functional stability, as the strength and effectiveness of interactions may change independently of network topology (Winfree et al., 2014).

Our second hypothesis regarding species turnover and functional shifts received strong support. Contributions to nestedness were taxonomically structured: Pieridae and Papilionidae increased nestedness through generalist interactions, whereas Hesperiidae and Lycaenidae reduced nestedness via specialized associations. These patterns are consistent with phylogenetic evidence showing that feeding specialization is evolutionarily conserved within butterfly families (Janz et al., 2006; Torres-Vázquez et al., 2023). Among plant families, those contributing positively to nestedness tended to be less species-rich and associated with generalist butterflies, whereas negative contributors were more abundant but concentrated interactions with fewer butterfly families. This replacement of specialist-rich assemblages by generalist-dominated communities represents a functional shift that may reduce specialized pollination services (Valiente-Banuet et al., 2015). Such contrasting changes in taxonomic composition and functional roles along disturbance gradients (Purschke et al., 2013) underscore that network stability should be evaluated beyond species richness alone, considering the functional consequences of compositional turnover. This taxonomic restructuring mirrors patterns of non-random interaction loss documented in other disturbed pollination networks

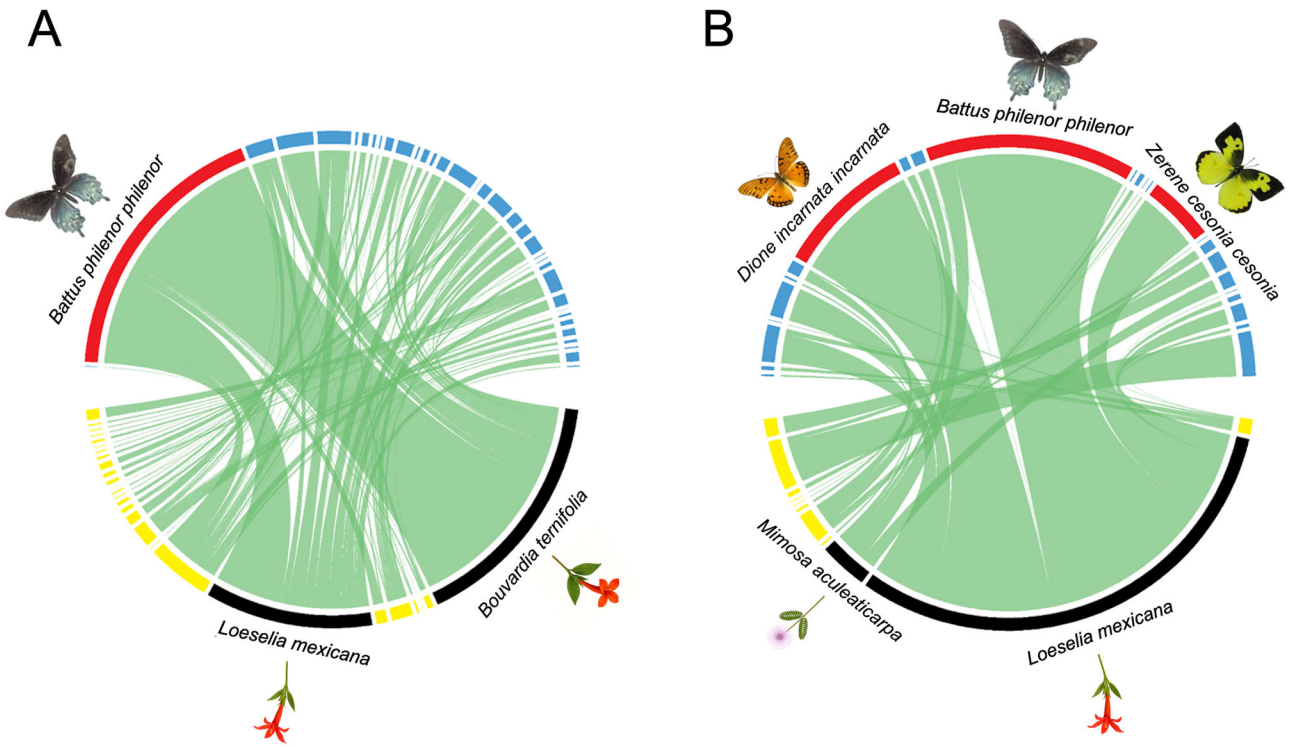

Fig. 3. Seasonal plant-butterfly interaction networks. (A) Wet season network and (B) dry season network. Blue nodes represent peripheral butterfly species and red nodes represent core butterfly species. Yellow nodes represent peripheral plant species and black nodes represent core plant species. Node size is proportional to species interaction frequency (degree). Link width (green lines) indicates pairwise interaction frequency. The wet season network shows more generalist butterfly behavior, while the dry season network exhibits increased specialization with distinct modularity (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

(Burkle et al., 2013), where specialist species and their unique interactions disappear first, leaving behind increasingly homogenized, generalist-dominated assemblages.

While taxonomic composition shifted predictably along the disturbance gradient, the mechanisms predicting interactions showed a different pattern. Contrary to our third hypothesis, neutral processes showed the strongest predictive power across most scenarios, including relatively undisturbed juniper-oak forest. We interpret this as evidence that abundance-driven encounter rates are the primary determinant of interaction frequencies in our system, though we acknowledge that other unmeasured processes (e.g., nectar rewards, floral volatiles, learned preferences) may also play important roles. This contrasts with views that specialized, coevolved interactions dominate network organization in natural communities (Bascompte and Jordano, 2007; Olesen et al., 2011), but aligns with empirical evidence that abundance-based models strongly predict interaction patterns in mutualistic networks (Krishna et al., 2008; He et al., 2025). The prominence of abundance-driven models reflects evidence that anthropogenic disturbance shifts network structure toward neutral mechanisms (Montoya et al., 2023; Burkle and Alarcon, 2011), with land-use intensification increasing the relative importance of neutral over trait-based processes (Weiner et al., 2014). Additionally, the generally flexible foraging behavior of butterflies, which are often less morphologically constrained than other pollinator groups (Forister et al., 2004; Stang et al., 2009; Rader et al., 2011), may contribute to the dominance of abundance-based patterns. In our networks, the most influential species (e.g., *Battus philenor philenor*, *Nathalis iole iole*) were generalists with broad foraging ranges, consistent with previous behavioral studies (Papaj, 1986). It is important to emphasize that while abundance best predicts interactions in our models, this does not mean that morphology and phenology are unimportant—rather, their effects may be secondary to, or mediated by, abundance patterns (Ponisio et al., 2017).

However, the dominance of abundance-based models was not universal across all habitats. An exception to the dominance of abundance-based models occurred in cropland environments, where the combination of abundance and phenology best explained interaction patterns. This result is consistent with evidence that agricultural systems impose strong temporal constraints on floral resource availability (Garibaldi et al., 2019). In landscapes characterized by synchronized and ephemeral flowering, phenological matching becomes critical for structuring interactions, a pattern also observed in community-wide analyses of plant–butterfly interactions under climatic variation (Rafferty and Ives, 2012). The shift toward phenology-dependent structuring in croplands may reflect a fundamental reorganization of how interactions are structured in highly disturbed systems, where resource availability becomes temporally concentrated rather than distributed throughout the growing season.

This context-dependent shift has implications for network stability. While neutral processes may buffer networks against species loss through functional redundancy (Blüthgen and Klein, 2011), increased reliance on phenological matching may heighten vulnerability to climate-driven mismatches (Both et al., 2006). Temporal asynchrony has been repeatedly identified as a threat to interaction stability under climate change (Rafferty et al., 2015; Kharouba et al., 2018). Our temporal analysis, spanning a full annual cycle, revealed substantial seasonal variation in network structure, with wet season networks showing greater richness (62 species) and lower specialization ($H_2' = 0.51$) than dry season networks (36 species, $H_2' = 0.79$). This temporal turnover suggests that the structuring mechanisms we documented operate dynamically across the year, with different subsets of the regional species pool interacting at different times. This seasonal turnover means that different subsets of species sustain interactions at different times of year, so the loss of one seasonal subset would not by itself collapse the entire network. Such temporal complementarity among phenologically

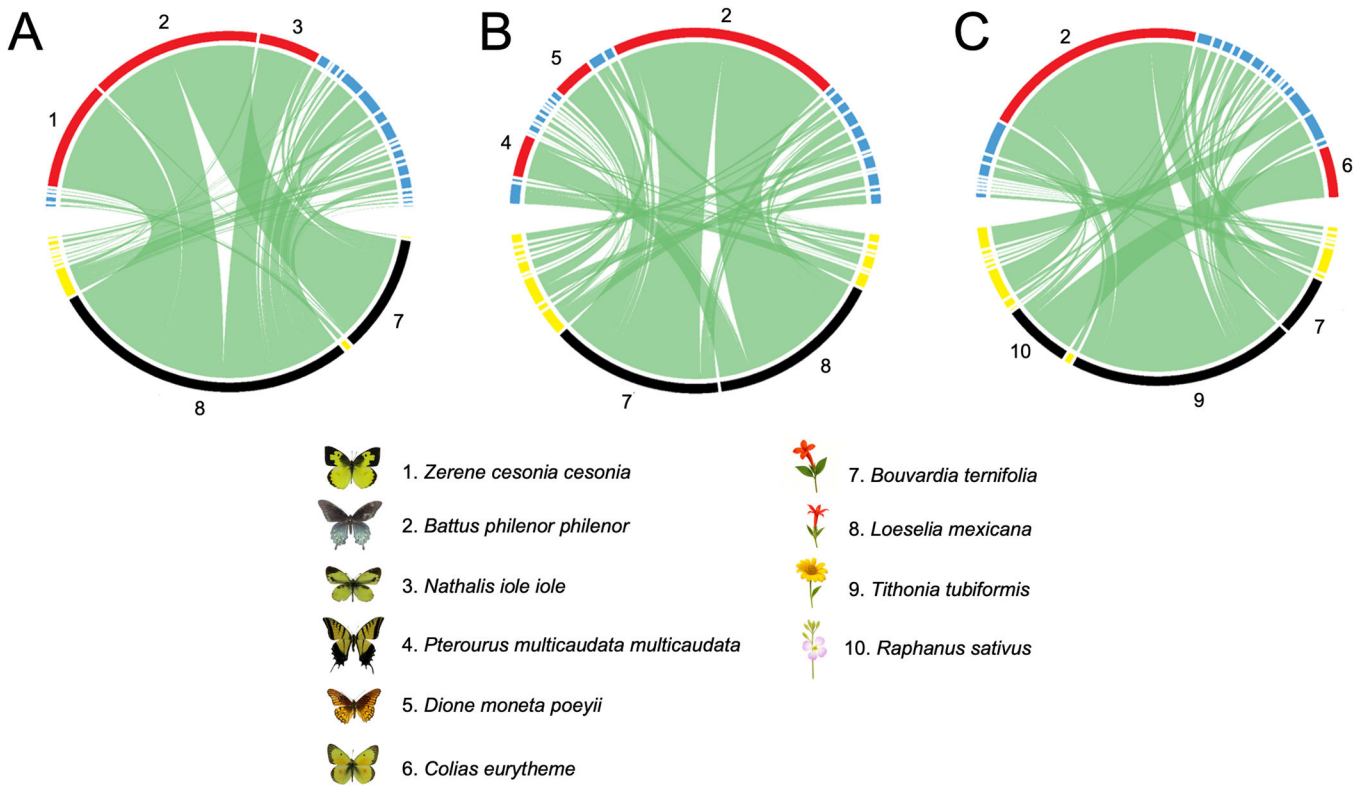

Fig. 4. Plant-butterfly interaction networks across vegetation types. (A) Juniper-oak forest, (B) eucalyptus forest, and (C) cropland. Blue nodes represent peripheral butterfly species and red nodes represent core butterfly species and yellow nodes represent peripheral plant species and black nodes core plant species. Numbers correspond to species identification in the legend below. Node size is proportional to species interaction frequency (degree). Link width (green lines) indicates pairwise interaction frequency. Species legend: butterflies (1–6) and plants (7–10) are listed with their corresponding network positions (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Table 1
Nestedness contribution (Nc) of butterfly and plant families within the full interaction network (Fig. 2). Nc values indicate nestedness contribution: positive values represent families that increase network nestedness, while negative values indicate families that decrease it. Characteristics describe the general pattern of associations.

Taxon	Family	Nc value	Characteristics
Butterflies	Pieridae	1.11	Generalist species that visit multiple plant families and sustain the network core
	Papilionidae	0.10	
	Nymphalidae	0.08	
	Hesperiidae	−1.87	More specialized, with fewer associated plant families
	Lycaenidae	−1.33	
	Erebidae	−0.47	
Plants	Phytolaccaceae	1.34	Species-poor families that couple with generalist butterflies
	Papaveraceae	1.11	
	Anacardiaceae	0.92	
	Convolvulaceae	0.85	
	Orchidaceae	0.82	
	Lamiaceae	0.18	
	Amaryllaceae	0.17	
	Brassicaceae	0.11	
	Solanaceae	0.09	
	Polemoniaceae	−1.26	
	Onagraceae	−1.24	Highly abundant families concentrated on few butterfly families
	Rubiaceae	−0.39	
	Asteraceae	−0.07	
	Fabaceae	−0.05	

segregated species may therefore provide a form of insurance against complete network collapse (CaraDonna et al., 2017). However, climate-driven phenological shifts could disrupt these temporal dynamics, particularly in cropland systems where assembly already depends heavily on phenological matching.

Complementing these network-level patterns, species-level analyses provide additional insight into how individual species respond to disturbance. Motif analysis revealed that *B. philenor philenor* maintained consistent functional roles across the disturbance gradient, consistent with evidence that highly generalist species maintain stable roles across environments (Olesen et al., 2008; Martín González et al., 2010; Vizentin-Bugoni et al., 2020). This functional stability may be facilitated by traits such as broad flight capacity and long proboscis (Lebeau et al., 2016), aligning with theoretical predictions of functional compensation whereby disturbance leads to role expansion by generalist species rather than complete network reorganization (Laliberté and Legendre, 2010; Peralta et al., 2020; Rabeau et al., 2025). The consistency of this species' functional role across habitats suggests that certain generalist species may act as network stabilizers, maintaining connectivity even as specialist species are lost during disassembly (Winfree et al., 2014). However, this functional stability at the species level should not be conflated with pollination effectiveness—*B. philenor philenor* may maintain similar network positions across habitats while varying in its actual contribution to plant reproductive success, which we did not measure.

Conservation implications and caveats

From a conservation perspective, our results suggest that maintaining high abundances of native flowering plants may be sufficient to preserve basic structural properties of plant-butterfly networks in

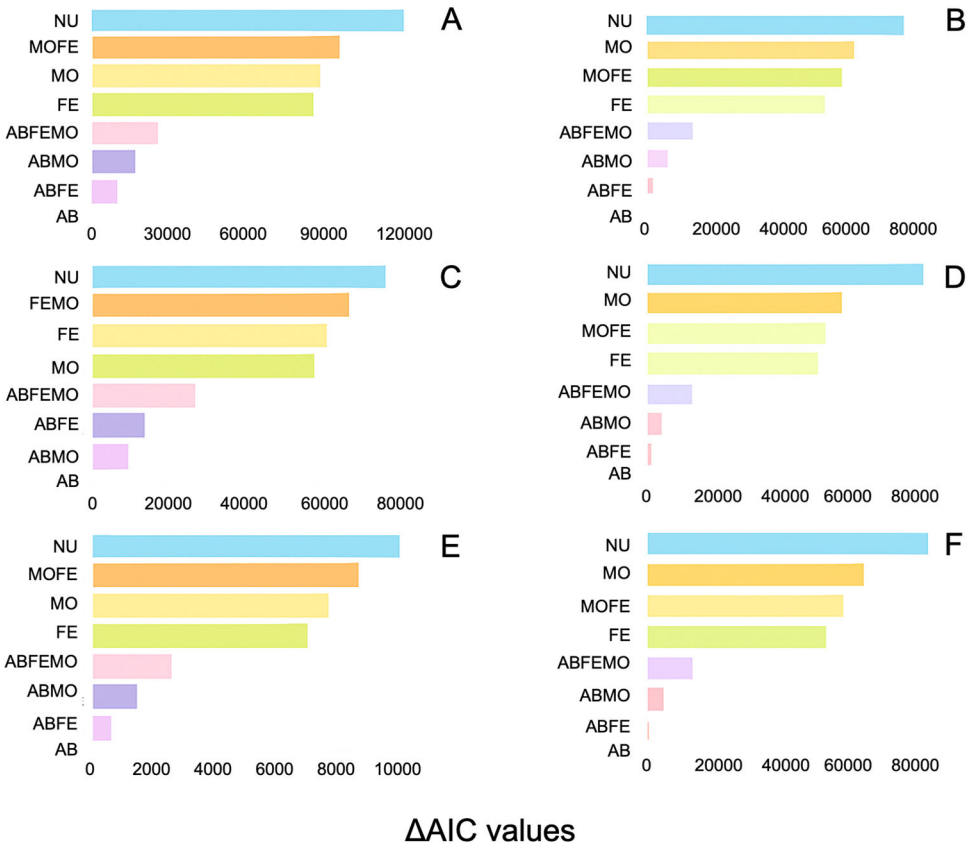

Fig. 5. ΔAIC values for probabilistic models predicting plant-butterfly interactions across different networks. Models include: abundance (AB), phenology (FE), morphology (MO), null model (NU), and all possible combinations (ABFE, ABFEMO, ABMO, FEMO). (A) Full network, (B) rainy season, (C) dry season, (D) juniper-oak forest, (E) eucalyptus forest, and (F) cropland. Lower ΔAIC values indicate better model performance. Models are ranked by performance within each network type.

human-modified landscapes (Winfree et al., 2011; Kennedy et al., 2013). The importance of mobile, generalist species suggests they may contribute disproportionately to network connectivity across heterogeneous landscapes (Harvey et al., 2017). In agricultural systems, management practices that extend or diversify flowering phenology may reduce dependence on synchronized interactions and enhance resilience (Scheper et al., 2013). These implications apply specifically to butterfly-mediated nectar-feeding interactions and should complement conservation strategies targeting other pollinator groups.

However, it is critical to emphasize that structural persistence does not guarantee functional persistence. Our study focused on network architecture and visitation patterns, not on pollination effectiveness or plant reproductive success. Networks may appear structurally intact while experiencing functional erosion if, for example, generalist visitors are less effective pollinators than the specialists they replace (Winfree et al., 2014). The shift from specialist-rich to generalist-dominated communities we documented may therefore represent a cryptic loss of pollination function that is not captured by network metrics alone. Future work should explicitly link network structure to pollination outcomes (seed set, fruit production, pollen transfer efficiency) to assess whether the structural stability we observed translates into functional stability. Additionally, our focus on adult nectar-feeding interactions overlooks the larval host plant requirements of butterflies, which may be more vulnerable to habitat modification than adult foraging patterns. Conservation strategies based solely on maintaining abundant floral resources may fail if host plants for specialist butterfly species are lost.

Similarly, while our models identify abundance as the primary predictor of interactions, this does not mean that conservation should focus exclusively on maximizing flower and butterfly abundances. Morphological matching and phenological synchrony, though secondary in our models, may still be critical for the maintenance of rare or specialized interactions that disproportionately contribute to ecosystem functioning (Bascompte and Jordano, 2007). Moreover, our modeling approach does not capture other potentially important factors such as nectar quality, floral scent chemistry, or behavioral plasticity, all of which may influence pollination effectiveness independently of visitation frequency.

Our findings should be interpreted within the context of several important considerations. By focusing exclusively on butterfly-plant nectar-feeding interactions, we examined only a subset of the complete pollination network, and other pollinator groups may respond differently to disturbance and rely on different structuring mechanisms (Williams et al., 2010; He et al., 2025). Additionally, our interaction data reflect visitation patterns rather than pollination effectiveness, which may not always correlate strongly. The probabilistic models we employed incorporated only a limited set of morphological and phenological traits, excluding potentially important factors such as nectar rewards, floral scent, and color preferences (Schiestl and Johnson, 2013). Our one-year sampling period, while capturing seasonal variation, cannot account for interannual fluctuations that are known to influence network structure and assembly processes (CaraDonna et al., 2017). Despite these constraints, our results provide robust evidence for the relative predictive power of neutral versus biological processes across a well-defined disturbance gradient.

Overall, our results highlight that the resilience of plant–butterfly interaction networks in human-modified landscapes may rely less on the preservation of specific interactions than on the maintenance of key

ecological processes, particularly species abundances and temporal resource availability. By showing that network structure can persist while underlying structuring mechanisms shift, this study underscores the need for conservation strategies that explicitly consider process-based resilience rather than structural patterns alone. Such an approach is particularly relevant in landscapes undergoing rapid land-use change, where apparent network stability may mask increasing vulnerability to climatic and phenological disruptions or cryptic losses of specialized pollination functions that are not captured by network topology.

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.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.pecon.2026.09.001.

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