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# Architecture and stability of tripartite ecological networks with two interaction types

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## Abstract

Over the past few decades, studies on empirical ecological networks have primarily focused on single antagonistic or mutualistic interactions. However, many species engage in multiple interactions that support distinct ecosystem functions. The architecture of networks integrating these interactions, along with their cascading effects on community dynamics, remains underexplored in ecological research. In this study, we compiled two datasets of empirical plant–herbivore/host–parasitoid (PHP) and pollinator–plant–herbivore (PPH) networks, representing two common types of tripartite networks in terrestrial ecosystems: antagonism–antagonism and mutualism–antagonism. We identified the patterns of subnetwork structures and interconnection properties in these networks and examined their relationships with community stability. Our findings revealed distinct pathway effects of network architecture on persistence and local stability in both PHP and PPH networks, with subnetwork modularity and nestedness showing a few strong direct effects and mediating the indirect effects of subnetwork size and connectance. In PHP networks, subnetwork modularity enhanced persistence and local stability, whereas subnetwork nestedness directly undermined them. However, both subnetwork topologies consistently mediated the destabilizing effects of subnetwork size and connectance on the entire network. In PPH networks, persistence was primarily affected by the plant–herbivore subnetwork, while the size, connectance, and modularity of different subnetworks had opposing effects on local stability. Regarding interconnection properties, the correlation of interaction similarity destabilized PHP networks, whereas the correlation of interaction degree promoted local stability in PPH networks. Further analysis indicated that structure–persistence relationships vary significantly across guilds, and the network-level effects of network architecture can be reversed, negligible, or biased in specific guilds. These findings advance our understanding of how network architecture influences ecosystem stability and underscore the importance of considering multiple interaction types when predicting community dynamics.

**KEYWORDS**
interconnection property, local stability, network architecture, persistence, subnetwork, tripartite network

# INTRODUCTION

Studies of ecological networks have significantly enhanced our understanding of how interaction complexity influences community stability (Delmas et al., 2019; Lewinsohn et al., 2006; May, 1972; McCann, 2000). However, most empirical studies have predominantly focused on single interaction types, such as food webs, mutualistic networks (pollination and seed dispersal), and host–parasite networks (Delmas et al., 2019; Landi et al., 2018; Thebault & Fontaine, 2010). Recent studies recognize that natural networks consist of multiple interaction types (Melián et al., 2009; Morrison et al., 2020; Pocock et al., 2012), often referred to as hybrid or multipartite networks, in which subnetworks linked by connector species—organisms involved in different interaction types (Fontaine et al., 2011). Studies suggest that variation in interaction types and subnetwork structures (such as connectance, nestedness, and modularity) disproportionately influences overall community stability (Sauve et al., 2014). Notably, the architecture of these networks includes not only subnetwork structures but also the interconnection properties that characterize how connector species interconnect different types of interactions—factors crucial for community stability (Domínguez-García & Kéfi, 2024; Sauve, Thebault, et al., 2016; Yan, 2022). However, general patterns of network architecture in empirical multipartite networks and their combined effects on community stability remain largely unexplored.

Network structure and its implications for community dynamics are key topics in ecological network research. Network size represents species richness, while connectance measures the proportion of realized links among all possible connections. These fundamental structural descriptors are closely related to community stability (Dunne et al., 2002; Landi et al., 2018; May, 1972). Theoretical and empirical studies have also explored how network topologies, such as modularity and nestedness, are distributed in natural ecosystems and influence network stability. For instance, the prevalence of nestedness and modularity varies across plant–herbivore, pollination, seed dispersal, and host–parasite networks, but this variation does not align with a simple mutualistic–antagonistic dichotomy (Pinheiro et al., 2022; Thebault & Fontaine, 2010). These network structures are closely related to various community stability measures (Landi et al., 2018). For example, high nestedness and connectance tend to stabilize mutualistic networks, whereas high modularity and low connectance stabilize herbivory networks (Thebault & Fontaine, 2010). However, the structure–stability relationships have largely been inferred from empirical networks with single interaction types.

Integrating multiple interaction types can produce dynamics that differ significantly from those observed in isolated pairwise interactions, as one interaction type can influence the outcomes of another (Jang, 2002; Yan, 2022). While some studies have shown that combining different interaction types affects community stability (Emary & Malchow, 2022; Garcia-Callejas et al., 2018; Kefi et al., 2016; Montesinos-Navarro et al., 2017; Mougi & Kondoh, 2012), three key gaps remain in our understanding of structure–stability relationships in ecological networks with multiple interaction types. First, the general patterns of subnetwork structures and interconnection properties in multipartite networks remain underexplored, especially in large datasets (but see Domínguez-García & Kéfi, 2024). Most studies have focused on structural differences among subnetworks within specific taxa in specific ecosystems (Genrich et al., 2016; Kefi et al., 2016; Lima et al., 2020; Martínez-Núñez & Rey, 2021; Mello et al., 2019; Morrison & Dirzo, 2020; Olesen et al., 2018; Vitali et al., 2022, 2023). The patterns of interconnection properties are even less understood. For instance, not all species engage in multiple interaction types, leading to a subset of connector nodes (species that have interactions in both subnetworks) in a shared set of species. In this context, Sauve, Thebault, et al. (2016) found that the correlation between plant mutualistic and antagonistic degrees was non-random in a tripartite network from an agroecosystem. Second, how subnetwork structures and connector species jointly affect community stability remains unclear in empirical multipartite networks. Simulation studies suggest that structures like modularity and nestedness have weak effects on stability, whereas interconnection properties, such as the correlation of interaction degree, may mitigate the destabilizing impacts of nestedness (Sauve et al., 2014; Yan, 2022). However, simulated networks may not capture the full diversity of empirical network structures, questioning the generality of structure–stability relationships. Third, different trophic groups of species may have varying sensitivities to disturbances, primarily explored in the context of species loss and robustness. For instance, Pocock et al. (2012) found that pollinators were particularly sensitive to plant loss in a hybrid agroecosystem network. A recent study also showed that the structural properties of connector species were related to the tolerance of different groups to species loss in 44 empirical tripartite networks (Domínguez-García & Kéfi, 2024). Notably, previous studies on hybrid or multipartite networks have primarily focused on overall community dynamics (Garcia-Callejas et al., 2018; Mougi & Kondoh, 2012; Sauve et al., 2014; Yan, 2022), with fewer exploring relationships between network architecture and community dynamics at the trophic group level.

To address these knowledge gaps, we collected empirical tripartite networks featuring two distinct interaction types: plant–herbivore/host–parasitoid (PHP) networks, interconnected by insects (herbivores and parasitoid hosts); and pollinator–plant–herbivore (PPH) networks, interconnected by plants. A PHP network consists of two subnetworks with antagonistic interactions (Figure 1a), whereas a PPH network includes one mutualistic and one antagonistic subnetwork (Figure 1b). These

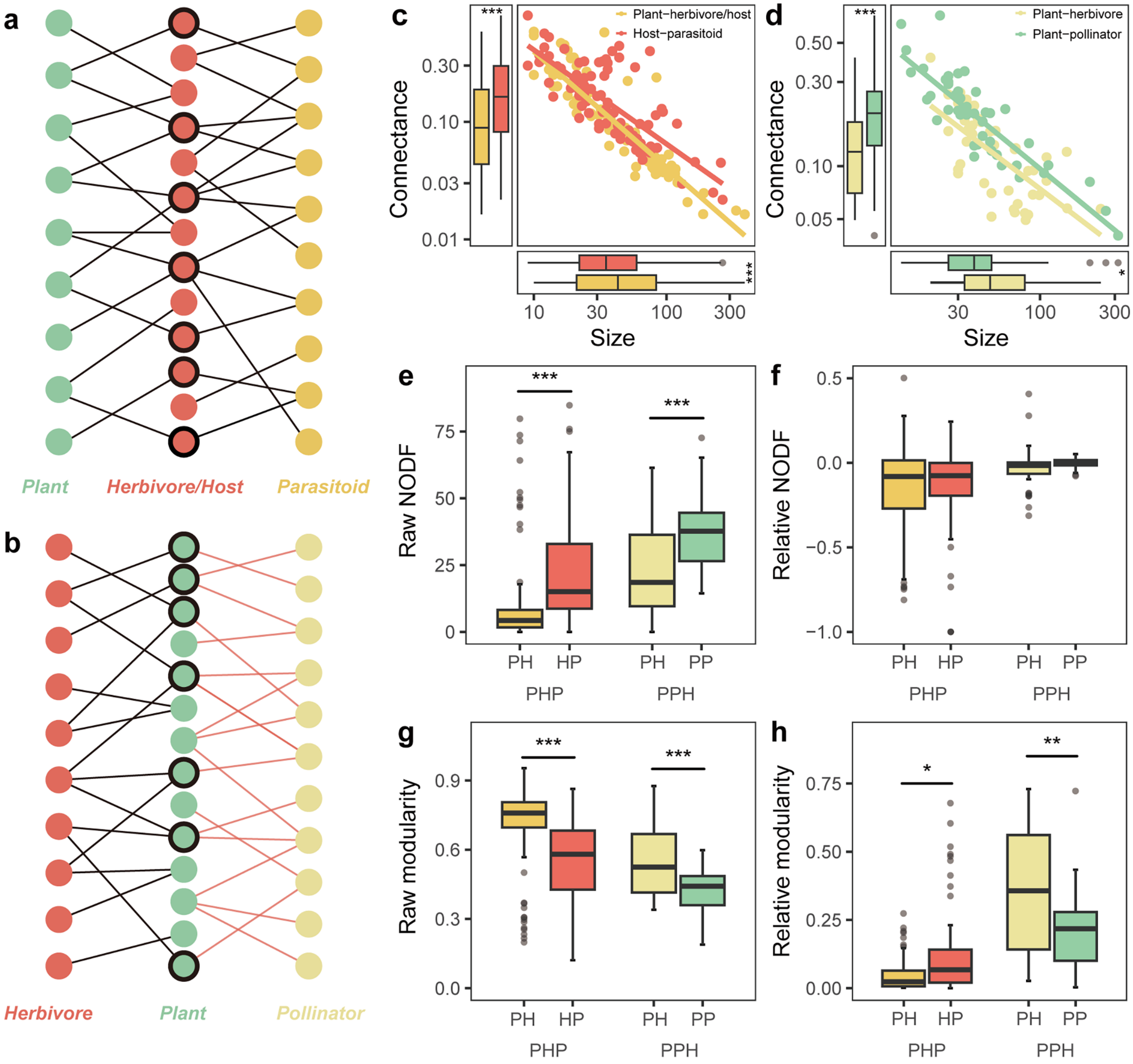

**FIGURE 1** Schematic representations of tripartite networks and the results on subnetwork structures. (a) Plant–herbivore/host–parasitoid (PHP) tripartite network. (b) Pollinator–plant–herbivore (PPH) tripartite network. (c, d) Relationship between subnetwork size and subnetwork connectance on logarithmic scales in the PHP and PPH networks. (e, f) Comparisons of raw and relative nestedness between subnetworks. (g, h) Comparisons of raw and relative modularity between subnetworks. $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$. NODF, a nestedness metric quantified using the overlap and decreasing fill.

tripartite networks represent distinct species guilds, ecosystem functions (pollination–herbivory vs. herbivory–parasitoidism), and interaction compositions (antagonism–antagonism vs. antagonism–mutualism). We addressed four main questions: (1) What are the structural differences between subnetworks? (2) How do connector species interconnect different subnetworks? The questions aimed to reveal the similarities and differences in the architecture of the two types of tripartite networks and their underlying biological constraints. We then examined how subnetwork structures and interconnection properties jointly affect the stability of the entire tripartite network (3) and different guilds (4), ultimately advancing our understanding of structure–stability relationships that have primarily been studied in single-interaction networks.

# MATERIALS AND METHODS

## Data collection

To compile a dataset of empirical tripartite ecological networks, we conducted two literature searches in the Web of Science database using the search terms "(TS = plant* AND host* AND parasitoid*) AND TS = (web* OR network*)" and "(TS = (pollinat* AND plant* AND herbivor*)) AND TS = (web* OR network*)" in June 2024. The search yielded 1301 articles, which were manually reviewed for relevant data. We included only studies with at least four species per guild, which yielded a total of 132 tripartite networks from various ecosystems: 87 PHP and 45 PPH networks (Appendix S1: Tables S1 and S2, Figure S1). Network data were extracted from tables, figures, and online data repositories. Seventy networks were reconstructed using nodes and links from high-resolution figures, 39 included link strengths, and the remaining were binary (1 for interaction and 0 for no interaction). We used the binary version of the networks because of the inconsistencies in interaction strength definitions and the limited availability of networks with quantified interaction strengths for comprehensive analysis.

## Subnetwork structure analyses

In this study, a PHP network consisted of a plant–herbivore/host (PH) subnetwork and a host–parasitoid (HP) network, while a PPH network comprised a plant–pollinator (PP) subnetwork and a plant–herbivore (PH) network. Subnetwork structure refers to the structural properties of a subnetwork. For each subnetwork, we measured size, connectance, nestedness, and modularity. Subnetwork size represents the total number of species within a subnetwork, while subnetwork connectance is the proportion of realized links relative to all possible links between species at two trophic levels. Nestedness was quantified using the overlap and decreasing fill (NODF) metric for bipartite networks (Almeida-Neto et al., 2008). Modules were detected using the algorithm developed by Beckett (2016), and modularity was calculated accordingly. As NODF and modularity are influenced by connectance and network size, we calculated relative values as (observed − $\text{mean}_{\text{null}}$)/$\text{mean}_{\text{null}}$, where the $\text{mean}_{\text{null}}$ was derived from 1000 randomized null networks. Null networks were generated by shuffling species interactions while maintaining the marginal totals of the subnetworks (Dormann et al., 2009; Olesen et al., 2007), implemented via the "quassiswap" algorithm in the R package "vegan" (Dixon, 2003). We also applied NODFc, a recent metric that directly accounts for connectance and size, facilitating nestedness comparisons across networks (Song et al., 2017). To indicate specific subnetworks, we prefixed subnetwork abbreviations to the metrics (e.g., PH-size for the size of the PH subnetwork and HP-size for the size of the HP subnetwork in PHP tripartite networks).

We further investigated (1) the correlation between log-transformed size and connectance within the same subnetworks using Spearman's correlation and (2) differences in nestedness and modularity between two subnetworks using the paired *t* test, following Thebault and Fontaine (2010). Analyses were performed in R using the "bipartite" (Dormann et al., 2008), "maxnodf" (Hoeppke & Simmons, 2021), and "vegan" (Dixon, 2003) packages.

## Interconnection properties of connector species

We characterized the interconnection properties of connector species using three different metrics (see examples in Appendix S1: Figure S2). At the trophic level bridging the two subnetworks, species were categorized as either connector species (CS), which occur in both subnetworks, or species exclusive to one subnetwork ($NS_1$ and $NS_2$). The first interconnection property, the proportion of connector species (PoC), represents the fraction of species present in both subnetworks (e.g., insects in PHP or plants in PPH) (Appendix S1: Figure S2a) and was calculated as $PoC = CS/(CS + NS_1 + NS_2)$. To evaluate whether one subnetwork contained more CS than the other, we calculated PoC for individual subnetworks as

PoC-$S_{1 \text{ or } 2} = CS/(CS + NS_{1 \text{ or } 2})$. Following Sauve, Thebault, et al. (2016), we used two additional metrics, correlation of interaction degree (CoID) and correlation of interaction dissimilarity (CoIS), to quantify how connector species link the two subnetworks. The CoID of connector species between the two subnetworks was calculated using Kendall's correlation coefficient (Appendix S1: Figure S2b), while CoIS was derived from the pairwise Jaccard index of interaction partners for connector species in each subnetwork. This resulted in two dissimilarity matrices, with CoIS represented as the Mantel correlation coefficient between them (Appendix S1: Figure S2c).

To determine whether the CoID and CoIS values deviated from random expectations, we applied the null model proposed by Sauve, Thebault, et al. (2016), which preserves the subnetwork structures while randomizing the connections between species bridging two subnetworks. This model splits a tripartite network into two subnetwork matrices, shuffles the rows (or columns) of connecting species (i.e., hosts/plants), and recombines them to create a tripartite network with randomized connections. Subsequently, we tested for significant differences in the CoID and CoIS values by comparing observed values with the distribution of these metrics from randomized networks using a two-tailed *p*-value test (George & Mudholkar, 1990). *Z*-scores were calculated to compare the two types of tripartite networks.

## Community stability

To ensure compatibility with previous theoretical studies (Neutel et al., 2002; Sauve, Thebault, et al., 2016; Thebault & Fontaine, 2010; Yan, 2022), we tested two stability measures: persistence and local stability.

Persistence represents the long-term survival of species within a community. For this measure, we simulated community dynamics using differential equations (Appendix S2), adopting parameter values from Thebault and Fontaine (2010) to facilitate comparisons between tripartite and bipartite networks. The differential equations for PHP and PPH networks were numerically solved using the "deSolve" package in R. Persistence was defined as the proportion of surviving species (density $> 1 \times 10^{-6}$) at the end of the simulation (after 20,000 time steps). Additionally, we conducted a sensitivity analysis of parameter values and assessed the robustness of structure–persistence relationships (*Structural equation modeling* and Appendix S3).

Local stability in ecology refers to a community's ability to return to equilibrium after small disturbances (May, 1972) and is most relevant when the system is in a steady state. To calculate local stability, we transformed a tripartite network into an adjacency matrix and randomly generated interaction coefficients from a normal distribution (mean = 0, SD = 3). This produced a weighted interaction matrix, A, where each element $a_{ij}$ represents the interaction strength. We assumed a linear Lotka–Volterra model to describe the community dynamics: $\frac{1}{N_i}\frac{dN_i}{dt} = r_i + \sum_j a_{ij}N_j$, where the per capita growth rate of species $i$ depends on its intrinsic per capita growth rate ($r_i$), self-effects ($a_{ii} < 0$), and interactions with other species ($a_{ij}$). The matrix A corresponds to the Jacobian matrix (Neutel et al., 2002; Novak et al., 2016; Sauve, Thebault, et al., 2016). Local stability was assessed by determining the minimum intraspecific negative feedback, which was calculated by evaluating the level of diagonal elements ($a_{ii}$), required for all eigenvalues of matrix A to have negative real parts, ensuring community stability (Sauve, Thebault, et al., 2016).

## Structural equation modeling

We used structural equation modeling (SEM) to investigate how subnetwork structures and interconnection metrics affect the stability of tripartite networks. Following previous studies (Sauve et al., 2014; Thebault & Fontaine, 2010), we hypothesized that all four subnetwork structures could directly affect stability, while size and connectance could influence stability indirectly through nestedness and modularity (see the full potential causal relationships in Appendix S1: Figure S3). Given that PoC represents the level of interdependence between subnetworks, it was included as a fixed term in the models irrespective of its statistical significance. Furthermore, we considered not only the overall persistence of the entire tripartite network but also the persistence of species across different guilds (i.e., plant, herbivore/host, and parasitoid; pollinator, plant, and herbivore). Given the large number of potential combinations of exploratory variables, we first selected the best-fit models for persistence or local stability with the lowest corrected Akaike information criterion ($\text{AIC}_c$) value, using the "dredge" function from "MuMIn" in R (Bartoń, 2024). These best-fit models were then integrated with other paths (from size and connectance to modularity and nestedness) for SEM analysis. Acceptable SEMs were those that passed Shipley's *d*-separation test ($p > 0.05$). The net effect of a variable on persistence or local stability was calculated by multiplying all coefficients on the respective path. All SEMs were performed using the "piecewiseSEM" package in R (version 4.2.2) (Lefcheck & Freckleton, 2015).

# RESULTS

## Subnetwork structure

In both PHP and PPH networks, subnetwork connectance was negatively correlated with subnetwork size (on logarithmic scales, for PHP, PH subnetwork, Spearman correlation $\rho = -0.913$, $p < 0.001$; HP subnetwork, $\rho = -0.735$, $p < 0.001$; for PPH, PP subnetwork, $\rho = -0.848$, $p < 0.001$; PH subnetwork, $\rho = -0.669$, $p < 0.001$) (Figure 1c,d). HP-connectance was significantly higher than PH-connectance in PHP networks, and PP-connectance was significantly higher than PH-connectance in PPH networks, whereas network size showed the opposite patterns (all $p < 0.05$). In PHP networks, raw PH-NODF was lower than HP-NODF ($t = -6.063$, $p < 0.001$), but no differences were observed for relative NODF ($t = -0.654$, $p = 0.515$) or NODFc ($t = 1.018$, $p = 0.311$) (Figure 1e,f, Appendix S1: Figure S4); raw PH-modularity was higher than HP-modularity ($t = 7.743$, $p < 0.001$), but relative modularity showed the opposite pattern ($t = -2.606$, $p = 0.011$) (Figure 1g,h). In PPH networks, raw PP-NODF was significantly higher than PH-NODF ($t = 5.371$, $p < 0.001$), but no significant differences were observed for relative NODF ($t = 1.505$, $p = 0.140$) or NODFc ($t = -1.447$, $p = 0.155$) (Figure 1e,f, Appendix S1: Figure S4); raw PP-modularity was significantly lower than PH-modularity ($t = -6.817$, $p < 0.001$), and the same trend was observed for relative modularity ($t = -2.310$, $p = 0.026$) (Figure 1g,h).

## Interconnection properties of connector species

On average, PHP networks had a higher PoC than PPH networks (Wilcoxon signed-rank test, $w = 3305.5$, $p < 0.001$) (Figure 2a). Further analysis revealed that many herbivores also served as hosts for parasitoids, whereas most insect-pollinated plants were consumed by herbivores, and few plants fed by herbivores were insect-pollinated (Appendix S1: Figure S5). The CoIS values were significantly higher in PHP networks than in PPH networks ($t$ test, $t = 4.645$, $p < 0.001$); however, no significant difference was observed for CoID ($t = 0.786$, $p = 0.434$) (Figure 2b,c). For CoID, nearly one third of the PHP networks exhibited significant deviations from the null models (23/74, 15 higher and 8 lower than expected) and slightly more than that observed in PPH networks (9/45, 6 higher and 3 lower than expected) (Figure 2b). Similarly, half of the PHP networks showed significant CoIS patterns relative to the null models (38/84, 32 higher and 6 lower than expected), whereas a much smaller proportion was observed in PPH networks (6/41, 4 higher and 2 lower than expected) (Figure 2c).

## Effects of subnetwork structure and interconnection properties on persistence and local stability

The persistence and local stability of the PHP and PPH networks varied significantly across different networks

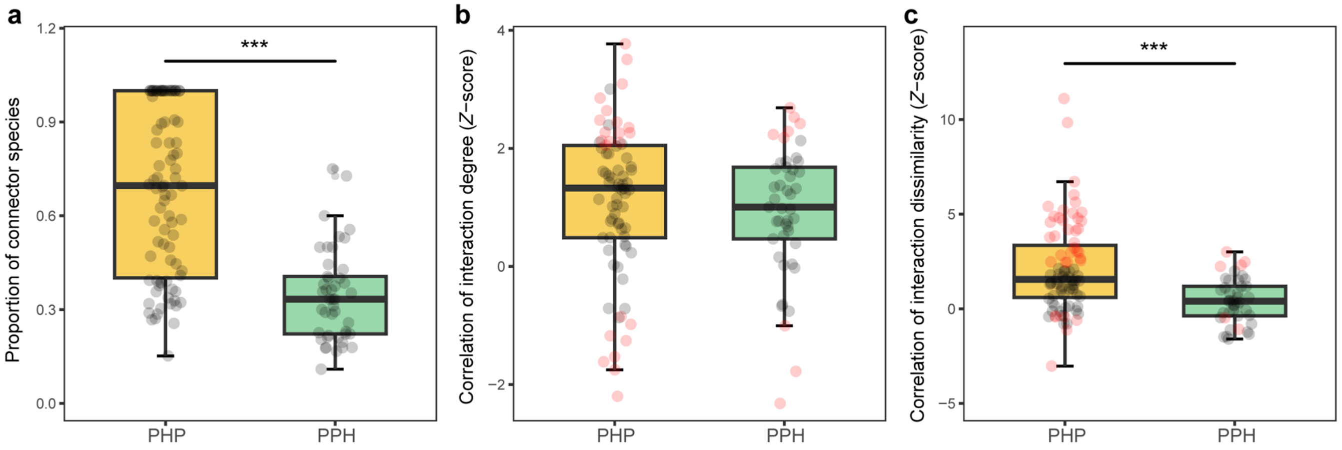

**FIGURE 2** Interconnection properties of plant–herbivore/host–parasitoid (PHP) and pollinator–plant–herbivore (PPH) tripartite networks. (a) Proportion of connector species in PHP and PPH networks. (b) Correlation of interaction degree in PHP and PPH networks. (c) Correlation of interaction dissimilarity in PHP and PPH networks. Red circles represent networks with significantly different interconnection properties compared to null models. $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

(Appendix S1: Figure S6). As shown in Figure 3, subnetwork structures and interconnection properties jointly affected the persistence and local stability of PHP networks (detailed SEM results in Appendix S1: Table S3). CoIS, HP-nestedness, and HP-size directly reduced persistence, whereas HP-connectance, HP-modularity, PH-modularity, and PH-size enhanced it (Figure 3a). PH-modularity mediated the negative effects of PH-connectance and PH-size, while both HP-nestedness and HP-modularity mediated the negative effects of HP-connectance and HP-size. For local stability, similar patterns were observed, except that HP-connectance, HP-nestedness, and PH-modularity did not affect local stability (and thus had no mediating effects), while PH-nestedness had a negative effect (Figure 3b).

In the SEM results for PPH networks (detailed in Appendix S1: Table S4), PH-size and PH-nestedness showed direct negative effects on persistence, whereas PP-size, PH-connectance, and PH-modularity showed direct positive effects (Figure 3c). PH-modularity and PH-nestedness mediate the negative effects of PH-connectance and PH-size on persistence. For local stability, CoID, PP-connectance, and PP-modularity had direct positive effects, whereas PH-connectance, PH-modularity, and PP-size had direct negative effects (Figure 3d). PP-modularity mediated the negative effects of PP-connectance and PP-size, whereas PH-modularity mediated their positive effects.

A sensitivity analysis of persistence indicated that the SEM results remained robust despite changes in the modeling parameters. Most path coefficients from the original results aligned with the average values obtained using resampled parameters. In cases where they did not, the signs of the coefficients remained consistent (Appendix S3).

## Effects of subnetwork structure and interconnection properties on guild-level persistence

Guild-level persistence varied substantially across networks (Appendix S1: Figure S7). The SEM results of network architecture for guild-level persistence differed from those for overall network persistence (Figure 4, detailed SEM results in Appendix S1: Tables S5 and S6).

In PHP networks (Figure 4a–c), HP-connectance promoted host and parasitoid persistence but decreased plant persistence, while HP-size reduced parasitoid persistence. HP-nestedness negatively affected host and parasitoid persistence, whereas HP-modularity positively affected host persistence but negatively affected plant persistence. PH-connectance promoted plant persistence but reduced parasitoid persistence, whereas PH-size enhanced parasitoid persistence (Figure 4a–c). PH-modularity had a positive effect on both plant and host persistence. Additionally, both CoIS and PoC reduced host persistence, whereas PoC promoted parasitoid persistence (Figure 4b,c).

In PPH networks (Figure 4d–f), PP-size positively affected plant and herbivore persistence, whereas PP-modularity negatively affected pollinator and herbivore persistence. PH-connectance promoted pollinator and plant persistence, whereas PH-size negatively affected plant and herbivore persistence. PH-modularity consistently promoted the persistence of all three guilds, whereas PH-nestedness decreased pollinator persistence. PoC and CoID decreased only pollinator persistence.

# DISCUSSION

This study highlights the complex pathways through which subnetwork structures and interconnection properties of connector species influence persistence and local stability in empirical tripartite networks. Specifically, the interactive effects among subnetworks suggest that both direct and indirect pathways contribute to community dynamics, underscoring the disproportionate impact of different interaction types. Our findings indicate that ecological network stability depends not only on the composition of interactions but also on how they are interconnected. Additionally, the structure–stability relationships differ at the guild and network levels, underscoring the need to consider differential trophic group responses to environmental disturbances. These findings enhance our understanding of the structure–stability relationships, which have largely been based on studies of single-interaction networks.

## Architecture of tripartite interaction networks

The difference in subnetwork structures between the PP and PH subnetworks in PPH networks generally supported the findings from single-interaction networks reported by Thebault and Fontaine (2010). The results from both PHP and PPH networks suggest that connectance was linked to significant differences in raw nestedness and modularity between subnetworks (Figure 3). However, the influence of connectance was weaker in PPH networks, where patterns of nestedness and modularity between subnetworks remained similar in both raw and relative values.

The high PoC in PHP networks emphasizes the role of herbivores as intermediate trophic species in

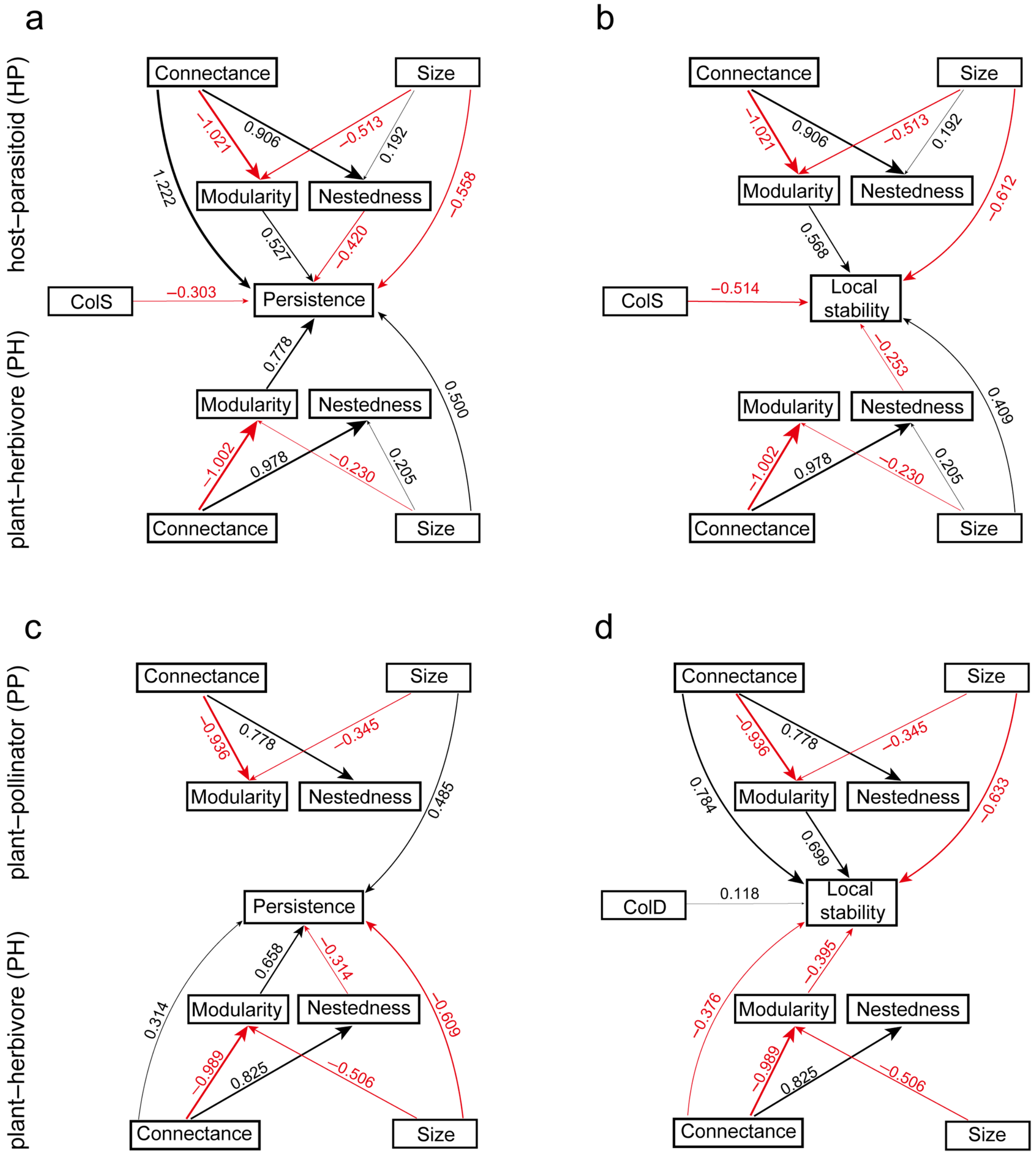

**FIGURE 3** Summary diagrams of the effects of network architecture on the persistence and local stability of plant–herbivore/host–parasitoid (a, b) and pollinator–plant–herbivore (c, d) tripartite networks. In panels (a) and (b), the upper section represents the host–parasitoid (HP) subnetwork, while the lower section represents the plant–herbivore (PH) subnetwork. In panels (c) and (d), the upper section represents the plant–pollinator (PP) subnetwork, while the lower section represents the plant–herbivore (PH) subnetwork. Only significant paths are shown ($p < 0.05$). Arrow thickness is scaled to standardized path coefficients, with values indicated next to arrows. Red arrows indicate negative effects, while black arrows indicate positive effects. CoID, correlation of interaction degree; CoIS, correlation of interaction dissimilarity.

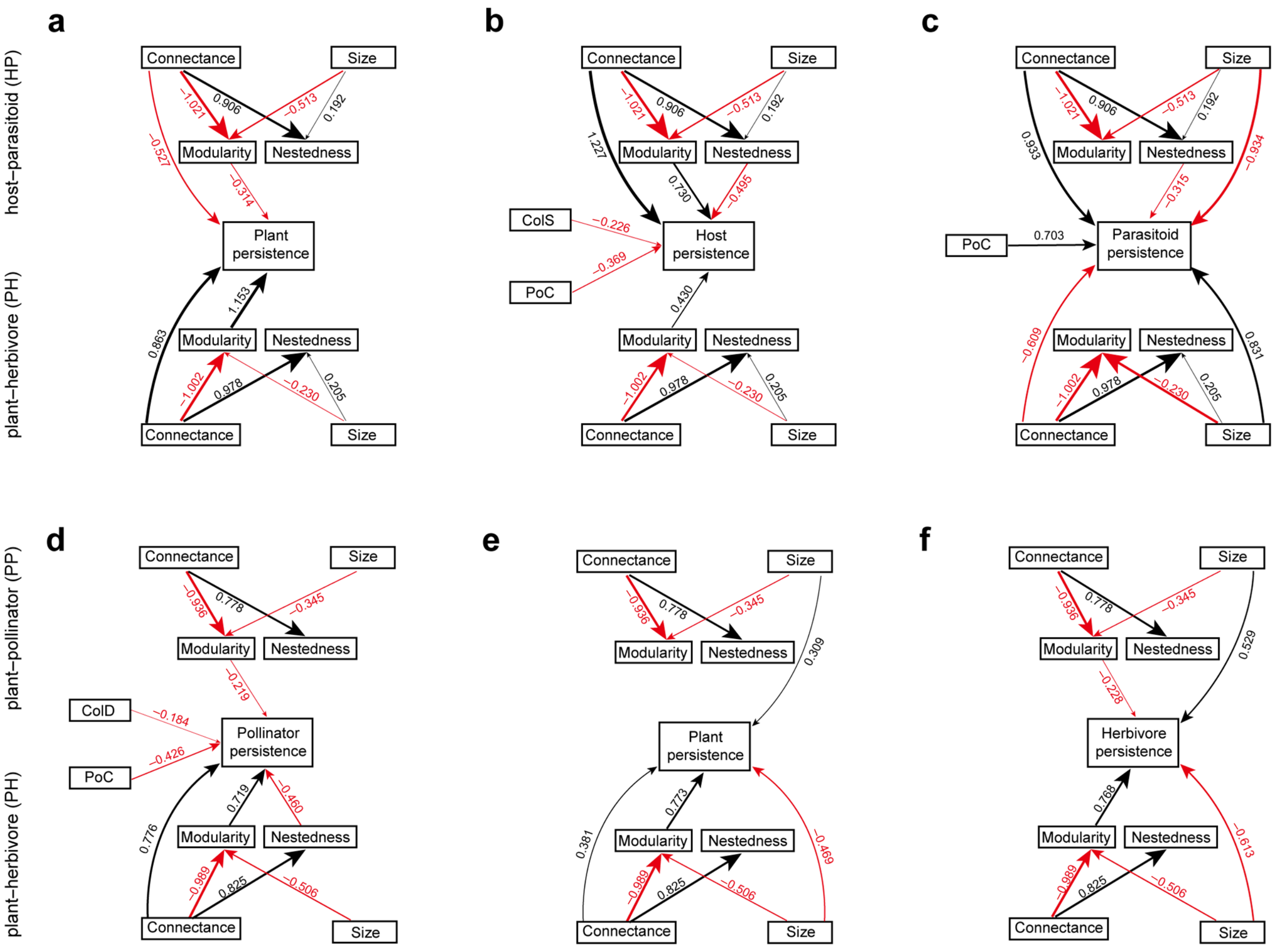

**FIGURE 4** Summary diagrams of the effects of network architecture on the persistence of different guilds in plant–herbivore/host–parasitoid (a–c) and pollinator–plant–herbivore (d–f) tripartite networks. Only significant paths are shown ($p < 0.05$). Arrow thickness is scaled to standardized path coefficients, with values indicated next to arrows. Red arrows indicate negative effects, while black arrows indicate positive effects. CoID, correlation of interaction degree; CoIS, correlation of interaction dissimilarity; PoC, proportion of connector.

plant–herbivore–parasitoid interactions. Conversely, the low PoC in pollinator–plant–herbivore interactions indicates that while most insect-pollinated plants are preyed upon by herbivores, only a limited number of herbivore-consumed plants are insect-pollinated (Appendix S1: Figure S5), aligning with the findings of a recent study (Domínguez-García & Kéfi, 2024). This may reflect the diversity of plant pollination strategies, including a large proportion of wind- and self-pollinated species. However, there could be sampling bias, as many studies on plant–herbivore–parasitoid dynamics focus primarily on herbivores with parasitoids (Alhmedi et al., 2018; Memmott et al., 1994).

For connector species, ecological and evolutionary factors may shape their non-random interconnection patterns (Nakadai & Kawakita, 2017; Sauve, Thebault, et al., 2016). However, our results only partially support this expectation, as non-random CoID and CoIS were observed in only half or fewer of the PHP and PPH networks, respectively. This suggests that alternative mechanisms influence species connectivity across interaction types. For instance, evolutionary constraints on similar interactions may be countered by competition-driven niche differentiation (Godoy et al., 2018). Thus, no universal interconnection patterns emerge in these tripartite networks, highlighting the need to integrate both niche and neutral processes to explain how different types of interactions are interconnected.

## Structure–stability relationships in PHP networks

While structure–stability relationships from isolated antagonistic networks (Grilli et al., 2016; Stouffer & Bascompte, 2011; Thebault & Fontaine, 2010) largely apply to PHP networks, such as the roles of modularity and nestedness, this study offers a more nuanced perspective. Specifically, the net effects of subnetwork complexity present a complex interplay: size stabilizes because of its direct effect, whereas connectance tends to introduce destabilizing dynamics (Appendix S1: Table S7). This suggests that network complexity functions differently in multi-interaction systems compared to single-interaction systems (Thebault & Fontaine, 2010). Furthermore, while modularity and nestedness exert contrasting direct effects on persistence and local stability, they consistently mediate the destabilizing effects of subnetwork complexity, underscoring their crucial roles in the indirect pathways of structure–stability relationships.

Species interconnecting different subnetworks play an important role in disturbance propagation, with their interconnections influencing how disturbances diversify (Domínguez-García & Kéfi, 2024; Fontaine et al., 2011; Sauve, Thebault, et al., 2016; Yan, 2022). In simulated mutualism–antagonism networks, CoIS stabilizes the system by offsetting positive and negative indirect effects (Sauve, Thebault, et al., 2016). However, in PHP networks, a high CoIS may intensify antagonistic interactions, facilitating disturbance propagation between subnetworks and leading to destabilization. This suggests that the impact of connector species depends not only on their interconnection properties but also on the types of interactions they interconnect.

## Structure–stability relationships in PPH networks

Our SEM analysis of persistence enabled a comparison of structure–stability relationships across simulated single-interaction networks (Thebault & Fontaine, 2010), simulated tripartite networks (Sauve et al., 2014), and empirical PPH networks (see the detailed comparison in Appendix S1: Figure S8). The empirical networks showed fewer significant pathways (e.g., no direct effects of PP-modularity and PP-nestedness on persistence) than the simulated single-interaction networks. However, where pathways were present in all three studies, their effects were mostly consistent, indicating robustness across both isolated and tripartite networks. Interestingly, PH-modularity promoted persistence in our PPH networks but reduced it in single-interaction PH networks. The exact mechanism for this discrepancy is unknown, but the mutualistic feedback from another subnetwork may counteract the destabilizing effects of PH-modularity, reversing its impact. Additionally, the lack of effects of subnetwork nestedness and modularity (Sauve et al., 2014) is plausible, as subnetworks are components of a tripartite network, where their influence may be weak or modified by connections to adjacent subnetworks. Compared to the simulated networks from Sauve et al. (2014), our findings showed no effect of subnetwork size on subnetwork nestedness. This could be because these effects were already weak in the simulations, and their absence in our results could be attributed to the smaller number of empirical networks compared to simulation studies, which limits the detection of such weak effects.

Although network complexity, referring to size and connectance in this study, typically reduces local stability in isolated networks (Allesina & Tang, 2012), our results showed that it can have opposing effects in PPH networks (Appendix S1: Table S8). This could be attributed to the fact that antagonistic interactions provide negative feedback that mitigates disturbances, whereas mutualistic interactions amplify them. Additionally, the contrasting effects of subnetwork modularity align with previous findings that its impact largely depends on overall interaction strength (Grilli et al., 2016). For example, May (1972) suggested that modularity enhances local stability in random networks; however, the opposite effect has been observed in antagonistic networks (Pimm, 1979; Solow et al., 1999). In multi-interaction networks, overall interaction strength is affected by the composition of interaction types, which may explain the varying effects of modularity across different interaction types. Regarding interconnection properties, the positive effect of CoID in empirical networks suggests that the balancing positive and negative interactions can enhance local stability of the entire system by neutralizing their effects (Sauve, Fontaine, & Thébault, 2016). However, the lack of significant effects from all three interconnection properties on overall persistence suggests that connector species may have a weak effect on the long-term maintenance of PHP networks.

## Structure–persistence relationships for different guilds

Decomposing persistence by guilds revealed distinct stabilizing and destabilizing effects of network architecture at the network and guild levels. While the signs of common path coefficients remained unchanged, differences arose from the loss or gain of direct effects and the reconfiguration of indirect pathways. Notably, some network structures had no effect on overall persistence but significantly influenced specific species subsets, sometimes reversing their effects or producing contrasting outcomes among guilds. Thus, analyzing the persistence of species subsets revealed hidden effects of network architecture and clarified the intricate structure–persistence relationships. More importantly, by identifying the guilds that were most affected by network architecture, our results highlight the differential vulnerability of functional groups to structural changes within multi-interaction networks. This is particularly relevant for biodiversity conservation and management, guiding efforts to prioritize specific taxa and ecological functions as ecological networks undergo rewiring under environmental changes.

## Limitations

Our study had several limitations owing to incompleteness and bias. First, we used binary networks and determined the interaction strengths of both subnetworks from the same random distribution. In reality, interaction strengths may vary between subnetworks, with stronger interactions likely having a greater impact on community stability. However, most empirical tripartite networks lack available interaction strength data, and definitions vary across studies (Emary & Malchow, 2022), making cross-network comparisons difficult. Future research could explore modeling parameters to account for varying interaction magnitudes across subnetworks. Second, we focused on tripartite networks with only three well-studied interaction types (herbivory, parasitoidism, and pollination) owing to their abundant network data. However, other less-studied multipartite networks involving seed dispersal, parasitism, and mycorrhizae are also common in ecosystems, and their inclusion could lead to different subnetwork structures and interconnection properties. Third, the empirical networks analyzed were geographically biased, primarily derived from temperate regions in the Northern Hemisphere. Overall, data deficiencies and research biases hinder a comprehensive understanding of multipartite networks in real ecosystems. Nonetheless, our study advances the understanding of complex structure–stability relationships in empirical networks with multiple interaction types.

## Conclusion

The joint effects of subnetwork structures and interconnection properties on persistence and local stability underscore the need to integrate traditional network structures from individual subnetworks with their specific interconnections to better understand ecosystem biodiversity and stability. As climate change and human activities continue to transform the structure and functioning of ecosystems, multipartite ecological networks are likely to be restructured. Thus, studying structure–stability relationships in these networks will be increasingly important for predicting and managing ecosystem responses and adaptability.

## AUTHOR CONTRIBUTIONS

Chuan Yan designed the study. Yangyang Zhao conducted data collection and analysis. Yangyang Zhao and Chuan Yan wrote the manuscript. Zhicheng Zhang, Xiyang Hao, Yongjun Zhang, and Xingfeng Si made substantial contributions to the data analysis, interpretation of results, and final written version of the manuscript.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data (Zhao et al., 2025) are available on Figshare at https://doi.org/10.6084/m9.figshare.24658215.v1.

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