

SYNTHESIS

The Hierarchical Coevolutionary Units of Ecological Networks

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ABSTRACT

In ecological networks, cohesive groups of species may shape the evolution of interactions, serving as coevolutionary units. Ranging across network scales, from motifs to isolated components, elucidating which cohesive groups are more determinant for coevolution remains a challenge in ecology. We address this challenge by integrating 376 empirical mutualistic and antagonistic networks and coevolutionary models. We identified cohesive groups at four network scales containing a significant proportion of potential direct coevolutionary effects. Cohesive groups displayed hierarchical organisation, and potential coevolutionary effects overflowing lower-scale groups were contained by higher-scale groups, underscoring the hierarchy's impact. However, indirect coevolutionary effects blurred group boundaries and hierarchy, particularly under strong selection from ecological interactions. Thus, under strong selection, indirect effects render networks themselves, and not cohesive groups, as the likely coevolutionary units of ecological systems. We hypothesise hierarchical cohesive groups to also shape how other forms of direct and indirect effects propagate in ecological systems.

1 | Introduction

Individuals of every species rely on interspecific interactions to obtain resources and services. Thus, interspecific interactions are important sources of selective pressure, potentially promoting coevolution (Thompson 1989). Coevolving species pairs, however, are rarely isolated, often being part of species-rich networks (Jordano 1987; Santamaría and Rodríguez-Gironés 2007). Thus, the structure of networks of direct ecological interactions is the frame over which indirect evolutionary effects between species propagate, potentially shaping coevolution (Andreazzi, Thompson, and Guimarães 2017; Guimarães et al. 2017). In this sense, a conspicuous structural pattern in ecological networks is the presence of cohesive groups (Olesen et al. 2007), which concentrate interactions when compared to surrounding network

regions (Wasserman and Faust 1994), and emerge across network scales.

At the highest scale, species-level networks are composed of one or more components (Guimarães 2020), groups of interacting species isolated from other components (Figure 1). Ecological networks range from disconnected, having several components, each encompassing a small proportion of species, to highly connected structures, composed of a giant component encompassing (almost) all species. Components, in turn, can be divided in two large and densely connected regions, called sectors (Slininger 2013). At intermediate network scales, ecological networks may be organised into modules (Olesen et al. 2007). The number of network modules depends on the number of species, and on the interaction distribution across

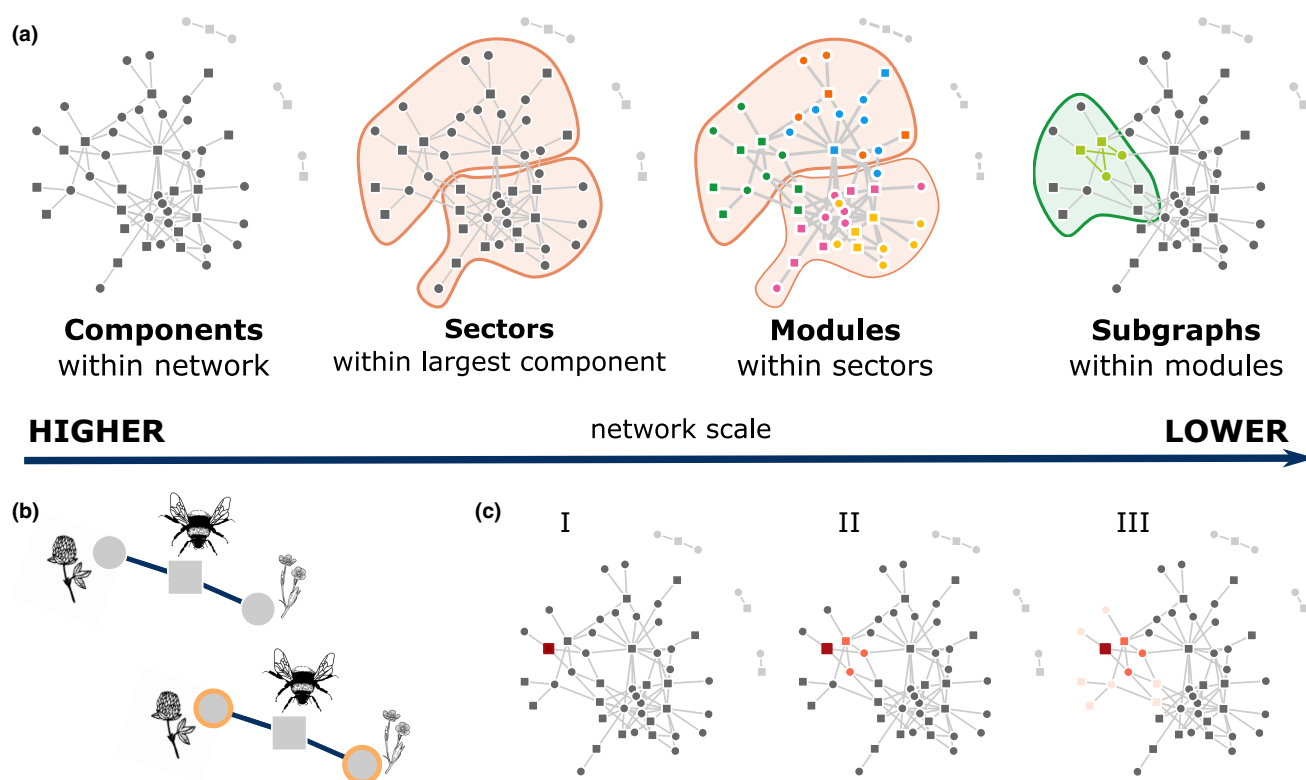


FIGURE 1 | Hierarchical structure in ecological networks. (a) Ecological networks present cohesive species groups which emerge across network scales: Components, sectors, modules and subgraphs (from highest to lowest). Ecological networks may also be hierarchically organised, i.e., cohesive groups at higher scales would be composed of groups at lower scales. If hierarchically organised, ecological networks would be composed of components (left to right: separate grey groups), composed of sectors (circled in orange), composed of modules (points of different colours), composed of subgraphs (four green points). (b) Direct ecological interactions between species (continuous lines) are the frame over which indirect interactions and coevolutionary effects (dashed lines) between non-interacting species (orange) emerge. (c) If present in ecological networks, the hierarchical organisation described in (a) may mediate the spread of coevolutionary effects described in (b) between network species. If so, coevolutionary effects initiated in a given species (dark red, I) should first affect species in its subgraph (medium red, II), then and with lower strength species in its module (light red, III) and successively with decreasing strength species in its sector and component. Coevolutionary effects are not exchanged between components as they depend on direct interactions to emerge.

species. Modules have been associated with trait syndromes (Carstensen, Sabatino, and Morellato 2016), resource heterogeneity (Pinheiro et al. 2019) and phylogenetic constraints (Cagnolo, Salvo, and Valladares 2011). At the lowest scale, a variety of small subgraphs are ecological networks' building blocks (Bascompte and Melián 2005; Milo et al. 2002; Stouffer et al. 2007). The fully connected subgraph composed of two species in each interacting set, for example, two pollinators visiting two plants, is the smallest possible cohesive group in bipartite networks (Figure 1a).

One enduring hypothesis in ecology and evolution is that coevolution is fuelled by groups of interacting species (Olesen et al. 2007; Thompson 2005), an idea dating back to Darwin's work on pollination and to hypotheses on trait syndromes (Fægri and van der Pijl 1979; Thompson 1989). In its most recent form, the hypothesis that modules represent coevolutionary units has been in the literature for over a decade (Olesen et al. 2007; Hutchinson, Cagua, and Stouffer 2017; Thompson 2005). Specifically, by concentrating interactions when compared to surrounding network regions, cohesive species groups could affect the spread of coevolutionary effects between species. Since modules are just one type of group

observed in ecological networks, cohesive groups emerging at different network scales (Figure 1) could also have the potential to mediate the propagation of coevolutionary effects and to represent coevolutionary units.

In complex systems, cohesive groups at different scales are often hierarchically organised, i.e., larger groups are composed of smaller groups (Figure 1a; Ravasz and Barabási 2003; Sales-Pardo et al. 2007). This hierarchical organisation, if also present in ecological networks, could strongly affect various ecological and evolutionary processes. For instance, the hierarchical organisation of ecological networks could affect the spread of coevolutionary effects among species, with consequences for community-level phenotypic patterns, interaction establishment and ecological processes. Specifically, a hierarchical organisation would imply that coevolutionary effects overflowing groups at smaller scales, should next reach the species forming the groups at the scale above (Figure 1c). For instance, coevolutionary effects released by phenotypic changes in a given species should first reach its direct partners, rapidly reaching all species in its subgraph (Figure 1c). As they propagate, effects should next reach species in the same module, and later sector, as the focal species. Finally, the absence of interactions

connecting components prevents the spread of coevolutionary effects between components. By now, we know that cohesive groups emerge across ecological network scales and could represent coevolutionary units (Figure 1a; Guimarães 2020; Olesen et al. 2007; Simmons et al. 2019). However, whether cohesive groups are hierarchically organised in ecological networks and the consequences of a potential hierarchy to coevolution are still open problems in ecology.

Here, we investigate the long-standing hypothesis that cohesive groups behave as coevolutionary units in 376 mutualistic and antagonistic networks of eight interaction types. We broaden the original hypothesis by including cohesive groups across network scales (components, sectors, modules and subgraphs), and by exploring if these groups are hierarchically organised. Importantly, we are not suggesting that groups emerge because of coevolution, but that they could mediate coevolutionary dynamics. We apply the analytical result of coevolutionary models for mutualistic and antagonistic networks to compute the potential for exchange of direct and indirect coevolutionary effects between species (Guimarães et al. 2017). We found coevolutionary units to be nested inside each other, but networks themselves become the potential coevolutionary units when ecological interactions are a strong selective pressure. Our results on the hierarchical organisation of ecological networks also have strong implications for ecological processes that trigger cascading effects, such as energy flow, coextinction dynamics and demographic changes in species assemblages.

2 | Material and Methods

We compiled a comprehensive dataset of 376 ecological bipartite networks from multiple environments and eight interaction types (Table 1), obtained from online repositories or publications (Table S1). We (i) identified species groups across network scales; (ii) tested for a hierarchical organisation, and (iii) explored whether the hierarchy mediated potential coevolution. We present an overview of our analyses below, and a step-by-step description of methods in the [Supporting Information](#).

2.1 | Cohesive Groups Across Network Scales

We characterised four types of cohesive species groups, each at a distinct network scale. At the highest scale, components are isolated groups of interacting species, so that all species are directly or indirectly connected to each other but disconnected from species in other components. We computed the number of network components and the component affiliation of each species with *igraph* (Czárđi and Nepusz 2006; Csárdi et al. 2024).

Descending network scales, we focused on the largest component (with the largest number of species) of each network, removing networks with multiple largest components ($N=5$), or star-shaped largest components, e.g., a single pollinator visiting all plants ($N=5$). We divided each network's largest component ($N=366$) in two sectors using Fiedler's vector (Slininger 2013). Sectors are two component regions which concentrate a higher interaction density than between-sector density. Networks can be represented by matrices, \mathbf{A} , in which species correspond to

rows and columns, $a_{ij}=1$ if i and j interact, and $a_{ij}=0$ otherwise. To every \mathbf{A} , a Laplacian matrix is defined as $\mathbf{L}=\mathbf{D}-\mathbf{A}$, where \mathbf{D} is a diagonal matrix in which d_{ii} is the number of interactions of i . The eigenvector associated with the smallest non-zero eigenvalue of \mathbf{L} , Fiedler's vector, divides components in two sectors by minimising the proportion of realised links between sectors.

We computed modules, groups of species that interact more frequently with each other than with species in other modules (Newman 2006), inside networks' largest components. With the MODULAR program (Marquitti et al. 2014) and a simulated annealing algorithm (Guimerà and Amaral 2005), we optimised a modularity function, Q_B (Barber 2007), to compute modularity, number of modules and species' module affiliation.

At the lowest scale, the fully connected subgraph with two species in each set (hereafter *subgraph*), is the smallest cohesive group with more than one species in each set (Simmons et al. 2019). We actively searched all subgraphs within networks' largest components, listing its four species (the same species can be in multiple subgraphs).

2.2 | Hierarchical Organisation of Cohesive Groups

We tested whether cohesive groups at lower scales occurred within groups at higher scales. We identified sectors, modules and subgraphs within largest components and tested the hierarchical organisation between lower-scales groups combining congruence coefficients with null models ([Supporting Information](#)). To test whether modules occurred inside sectors, we calculated the module-sector congruence coefficient of each network with Goodman & Kruskal's τ statistic, a directional measure of association between two categorical variables, i.e., modules associations to sectors. The coefficient ranges from 0 if there is no association between modules and sectors to 1 if there is perfect association, i.e., all species of each module fall within the same sector across all modules. Congruence coefficients involving subgraphs were computed as the proportion of subgraphs with all four species inside the same module, the same sector and concomitantly inside the same module and sector (i.e., 'double hierarchy'). Therefore, congruence coefficients measure the association between groups in two scales, but 'double hierarchy' measures the association between groups at three scales. We assessed observed congruence using null models that randomly swapped species' affiliations to groups among species of the same set in one scale, whilst keeping network structure fixed (e.g., swapped species' affiliations to sectors to test module-sector congruence).

2.3 | Potential Coevolutionary Dynamics

We used as reference two coevolutionary models for ecological networks in which species i is characterised by a quantitative trait z_i that mediates interactions between species and evolves in response to selection imposed by interactions and the environment (Andreazzi, Thompson, and Guimarães 2017; Guimarães et al. 2017). For instance, z could represent beak and seed sizes for seed disperser-plant networks. In these models,

TABLE 1 | Summary of network group structure across interaction types.

| Sign | Type | N | S | Connectance | Number of components | Largest component | Number of modules | Number of subgraphs |
|------|-------|----------------------|---------------|-------------|--------------------------------|-------------------|-------------------------------|------------------------------------|
| A | Pa-Ho | 81 (52/78/79) | 71.04 ± 88 | 0.26 ± 0.15 | 2.43 ± 3.53 (2.02 ± 3.39) | 0.95 ± 0.1 | 5.12 ± 2.05 (-0.74 ± 1.18) | 1204.6 ± 2771.3 (3.11 ± 3.27) |
| A | Ph-B | 38 (8/25/26) | 33.58 ± 22.78 | 0.5 ± 0.22 | 1.47 ± 0.86 (3.35 ± 2.97) | 0.94 ± 0.12 | 3.26 ± 1.22 (-1.22 ± 1.16) | 3417.6 ± 6266.6 (3.57 ± 4.52) |
| A | Her-P | 33 (25/30/30) | 152.4 ± 304.3 | 0.14 ± 0.14 | 11.39 ± 15.51 (1.89 ± 2.79) | 0.71 ± 0.35 | 5.44 ± 2.4 (-1.23 ± 1.51) | 6627.7 ± 23,502.7 (3.32 ± 9.07) |
| A | Pr-Pr | 3 (0/3/3) | 24.33 ± 2.52 | 0.66 ± 0.15 | 1 ± 0 — | 1 ± 0 | 3.33 ± 0.58 (-0.1 ± 1.03) | 597.7 ± 448.4 (-0.47 ± 0.49) |
| M | Pol-P | 154 (125/152/150) | 104.5 ± 187.5 | 0.19 ± 0.11 | 1.64 ± 1.16 (0.06 ± 1.44) | 0.97 ± 0.07 | 5.48 ± 1.78 (-0.91 ± 1.23) | 5196.8 ± 46,082.8 (0.57 ± 3.29) |
| M | SD-P | 39 (19/35/35) | 53.13 ± 57.59 | 0.33 ± 0.18 | 1.18 ± 0.68 (-0.13 ± 0.55) | 0.99 ± 0.03 | 4.26 ± 1.14 (-0.95 ± 1.4) | 1817.2 ± 4300.1 (1.35 ± 2.83) |
| M | F-Ane | 17 (9/9/10) | 9.53 ± 7 | 0.41 ± 0.1 | 1.71 ± 0.92 (-0.53 ± 0.25) | 0.8 ± 0.25 | 2.92 ± 0.86 (-0.04 ± 0.7) | 22.46 ± 80.98 (-0.49 ± 0.26) |
| M | Ant-P | 11 (7/3/3) | 25.55 ± 22.44 | 0.19 ± 0.12 | 4.73 ± 2.15 (1.6 ± 1.86) | 0.46 ± 0.3 | 3 ± 1.15 (-0.7 ± 1.96) | 429 ± 1125.78 (1.28 ± 1.19) |

Note: Interaction sign (A: Antagonism, M: Mutualism) and type, number of networks (N) and structural attributes (mean ± SD): Number of species (S), connectance, number of components, proportion of network species in the largest component, number of modules and of subgraphs. Inside parenthesis (second row for each interaction type) are z-scored values using a null model that maintains network S and connectance (null model 1, Bascompte et al. 2003); N values (one for each z-score) may be lower for z-scored values due to lack of variance in null model results. Code for interaction types: Ant-P, Ant-Plant; F-Ane, Fish-Anemone; Her-P, Herbivore-Plant; Pa-Ho, Parasite-Host; Ph-B, Phage-Bacteria; Pol-P, Pollinator-Plant; Pr-Pr, Predator-Prey, SD-P, Seed Disperser-Plant.

environmental selection favours a trait value (θ_i) for each species i . The coevolutionary model for mutualisms assumes selection to favour trait matching between interacting species, while the model for antagonisms assumes selection to favour matching for predators and mismatching for prey.

In the equilibrium, one analytical result of the coevolutionary model for mutualistic networks is the **T-matrix**, which contains the sum of direct and indirect potential coevolutionary effects exchanged between species under the assumptions of this model. **T** effects describe the relative impact of species on the adaptive peaks of other species, through direct and indirect pathways. We derived for the first time the **T-matrix** for the antagonistic model (Andreazzi, Thompson, and Guimarães 2017, see [Supporting Information](#) for the derivation of **T** from both models). Here, we emphasise that the definition of **T** is identical for mutualisms and antagonisms. This result emerges because **T** is independent of the type of the impact (positive or negative) of direct and indirect effects on species mean fitness, depending instead on the combination of the multiplicity of pathways connecting species and the decay of effects with pathway length ([Supporting Information](#)). In fact, similar matrices containing the sum of direct and indirect potential effects between interacting elements is a general result for multiple network dynamic models, as those describing social (Katz 1953), economic (Leontief's input-output model) and ecological processes (Higashi and Nakajima 1995; Pires et al. 2020). These matrices emerge as long as effects between interacting elements are assumed to weaken along network paths. The **T-matrices** computed here are rooted on coevolutionary models for ecological networks and effects are interpreted as potential coevolutionary effects between species.

In order to search for potential coevolutionary units, we directly computed the **T-matrix** of each network, i.e., instead of running the coevolutionary models we used their analytical results. We emphasise that ecological interactions do not imply selection. Therefore, it was not our aim and we did not measure coevolution in the networks. Our aim was to explore and estimate the potential for coevolution within ecological networks under the assumption that coevolutionary effects propagate along the interactions depicted in each network. We used basic network architecture (binary interactions) as the association between interaction frequency and selective pressure is far from straightforward (Benkman 2013), but computing coevolutionary effects from weighted interactions produces qualitatively similar results ([Supporting Information](#)). **T** is defined as $\mathbf{T} = (\mathbf{I} - \mathbf{Q})^{-1}$, where **I** is the identity matrix, and **Q** describes the strength of selection (interaction weight) between every species pair. **Q** is an $S \times S$ matrix, with $q_{ij} = m(a_{ij}/k_i)$, where S is network species richness, m , $0 < m < 1$ (here, $m = [0.1, 0.5, 0.9]$), is the parameter that modulates the strength with which direct ecological interactions act as a source of selective pressure, and k_i is the number of interactions of species i . Note that $\mathbf{T} = (\mathbf{I} - \mathbf{Q})^{-1} = \sum_{l=0}^{\infty} \mathbf{Q}^l$, l being the length of network paths, so that \mathbf{Q}^1 describes the direct interaction weights ($l=1$) connecting network species, \mathbf{Q}^2 describes pathways of $l=2$, e.g., $q_{ik}^{(2)} = \sum_{j=1}^N q_{ij} * q_{jk}$ and so on. Thus, **T** contains information on the direct and indirect potential effects of any length connecting every network species pair. From **Q** we extracted direct effects between interacting species (e.g., effect of j on i). From **T** we extracted indirect effects between

non-interacting species (e.g., j on $i \rightarrow i$ on k), contained in **G**, defined as $g_{ij}=0$ if $i=j$ or if $q_{ij}>0$, and $g_{ij}=t_{ij}$ otherwise (Figure S1; Guimarães et al. 2017).

We explored the amount of potential coevolutionary effects conforming to the hierarchical organisation of each network, by computing the proportion of effects exchanged inside and between groups, from the lowest to the highest scale. Starting with subgraphs and modules, we divided potential coevolutionary effects of each network in: (i) effects inside both subgraphs and modules (exchanged by species cooccurring in at least one subgraph and in the same module), (ii) effects between subgraphs and inside modules (exchanged by species not cooccurring in any subgraph, but in the same module), (iii) effects inside subgraphs and between modules (exchanged by species cooccurring in at least one subgraph, but in different modules), and (iv) effects between both subgraphs and modules. We summed the effects in each of these four groups for each network. The first two conform to the hierarchical organisation being contained at least in the group at the higher scale. Effects inside subgraphs and between modules do not conform to the hierarchy, as they are contained in the group at lower but not at higher scale. Effects between both subgraphs and modules do not conform to the hierarchy at these scales, overflowing both groups. Ascending the network, we divided potential coevolutionary effects in (i) inside modules and sectors, (ii) between modules and inside sectors, (iii) inside modules and between sectors, and (iv) between modules and sectors, and summed the effects in each of these four groups for each network. Effects inside modules and between sectors do not conform to a hierarchical organisation, and effects between both also do not conform, overflowing groups at this scale.

Finally, we explored how much of the direct and indirect effects inside groups are explained by the number of links inside these groups. To do so, we calculated the proportion of links of networks' largest components inside groups across scales (links part of multiple subgraphs were counted once). Then, we calculated the ratio between the proportion of potential coevolutionary effects and the proportion of links inside groups across scales.

3 | Results

3.1 | Cohesive Groups Across Network Scales

We present results from the highest to the lowest scale. Most networks (233 out of 376, 62%) were composed of a single component which included all species. Single-component networks occurred in all interaction types, and were frequent in mutualisms (Seed Disperser–Plant: 35 out of 39, 90%, Pollinator–Plant: 97/154, 63%) and antagonisms (Predator–Prey: 3 out of 3, 100%, Phage–Bacteria: 28/38, 74%), being still numerous in the remaining interaction types (Parasite–Host: 48/81, 59%, Fish–Anemone: 9/17, 53%, Herbivore–Plant: 11/33, 33%, Ant–Plant: 2/11, 18%). Despite their higher connectance (antagonistic: 0.3 ± 0.21 , mutualistic: 0.23 ± 0.15 , mean \pm SD; $F_{(1,374)} = 14.5$, $p < 0.001$), antagonistic networks were more fragmented than mutualistic networks ($F_{(1,374)} = 16.7$, $p < 0.001$; Table 1; Figure S5), having on average twice as many components (antagonistic: 4.08 ± 8.45 , mutualistic: 1.71 ± 1.34). Although antagonistic and mutualistic networks had similar species richness (antagonistic: 78.3 ± 158.6 ,

mutualistic: 84.2 ± 161.6 ; $F_{(1,374)} = 0.12$, $p = 0.7$), their largest components did not ($F_{(1,374)} = 4.2$, $p < 0.05$; Figure S5; Table 1): mutualistic networks concentrate a larger proportion of species in their largest components (0.94 ± 0.16) when compared to antagonistic networks (0.90 ± 0.21). Except for plant–herbivore and plant–ant networks, largest components concentrated on average more than 80% of network species (Table 1; Figure S5). Plant–herbivore networks presented the highest variation, ranging from extremely fragmented (one galling-plant network had 29 two-species components) to single-component networks (Figure S5). Additional network components ($N = 601$) were often small, mostly having two ($N = 394$, 66%) or three species ($N = 99$, 16%; Figure S6).

We analysed sectors, modules and subgraphs within the largest components of 366 networks. On average, the largest components had a larger sector, with relative sector sizes varying widely across networks (Figure S7). The largest component of mutualistic networks had, on average, higher levels of modularity (antagonistic: 0.34 ± 0.15 , mutualistic: 0.4 ± 0.1 , mean \pm SD; $F_{(1,364)} = 20.96$, $p < 0.001$; Figure S8), while the number of modules was indistinguishable between mutualistic (5.01 ± 1.81) and antagonistic networks (4.69 ± 2.12 ; $F_{(1,366)} = 2.4$, $p = 0.12$; Table 1). At the lowest scale, subgraphs were pervasive in most network types: out of 366 networks, only 21 had none in their largest components (1 phage–bacteria, 2 herbivore–plant, 3 pollinator–plant, 12 fish–anemone and 3 ant–plant), and the number of subgraphs increased with the size of largest components (Figure S9). The number of subgraphs was indistinguishable between mutualistic and antagonistic networks (antagonistic: $2865.75 \pm 11,403.15$, mutualistic: $4100.35 \pm 39,198.08$; $F_{(1,364)} = 0.14$, $p = 0.7$; Table 1).

3.2 | Hierarchical Organisation of Cohesive Groups

Because we characterised sectors, modules and subgraphs inside networks' largest components, we started testing the level of congruence between sectors and modules. Module-sector

congruence was high (average above 0.71) for all interaction types (Figure 2a), and higher than expected by the null model for most networks of most interaction types (Figure 2b), indicating that modules are mostly contained within sectors, despite the high variation on how observed congruence compared with null model expectations (Figure 2c; Figures S10 and S11).

We then tested whether subgraphs occurred inside sectors and modules. Across interaction types, on average 60.84% of subgraphs (± 29.05 , mean \pm SD; Figure 3a) occurred inside sectors and this proportion was higher than expected by the null model in 46.96% of networks (Figure 3b). A smaller proportion of subgraphs ($18.79\% \pm 21.05$) occurred inside modules (below sectors, Figure 3d), but this proportion was higher than expected by the null model in 80.58% of networks (Figure 3e). Despite the high proportion of networks with congruence coefficients surpassing null model expectations, how observed coefficients compare with null models varies widely across networks (Figure 3c,f; Figures S10 and S11). Finally, 16.2% (± 20.97) of subgraphs concomitantly occurred inside sectors and modules ('double hierarchy'), a proportion that was higher than expected by the null model in 77% of networks (Figure S12).

Thus, ecological networks simultaneously present cohesive groups at four network scales and, despite deviations, groups at higher scales are collections of groups at lower scales. A sensitivity analysis on network sampling completeness produced qualitatively similar results (Supporting Information). We then explored the potential consequences of this hierarchical organisation for coevolution.

3.3 | Potential Coevolutionary Dynamics

At all network scales, the largest part of potential direct effects is contained within cohesive groups, and this proportion increases with scale. At the lowest scale, 55.2% (± 25.28 , mean \pm SD) of direct effects are contained within subgraphs, 75.6% (± 11) of direct effects are contained within modules, and 89.51% (± 8.03) within sectors. By definition, 100% of direct effects are contained

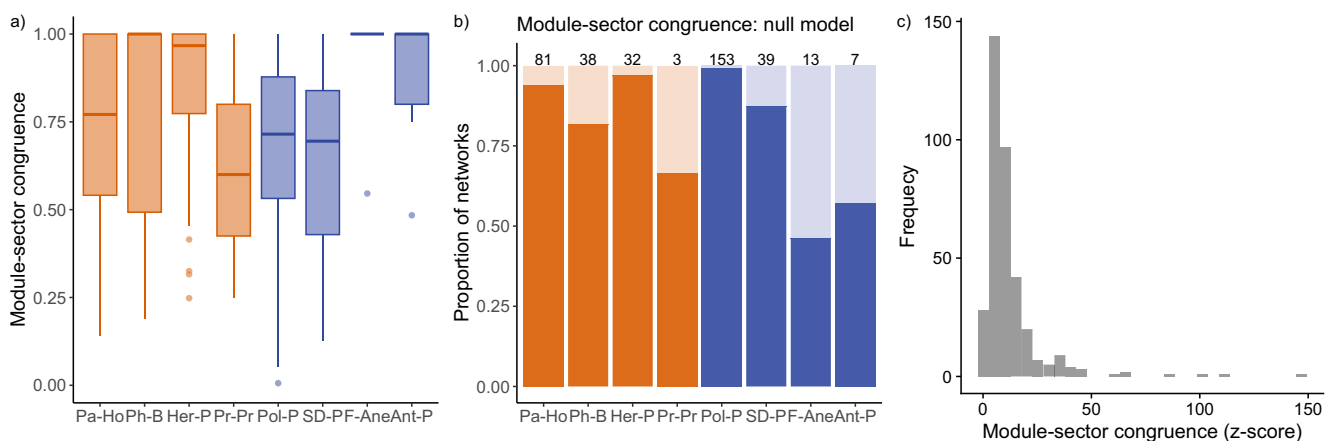


FIGURE 2 | Module-sector congruence. (a) Module-sector congruence per interaction type. (b) Proportion of networks with a significant (compared to a null model) level of module-sector congruence per interaction type (N above bars). (c) Values of module-sector congruence across interaction types z-scored in relation to a null model. Antagonistic interactions in orange and mutualistic interactions in blue. Code for interaction types: Ant–P, Ant–Plant; F–Ane, Fish–Anemone; Her–P, Herbivore–Plant; Pa–Ho, Parasite–Host; Ph–B, Phage–Bacteria; Pol–P, Pollinator–Plant; Pr–Pr, Predator–Prey; SD–P, Seed Disperser–Plant.

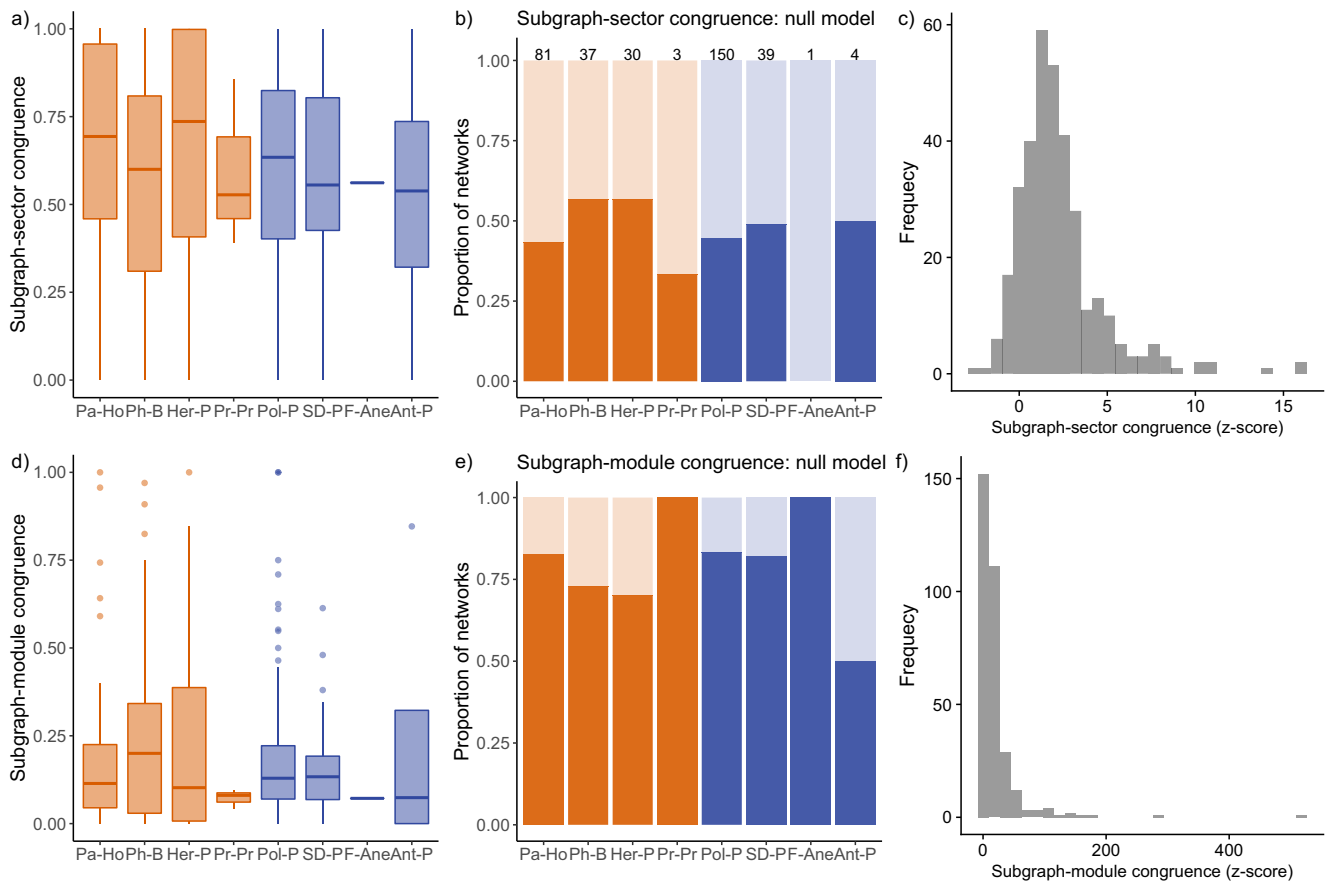


FIGURE 3 | Subgraph-module and subgraph-sector congruence. Measured as the proportion of network subgraphs inside (a) sectors and (d) modules of networks' largest components per interaction type. Proportion of networks with significant levels (compared to a null model) of (b) subgraph-sector and (e) subgraph-module congruence (N above bars). Values of (c) subgraph-sector and (f) subgraph-module congruence across interaction types z-scored in relation to a null model. Antagonistic interactions in orange and mutualistic interactions in blue. Code for interaction types: Ant-P, Ant-Plant; F-Ane, Fish-Anemone; Her-P, Herbivore-Plant; Pa-Ho, Parasite-Host; Ph-B, Phage-Bacteria; Pol-P, Pollinator-Plant; Pr-P, Predator-Prey; SD-P, Seed Disperser-Plant.

within largest components. These results are independent of the strength of selection imposed by the ecological interactions (m). Thus, cohesive groups, especially at higher scales, contain the majority of direct potential coevolutionary effects. Contrastingly, the proportion of links inside groups did not increase with network scale: modules (intermediate groups) often hold a smaller proportion of links than subgraphs (lowest groups; Figure S13). Consequently, modules were the groups with the highest direct effect-link ratio (between the proportion of direct effects and of links) for all interaction types (Figure S14); and both modules and sectors held a higher proportion of direct coevolutionary effects than of links (ratio >1).

We then explored if direct coevolutionary effects conform to the hierarchical organisation, starting with lower-scale groups, subgraphs and modules. Of the 75.6% of direct effects inside modules, i.e., respecting the hierarchical organisation at this scale, 32.9% (± 16.6 , mean \pm SD) are exchanged between species also in the same subgraph, and the remaining 42.7% (± 22.7) are exchanged by species in different subgraphs (Figure 4; Table S2; Figures S15 and S16). An additional 22.3% (± 12.9) of direct effects do not follow the hierarchy, being exchanged by species in the same subgraphs but not modules. The remaining 2.13% (± 4.41) of direct effects escape both groups. For indirect effects, the proportion conforming to the hierarchical organisation decreases

(inside both subgraphs and modules: $17.4\% \pm 13.4$; between subgraphs and inside modules: $27.4\% \pm 16.7$), while the proportion of unconforming effects (inside subgraphs and between modules: $23.5\% \pm 16.8$; between both subgraphs and modules: $31.7\% \pm 14$) increases (for $m = 0.1$; Figure 4; Table S2; Figures S15 and S16). As the selection imposed by ecological interactions increases (m), the proportion of indirect effects conforming to the hierarchy decreases (Figure 4; Table S2; Figures S15 and S16). Escaping effects reach the scale above (below).

Ascending to modules and sectors, similar patterns emerge. At higher scales, a larger proportion of effects conforms to the hierarchical organisation of ecological networks (Figure 5). Of the 89.6% of direct effects conforming to the hierarchy by being contained by sectors, 72% (± 13 , mean \pm SD) of effects are also inside modules, and the remaining 17.6% (± 9.17) are between modules (Figure 5; Table S3; Figures S17 and S18). An additional 10.4% of direct effects do not conform to the hierarchy (inside modules and between sectors: $3.65\% \pm 4.77$; between both modules and sectors: $6.84\% \pm 6.28$; Figure 5; Figures S17 and S18). For indirect effects, the proportion conforming to the hierarchy is smaller than for direct effects, but higher when compared to lower scales (Figure 5; Table S3). When interactions are a weak selective pressure ($m = 0.1$), on average 77.9% of indirect effects conform to a hierarchical

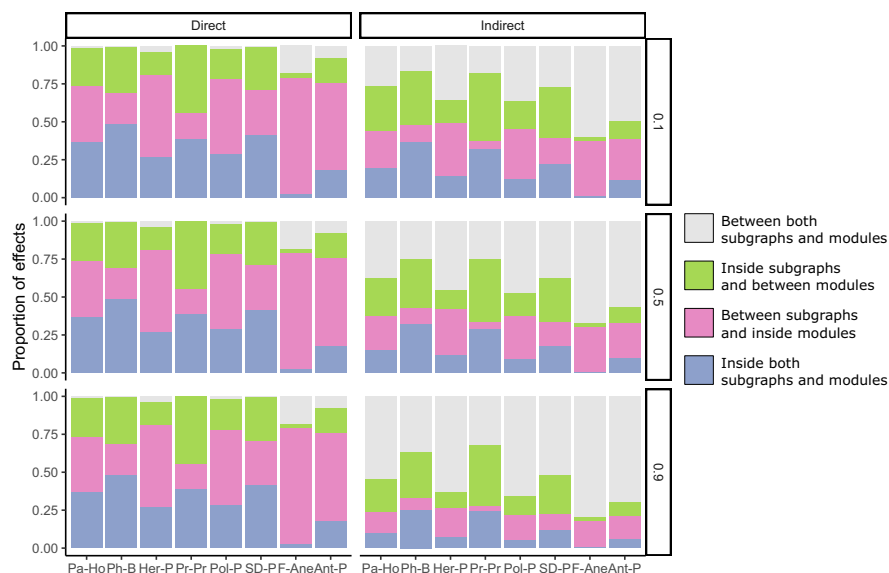


FIGURE 4 | Coevolutionary effects in subgraphs and modules. Direct and indirect coevolutionary effects partitioned in four groups: Effects inside both subgraphs and modules, effects between subgraphs and inside modules, effects inside subgraphs and between modules and effects between both subgraphs and modules. Plot rows represent effects for different values of m —0.1, 0.5 or 0.9—the strength with which network interactions act as selective pressures. Code for interaction types: Ant-P, Ant-Plant; F-Ane, Fish-Anemone; Her-P, Herbivore-Plant; Pa-Ho, Parasite-Host; Ph-B, Phage-Bacteria; Pol-P, Pollinator-Plant; Pr-Pr, Predator-Prey; SD-P, Seed Disperser-Plant.

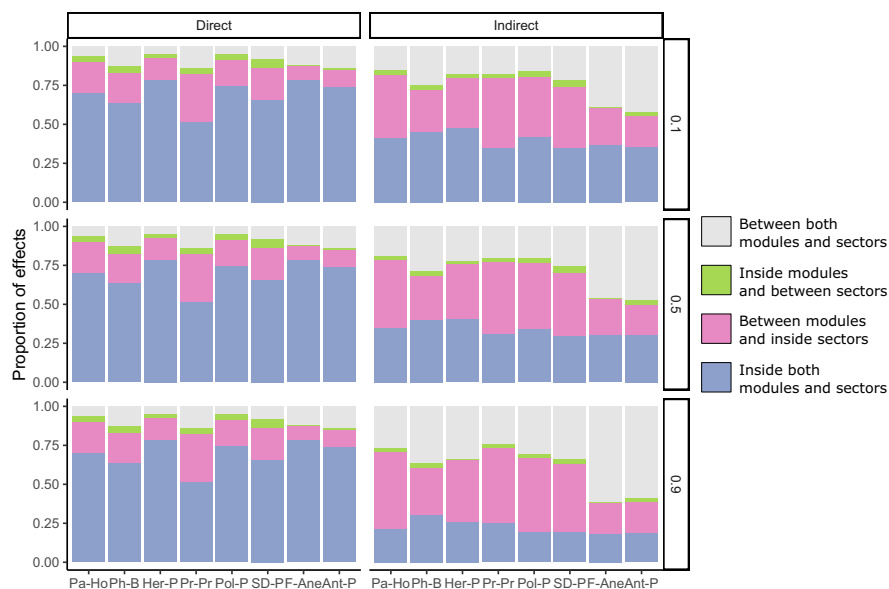


FIGURE 5 | Coevolutionary effects in modules and sectors. Direct and indirect coevolutionary effects divided in four groups: Effects inside both modules and sectors, effects between modules and inside sectors, effects inside modules and between sectors and effects between both modules and sectors. Plot rows represent effects for different values of m —0.1, 0.5 or 0.9—the strength with which network interactions act as selective pressures. Code for interaction types: Ant-P, Ant-Plant; F-Ane, Fish-Anemone; Her-P, Herbivore-Plant; Pa-Ho, Parasite-Host; Ph-B, Phage-Bacteria; Pol-P, Pollinator-Plant; Pr-Pr, Predator-Prey; SD-P, Seed Disperser-Plant.

organisation (inside both modules and sectors: $41.6\% \pm 14.1$, between modules and inside sectors: $36.3\% \pm 13.5$), and the remaining 22.1% do not (inside modules and between sectors: $3.27\% \pm 3.38$, between both modules and sectors: $18.8\% \pm 12.9$; Figure 5; Figures S17 and S18). Here again, as selection imposed by interactions becomes stronger (m), the proportion of conforming indirect potential effects decreases while effects escaping groups increases (Figure 5; Table S3; Figures S17–S19). Groups at any scale concentrate a higher proportion of indirect effects than of links (Figure S14). We emphasise that

Figures 4 and 5 correspond to averages and, due to the high variation across networks, the most complete description of results is available in Figures S15–S18.

Thus, direct effects tend to occur inside groups and to follow group hierarchy, but indirect effects overflow groups at every scale, leaking through network structure, especially when ecological interactions impose strong selection. Our sensitivity analysis on the effect of sampling completeness produces similar results (Figures S23 and S24).

4 | Discussion

A long-standing hypothesis suggests that coevolution operates in groups of species and that modules could represent coevolutionary units within ecological networks. Experimental (Gilarranz et al. 2017) and theoretical (Fortuna et al. 2009; Grilli, Rogers, and Allesina 2016; Stouffer and Bascompte 2011) research have shown that cohesive groups have the potential to influence dynamics in networks. Expanding the hypothesis, we show that coevolutionary units may broadly occur in ecological networks, where they are hierarchically organised. We did so by (i) describing a consistent four-level hierarchical group structure in over 300 ecological networks of eight interaction types, (ii) analytically deriving the matrix for direct and indirect effects from the coevolutionary model for antagonisms for the first time and (iii) by exploring how potential coevolutionary effects propagate inside and between cohesive groups across network scales. Our study maps under which conditions and scales coevolutionary units may emerge in ecological networks, contributing to our understanding of how coevolution, but also ecological processes, potentially occur within species-rich assemblages.

We demonstrate that cohesive groups emerge at various scales within the same network, ranging from fully connected small subgraphs to components. The formation of different cohesive groups varies across the spectrum of ecological networks. At larger network scales, interactions such as herbivore–plant form fragmented networks with multiple components, while others such as seed disperser–plant, often display a single giant component, crucial for the propagation of cascading effects throughout most of the network. Here, we are interested in the consequences of cohesive groups to coevolution. However, we do not claim that coevolution leads to cohesive group formation. Instead, several other mechanisms could explain their emergence, including heterogeneity in space, time and resources (Fortuna et al. 2009; Pinheiro et al. 2019; Schleuning et al. 2014), competition (Tinker et al. 2012) and evolutionary history (Cagnolo, Salvo, and Valladares 2011; Lewinsohn et al. 2006). At higher network scales, fragmented or highly connected networks may emerge due to the variation in number of interactions across species, as predicted by random graph theory (Figures S25 and S26; Guimarães 2020; Newman, Strogatz, and Watts 2001). Hence, developing a theory on cohesive group emergence across scales requires a deeper understanding on the interplay between scales (Guimarães 2020).

We found cohesive groups to exhibit hierarchical organisation in ecological systems, a conclusion based on multiple tests, which together suggest the presence of a hierarchy despite the variation on the hierarchy strength at different scales. The presence of a hierarchy corroborates our theoretical prediction, since the higher density of interactions inside (than between) groups, should favour a hierarchical organisation. This result, however, is not obvious, since the level of hierarchical organisation identified was not predicted by our conservative null models. Moreover, this result is not inevitable, since we found an imperfect hierarchy, illustrated by the many isolated small components, and by congruence values which get lower as we descend network scales (e.g., the proportion of subgraphs inside modules is lower than inside sectors). Different forms of hierarchy have been shown in ecological networks (compound

topologies; Kondoh, Kato, and Sakato 2010; Pinheiro, Felix, and Lewinsohn 2022), and a hierarchical group structure resembling the one reported here is observed in disparate systems, such as metabolic networks, language networks and the WWW (Ravasz et al. 2002; Ravasz and Barabási 2003). A hierarchical group structure enables networks to simultaneously have cohesive groups loosely connected to one another and to exhibit heterogeneous interaction distributions (Ravasz and Barabási 2003). Ecological networks can indeed display modularity (Guimerà et al. 2010; Krasnov et al. 2012) and exhibit high interaction heterogeneity across species (Jordano, Bascompte, and Olesen 2003). The reason why cohesive groups are hierarchically organised, however, remains unclear. One explanation is that, as observed in butterfly host use and carnivore–prey interactions (Braga et al. 2018; Slater and Friscia 2019), specialisation evolves within groups, with closely related clades specialising in slightly different resources, while some species also interact with a wide resource range. Moreover, as coevolution could also lead to the formation of cohesive groups (Andreazzi, Thompson, and Guimarães 2017), feedback between structure and dynamics is likely, but whether it leads to the emergence of hierarchical structures is yet to be explored. Regardless of the processes involved in the emergence of cohesive groups and their hierarchical organisation, the potential consequences of a hierarchical group organisation for coevolutionary and ecological dynamics within networks are profound.

Our results provide insights into how cohesive groups interact with hierarchical organisation in order to affect dynamics in ecological networks. Cohesive groups, known to influence the propagation of perturbations (Gilarranz et al. 2017; Grilli, Rogers, and Allesina 2016; Stouffer and Bascompte 2011), were expected to also constrain evolutionary cascades. Our results indicate that, under the assumptions of coevolutionary models, cohesive groups across four scales hold a significant proportion of direct potential coevolutionary effects, a proportion that increases with network scale and the species richness within these groups. The ability of cohesive groups to contain direct effects is partially explained by their number of links, but modules and sectors hold a higher proportion of direct effects than of links. This indicates that, at these scales, the influence of cohesive groups on coevolutionary dynamics extends beyond their link density. In contrast, the interaction heterogeneity across species, a conspicuous feature of network hierarchy, is associated with small-world properties that fuel cascading effects (Guimarães 2020). Therefore, the hierarchical group organisation implies that groups are not as isolated as they might appear at each scale independently. Indeed, while cohesive groups capture many direct effects, a notable proportion still escape groups, particularly at lower scales. The hierarchy ensures that effects escaping smaller groups, are encapsulated by larger groups, maintaining these effects within the vicinity of their origin, supporting the concept of coevolutionary units (Olesen et al. 2007) even if with blurred boundaries. Thus, our findings suggest that coevolutionary units are not independent but rather hierarchically structured.

Considering indirect effects, the proportion of potential effects escaping groups across all scales is considerably larger and increases with the strength of selection imposed by interactions (m). While, individually, indirect effects are ‘weaker’

than direct effects, when summed, they become a substantial proportion of overall coevolutionary effects (Figure S19), potentially impacting trait evolution (Guimarães et al. 2017) and species fitness (Cosmo et al. 2023). Thus, even if cohesive groups and hierarchical organisation indeed mediate the spread of potential coevolutionary effects, indirect effects blur group boundaries, especially when ecological interactions are a strong source of selection (Abdala-Roberts et al. 2014; Campbell et al. 2022). Any potential cascade is confined within components. Therefore, networks composed of multiple components suggest isolated and divergent evolutionary trajectories, a phenomenon observed in certain intimate antagonisms (e.g., galler-plants) and mutualisms (e.g., ant-mycorrhizal plants), which form fragmented networks. Our results, however, demonstrate that fragmented networks are rare in ecological systems, as most ecological networks tend to form a giant component encompassing most network species (Guimarães 2020). Therefore, indirect effects blurring the hierarchical group structure of ecological systems and reaching multiple species is a likely scenario, in which networks themselves act as coevolutionary units (Thompson 2005).

Our approach based on the **T-matrix**, allowed us to study over 300 ecological communities, and to find general patterns spanning eight mutualistic and antagonistic interaction types. Moreover, the implications of our results extend beyond coevolutionary dynamics. We extracted potential coevolutionary effects from the **T-matrix** of each network, an analytical result of coevolutionary models (Andreazzi, Thompson, and Guimarães 2017; Guimarães et al. 2017). This matrix encompasses the cumulative effects of all lengths exchanged between every network species pair. The fact that an identical matrix emerges from the coevolutionary models for mutualisms and antagonisms is an interesting result which suggests that despite undergoing different coevolutionary trajectories and resulting in different phenotypic patterns, mutualistic and antagonistic systems may do so through potentially similar exchanges of potential coevolutionary effects between species. Moreover, matrices similar to **T** also emerge from ecosystem (Higashi and Nakajima 1995), social (Katz 1953) and economic models (Leontief's Input-Output analysis). In fact, **T-matrices** arise from any model of flow dynamics in networks, provided that the strength of effects is assumed to decrease with the length of the path. The emergence of similar **T-matrices** across disparate dynamics models indicates potential generality on the way that direct and indirect effects propagate in apparently unrelated problems. As a result, our findings and conclusions can be extrapolated to processes cascading through ecological networks, such as the spread of perturbations and extinction dynamics (Pires et al. 2020). For instance, species in the group where a perturbation initiated may preferentially be affected, but (almost) every network species could be at harm as the group hierarchy of ecological networks blurs groups boundaries. Moreover, isolated components, which could represent separate coevolutionary trajectories, could also imply lower susceptibility for species in isolated groups. The implications of **T**, however, depend on the nature of the process being modelled. For now, we suggest that the hierarchical cohesive group structure of ecological networks may not restrict the propagation of cascading effects, but the hierarchy can inform us about the pathways through which cascading effects are more likely to propagate. In scenarios with

strong selection imposed by interactions, we expect coevolution to be essentially a network-level phenomenon.

Author Contributions

K.P.M. and P.R.G. designed the study, K.P.M. performed the analyses, K.P.M. wrote the first draft, and K.P.M. and P.R.G. substantially contributed to the final draft.

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Data Availability Statement

Data and code needed to perform and reproduce the analysis and figures in the main text and Supporting Information are available at https://github.com/katemaia/Maia-Guimaraes_HierarchyCoevoUnits and at curated repository (<https://zenodo.org/doi/10.5281/zenodo.12628129>).

Peer Review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14501>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.