
NETWORK STRUCTURE AND SPECIES CONNECTIVITY DRIVE ASYMMETRIC FITNESS OUTCOMES IN COEVOLVING ANTAGONISTIC COMMUNITIES

A PREPRINT

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October 5, 2026

ABSTRACT

Antagonistic interactions are fundamental drivers of ecological community structure, generating strong reciprocal selective pressures that shape the evolution of functional traits across interacting species. Despite their ecological importance, the coevolutionary dynamics of antagonistic communities remain far less understood than those of mutualistic systems. Here, we develop a trait-based coevolutionary model in which exploiters and victims evolve under symmetric dynamical equations governed by two additive selective forces: a stabilising component directed towards a species-specific environmental optimum, and a directional component arising from antagonistic interactions within the ecological network. Using this framework alongside a trait-based fitness measure, we show that connectivity shapes fitness asymmetrically across guilds: generalist exploiters outperform specialists under weak interaction-driven selection while the advantage reverses under strong selection, whereas victim fitness is buffered by exposure to multiple exploiters through selective dilution. A principal component analysis of structural network descriptors further reveals that global network architecture predicts community-level exploiter fitness only under regimes of reciprocal antagonistic selection, while victim fitness remains largely insensitive to network structure. Together, these results demonstrate that antagonistic coevolutionary asymmetries are emergent consequences of the interplay between opposing selective pressures and the ecological networks through which they propagate, with implications for predicting the eco-evolutionary consequences of anthropogenic change.

Keywords coevolution · antagonistic interactions · ecological networks · fitness landscapes · trait-based modelling

1 Introduction

Darwin’s “entangled bank” remains a powerful metaphor for the densely interconnected ecological interactions that sustain and structure the diversity of life. Among these interactions, antagonistic relationships, including predation, parasitism, and herbivory, play a fundamental role in the organisation of ecological communities. They form the structural backbone of food webs [1, 2], regulate population dynamics across trophic levels [3], and give rise to indirect effects that cascade throughout ecological communities [4, 5].

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In contrast to interactions characterised by reciprocal fitness benefits, antagonistic interactions impose a net fitness cost on at least one participant, generating persistent selective asymmetries and the conditions for sustained evolutionary conflict. These conflicts produce some of the most striking adaptive phenomena in nature, including predator-prey arms races and host-parasite coevolutionary cycles, driving the evolution of extreme defensive and exploitative traits whose diversity and complexity can only be understood in the context of the shared coevolutionary history of the interacting lineages [6, 7]. The directionality and intensity of antagonistic selection shape the evolution of functionally important traits, including defensive morphology and behaviour in prey, exploitation efficiency in predators [8], and virulence and immune evasion in parasites [9], thereby linking microevolutionary trait dynamics to the emergent patterns of community structure [10, 11].

Antagonistic interactions have long served as the paradigmatic model system for understanding coevolutionary arms races, with predator-prey dynamics in particular shaping theoretical perspectives on reciprocal selection for decades. The life-dinner principle, one of the earliest and most influential hypotheses in coevolutionary theory, posits that preys should experience systematically stronger selection than predators because the asymmetric cost of failure (death for prey versus loss of a single meal for predator) generates a persistent asymmetry in the intensity of selection acting on the two parties [12]. However, subsequent empirical and theoretical advances have increasingly challenged the generality of this principle, revealing that the magnitude and direction of selective asymmetries depend strongly on the ecological context in which antagonistic interactions occur [6, 13–15].

In many systems, predators interacting with dangerous, toxic, or otherwise costly prey experience selection pressures comparable to those acting on their prey, producing tight phenotypic matching and genuinely reciprocal coevolutionary arms races [13]. Moreover, coevolutionary dynamics are rarely spatially uniform across ecological landscapes. In the well-studied system involving toxic newts (*Taricha spp.*) and resistant garter snakes (*Thamnophis spp.*), coevolutionary hotspots, i.e. localities where reciprocal selection is intense and traits are closely matched, coexist with coldspots, where phenotypic mismatches weaken or even halt reciprocal escalation. In some populations, snakes have evolved toxin resistance so extreme that prey newts no longer impose meaningful selection, effectively dissolving the coevolutionary arms race [14, 16]. More recent theoretical work further suggests that selective asymmetries may arise not only from differences in the fitness consequences of failure, but also from the behavioural economics of pursuit itself [17]. Prey may adopt risk-prone escape strategies, whereas predators must balance nutritional gain against the risk of injury. These behavioural differences can generate asymmetries in the willingness to escalate conflict, independently of the intrinsic evolutionary capacity of either party. Collectively, these findings demonstrate that antagonistic coevolution is more mechanistically diverse, spatially heterogeneous, and ecologically contingent than classical theory originally predicted [14, 17].

At the community level, the network structure of antagonistic interactions introduces an additional layer of complexity that cannot be captured by two-species models alone [18]. The topology of species interactions mediates how selection arising from any given interaction propagates through the broader community, generating indirect evolutionary effects that can amplify, attenuate, or qualitatively transform pairwise coevolutionary dynamics [18, 19]. A growing body of theoretical and empirical research has begun to address these network-level effects in mutualistic communities, demonstrating that nested and modular network architectures can constrain trait divergence through indirect selection while enhancing community stability [20, 21]. Comparable theoretical development for antagonistic communities, however, remains incipient.

Existing models of antagonistic network coevolution have either imposed structurally asymmetric dynamical rules on exploiters and victims, thereby embedding selective asymmetry into the model itself, or restricted analyses to extreme parameter regimes that limit systematic exploration of the broader coevolutionary landscape [11, 22]. This theoretical gap has become increasingly important as anthropogenic drivers, including climate change, habitat loss, and biological invasions, rapidly reshape ecological communities. Growing empirical evidence indicates that these drivers not only reorganise ecological network structure but can also alter the nature of species interactions, shifting previously mutualistic relationships towards antagonism as environmental change erodes the ecological conditions that sustain reciprocal benefits [23–25]. Understanding how network structure shapes antagonistic coevolution is therefore becoming increasingly important for predicting the ecological and evolutionary consequences of global environmental change.

To address this gap, here we extend the framework of Andreazzi et al. [11] by modelling the coevolution of exploiters and victims within a unified dynamical system governed by structurally symmetric equations. A key feature of our formulation is that the asymmetry characteristic of antagonistic coevolution is not imposed through different mathematical rules for exploiters and victims. In this model, the evolutionary dynamics of each species are determined by two additive selective components: a stabilising force that drives the trait towards a species-specific environmental optimum and a directional force arising from antagonistic interactions within the network. Because the equations are identical for both guilds, exploiters and victims differ only in the direction of interspecific selection: exploiters

evolve towards trait matching with their victim partners, whereas victims evolve towards maintaining or increasing trait mismatch with their exploiters. Consequently, any asymmetry in the resulting coevolutionary dynamics reflects biological mechanisms rather than structural asymmetries embedded in the model. Building on this formulation, we introduce a fitness measure that integrates the environmental and interaction-mediated components of selection into a single, biologically interpretable index of species performance, enabling direct comparisons across species, guilds, and network architectures.

Using this framework, we investigate how trait heterogeneity, species connectivity, and network structure jointly shape fitness asymmetries across a range of coevolutionary regimes. We identify the conditions under which species become effectively decoupled in fitness space, either escaping reciprocal selection or remaining locked in persistent antagonistic arms races, and determine which structural properties of ecological networks best predict these evolutionary outcomes. By explicitly separating structural and biological sources of asymmetry, our framework provides a mechanistic understanding of how network architecture governs antagonistic coevolution and shapes the emergence, persistence, and amplification of evolutionary conflict in ecological communities.

2 Methods

2.1 Coevolutionary model for antagonistic communities

Building upon established theoretical frameworks [11, 26], we propose a coevolutionary model in which species trait dynamics are governed by two distinct selective pressures: selection imposed by the environment, and selection arising from antagonistic interspecific interactions. To this aim, we consider a community composed of M_E exploiter and M_V victim species. Each species is characterised by a single quantitative trait, represented by its population mean value: $x_i \in \mathbb{R}$ for exploiter i and $z_i \in \mathbb{R}$ for victim i . Traits are therefore dimensionless scalars evolving along a common one-dimensional axis shared by both guilds, so that trait matching and mismatching between an exploiter and a victim are measured as distances along this axis. Accordingly, the temporal evolution of x_i and z_i is described by the following system of differential equations:

$$\dot{x}_i(t) = \xi_{e,E} \cdot S_i^E(t) + \xi_{r,E} \sum_{j=1}^{M_V} M_{ij}(t), \quad (1)$$

$$\dot{z}_i(t) = \xi_{e,V} \cdot S_i^V(t) + \xi_{r,V} \sum_{j=1}^{M_E} M_{ji}(t), \quad (2)$$

where $\xi_{e,E}$ and $\xi_{e,V}$ denote the intensity of environmental selection acting on exploiters and victims, respectively, while $\xi_{r,E}$ and $\xi_{r,V}$ quantify the relative intensity of antagonistic interaction selection pressure to trait evolution. These parameters are constrained such that $\xi_e + \xi_r = 1$ for both guilds. Therefore, larger values of ξ_r , imply a proportionally greater influence of antagonistic interactions, relative to environmental selection, on the combined differential of selection. This constraint also allows the introduction of a single control parameter for each guild, namely $\xi_{r,E} \rightarrow \xi_E$ and $\xi_{r,V} \rightarrow \xi_V$, which serve as the primary variables through which distinct coevolutionary regimes arise [11].

The partial selection differentials caused by environmental pressure, $S_i^E(t)$ and $S_i^V(t)$, represent a stabilizing force directed towards a species-specific environmental optimum (see Fig. 1b) and are defined as

$$S_i^E(t) = \theta_i^E - x_i(t), \quad S_i^V(t) = \theta_i^V - z_i(t), \quad (3)$$

where θ_i^E and θ_i^V denote the environmental optima for exploiters and victims, respectively. Throughout the present study, the environmental optimum of each species is set equal to its initial trait value, so that $\theta_i^E = x_i(t=0)$ and $\theta_i^V = z_i(t=0)$. This choice reflects a standard and biologically well-motivated assumption in trait-based coevolutionary models: the initial trait value of each species represents the phenotype that has been shaped by environmental selection over evolutionary time prior to the onset of the coevolutionary dynamics under study. In the absence of interspecific interactions, a population at evolutionary equilibrium would be expected to reside at or near its environmental optimum, since any deviation would be penalised by stabilising selection.

The partial selection differential arising from antagonistic interactions assumes that the fitness consequences of an interaction depend on the degree of trait matching, thereby encoding the selective asymmetry intrinsic to antagonistic

interactions: exploiters are selected to achieve functional matching with the traits of their victim partners, whereas victims experience opposing selection to maintain or increase functional mismatch with their exploiters (see Fig. 1b). This asymmetry in selection is captured by the following expression

$$M_{ij}(t) = \frac{f_{ij} e^{-\alpha(z_j - x_i)^2}}{\sum_k^R f_{ik} e^{-\alpha(z_k - x_i)^2}} \cdot \frac{z_j - x_i}{|z_j - x_i|}, \quad (4)$$

where f_{ij} is a binary indicator specifying whether species i and j interact ($f_{ij} = 1$) or not ($f_{ij} = 0$). In a bipartite network representation of ecological communities [27], species are partitioned into two distinct guilds (exploiters and victims) as nodes, with edges connecting species exclusively across guilds, such that f_{ij} corresponds to the entries of the community adjacency matrix. The parameter α controls how the degree of trait (mis)matching modulates the fitness consequences of an interaction: higher values of α strengthen the selective effect on interactions where traits are closely matched, thereby increasing the intensity of coevolutionary coupling. The value chosen in this work is $\alpha = 0.1$. We verified the robustness of this choice by repeating the fitness landscape analysis of Section 3.2 across a range of alternative values of α ($\alpha = 0.01, 0.05, 0.2$; see Supplementary Figs. S2, S3 and S4). The qualitative structure of the fitness landscapes, including the location of the generalist-specialist trade-off, remained unchanged across this range. We therefore fixed $\alpha = 0.1$ for the remainder of the study for computational convenience. Notably, despite the intrinsically asymmetric effect of trait matching on exploiters and victims, the functional form of $M_{ij}(t)$ is identical for both guilds: directional asymmetry emerges from the structure of the interaction term itself, through the sign of the trait difference ($z_j - x_i$).

2.2 Fitness landscape of the coevolutionary model

Having defined the dynamical equations governing trait evolution, we now specify the definition of species fitness within this framework. Fitness is a central quantity in evolutionary theory, and its precise interpretation depends on the modelling approach. Here, we adopt a trait-based formulation grounded in quantitative genetics and phenotypic evolution [28], in which fitness is determined by the match between organismal traits and the selective pressures acting upon them. In this view, fitness is maximized when functional traits are optimally aligned with both abiotic environmental optima and the biotic pressures arising from interactions within the ecological network.

Applied to antagonistic systems, this general principle yields distinct fitness criteria for each guild (see Fig. 1c). The fitness of an exploiter species is maximal when its trait is simultaneously aligned with the environmental optimum and functionally matched to the traits of the victim species with which it interacts. In contrast, the fitness of a victim species is maximized when its trait aligns with the environmental optimum while maintaining or increasing functional mismatch with its exploiters, thereby reducing interaction efficacy. These definitions directly reflect the selective asymmetry encoded in the interaction term $M_{ij}(t)$ and are consistent with the match–mismatch framework widely used in studies of antagonistic coevolution [11, 29, 30].

Taking these definitions as a starting point, we express the fitness w_i of species i in terms of the model parameters and the instantaneous trait values of all relevant species. Specifically, fitness is decomposed into an environmental component, which penalizes deviation from the abiotic optimum, and an interaction component, which rewards trait matching for exploiters and trait mismatching for victims:

$$w_i^E = (1 - \xi_E) (1 - \Delta\mathcal{S}_i) + \frac{\xi_E}{k_i^E} \sum_j^{k_i^E} (1 - \Delta\mathcal{M}_{ij}), \quad (5)$$

$$w_i^V = (1 - \xi_V) (1 - \Delta\mathcal{S}_i) + \frac{\xi_V}{k_i^V} \sum_j^{k_i^V} \Delta\mathcal{M}_{ij}, \quad (6)$$

where the two adding terms in each expression correspond, respectively, to the environmental and interspecific interaction contributions to overall fitness, weighted by the same selective parameters ξ_E and ξ_V introduced in the trait dynamics.

The quantities $\Delta\mathcal{S}_i$ and $\Delta\mathcal{M}_{ij}$ represent normalized phenotypic distances bounded between 0 and 1, measuring deviations from the corresponding selective targets. Specifically, $\Delta\mathcal{S}_i = \Delta_{X_i}/h(\xi_X)$ is the fractional deviation

of species i from its environmental optimum, and $\Delta\mathcal{M}_{ij} = \Delta_{E_i V_j} / [h(\xi_E) + h(\xi_V) + \Theta_{ji}]$ is the normalised trait distance between exploiter i and victim j . The normalisation function $h(y) = y/(1-y)$ defines the maximum attainable trait displacement from the environmental optimum for a given selection strength (see Supplementary Section S1), and ensures that fitness remains comparable across the full parameter space. The auxiliary quantities are defined as follows: $\Theta_{ij} = |\theta_i^E - \theta_j^V|$, the difference between environmental optima of an interacting pair; $\Delta_{E_i} = |x_i - \theta_i^E|$ and $\Delta_{V_i} = |z_i - \theta_i^V|$, the deviations of each species from its own optimum; and $\Delta_{E_i V_j} = |x_i - z_j|$ measures the phenotypic distance between exploiter i and victim j . The interaction component is normalised by species degree (k_i^E or k_i^V) to prevent highly connected species from getting disproportionate interaction contributions, ensuring fitness is comparable across species regardless of connectivity.

Together, these fitness functions provide a unified representation of the opposing selective pressures experienced by exploiters and victims. Exploiter fitness increases as traits converge towards both the environmental optimum and the traits of their victim partners, reflecting the adaptive advantage of functional matching. Conversely, victim fitness increases as traits remain close to the environmental optimum while diverging from those of their exploiters, reflecting the adaptive advantage of functional mismatch.

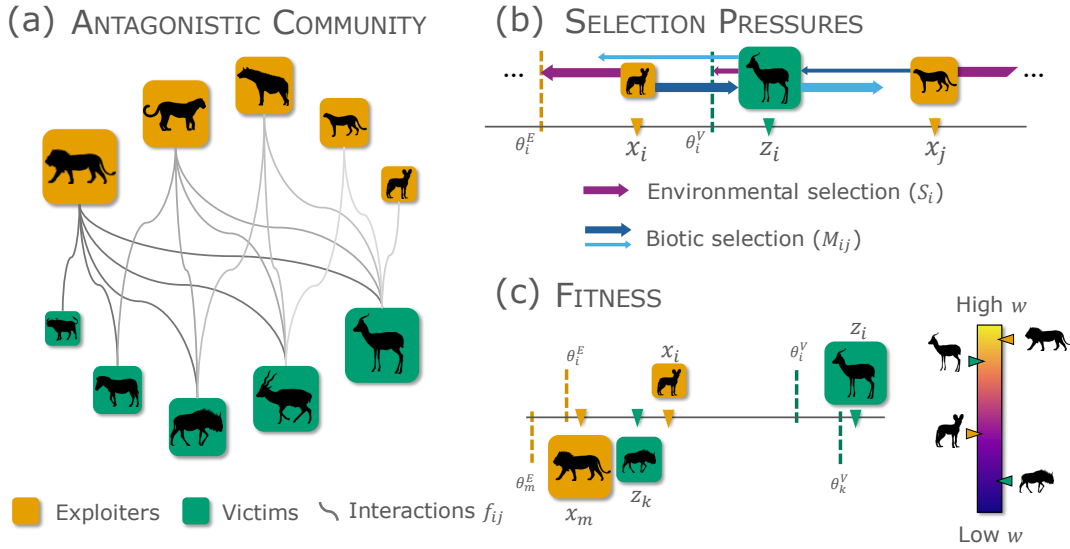


Figure 1: Conceptual overview of the trait-based coevolutionary model for antagonistic communities. (a) Ecological community represented as a bipartite network in which exploiter species (amber nodes) and victim species (green nodes) are connected by edges f_{ij} encoding permissible pairwise antagonistic interactions. Node size reflects species connectivity, with larger nodes representing more highly connected species within the community. This network is the one used for the results of Sections 3.1 and 3.2. (b) The two selective forces acting on species traits along a one-dimensional trait axis. Environmental selection (S_i , purple arrows) drives each species towards its environmental optimum (θ_i^E for exploiters, θ_i^V for victims, marked by amber and green dashed lines respectively), while biotic interaction selection (M_{ij} , blue arrows) acts asymmetrically: exploiters evolve towards victim traits (dark blue) and victims evolve away from exploiter traits (light blue). The second exploiter x_j illustrates that victims can face simultaneous selective pressures from multiple exploiters at different trait positions. (c) Qualitative fitness configurations for each guild along the trait axis. Upper row: low-fitness exploiter (x_i , far from both its optimum and its victim) and high-fitness victim (z_i , close to its optimum and distant from the exploiter). Lower row: the contrasting case, with a high-fitness exploiter (x_m) and a low-fitness victim (z_k). The colourbar encodes relative fitness from low (purple) to high (yellow).

2.3 Numerical simulations and data analysis

Numerical simulations were used to investigate the coevolutionary dynamics predicted by the model across both synthetic and empirical antagonistic networks. The analysis comprised three complementary stages. First, we characterized the dynamical regimes emerging in a controlled synthetic network. Second, we quantified how species connectivity influenced evolutionary performance across the coevolutionary parameter space. Finally, we evaluated the robustness of

these patterns across a large collection of empirical antagonistic networks and examined how species fitness varied with global network structure.

We first examined trait dynamics in a synthetic nested bipartite network comprising five exploiters and five victims, as the one illustrated in the Fig. 1a. Nested networks are characterised by a hierarchical interaction pattern in which specialist species interact exclusively with subsets of the partners of more generalist species, while modular networks are organised into internally dense and externally sparse groups of species that interact preferentially within but rarely across modules. Although antagonistic ecological networks span a broad range of topological structures, ranging from highly nested to strongly modular architectures, many empirical systems exhibit pronounced nestedness, and nested networks have become a standard benchmark for theoretical studies of antagonistic coevolution [11, 22]. Adopting a synthetic network architecture provides a simple and controlled model system for exploring the range of coevolutionary behaviours generated by our framework before extending the analysis to empirical networks with more diverse topologies.

To evaluate the model under realistic ecological conditions, we analysed 122 empirical antagonistic networks compiled from the Interaction Web Database (<https://www.nceas.ucsb.edu/interactionweb/index.html>), the Web of Life database (<https://www.web-of-life.es>), and the datasets assembled by [22, 31–33]. These networks span a broad range of interaction types, community sizes, and network architectures, including both nested and modular systems.

For each empirical network, simulations were performed across the explored coevolutionary parameter space by independently varying the interaction-driven selection parameters ξ_E and ξ_V . Each parameter combination was simulated using 100 independent realizations, with initial trait values drawn from a normal distribution, $\mathcal{N}(0, 0.5)$, to minimize the influence of initial conditions on the resulting evolutionary trajectories.

To characterize species-level patterns, we computed the fitness of every species using Eqs. (5) and (6) and examined its relationship with species degree for the four extreme combinations of interaction-driven selection, corresponding to low and high values of ξ_E and ξ_V . Species from all empirical networks were then grouped according to their degree, irrespective of network identity, and the mean fitness was computed for each degree class across the complete dataset. This procedure allowed us to identify general relationships between species connectivity and evolutionary performance that are independent of the structural characteristics of any individual network.

To investigate how guild-level evolutionary outcomes depend on global network architecture, we quantified eight structural descriptors for each empirical network: number of exploiters (M_E), number of victims (M_V), exploiter-to-victim ratio (EV), mean exploiter degree ($\langle k_E \rangle$), mean victim degree ($\langle k_V \rangle$), connectance (ρ_L), modularity (Q_{HSP} , a hybrid of simulated annealing and spectral partitioning algorithm [34]), and nestedness (NODF [35]). Together, these descriptors capture complementary aspects of network organization, including guild composition, connectivity, and topology. We then performed a principal component analysis (PCA) on the matrix of standardised network descriptors (zero-meaned and scaled to unit variance to ensure that metrics of different magnitudes contribute equally) to summarise the major axes of structural variation among the 122 empirical networks. PCA identifies orthogonal linear combinations of the original variables, ranked by the proportion of total variance they explain, that project each network onto a low-dimensional structural space while preserving as much of the original variation as possible. Each network is thereby represented as a point in this reduced space, and the loading vectors of the original metrics onto each principal component provide a mechanistic interpretation of what each axis captures structurally.

3 Results

3.1 Trait dynamics in synthetic networks: emergent coevolutionary regimes

Four combinations of exploiter and victim selection strengths (ξ_E and ξ_V), spanning weak to strong interaction-driven selection, were simulated in the 10 species synthetic network to characterize the dynamical regimes emerging from the model. The resulting trajectories (Fig. 2) reveal four qualitatively distinct coevolutionary regimes.

When interaction-driven selection is weak in both guilds ($\xi_E = 0.1$, $\xi_V = 0.1$), trait evolution is dominated by environmental selection, and species stay near their environmental optimum. In some species, there is a slight deviation from it, which depends on the relative position with their antagonistic partners (Fig. 2a). Increasing interaction-driven selection for exploiters while maintaining weak selection on victims ($\xi_E = 0.9$, $\xi_V = 0.1$) produces directional tracking dynamics, in which victims remain close to their environmental optima whereas exploiters evolve towards the traits of their interaction partners (Fig. 2b). When both guilds experience strong interaction-driven selection ($\xi_E = 0.9$, $\xi_V = 0.9$), reciprocal selection generates persistent oscillatory trait dynamics (Fig. 2c). These oscillations arise from the reciprocal feedback between exploiter tracking and victim escape: any reduction in trait distance by the exploiter intensifies selection on the victim to increase it, and vice versa, preventing either guild from reaching a

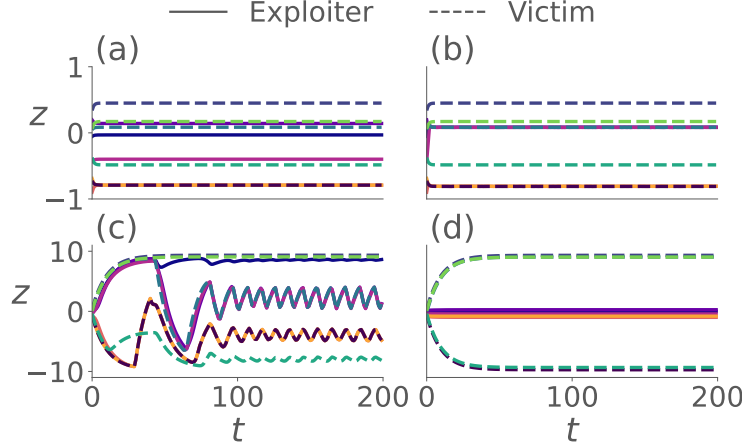


Figure 2: Temporal evolution of functional traits in the synthetic nested bipartite network comprising five exploiters and five victims of Fig. 1a, under four combinations of interaction-driven selection strengths: (a) $\xi_E = 0.1$, $\xi_V = 0.1$; (b) $\xi_E = 0.9$, $\xi_V = 0.1$; (c) $\xi_E = 0.9$, $\xi_V = 0.9$; and (d) $\xi_E = 0.1$, $\xi_V = 0.9$. In nested ecological networks, highly connected generalists interact with many partners, whereas specialists interact primarily with generalists, producing the characteristic staircase pattern in the adjacency matrix. Solid and dashed lines represent exploiter and victim trait trajectories, respectively.

stable evolutionary equilibrium. Finally, when interaction-driven selection is stronger for victims than for exploiters ($\xi_E = 0.1$, $\xi_V = 0.9$), victims rapidly diverge from exploiter traits, whereas exploiter responses remain comparatively weak because the selective effects imposed by multiple phenotypically divergent victims can partially offset one another (Fig. 2d).

These simulations demonstrate that the balance between environmental and interaction-driven selection determines whether antagonistic coevolution converges towards environmental optima, produces directional tracking or escape dynamics, or generates persistent oscillatory behaviour. Trait trajectories alone, however, do not quantify evolutionary performance because similar patterns of trait matching may correspond to markedly different fitness outcomes. We therefore next apply the fitness functions introduced in the Methods to integrate the environmental and interaction-mediated components of selection and compare evolutionary outcomes across species and coevolutionary regimes, with particular attention to how species connectivity within the network shapes the fitness landscape of each guild.

3.2 Connectivity shapes asymmetric fitness landscapes

Species within antagonistic networks differ not only in their functional traits but also in the number and identity of their interaction partners, a structural heterogeneity that the trait dynamics alone cannot capture. To quantify how this connectivity difference translates into differences in evolutionary performance, we evaluated species fitness using the functions defined in Eqs. (5) and (6). Since these expressions explicitly incorporate species connectivity through the interaction term, we compared the fitness landscapes of four representative species spanning the range of connectivity within the nested network: a generalist exploiter, a specialist exploiter, a victim attacked by multiple exploiters, and a victim attacked by a single exploiter (Fig. 3; see Supplementary Section S1 for an analytical treatment of limiting cases). Owing to the nested architecture, these categories are not independent: specialist exploiters necessarily interact with highly connected victims, whereas victims attacked by a single exploiter are linked to generalist exploiters.

The resulting fitness landscapes reveal that connectivity affects exploiters and victims in fundamentally different ways. Generalist exploiters (Fig. 3a) maintain relatively high fitness across most of the parameter space because they can either achieve partial trait matching with multiple victims simultaneously or remain close to their environmental optimum when tracking several divergent victims becomes ineffective. Their fitness declines primarily when victim selection is strong and exploiter selection is intermediate, a regime in which victims rapidly escape through trait divergence while exploiters incur simultaneous costs from increased interaction mismatch and departure from the environmental optimum. Specialist exploiters (Fig. 3c) exhibit a more polarized response. Under strong interaction-driven selection, focusing on a single victim provides a fitness advantage by concentrating evolutionary effort on a unique target. Conversely, when interaction-driven selection is weak, the absence of alternative interaction partners leaves specialists with little opportunity to compensate for poor trait matching, resulting in consistently lower fitness.

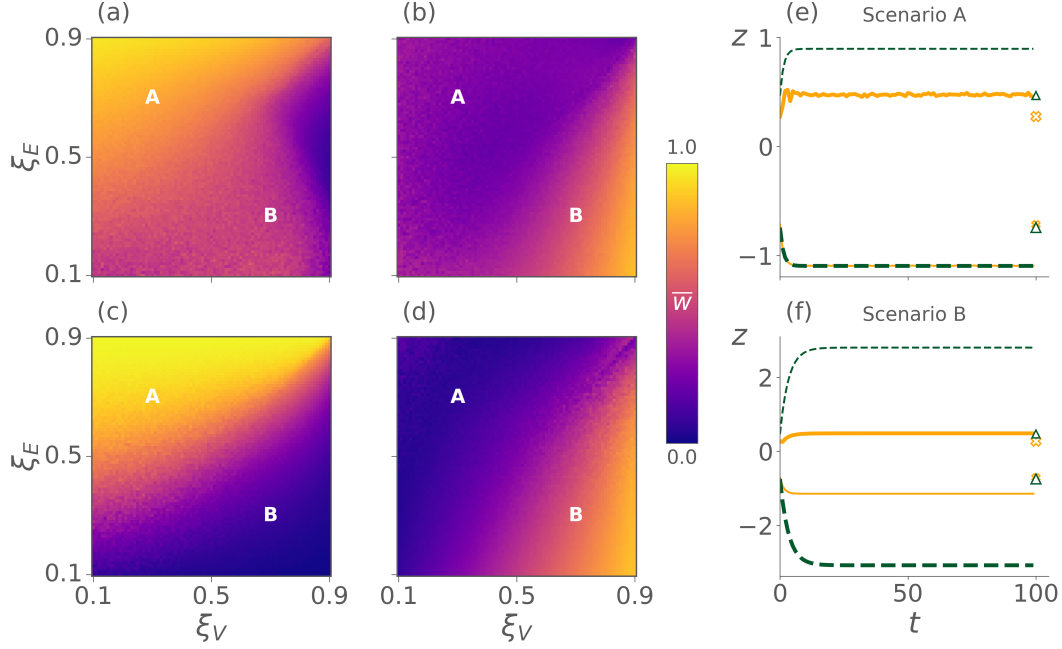


Figure 3: Fitness landscapes and representative trait dynamics for four focal species selected from the nested bipartite network to illustrate how connectivity shapes evolutionary performance. Panels (a)–(d) show fitness across the coevolutionary parameter space ($\xi_E, \xi_V \in [0.1, 0.9]$) for a generalist exploiter interacting with all victim species (a), a victim attacked by multiple exploiters (b), a specialist exploiter interacting with a single victim (c), and a victim attacked by a single exploiter (d). Owing to the nested architecture, the specialist exploiter necessarily interacts with a highly connected victim, whereas the victim attacked by a single exploiter is linked to a generalist exploiter. Warmer colours indicate higher fitness. White circles identify the parameter combinations used in panels (e) and (f), which show representative trait trajectories for two contrasting coevolutionary regimes: Scenario A ($\xi_E = 0.7, \xi_V = 0.3$), where interaction-driven selection dominates exploiters, and Scenario B ($\xi_E = 0.3, \xi_V = 0.7$), where interaction-driven selection dominates victims. Solid and dashed lines represent exploiter and victim traits, respectively, with bold lines denoting the highly connected focal species and thin lines the low-connectivity focal species.

Victims exhibit a contrasting pattern. Victims attacked by multiple exploiters (Fig. 3b) consistently achieve higher fitness than victims attacked by a single exploiter (Fig. 3d). Although interactions with multiple exploiters increase the number of antagonistic partners, they also generate competing directional selective pressures because different exploiters generally occupy different positions in trait space. Consequently, no single exploiter dominates the victim’s selective environment, allowing the victim to maintain mismatch with part of its exploiter assemblage while remaining relatively close to its environmental optimum. In contrast, victims attacked by a single exploiter experience a much more focused selective pressure and successful escape requires divergence from a single antagonist, often at the expense of environmental adaptation. As a consequence, these victims attain comparatively low fitness across most of the parameter space, except when victim selection is sufficiently strong to overcome exploiter tracking.

Together, these results demonstrate that species connectivity strongly influences evolutionary performance, although its effects differ markedly between the two guilds. For exploiters, the relative advantage of generalism or specialism depends on the balance between environmental and interaction-driven selection. For victims, by contrast, interactions with multiple exploiters generate a more heterogeneous selective environment in which competing selective pressures, together with degree normalization, buffer the fitness costs of antagonistic interactions. These contrasting responses reveal a pronounced asymmetry in how network topology shapes the selective environment experienced by exploiters and victims.

The diverging fitness landscapes are illustrated by the temporal trait dynamics shown in Fig. 3e,f for two representative coevolutionary regimes. In Scenario A ($\xi_E = 0.7, \xi_V = 0.3$), exploiters experience strong interaction-driven selection whereas victims remain primarily under environmental selection. Consequently, exploiters closely track victim traits while maintaining relatively high fitness, whereas both victim species incur substantial fitness costs through departure from their environmental optima. In Scenario B ($\xi_E = 0.3, \xi_V = 0.7$), the selective balance is reversed. Victims rapidly escape through trait divergence, increasing fitness by maintaining mismatch with exploiters, whereas exploiters

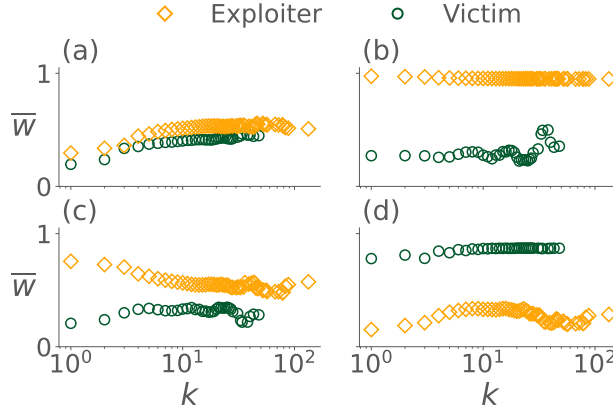


Figure 4: Relationship between species degree and fitness for exploiters (yellow diamonds) and victims (green circles), computed across 122 empirical antagonistic networks under four representative coevolutionary parameter combinations: (a) $\xi_E = 0.1$, $\xi_V = 0.1$, (b) $\xi_E = 0.9$, $\xi_V = 0.1$, (c) $\xi_E = 0.9$, $\xi_V = 0.9$ and (d) $\xi_E = 0.1$, $\xi_V = 0.9$. Each point represents the mean fitness of a single degree-class averaged across all 122 networks and 100 independent simulation replicates. Lines of best fit are shown separately for each guild to aid visual interpretation of the degree–fitness relationship across coevolutionary regimes.

experience reduced fitness because they are unable to simultaneously track diverging victims and remain close to their environmental optima. These contrasting scenarios illustrate how the same network structure can produce markedly different evolutionary outcomes depending on the relative strengths of environmental and interaction-driven selection.

The synthetic-network analyses revealed that both species connectivity and the balance between environmental and interaction-driven selection strongly influence coevolutionary outcomes. To evaluate the generality of these findings, we applied the model to 122 empirical antagonistic networks spanning a broad diversity of interaction types and network architectures, including both nested and modular communities.

We first examined how species connectivity influences evolutionary performance by analysing the relationship between fitness and degree across all empirical networks (Fig. 4). The patterns identified in the synthetic network proved remarkably robust. For exploiters, the sign of the degree–fitness relationship depends on the strength of interaction-driven selection. When ξ_E is low (Figs. 4a,d), fitness increases with degree, indicating that generalist exploiters benefit from interacting with multiple victims. Under weak interaction-driven selection, a broader range of victims allows exploiters to maintain adequate trait matching with at least a subset of their victims, thereby maximizing the average interaction component of fitness without incurring a large environmental fitness penalty. As ξ_E increases (Figs. 4b,c), this relationship reverses. Generalist exploiters become progressively less able to track multiple diverging victims simultaneously, whereas specialists, whose evolutionary response is concentrated on a single interaction partner, achieve higher fitness. Across the empirical dataset, species connectivity therefore reveals a consistent trade-off between the flexibility associated with generalism and the precision afforded by specialization, with the balance between these strategies depending on the strength of interaction-driven selection.

Victims exhibit a markedly different pattern. Across the empirical networks, no relationship emerges between fitness and degree. Weak positive correlations appear under some parameter combinations, but they are considerably less pronounced and less consistent than those observed for exploiters. This result indicates that, unlike exploiters, victim fitness cannot be predicted from connectivity alone, reflecting the more complex interplay between network structure, environmental adaptation, and escape from multiple exploiters.

Together, these results demonstrate that the asymmetric effects of connectivity identified in the synthetic network persist across empirical antagonistic communities despite their wide structural diversity. Species degree, however, captures only one aspect of network organization. We therefore next investigated whether broader properties of network architecture also shape coevolutionary outcomes at the community level.

3.3 Coevolutionary outcomes across empirical antagonistic networks

To characterize structural variation among the empirical networks, we summarized the eight network descriptors using principal component analysis (PCA) described in the Methods. We retained the first three principal components, which

together account for 86.0% of the total structural variance, and used the resulting projections to evaluate how guild-level mean fitness varied along these structural gradients across the explored coevolutionary parameter space. PC1 primarily describes a gradient from modular communities with relatively large exploiter guilds to densely connected, highly nested networks, whereas PC2 captures variation in victim connectivity and guild composition. PC3 accounts for the remaining variation associated with victim richness and exploiter connectivity. Together, these three axes provide a low-dimensional representation of the major structural differences among the empirical networks. The loadings of each metric in the three principal components can be seen in Supplementary Fig. S5.

We then examined how these structural gradients relate to guild-level fitness (Fig. 5). Although the three-dimensional projection spanned by PC1, PC2, and PC3 provides the most complete representation of the structural organisation of the empirical networks, we restrict the primary visualisation to the two-dimensional subspace defined by PC1 and PC2, which together account for 68.0% of the total structural variance, in the interest of readability and direct visual accessibility. The full three-dimensional plots for all scenarios and both guilds are provided in the Supplementary Material (Figs. S7 and S8). For exploiters, network architecture has little predictive power under strongly asymmetric selective regimes. When exploiters experience strong interaction-driven selection while victims do not ($\xi_E = 0.9$, $\xi_V = 0.1$, Fig. 5b), exploiter fitness remains uniformly high across network architectures. Conversely, when victims dominate the coevolutionary dynamics ($\xi_E = 0.1$, $\xi_V = 0.9$, Fig. 5d), exploiter fitness remains uniformly low regardless of network structure. In both cases, the asymmetry in selective pressures overwhelms any effect of network topology.

In contrast, clear structural gradients emerge when both guilds experience comparable interaction-driven selection. Under strong reciprocal selection ($\xi_E = \xi_V = 0.9$, Fig. 5c), exploiter fitness varies primarily along PC1, with modular networks consistently supporting higher mean fitness than densely connected, highly nested networks. When interaction-driven selection is weak for both guilds ($\xi_E = \xi_V = 0.1$, Fig. 5a), this gradient reverses, and nested networks become associated with slightly higher exploiter fitness. Thus, the influence of network architecture depends critically on the prevailing coevolutionary regime: structural effects become apparent only when reciprocal selection generates sustained evolutionary conflict between exploiters and victims.

The corresponding analysis for victims (Supplementary Fig. S6) reveals a totally distinct behaviour. Across most coevolutionary regimes, victim fitness shows little association with the principal structural gradients identified by the PCA. Although modest trends emerge under some parameter combinations, particularly along PC2, these effects are substantially weaker than those observed for exploiters, in line with the results obtained in the previous section for victims, where there were weak correlations between its connectivity and fitness. Instead, victim fitness is determined primarily by the balance between exploiter and victim selection strengths rather than by global network architecture.

Taken together, the empirical analyses reveal complementary roles of local and global network structure in shaping antagonistic coevolution. Species connectivity consistently influences exploiter fitness but has weaker and less predictable effects on victims. At the community scale, global network architecture modulates evolutionary outcomes primarily under regimes of reciprocal interaction-driven selection, whereas strongly asymmetric selective regimes largely override structural effects. These findings demonstrate that both local connectivity and global network organization contribute to coevolutionary dynamics, but that their relative importance depends fundamentally on the balance of selection acting on the two interacting guilds.

4 Discussion

Antagonistic coevolution is fundamentally asymmetric because exploiters are selected to increase functional matching with their interaction partners, whereas victims are selected to reduce such matching. Classical theory has largely attributed this asymmetry to the unequal fitness consequences of failure, exemplified by the life-dinner principle, according to which victims generally experience stronger selection because the cost of failure is greater than for exploiters [12]. Subsequent empirical and theoretical work, however, has shown that the magnitude and even the direction of these asymmetries depend on the ecological context and the strength of reciprocal selection [13, 15, 16]. Our results extend this perspective by demonstrating that antagonistic asymmetries are also mediated by ecological network structure. By describing exploiters and victims within the same mathematical framework, we disentangle asymmetries arising from model assumptions from those emerging through biological interactions. Even under structurally symmetric evolutionary equations, pronounced asymmetries arise in species fitness, in the effects of connectivity, and in the influence of network architecture. Selection asymmetry should therefore be viewed not simply as a property of pairwise interactions, but as an emergent consequence of the interplay between opposing selective pressures and the ecological network through which those pressures propagate [20, 36].

The context dependence of the generalist-specialist trade-off emerges as a second major implication of our results. Ecological theory has long recognized that neither strategy is universally advantageous, and that specialization arises through trade-offs between the breadth of resource use and the efficiency with which particular resources are exploited

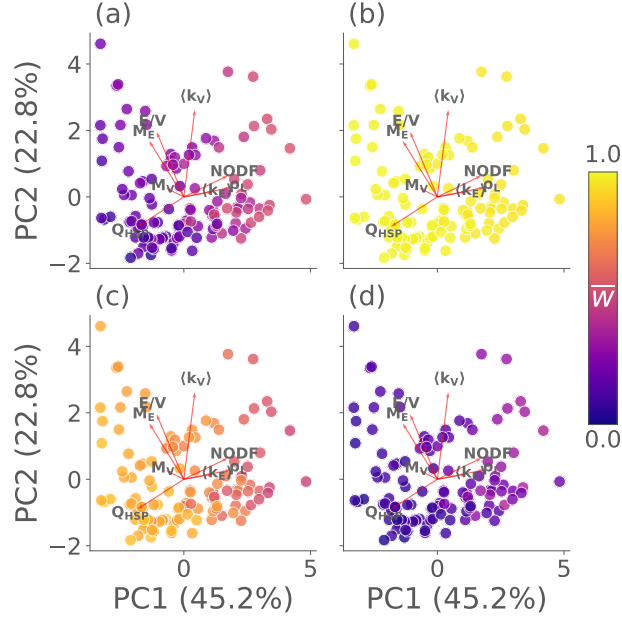


Figure 5: Two-dimensional PCA plots of 122 empirical antagonistic networks for mean exploiter fitness $\langle w_E \rangle$ under four limiting coevolutionary scenarios: (a) $\xi_E = 0.1$, $\xi_V = 0.1$, (b) $\xi_E = 0.9$, $\xi_V = 0.1$, (c) $\xi_E = 0.9$, $\xi_V = 0.9$ and (d) $\xi_E = 0.1$, $\xi_V = 0.9$. Colour encodes mean exploiter fitness on a unified normalised scale (0–1) identical across all panels, enabling direct cross-scenario comparison of both absolute fitness values and spatial gradient structure. Red loading vectors show the contribution of each of the eight structural network metrics to the PC axes. The point cloud geometry is identical across panels; only the colouring changes.

[37]. More recent syntheses have further emphasized that specialization should be viewed as an emergent property of ecological and evolutionary interactions rather than as a fixed characteristic of species [38, 39]. Our results support and extend this perspective by revealing a coevolutionary mechanism through which ecological network structure and the balance between environmental and antagonistic selection jointly determine the relative advantages of generalism and specialization.

The regime-dependent reversal we report (Fig. 4) identifies one such mechanism, and it emerges from the interplay between selective asymmetry and network structure rather than from fixed differences among species. Our findings therefore suggest that the evolution of ecological specialization cannot be understood solely from the intrinsic properties of organisms, but must also be viewed as an emergent consequence of the coevolutionary and structural context in which antagonistic interactions occur.

The influence of network architecture on guild-level fitness provides a broader perspective on how antagonistic interactions scale from pairwise encounters to entire ecological communities. A growing body of theory has shown that coevolution in species-rich communities is mediated not only by direct interactions but also by indirect effects that propagate through ecological networks, linking local selection to community-wide evolutionary dynamics [18, 19, 36]. In antagonistic systems, this perspective has been further developed by demonstrating that network structure and selection asymmetry jointly determine patterns of trait evolution and coevolutionary coupling across interacting guilds [11]. More recently, Fuster-Calvo et al. [30] showed that network architecture can constrain adaptation by spreading biotic selection across multiple interaction partners, generating conflicting selective pressures that slow exploiter evolution while producing more variable responses in victims. Our results build upon these theoretical advances by demonstrating that the evolutionary consequences of network structure extend beyond trait dynamics to the fitness landscape itself. Specifically, we show that network architecture becomes a major determinant of guild-level fitness only when reciprocal interaction-driven selection is sufficiently strong to sustain persistent coevolutionary conflict. Under strongly asymmetric selective regimes, by contrast, the balance between environmental and interaction-driven selection largely overrides the influence of network topology, leading to similar evolutionary outcomes across structurally distinct communities. Ecological networks therefore do not impose fixed evolutionary constraints. Instead, they act as filters through which selective pressures are transmitted and redistributed, determining the extent to which local antagonistic interactions propagate into community-wide evolutionary patterns.

The lower predictability of victim fitness, which depends far more weakly than exploiter fitness on connectivity and network architecture, reflects a fundamental difference in the evolutionary challenges faced by the two guilds. Exploiters ultimately pursue a common functional objective: successfully locating, infecting, or consuming their victims; whereas victims can escape exploitation through a much broader diversity of evolutionary solutions. Empirical studies across antagonistic systems illustrate this asymmetry. Hosts confronted by parasites may evolve resistance, immune priming, tolerance, behavioural avoidance, or life-history shifts, while prey reduce predation risk through strategies as diverse as crypsis, aposematism, mimicry, chemical defence, armour, and behavioural escape [7, 13, 40]. These alternative defensive strategies are often functionally equivalent in reducing exploitation, yet they correspond to distinct evolutionary trajectories. Our model provides a mechanistic explanation for this diversity by showing that victim fitness emerges from balancing environmental adaptation with escape from exploitation, rather than from optimizing a single phenotypic target. Consequently, the evolutionary responses of victims are intrinsically more contingent on local ecological conditions and historical trajectories than those of exploiters. More broadly, these findings suggest that one of the defining features of antagonistic coevolution is not simply the asymmetry in the strength of reciprocal selection, but also the asymmetry in the predictability of adaptive responses across the two interacting guilds.

Several limitations of the present framework also point to promising directions for future research. First, we assumed that interaction networks remain fixed throughout the coevolutionary process, whereas ecological interactions are increasingly recognized as dynamic properties of communities that can be rewired as species evolve or environmental conditions change [36, 41]. Coupling trait evolution with adaptive network rewiring would allow reciprocal feedbacks between species traits and community structure to emerge explicitly. Second, our model focuses on phenotypic evolution while treating population dynamics implicitly. Integrating trait evolution with demographic processes, species abundances, and extinction risk would provide a more comprehensive understanding of eco-evolutionary dynamics under antagonistic interactions, particularly in rapidly changing environments [42, 43]. Finally, extending the framework to specific systems, such as host–parasite, predator–prey, and herbivore–plant, would reveal how differences in life history, interaction strength, and network organisation shape coevolutionary outcomes across ecological contexts.

By linking network architecture, species connectivity, and fitness within a unified coevolutionary framework, our study demonstrates that the evolutionary consequences of antagonistic interactions depend not only on the identities and traits of interacting species, but also on the structural context in which those interactions are embedded.

Because anthropogenic drivers are simultaneously restructuring ecological networks and shifting the nature of species interactions, predicting their eco-evolutionary consequences will require understanding how changes in network architecture alter the balance between environmental and interaction-driven selection, and thereby reshape the adaptive trajectories of interacting species. Integrating ecological network structure with trait evolution and species fitness thus provides a promising route towards a predictive eco-evolutionary theory of antagonistic communities in a rapidly changing world.

Data accessibility

The empirical antagonistic networks analysed in this study are publicly available and were compiled from the Interaction Web Database (<https://www.nceas.ucsb.edu/interactionweb/index.html>), the Web of Life database (<https://www.web-of-life.es>), and the datasets assembled by [22, 31–33]. A curated, harmonised version of the 122 networks used in this work, together with the associated structural descriptors computed for the principal component analysis, is available at <https://doi.org/10.5281/zenodo.22689388>. The code implementing the coevolutionary model and the fitness functions described in the Methods, and the analyses and figures presented in this article and its Supplementary Material is openly available at <https://doi.org/10.5281/zenodo.22689388>.

Authors' contributions

P.G.S.: conceptualization, data curation, formal analysis, methodology, software, visualization, writing—original draft, writing—review and editing; S.L.O.: conceptualization, formal analysis, methodology, validation, visualization, writing—original draft, writing—review and editing; J.G.G.: conceptualization, methodology, project administration, supervision, validation, writing—original draft, writing—review and editing.; C.S.A.: conceptualization, data curation, methodology, project administration, supervision, validation, writing—original draft, writing—review and editing. All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Acknowledgements

P.G.S., S.L.O. and J.G.G. acknowledge financial support from the Departamento de Industria e Innovación del Gobierno de Aragón y Fondo Social Europeo (FENOL group grant E36-23R), and from Ministerio de Ciencia, Innovación y Universidades (grant PID2023-147734NB-I00). P.G.S. and S.L.O. acknowledges financial support from Gobierno de Aragón through a doctoral fellowship. CSA acknowledges financial support from Comunidad Autónoma de Madrid, 2022-T1/AMB-24091.

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SUPPLEMENTARY MATERIAL

Network structure and species connectivity drive asymmetric fitness outcomes in coevolving antagonistic communities

S1 Two-species scenario: defining trait boundaries

The case of a single victim and a single exploiter represents the minimal configuration of the coevolutionary model and serves as an analytical baseline for establishing the intrinsic bounds on trait values that constrain the system’s long-term behaviour. To characterise this limiting case, we seek the stationary solutions of the dynamical equations (1) and (2), defined by the conditions $\dot{x} = 0$ and $\dot{z} = 0$.

In the two-species system, the interaction term (4) reduces considerably. With a single interaction partner, the weighted sum in the denominator of M_{ij} collapses to a single term, and the Gaussian weighting cancels identically, leaving $M_{ij}(t) = \sigma(z - x)$, where $\sigma(\cdot)$ denotes the sign function of the trait difference between the two species. Substituting this simplified expression into the stationary conditions yields

$$0 = (1 - \xi_E) \cdot (x(t \rightarrow \infty) - \theta^E) + \xi_E \cdot \sigma(z - x), \quad (\text{S1})$$

$$0 = (1 - \xi_V) \cdot (z(t \rightarrow \infty) - \theta^V) + \xi_V \cdot \sigma(z - x). \quad (\text{S2})$$

Setting the environmental optima equal to the initial trait values, $\theta^E = x(t = 0)$ and $\theta^V = z(t = 0)$, as assumed throughout this work, and noting that $\sigma(z - x) = \pm 1$ at stationarity, these equations can be solved directly to yield the long-term asymptotic trait values

$$x(t \rightarrow \infty) = x(t = 0) \pm \frac{\xi_E}{1 - \xi_E}, \quad (\text{S3})$$

$$z(t \rightarrow \infty) = z(t = 0) \pm \frac{\xi_V}{1 - \xi_V}, \quad (\text{S4})$$

These expressions reveal that the maximum attainable displacement of each species’ trait from its environmental optimum is determined solely by the ratio $\xi/(1 - \xi)$, that is, by the relative strength of interaction-driven selection with respect to environmental selection, and is independent of the traits of the interaction partner. This quantity, which we denote $h(\xi) = \xi/(1 - \xi)$ in the main text, therefore defines a natural scale for trait variation within the model and provides the normalisation factor used in the construction of the fitness functions in Eqs. (5) and (6) of the main text.

The sign of the $\pm$ term is determined by the initial conditions: since the victim evolves in the direction opposite to the exploiter’s trait, the sign of $\sigma(z - x)$ is set at $t = 0$ and maintained throughout the evolutionary trajectory provided the relative selection intensities do not permit a reversal. Whether the exploiter ultimately converges onto the victim’s trait value, achieving full phenotypic matching and thus successful exploitation, depends on the interplay between the two selection strengths and the initial trait separation. If the victim evolves “fast” enough ($\xi_V/(1 - \xi_V) > \xi_E/(1 - \xi_E)$) or starts sufficiently far from the exploiter, it succeeds in mismatching and escaping the exploitation; otherwise, if these conditions are not met, the exploiter converges onto the victim’s trait value.

Figure S1 illustrates this two-species analysis schematically, showing the admissible trait regions for the exploiter and the victim under a representative parameter combination in which $\xi_V > \xi_E$. In this case, the victim’s allowed displacement region is wider than the exploiter’s, and the two regions do not overlap, a configuration corresponding to successful escape, in which exploitation is prevented and the coevolutionary arms race is resolved in favour of the victim.

S2 Robustness of fitness landscapes to the interaction-matching parameter α

In the main text, the parameter α , which controls how strongly the degree of trait (mis)matching modulates the fitness consequences of an interaction (Eq. 4), was fixed to $\alpha = 0.1$ for computational convenience. To confirm that this

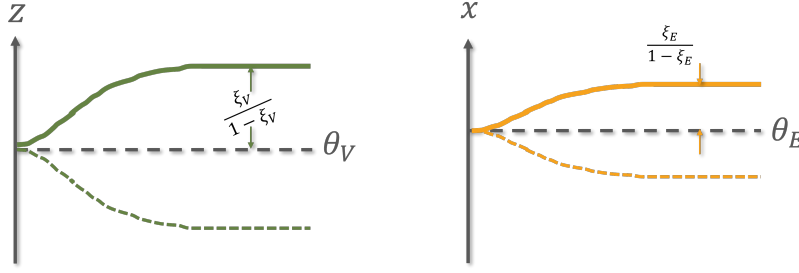


Figure S1: Schematic representation of the two-species scenario, illustrating the admissible ranges of trait values for a single victim and a single exploiter.

choice does not qualitatively affect our conclusions, we repeated the fitness landscape analysis of Section 3.2 of the main text, computed for the same four representative species of the synthetic nested network (a generalist exploiter, a victim attacked by multiple exploiters, a specialist exploiter, and a victim attacked by a single exploiter) across the full coevolutionary parameter space (ξ_E, ξ_V) , for three additional values of α spanning an order of magnitude below and above the value used in the main text: $\alpha = 0.01$, $\alpha = 0.05$, and $\alpha = 0.2$ (Figs. S2, S3 and S4, respectively).

Across all three values, the fitness landscapes reproduce the same qualitative structure reported for $\alpha = 0.1$ in Fig. 3 of the main text. Panel (a) (generalist exploiter) consistently shows high fitness across most of the parameter space, with a marked decline confined to the region of strong victim selection and intermediate exploiter selection. Panel (b) (victim attacked by multiple exploiters) remains dominated by low-to-moderate fitness, with a high-fitness region restricted to strong victim selection combined with weak-to-moderate exploiter selection. Panel (c) (specialist exploiter) reproduces the polarised response described in the main text, with fitness increasing sharply along the diagonal of strong reciprocal selection. Panel (d) (victim attacked by a single exploiter) shows the same diagonal gradient, with high fitness confined to the region where victim selection dominates over exploiter selection.

These results indicate that the generalist–specialist trade-off for exploiters and the connectivity-dependent fitness asymmetry for victims, both central to our conclusions, are not artefacts of the specific value of α adopted in the main text, but reflect a robust property of the coevolutionary model across the range of interaction-matching sensitivities tested.

S3 PCA loadings of the structural network metrics

The biological interpretation of the three main principal components is established by the loadings of each structural metric, shown in Figure S5. These three components capture distinct and interpretable axes of structural variation, and their identification provides the mechanistic foundation for understanding the fitness gradients described below.

PC1 (45.2% of variance) emerges as a contrast between two opposing structural archetypes. On one side, high negative loadings are mainly contributed by modularity (Q) and number of exploiters (M_E), both of them which load negatively and with comparable magnitude (~ -0.47 , ~ -0.35). On the other side, link density (ρ_L) and nestedness (NODF) load strongly in the positive direction (~ 0.48 and ~ 0.45 , respectively). PC1 therefore encodes a fundamental structural opposition between networks that are modular and with large exploiters guild, located at negative PC1 values, and networks that are densely connected and highly nested, located at positive PC1 values. Mean exploiter degree ($\langle k_E \rangle$) contributes a modest additional positive loading on this axis (~ 0.20), further associating positive PC1 with architectures in which individual exploiters maintain a high number of interaction partners. This structural axis is consistent with a well-documented empirical pattern in antagonistic communities, wherein nestedness and modularity tend to co-vary negatively across network types [44, 45], and its dominance in the variance decomposition confirms that this opposition is the primary dimension along which empirical antagonistic networks are structurally differentiated.

PC2 (22.8% of variance) captures an orthogonal dimension of structural variation, dominated by mean victim degree ($\langle k_V \rangle$, loading ~ 0.68) and the exploiter-to-victim ratio (E/V , loading ~ 0.51), with a positive contribution from the number of exploiters (M_E , ~ 0.35) and a negative contribution from modularity (Q_{HSP} , ~ -0.23). Networks positioned at high positive PC2 values are therefore those in which individual victim species maintain a large number of interaction partners on average, the exploiter guild is proportionally large relative to the victim guild, and the community as a whole is weakly compartmentalised. This axis is interpretable as a connectivity intensity dimension that is largely independent of raw community size: it reflects how intensively connected individual species are within the interaction structure, and

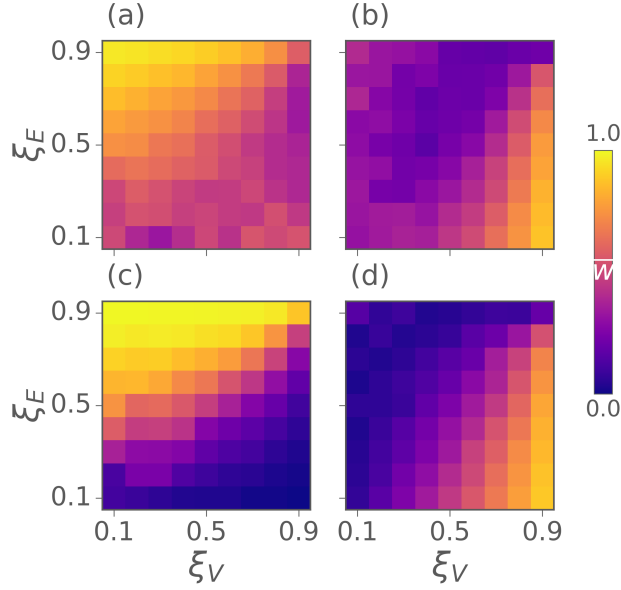


Figure S2: **Robustness of fitness landscapes to the interaction-matching parameter α .** Fitness landscapes across the coevolutionary parameter space (ξ_E, ξ_V) for the four focal species of the synthetic nested network defined in Fig. 3 of the main text (a generalist exploiter interacting with all victim species (panel a), a victim attacked by multiple exploiters (panel b), a specialist exploiter interacting with a single victim (panel c), and a victim attacked by a single exploiter (panel d)) computed for $\alpha = 0.01$. Warmer colours indicate higher fitness, on the same normalised colour scale (0–1) used throughout the main text.

how asymmetrically the two guilds are represented numerically, rather than how many species the community contains in total.

PC3 (18.0% of variance) encodes a more specific and structurally asymmetric contrast. The number of victims (M_V) and mean exploiter degree ($\langle k_E \rangle$) load strongly in the positive direction (~ 0.74 and ~ 0.55 , respectively), while the exploiter-to-victim ratio (E/V) contributes a negative loading (~ -0.29). PC3 therefore differentiates communities characterised by a numerically large victim guild in which each exploiter maintains many interaction partners.

Taken together, PC2 and PC3 jointly encode a guild-level asymmetry in the distribution of interaction burden across the community. Whereas PC2 reflects the overall intensity of connectivity and the numerical balance between guilds, PC3 captures whether that interaction load is concentrated on a small victim guild or dispersed across a larger one facing a highly connected exploiter guild. These two complementary axes, together with the nestedness–modularity opposition encoded in PC1, provide the structural foundation for interpreting the regime-dependent fitness gradients described in the following section. The fitness gradients reported in the following section are interpretable directly in terms of these axes, providing a mechanistic link between measurable network properties and guild-level coevolutionary outcomes.

S4 PCA projections of mean victim fitness across coevolutionary scenarios

The following figures complement the exploiter fitness PCA analysis presented in Section 3.3 of the main text, providing the analogous two-dimensional projections of mean victim fitness $\langle w_V \rangle$ (Figure S6) and the three-dimensional projections of mean exploiter and victim fitness (Figures S7 and S8), across the same 122 empirical antagonistic networks and under the same four limiting coevolutionary scenarios: (a) $\xi_E = 0.1$, $\xi_V = 0.1$, (b) $\xi_E = 0.9$, $\xi_V = 0.1$, (c) $\xi_E = 0.9$, $\xi_V = 0.9$ and (d) $\xi_E = 0.1$, $\xi_V = 0.9$.

The position of each network in the two-dimensional space spanned by PC1 and PC2 is identical to that shown in Fig. 5 of the main text (the PCA geometry is fixed and determined solely by the eight structural metrics) and only the colouring of each point changes, now reflecting mean victim rather than mean exploiter fitness. These supplementary figures are provided to allow direct visual comparison between the structured exploiter fitness gradients reported in the main text and the spatially diffuse victim fitness distributions described in Section 3.3, and to make the full dataset of guild-level fitness outcomes across all scenarios and both guilds available for inspection.

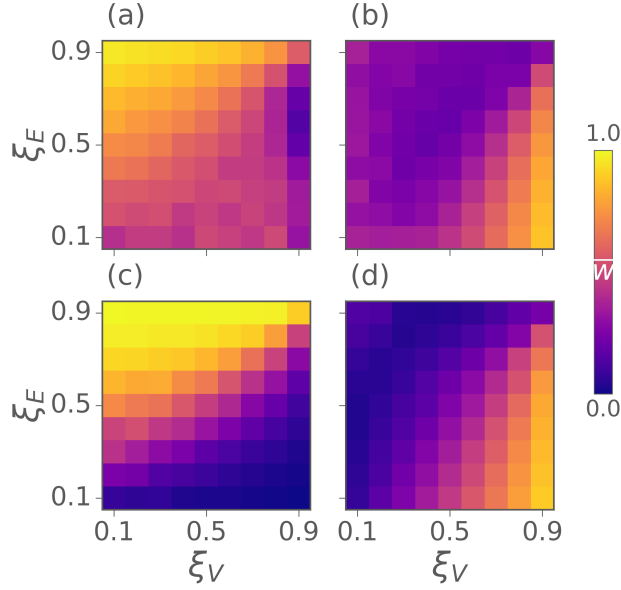


Figure S3: **Robustness of fitness landscapes to the interaction-matching parameter α .** Fitness landscapes across the coevolutionary parameter space (ξ_E, ξ_V) for the four focal species of the synthetic nested network defined in Fig. 3 of the main text (a generalist exploiter interacting with all victim species (panel a), a victim attacked by multiple exploiters (panel b), a specialist exploiter interacting with a single victim (panel c), and a victim attacked by a single exploiter (panel d)) computed for $\alpha = 0.05$. Warmer colours indicate higher fitness, on the same normalised colour scale (0–1) used throughout the main text.

The three-dimensional projections (Figures S7 and S8) extend the two-dimensional representations by incorporating the third principal component (PC3, 18.0% of variance), providing a more complete view of the structural organisation of the empirical networks and the fitness gradients embedded within it. For exploiters (Figure S7), the three-dimensional representation confirms and sharpens the patterns identified in the main text. Under scenario (b) ($\xi_E = 0.9, \xi_V = 0.1$), the point cloud is uniformly yellow throughout the full three-dimensional space, confirming that strong unilateral exploiter selection produces universally high fitness regardless of network position along any structural axis. Under scenario (d) ($\xi_E = 0.1, \xi_V = 0.9$), the cloud is uniformly deep purple, reflecting the pervasive fitness depression imposed by strong victim counter-selection in the absence of effective exploiter tracking. The intermediate scenarios (a) and (c) reveal the most informative structural gradients: in scenario (c) ($\xi_E = 0.9, \xi_V = 0.9$), a fitness gradient is visible primarily along PC1, with networks at positive PC1 values reaching higher mean exploiter fitness, while the inclusion of PC3 reveals a secondary gradient in which networks with larger victim guilds and higher mean exploiter degree achieve marginally elevated fitness within the same PC1 band. For victims (Figure S8), the three-dimensional representation confirms the structural unpredictability of victim fitness across most scenarios: the colour distributions remain spatially diffuse across all three axes in scenarios (a), (c), and (d), with no principal component emerging as a consistent predictor of performance. The sole exception is scenario (b) ($\xi_E = 0.9, \xi_V = 0.1$), where the point cloud presents a gradient along PC1, the same as in the two-dimensional projection.

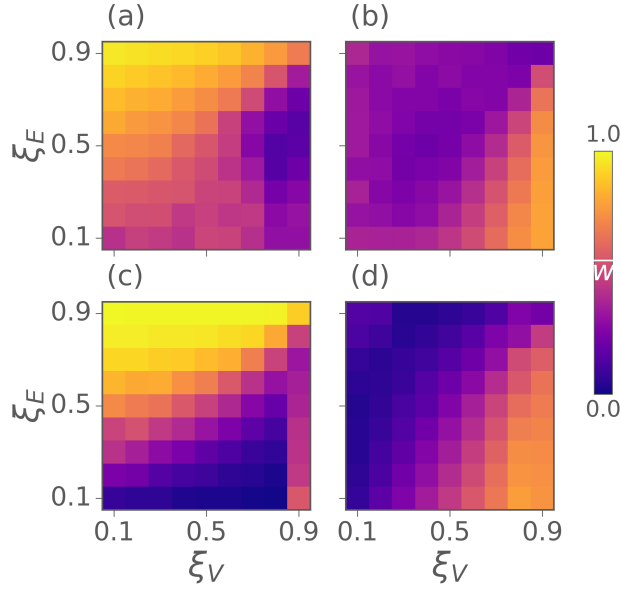


Figure S4: **Robustness of fitness landscapes to the interaction-matching parameter α .** Fitness landscapes across the coevolutionary parameter space (ξ_E, ξ_V) for the four focal species of the synthetic nested network defined in Fig. 3 of the main text (a generalist exploiter interacting with all victim species (panel a), a victim attacked by multiple exploiters (panel b), a specialist exploiter interacting with a single victim (panel c), and a victim attacked by a single exploiter (panel d)) computed for $\alpha = 0.2$. Warmer colours indicate higher fitness, on the same normalised colour scale (0–1) used throughout the main text.

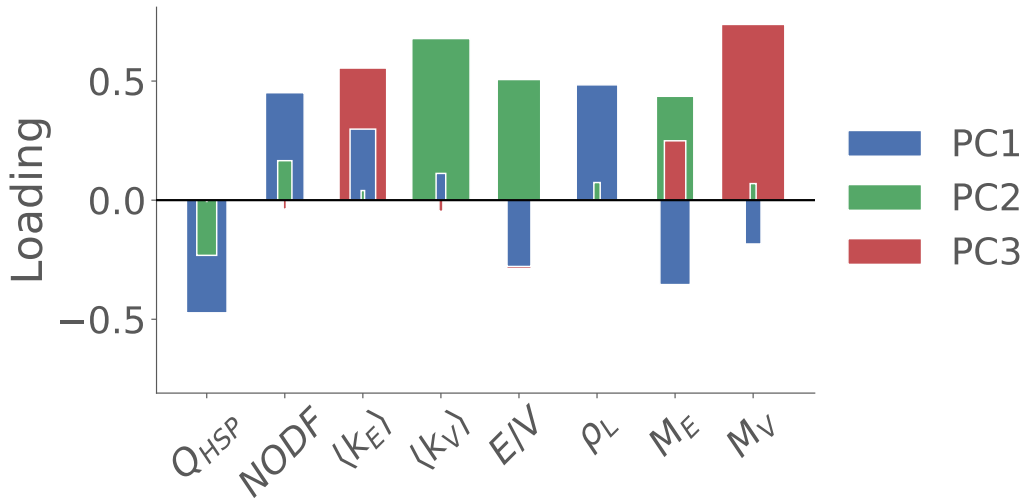


Figure S5: Loadings of the eight structural network metrics onto the three principal components retained from the PCA of 122 empirical antagonistic networks. Bars show the loading magnitude and sign for each metric on PC1 (blue, 45.2% of variance), PC2 (green, 22.8%), and PC3 (red, 18.0%), together accounting for 86.0% of total structural variance.

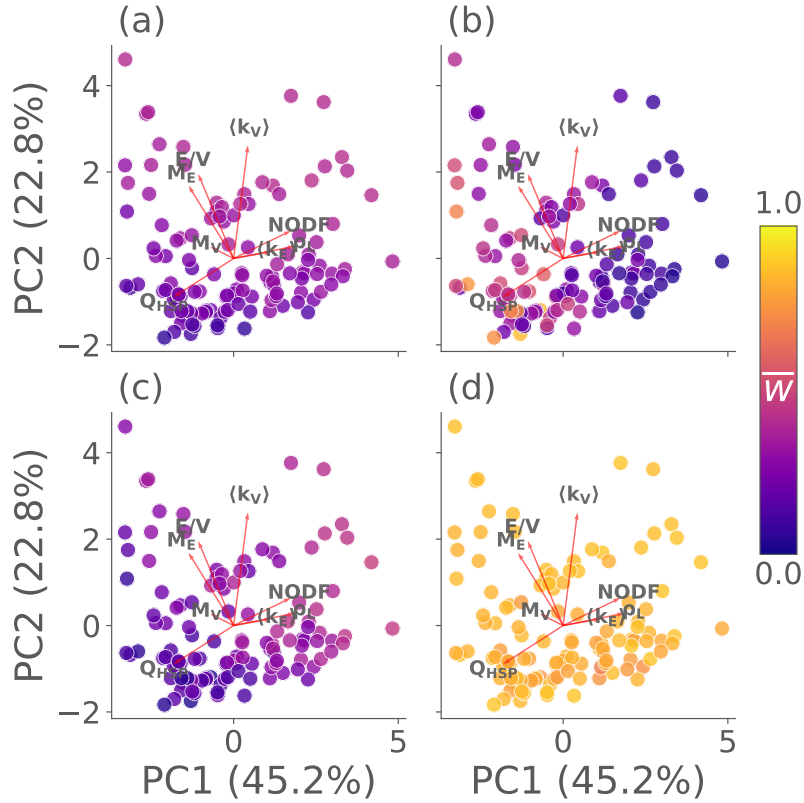


Figure S6: Two-dimensional PCA plots of 122 empirical antagonistic networks for mean victim fitness $\langle w_V \rangle$ under four limiting coevolutionary scenarios: (a) $\xi_E = 0.1$, $\xi_V = 0.1$, (b) $\xi_E = 0.9$, $\xi_V = 0.1$, (c) $\xi_E = 0.9$, $\xi_V = 0.9$ and (d) $\xi_E = 0.1$, $\xi_V = 0.9$. Colour encodes mean victim fitness on a unified normalised scale (0–1) identical across all panels, enabling direct cross-scenario comparison of both absolute fitness values and spatial gradient structure. Red loading vectors show the contribution of each of the eight structural network metrics to the PC axes. The point cloud geometry is identical across panels; only the colouring changes.

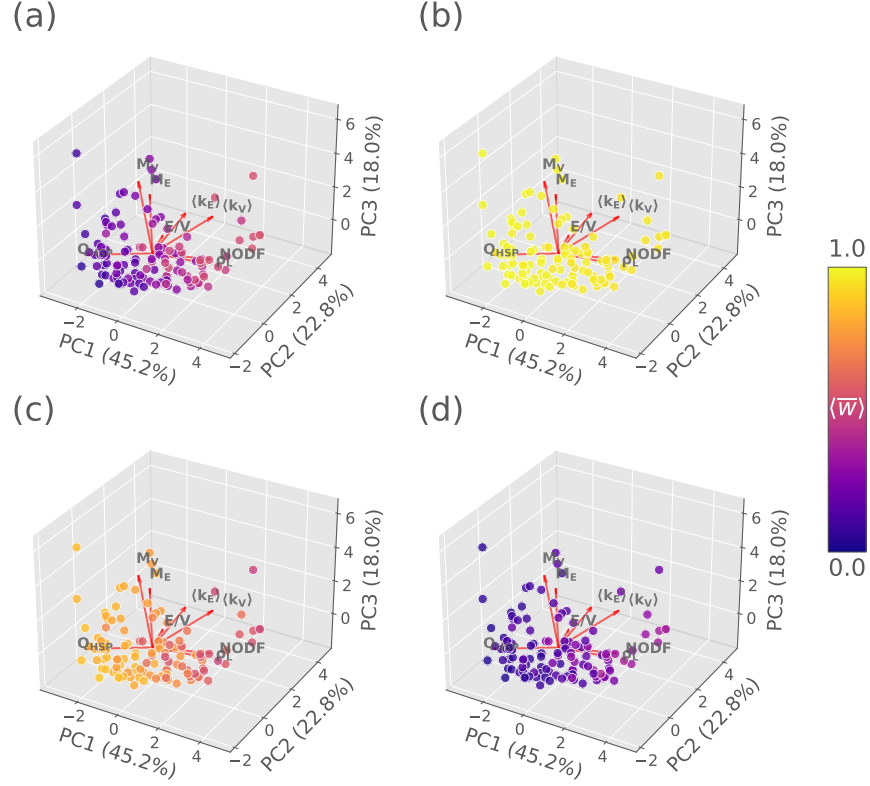


Figure S7: Three-dimensional PCA plots of 122 empirical antagonistic networks for mean exploiter fitness $\langle w_E \rangle$ under four limiting coevolutionary scenarios: (a) $\xi_E = 0.1, \xi_V = 0.1$, (b) $\xi_E = 0.9, \xi_V = 0.1$, (c) $\xi_E = 0.9, \xi_V = 0.9$ and (d) $\xi_E = 0.1, \xi_V = 0.9$. Colour encodes mean exploiter fitness on a unified normalised scale (0–1) identical across all panels, enabling direct cross-scenario comparison of both absolute fitness values and spatial gradient structure. Red loading vectors show the contribution of each of the eight structural network metrics to the PC axes. The point cloud geometry is identical across panels; only the colouring changes.

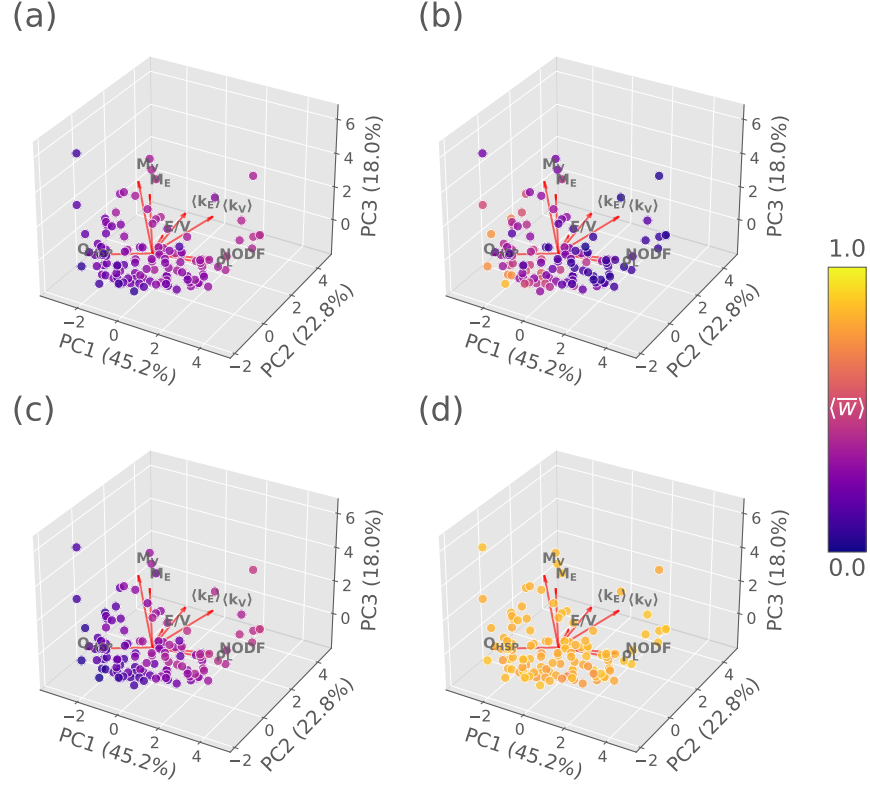


Figure S8: Three-dimensional PCA plots of 122 empirical antagonistic networks for mean victim fitness $\langle w_V \rangle$ under four limiting coevolutionary scenarios: (a) $\xi_E = 0.1$, $\xi_V = 0.1$, (b) $\xi_E = 0.9$, $\xi_V = 0.1$, (c) $\xi_E = 0.9$, $\xi_V = 0.9$ and (d) $\xi_E = 0.1$, $\xi_V = 0.9$. Colour encodes mean victim fitness on a unified normalised scale (0–1) identical across all panels, enabling direct cross-scenario comparison of both absolute fitness values and spatial gradient structure. Red loading vectors show the contribution of each of the eight structural network metrics to the PC axes. The point cloud geometry is identical across panels; only the colouring changes.