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Can Multiple Natural Enemies Cooperate without Destabilizing Control? An Ecological-Network Theory of Complementarity, Competition, and Intraguild Predation

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ABSTRACT

Biological control increasingly relies on assemblages of predators, parasitoids, pathogens, and other beneficial organisms whose combined actions may broaden pest suppression but may also generate competition, behavioural interference, intraguild predation, and unstable trophic feedbacks. The central scientific and decision problem is therefore not whether multiple natural enemies can attack the same pest, but under which ecological conditions their joint action produces complementary, persistent control rather than redundancy, antagonism, or transient suppression. This theory article develops an evidence-grounded ecological-network synthesis that integrates natural-enemy richness and composition, functional complementarity, niche partitioning, resource overlap, competition, intraguild predation, environmental context, network structure, and programme implementation. The synthesis distinguishes observed interactions from inferred mechanisms and separates species richness from complementarity, niche difference from cooperation, pairwise compatibility from network stability, and short-term additive effects from durable control. The strongest defensible conclusion is that multi-enemy performance emerges from the balance of positive and negative interaction pathways whose direction and strength vary with agent identity, pest stage, resource availability, trophic structure, spatial scale, environmental conditions, and operational practice. Current evidence remains limited by short experimental durations, incomplete interaction networks, inconsistent trait–function relationships, scale-dependent outcomes, and insufficient linkage between interaction detection and population-level pest suppression. The proposed theory therefore treats multi-agent design as a staged, context-sensitive network problem rather than a species-accumulation exercise. Progress requires mechanism-specific compatibility tests, explicit treatment of uncertainty and indirect effects, cross-scale validation, and programme governance that permits combinations to advance, be redesigned, or be discontinued according to pre-specified biological and operational evidence.

Keywords: Biological control, Multi-enemy ecological networks, Predators, Parasitoids, Natural-enemy traits, Host finding.

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INTRODUCTION

Biological control is often described through the effects of an individual predator, parasitoid, pathogen, or antagonist on a focal pest. Yet agricultural communities rarely operate through isolated consumer–resource pairs. Several natural enemies may encounter the same pest

population, attack different developmental stages, forage in different crop strata, use overlapping resources, consume one another, or respond differently to seasonal and landscape conditions. Recent syntheses indicate that natural-enemy diversity can strengthen pest suppression, but the sign and magnitude of the relationship depend on functional traits, species identity, and ecological context [1–3]. This conditional evidence creates an important distinction between the presence of multiple enemies and the existence of a biologically coherent control assemblage. A species-rich assemblage may contain complementary functions, but it may also contain redundant, competitively inferior, behaviourally disruptive, or intraguild-predatory members. Greater enemy richness is therefore not equivalent to functional complementarity.

The distinction is consequential because biological-control decisions frequently require choices among conserving resident communities, releasing one agent, combining several agents, or integrating introduced enemies with existing food webs. Experimental evidence shows that enemy composition can explain suppression more directly than richness alone [4]. The identity of the agents included, their relative densities, the pest stages they attack, and their responses to local conditions may determine whether an assemblage outperforms its strongest member. A positive mixture outcome may reflect genuine partitioning or facilitation, but it may instead arise from a dominant species, a greater total density of consumers, or a short-lived response under favourable experimental conditions. Conversely, a detected antagonistic interaction need not eliminate the possibility of useful net control if other pathways compensate for its cost. Biological interpretation must therefore move beyond categorical labels such as compatible, incompatible, synergistic, or disruptive.

The unresolved gap is the absence of a sufficiently explicit ecological-network theory connecting natural-enemy composition to mechanisms, boundary conditions, failure modes, and validation requirements. Existing evidence spans biodiversity experiments, field food webs, behavioural assays, landscape studies, molecular interaction detection, and operational release programmes. These approaches illuminate different parts of the problem but do not measure interchangeable constructs. Detection of feeding is not equivalent to a demographic effect; a demographic effect is not equivalent to crop protection; pairwise compatibility is not equivalent to network stability; and a short-term additive response is not equivalent to durable multi-agent control. Without these distinctions, multi-enemy programmes risk advancing combinations on the basis of nominal diversity or isolated efficacy tests while overlooking indirect effects, changing environmental conditions, resident enemies, and implementation constraints.

This article develops an original, explicitly non-validated ecological-network synthesis for analysing when multiple natural enemies may cooperate without destabilizing control. Its scope is limited to biological-control systems in which two or more control agents, resident enemies, pests, shared resources, or higher trophic actors form interacting ecological pathways. The central argument is that realized control emerges from a context-dependent balance among complementary attack, niche separation, competition, resource overlap, intraguild predation, behavioural interference, environmental filtering, and operational implementation. The proposed organization does not replace empirical evaluation or predict universal outcomes. Instead, it defines the constructs that must be distinguished, the relationships that require evidence, the points at which a candidate combination should be questioned, and the observations needed to test whether an apparently beneficial assemblage remains effective and stable across time and scale.

Multi-enemy biological control as a network problem

A multi-enemy system becomes a network problem when the performance of one control agent depends on the presence, behaviour, resources, or consequences of other organisms. Field evidence indicates that species diversity and food-web structure can jointly determine parasitism, hyperparasitism, and realized biological-control function [5]. This finding changes the analytical unit from a list of agents to a connected trophic structure. Nodes may include pests, predators, primary parasitoids,

hyperparasitoids, alternative prey, host plants, microbial partners, and non-target organisms. Edges may represent consumption, parasitism, competition, facilitation, avoidance, resource sharing, or indirect effects. Each edge may vary in strength, direction, timing, and environmental sensitivity. Network representation is therefore useful only when it preserves these biological meanings; a diagram based solely on co-occurrence can imply interactions that were not observed. Management gradients can reorganize enemy–herbivore network properties, but co-occurrence links must not automatically be interpreted as attacks or causal control pathways [6].

Network-level reasoning also prevents local responses from being mistaken for whole-system stability. Large-scale analyses indicate that marked responses by individual taxa need not produce equivalent changes in overall network structure [7]. The reverse is also possible: apparently stable abundance patterns may conceal changes in interaction strength, trophic routing, or the identity of agents delivering suppression. Dynamic analysis further shows that antagonistic and beneficial pathways may coexist. A predator may consume parasitized hosts while predators and parasitoids still generate positive net control under particular demographic conditions [8]. Similarly, molecularly resolved diet networks can identify predators that occupy central or specialized positions in a pest-consumption network, but detection of prey DNA establishes consumption rather than the magnitude or persistence of pest-population suppression [9]. The network problem therefore requires explicit separation of interaction occurrence, interaction strength, demographic consequence, pest suppression, and durability.

The proposed synthesis organizes multi-enemy control around five linked analytical decisions. First, the system boundary must identify the agents, pest stages, shared resources, resident enemies, and higher trophic actors relevant to the intended intervention. Second, evidence must distinguish observed links from assumed links and specify whether each relationship is positive, negative, conditional, or unresolved. Third, the expected output must be stated as a biological construct, such as expanded pest-stage coverage, reduced pest growth, lower crop injury, or increased temporal stability, rather than as an undefined claim of synergy. Fourth, boundary conditions must include species identity, release density, life stage, habitat complexity, resource availability, season, landscape setting, and experimental scale. Fifth, validation must test whether the proposed network predicts outcomes beyond the conditions from which it was derived. Failure modes include missing trophic links, treating richness as a mechanism, confusing structural persistence with effective control, extrapolating pairwise results to larger assemblages, and accepting short-duration suppression as evidence of stability. The proposed components, evidence bases, boundary conditions, failure modes, and validation requirements are organized in **Table 1**.

Table 1. Multi-Enemy Biological Control as a Network Problem: Components, Evidence Basis, Relations, Boundary Conditions, Failure Modes, and Validation Requirements

Proposed component	Purpose	Evidence basis	Relation or mechanism	Input or precondition	Expected output	Boundary condition or failure mode	Validation requirement
Network boundary	Define which organisms and resources belong to the analysed control system	Field food-web evidence shows that higher trophic links can alter realized control	Connect pests, control agents, alternative resources, and higher trophic actors	Biologically justified system boundary	A tractable representation of relevant direct and indirect pathways	Excluding hyperparasitoids, resident enemies, or alternative prey can misrepresent control	Compare predictions from reduced and expanded network boundaries
Verified interaction layer	Separate demonstrated ecological links from co-occurrence or assumed compatibility	Field networks and molecular diet studies identify different levels of interaction evidence	Classify feeding, parasitism, competition, facilitation, and behavioural effects	Direct observation, diagnostic detection, or defensible mechanistic evidence	Interaction map with explicit evidence status	Co-occurrence or molecular detection may be mistaken for population-level control	Link interaction evidence to demographic and suppression outcomes
Agent identity and composition	Prevent richness from functioning as a proxy for compatibility	Experimental assemblages show that species composition can	Agent identity determines attack role, competitive ability, and trophic position	Defined species, life stages, densities, and provenance	Composition-specific expectation of control	Species number is increased without testing which agents contribute	Compare combinations with component species and the

		dominate richness effects					strongest single-agent treatment
Dynamic interaction balance	Integrate positive and negative pathways rather than assign a fixed compatibility label	Dynamic predator–parasitoid analysis demonstrates that antagonism and net control can coexist	Complementary attack is balanced against competition, intraguild predation, and indirect effects	Time-dependent attack, survival, and reproduction information	Estimated net contribution through time	Static interaction signs conceal compensatory or delayed effects	Test predictions across relevant pest and enemy generations
Network structure and resilience	Distinguish responses of individual taxa from persistence of network organization and control	Large-scale network analysis shows that taxon-level change and network-level resilience are not equivalent	Modularity, redundancy, and trophic routing mediate disturbance responses	Replicated network observations under contrasting conditions	Conditional expectation of structural and functional persistence	Structural resilience is interpreted as proof of stable pest suppression	Measure both network reorganization and biological-control outcomes
Functional-role mapping	Identify whether enemies provide distinct, overlapping, or antagonistic functions	Interaction networks can reveal central and specialized consumers	Map agents to pest stages, microhabitats, times, and alternative resources	Verified attacks and ecologically relevant trait information	Mechanistic hypothesis of complementarity or redundancy	Network position is inferred from incomplete sampling	Repeat interaction sampling and test whether mapped roles predict suppression
Context-conditioned network state	Represent interactions as environment-dependent rather than fixed	Network properties change along management and landscape gradients	Environmental conditions modify node performance and edge strength	Habitat, resource, management, and landscape information	Context-specific rather than universal compatibility prediction	A combination is transferred without recalibration	Validate under independent environmental and management contexts
Decision and validation gate	Prevent conceptual synthesis from being treated as operational proof	Convergent evidence shows scale, method, and outcome non-equivalence	Advance, redesign, or discontinue combinations according to pre-specified evidence	Defined outcome, comparator, uncertainty, and stopping criteria	Falsifiable programme hypothesis	Positive short-term response is treated as durable control	Staged laboratory, semi-field, field, and longitudinal evaluation

Functional complementarity and niche partitioning

Functional complementarity refers to improved joint performance arising because agents contribute different, mutually useful control functions. These functions may involve attacking different pest species, developmental stages, plant strata, seasons, or behavioural states. Niche partitioning can reduce overlap and create the opportunity for such complementarity, but it does not establish that the combined assemblage suppresses pests more effectively. Complementarity may improve control when enemies partition resources or attack different pest components, yet trait diversity and realized joint efficacy remain non-equivalent [10–12]. Field evidence supports enhanced suppression in some complementary assemblages, whereas experimental work also shows that selected functional-diversity measures may fail to explain control efficiency. In greenhouse systems, contrasting within-plant preferences can broaden control when one predator performs better against flower-associated pests and another contributes more strongly in foliar habitats. The relevant mechanism is therefore not difference alone, but difference that expands effective attack without creating an equal or greater antagonistic cost.

The operational composition and release design of an assemblage can obscure this mechanism. Repetitive-release experiments demonstrate that adding multiple commercial enemies does not automatically improve control relative to a carefully selected single-agent treatment [13]. Apparent benefits may depend on release frequency, total enemy density, pest distribution, or one particularly effective member. The appropriate comparator is consequently not an untreated system alone, but also each component agent and the strongest single-agent treatment under equivalent density and timing. A further interpretive problem is that mixture overperformance is often labelled complementarity without identifying the pathway that produced it. Ecological synthesis distinguishes resource partitioning, facilitation, and biotic feedbacks as different processes that can generate superficially similar outcomes [14]. In a biological-control network, these processes should be represented separately because they

imply different persistence requirements and different risks of failure.

A defensible claim of functional complementarity therefore requires three linked demonstrations. First, agents must differ in an ecologically relevant function, such as prey-stage use, plant-stratum use, host-finding period, or response to pest density. Second, that difference must alter joint attack or pest-demographic outcomes rather than merely describe trait dissimilarity. Third, the advantage must remain after accounting for identity, density, and experimental-design effects. Niche partitioning is best treated as a candidate mechanism that may reduce competitive overlap or extend pest coverage, not as evidence of cooperative suppression by itself. Complementarity may also vary over time: an initially useful division of labour may disappear if pest stages shift, resources become scarce, or one enemy excludes another. The synthesis therefore treats complementary edges as conditional and testable, with their expected contribution tied to the pest complex, crop architecture, release schedule, and environmental context in which the combination is intended to operate.

Competition and resource overlap

Competition enters multi-enemy networks when agents depend on the same limiting host, prey, refuge, oviposition site, or spatial foraging domain. Resource overlap increases the opportunity for competition but does not prove that competition is occurring or that it has a meaningful effect on control. Outcomes may involve exploitative depletion, direct interference, priority effects, intrinsic competition within a shared host, or changes in foraging behaviour. Competitive interactions among parasitoids may also be altered by microbial symbionts, making visible species traits and nominal host ranges incomplete predictors of compatibility [15]. Direct evaluation of candidate parasitoids shows that competition and intraguild predation can change their expected joint contribution against a shared pest [16]. These findings argue against fixed species-level compatibility labels. The same pair may interact differently according to host stage, sequence of attack, host quality, symbiont status, agent density, or availability of alternative resources.

Competition is especially consequential when introduced agents encounter indigenous natural enemies. Reproductive comparisons between native and imported parasitoids sharing a host indicate that classical biological-control candidates must be assessed not only for their individual performance but also for their potential to alter the contribution or persistence of resident enemies [17]. Similar constraints arise beyond predator–parasitoid systems. In multiple-agent weed biological control, intra- and interspecific interference reduced larval survival, and a mixed treatment failed to increase plant impact [18]. The absence of an additional effect in such a combination may reflect direct aggression, reduced establishment, resource limitation, or a shift in plant-mediated conditions rather than simple functional redundancy. These mechanisms require different responses: redesigning release timing may address priority effects, whereas reducing overlap, changing density, or abandoning the combination may be necessary when interference is intrinsic.

The proposed theory therefore represents resource overlap as a precondition that modifies the probability and potential strength of competitive edges. Competition itself must be demonstrated through changes in attack, development, survival, reproduction, establishment, or target suppression. This distinction matters because agents can share a nominal resource without limiting one another when the resource is abundant, spatially partitioned, or renewed quickly. Conversely, apparently different agents may compete strongly if their effective host-finding zones converge during a vulnerable pest stage. Pairwise tests remain necessary but insufficient: adding further agents can create indirect release from competition, new intraguild pathways, or altered resource use that was absent from the pair. Competition and complementarity can therefore coexist within the same assemblage, and their balance may change across pest density, crop development, season, and release sequence. A candidate programme should advance only when its expected complementary contribution exceeds demonstrated competitive costs under conditions that resemble the intended operational context.

Intraguild predation and behavioural interference

Intraguild predation must be separated into event occurrence, demographic cost, and measurement certainty because these dimensions can lead to different predictions of control [19–21]. Alternative prey may alter focal-prey consumption and parasitism without changing measured intraguild-predation intensity [19]. In other systems, intraguild feeding can reduce predator fitness while producing context-dependent consequences for pathogen transmission [20]. Diagnostic methods can establish that feeding occurred and identify the life stages involved, but detection alone cannot determine whether the event destabilized pest suppression [21].

The direction of an intraguild link is therefore insufficient for predicting programme performance. Food-web theory indicates that intraguild predation is not universally destabilizing and may support biodiversity or functioning under particular network configurations [22]. Positive net suppression can also coexist with consumption of parasitized hosts when compensatory attack pathways remain strong [8]. Behavioural interference adds a non-consumptive dimension: avoidance, disturbance, aggression, or altered foraging can reduce effective attack without generating visible mortality among enemies. These effects may intensify under confinement, high agent density, or resource scarcity and weaken under structurally complex field conditions.

The proposed interpretation treats intraguild predation, exploitative competition, and behavioural interference as separate, context-dependent edges. Compatibility assessment should measure feeding events, encounter rates, agent survival, reproduction, behavioural displacement, pest suppression, and persistence through time. Pairwise compatibility cannot establish network stability because additional agents, alternative prey, habitat structure, or higher trophic actors may alter both encounter probabilities and demographic consequences. The evidence dimensions and interpretive boundaries for intraguild predation and behavioural interference are summarized in **Table 2**.

Table 2. Intraguild Predation and Behavioural Interference: Agent Traits, Ecological Interactions, Persistence, Compatibility, Context Dependence, and Programme-Design Implications

Agent, trait, or interaction	Target and ecological context	Mechanism	Expected contribution	Persistence requirement	Compatibility risk	Context dependency	Programme-design implication
Predator–parasitoid intraguild predation	Shared prey or hosts in multi-enemy systems	Predator consumes parasitized hosts or parasitoid stages	May retain net control when predator and parasitoid attack compensate	Both guilds must persist sufficiently to maintain complementary attack	Loss of parasitoids, altered host mortality, delayed control	Pest density, attack sequence, alternative prey, habitat structure	Compare demographic and suppression outcomes, not interaction sign alone
Alternative-prey pathway	Predator–parasitoid system with focal and alternative prey	Resource switching alters prey consumption and parasitism	May redistribute attack among pest components	Alternative resources must remain available without sustaining pests	Reduced attack on the focal pest or continued intraguild feeding	Relative prey abundance and accessibility	Test focal-pest control under changing resource conditions
Fitness-mediated intraguild cost	Predator and pathogen acting through a shared herbivore	Intraguild feeding reduces predator performance	Potential suppression through multiple mortality pathways	Predator fitness and pathogen transmission must remain sufficient	Lower predator persistence or altered disease transmission	Predator stage, infection state, prey condition	Measure reproduction and transmission as well as immediate mortality
Life-stage-specific feeding detection	Cannibalism or intraguild predation among arthropod enemies	Diagnostic identification of consumed life stages	Establishes which feeding links occur	Detection must be repeatable within relevant sampling windows	Detection may be mistaken for population-level importance	Digestion, sampling time, secondary predation	Pair diagnostic evidence with demographic and pest-suppression measures

Network-position effect	Complex food webs containing intraguild links	Topology redistributes energy and interaction pressure	May stabilize or enhance functioning under some configurations	Relevant network structure must persist through disturbance	General theory may not transfer to a focal crop system	Connectance, productivity, body-size structure, interaction strength	Test topology-specific predictions in biological-control systems
Behavioural interference	Enemies sharing foraging space or hosts	Avoidance, aggression, disturbance, or altered searching	Usually no direct contribution; may reveal hidden antagonism	Behaviour must persist outside confined assays	Reduced effective attack without direct enemy mortality	Density, arena size, crop architecture, resource scarcity	Include semi-field behavioural tests before combined release

Environmental conditions that reshape interactions

Environmental context changes both node performance and interaction strength. Landscape diversity is not synonymous with effective pest control because habitats may provide resources to irrelevant species, support antagonists, or fail to connect with the crop at the spatial scale used by effective enemies [23]. Temperature, humidity, crop architecture, plant phenology, disturbance, and alternative resources can similarly alter host finding, development, retention, and encounter rates. A combination that appears complementary in one setting may become redundant or competitive when the pest distribution or resource environment changes.

Landscape configuration can restructure herbivore–parasitoid communities by altering movement, colonization, and encounter opportunities [24]. Augmentative-control efficacy can also depend on surrounding landscape context even when the nominal agent and release protocol remain unchanged [25]. Such differences may reflect dispersal from the treated crop, variation in resident enemies, background pest pressure, or resource continuity. Environmental variables should therefore be treated as mechanistic modifiers rather than descriptive covariates appended after compatibility has been assessed.

Landscape structure consequently functions as a boundary condition on realized natural pest suppression [26]. Context-conditioned network analysis should identify the spatial and temporal scale at which agents locate hosts, persist between pest generations, and encounter competitors or intraguild prey. Progress requires replication across relevant environmental states and measurement of both agent persistence and pest outcomes. Transferability should be claimed only when the same proposed relations predict performance under independent crop, season, habitat, or management conditions.

Proposed ecological-network theory

The proposed ecological-network theory treats each natural enemy as a node embedded in a multilevel system rather than as an independently acting control input. Ecological-network effects emerge across organizational levels, so local attack, pairwise interaction, community composition, and whole-network persistence cannot be assumed to vary together [27]. The theory contains four evidence layers: verified organisms and resources; observed or strongly supported interactions; context-dependent modifiers; and proposed predictions requiring validation. Its output is not a universal readiness score, but a conditional explanation of why a combination may produce complementary, redundant, antagonistic, or unstable control.

Network characterization can broaden biological-control assessment beyond isolated candidate–host pairs by including indirect and non-target pathways [28]. Molecularly resolved networks may improve candidate selection when interaction detection is combined with ecological-performance evidence [29]. Hierarchical topology can further reveal modules and cross-module connections concealed by a single aggregate compatibility measure [30]. **Figure 1** shows alternative multi-enemy interaction networks within the analytical logic developed in this section.

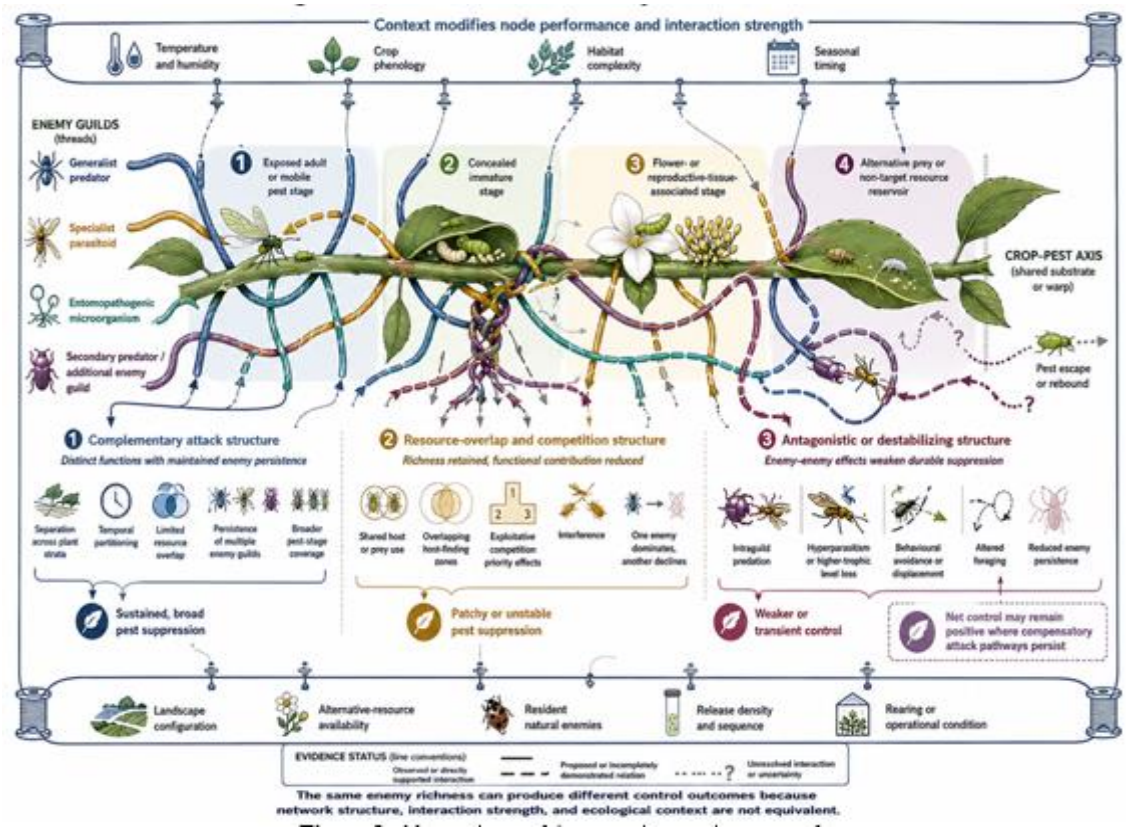

Figure 1. Alternative multi-enemy interaction networks

Alt text

A structured conceptual diagram that shows alternative multi-enemy interaction networks, with labelled components, directional relations, contextual modifiers, uncertainty points, and a clear boundary between observed evidence and proposed synthesis.

Node attributes should include agent identity, life stage, provenance, traits, population history, and operational condition because hidden demographic structure may alter contemporary trophic interactions [31]. Positive edges represent demonstrated or hypothesized mechanisms such as complementary attack, facilitation, or temporal insurance. Negative edges represent competition, interference, intraguild predation, or higher-trophic-level loss. Context modifiers alter edge direction or strength. Complementarity is favoured when distinct functions increase pest coverage, agent persistence is maintained, antagonistic costs remain limited, and the network retains those relations across relevant environments. Destabilization becomes more plausible when resource overlap intensifies, agent mortality or displacement reduces functional coverage, trophic feedbacks promote pest release, or an initially positive response fails during scale-up. **Figure 2** depicts conditions favouring complementarity or control destabilization within the analytical logic developed in this section.

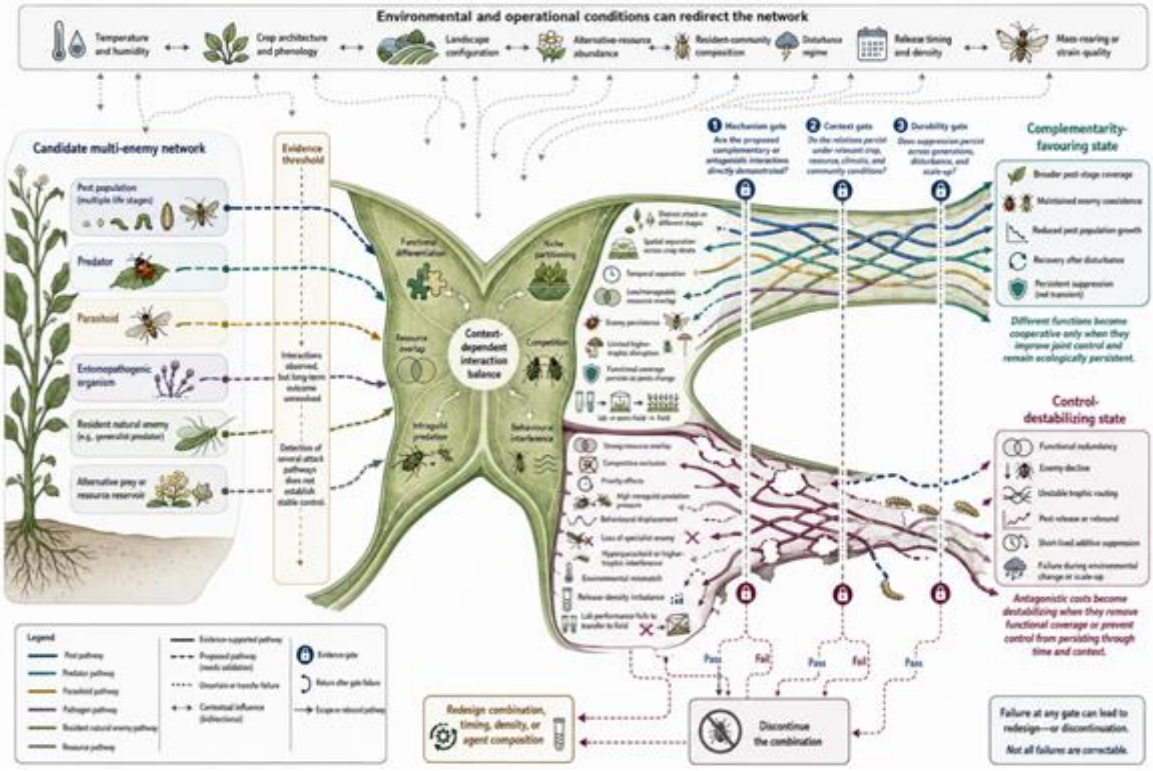

Figure 2. Conditions favouring complementarity or control destabilization

Alt text

A structured conceptual diagram that depicts conditions favouring complementarity or control destabilization, with labelled components, directional relations, contextual modifiers, uncertainty points, and a clear boundary between observed evidence and proposed synthesis.

The theory uses staged decision points. A candidate network first requires verified nodes and ecologically relevant links. It then requires mechanism-specific evidence that positive pathways exceed antagonistic costs under controlled conditions. Semi-field and field evaluation must test whether the interaction balance persists under realistic density, habitat, resident-community, and environmental conditions. Longitudinal evaluation must finally distinguish transient suppression from durable control. Failure at any point should trigger network revision, altered release timing or density, removal of an agent, or termination of the combination. The proposed components, evidence bases, boundary conditions, failure modes, and validation requirements are organized in **Table 3**.

Table 3. Proposed Ecological-Network Theory: Components, Evidence Basis, Relations, Boundary Conditions, Failure Modes, and Validation Requirements

Proposed component	Purpose	Evidence basis	Relation or mechanism	Input or precondition	Expected output	Boundary condition or failure mode	Validation requirement
Multilevel node structure	Represent agents and ecological associates across organizational levels	Ecological-network theory	Nodes contain species, stage, trait, population, and operational attributes	Verified identity and relevant biological information	Explicit network membership and node roles	Important population or life-stage variation is omitted	Test whether node attributes improve independent predictions
Interaction-evidence layer	Distinguish observed links from proposed relations	Network risk assessment	Direct and indirect links are labelled by evidence status	Observation, molecular evidence, or defensible mechanism	Traceable interaction architecture	Assumed links are presented as established pathways	Confirm links with independent ecological methods
Molecularly informed network	Improve resolution of	Metabarcoding-supported	Molecular detections identify	Representative sampling and	Refined candidate and interaction map	Detection is interpreted as	Connect detection with abundance and

	feeding or host-use relations	candidate selection	otherwise hidden interactions	validated markers		effect size or suppression	demographic outcomes
Hierarchical topology	Detect modules and cross-module pathways	Compound network topology	Nested subnetworks organize local and system-level effects	Sufficiently resolved network data	Identification of structurally distinct interaction pathways	Aggregate metrics conceal destabilizing substructures	Compare hierarchical predictions with observed outcomes
Context-modifier layer	Make interaction strength conditional on environment and management	Landscape and field evidence	Habitat, resources, climate, crop stage, and management alter nodes and edges	Defined environmental state	Context-specific prediction	Compatibility is treated as fixed across settings	Replicate under independent environmental contexts
Complementarity pathway	Represent positive joint function without equating it with richness	Mechanistic and experimental evidence	Distinct attack functions broaden or stabilize pest coverage	Verified functional difference and maintained agent persistence	Improved joint suppression relative to valid comparators	Identity, density, or transient effects imitate complementarity	Compare with component and best single-agent treatments
Antagonism pathway	Represent competition, interference, and intraguild predation separately	Experimental and food-web evidence	Negative edges reduce survival, attack, or persistence	Demonstrated encounter and consequence	Estimated antagonistic cost	Interaction occurrence is equated with destabilization	Measure demographic and pest-level consequences
Network-stability test	Separate pairwise compatibility from system persistence	Network-resilience and dynamic evidence	Direct and indirect pathways respond to disturbance through time	Multi-agent and longitudinal observations	Conditional estimate of functional stability	Stable structure without stable pest suppression	Test recovery, persistence, and suppression after perturbation
Decision and revision gate	Prevent proposed synthesis from being treated as validation	Cross-scale evidence and methodological gaps	Advance, redesign, remove agents, or terminate combinations	Pre-specified outcomes, uncertainty, and stopping conditions	Falsifiable programme decision	Laboratory advantage is assumed to transfer operationally	Staged laboratory, semi-field, field, and longitudinal assessment

Design implications for multi-agent programmes

Multi-agent design should begin with multivariate, context-explicit profiles rather than a search for a single predictive trait [32]. Candidate records should specify host-finding behaviour, attacked pest stages, spatial and temporal niches, reproductive strategy, dispersal, resource use, climatic response, symbiont status, rearing history, and known antagonistic interactions. Progress would be demonstrated when these attributes predict independent differences in establishment, interaction strength, and suppression more reliably than species identity or richness alone.

Ex-ante analysis can define falsifiable expectations and identify conditions under which an agent or combination may fail [33]. Each programme should specify its system boundary, expected complementary pathways, plausible negative edges, environmental assumptions, comparator treatments, and uncertainty. Advancement should require evidence that positive joint effects persist after controlling for total agent density and dominant-species effects. Pairwise tests should be followed by larger-network and context tests rather than interpreted as sufficient proof of stability.

Operational quality can filter or overwhelm biological potential. Long-running parasitoid programmes show that mass rearing, storage, strain quality, release timing, and monitoring are integral determinants of performance [34]. Cross-scale experiments further demonstrate that combinations performing well in the laboratory may lose their advantage in greenhouse or field conditions [35]. Programme governance should therefore include identity assurance, quality-control records, staged scale-up, monitoring of resident enemies and unintended trophic effects, and explicit revision or stopping rules. Progress is shown not by one favourable trial, but by reproducible, mechanism-consistent control across relevant scales and environmental states.

CONCLUSION

Multiple natural enemies can cooperate without destabilizing control, but cooperation cannot be inferred from species number, nominal niche difference, or pairwise coexistence. The strongest defensible synthesis is that multi-enemy performance emerges from a context-dependent balance among complementary attack, resource partitioning, competition, behavioural interference, intraguild predation, higher trophic interactions, environmental filtering, and operational implementation. Greater richness is not equivalent to functional complementarity; niche difference is not equivalent to cooperative suppression; pairwise compatibility is not equivalent to network stability; and short-term additive effects are not equivalent to durable multi-agent control. The highest-priority implication is to replace categorical compatibility judgments with staged, mechanism-specific network evaluation that links verified interactions to demographic effects, pest suppression, persistence, and cross-scale transfer. The proposed theory provides an organized and falsifiable structure for that work, but its components and relations require prospective validation before they can support operational decisions.

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