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A mechanistic perspective of ecological networks highlights the contribution of alternative interaction strategies

Danis Kiziridis[1, 2, @], Lynne Boddy[3], Daniel C. Eastwood[2], Chenggui Yuan[1] and Mike S. Fowler[2]

[1]Department of Mathematics, Swansea University, Swansea, UK
[2]Department of Biosciences, Swansea University, Swansea, UK
[3]Cardiff School of Biosciences, Cardiff University, Cardiff, UK

[@]email@danis.nichesite.org
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Abstract

Trait-based approaches in direct intraspecific and interspecific interactions address proximate and evolutionary questions across biological systems. However, interest in particular questions or systems has led to specialised descriptions of how interactions occur. We propose a generalised description in which interactions can be: defined by goals (e.g. consumption, parasitism, pollination); charted systematically (with logic statements); and explained by performance inequalities (comparing traits of individuals). Consequently, goal failures ('forbidden links') are interaction outcomes; alternative strategies to goal success exist; and matching traits are reformulated as difference traits. To illustrate, we introduce a new network measure: minimum mechanistic dimensionality, the minimum number of traits for the mechanistic explanation of the outcomes. Our dimensionality offers alternative explanations for intransitive networks. We show that previous approaches underestimate the dimensionality of 658 published empirical ecological networks (animal dominance, food webs, pollination, parasitism, seed dispersal) by omitting concepts emerging from the framework (mechanistic perspective, trait-mediated goal failures, generalisation to alternative interaction strategies). Such underestimation can prevent models from generating networks at the interaction outcome level. The framework provides a common mechanistic basis for proximate and evolutionary questions, inspiring hypotheses and trait-based models of social network dynamics, antagonistic or mutualistic community assembly or invasion, and coevolution.

Keywords: Theoretical ecology, multilayer networks, niche space, phenotype space, morphospace, trophic interactions, commensalism, interference competition, cooperation, rock–paper–scissors.

INTRODUCTION

A wide range of questions about direct intra- and interspecific interactions are addressed with trait-based approaches. These questions can be categorised as proximate or evolutionary (Dewsbury, 1999). For example, proximate ('how') questions address which key traits best explain interaction outcomes (Eklöf *et al.*, 2013; Vieira & Peixoto, 2013; Olito & Fox, 2015; Dehling *et al.*, 2016), and how are key traits involved in the interactions and outcomes (Ibanez *et al.*, 2012; Ryan & Cummings, 2013; Dy *et al.*, 2014); evolutionary ('why') questions focus on justifying key traits correlating with individual fitness (Sih *et al.*, 2012; Seppälä, 2015), on the relative impact of phylogenetic history (Becerra, 2003; Sanders *et al.*, 2014), and on the evolution of traits and population or community structure (Pinter-Wollman *et al.*, 2014; Strauss, 2014). Two main categories of trait-based approaches are the phenomenological and mechanistic (Ings *et al.*, 2009). For instance, explanation of food web structure can be attempted phenomenologically by assuming exploitation of resources with mainly smaller trait values in a range (Williams & Martinez, 2000), or by assuming mechanistic rules of allometric foraging behaviour (Petchey *et al.*, 2008).

Addressing study questions related to direct biotic interactions requires a conceptual or mathematical description of how interactions occur. For example, investigating key traits in phage–bacterium interactions requires a conceptual representation of the infection process (Dy *et al.*, 2014). Studying plant–herbivore coadaptation relies on understanding how plants and herbivores interact via defences and counterdefences (Becerra, 2003). Interaction mechanisms of trait complementarity and exploitation barriers underlie the theoretical study of plant–pollinator community structure (Santamaría & Rodríguez-Gironés, 2007).

Direct biotic interactions in different systems appear to occur sharing four common features: (*i*) interactions can be of various types within a system; (*ii*) for each interaction type, there can be alternative associated strategies; (*iii*) in each interaction strategy, there can be multiple required tasks; and (*iv*) the outcome of each task depends on the comparison between specific traits of the interacting individuals. Interaction types range from mutualistic, to antagonistic or victim–exploiter interactions, to intra- and interspecific helping, dominance, fighting, and territoriality (Morin, 2011; Davies *et al.*, 2012). For one type of interaction, examples of alternative interaction strategies are different feeding modes (Kiørboe, 2011), various visual or olfactory floral signals (Schiestl & Johnson, 2013), novel pathways to bacterial infection (Meyer *et al.*, 2012), and alternative combative mechanisms employed in fungal competition for space (Boddy, 2000). An interaction strategy usually includes multiple tasks: from the encounter–detection–identification–approach–subjugation–consumption steps of a typical predation

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sequence (Endler, 1991), to the attachment–DNA injection–replication–transcription–translation–assembly–lysis phases of a phage infection process (Dy *et al.*, 2014). For a specific task, the competing traits involved are measurable features of the interacting individuals (Arnold, 1983; McGill *et al.*, 2006; Violle *et al.*, 2007): from physiological (e.g. plant–herbivore toxin–detoxification enzyme concentrations), to morphological (e.g. animal–plant proboscis length–depth of nectar in floral tube), to behavioural (e.g. cheating–punishment in cleaner–client fish), to phenological (e.g. predator–prey temporal presence–absence) properties.

Despite the accumulated empirical knowledge about how interactions occur, previous theoretical works lack an explicit incorporation of the feature of alternative interaction strategies, and frequently other features in their mathematical descriptions. On one hand, theoretical works have focused on particular types of interaction in one strategy, for example, on mutualistic (Santamaría & Rodríguez-Gironés, 2007; Vázquez *et al.*, 2009a; Campbell *et al.*, 2011; Guimarães Jr *et al.*, 2011; Nuismer *et al.*, 2013), antagonistic (Abrams, 2000; Nuismer *et al.*, 2005; Nuismer & Thompson, 2006; Gilman *et al.*, 2012), or trophic interactions (Cohen & Newman, 1985; Williams & Martinez, 2000; Cattin *et al.*, 2004; Stouffer *et al.*, 2006; Allesina *et al.*, 2008; Petchey *et al.*, 2008; Gravel *et al.*, 2013). On the other hand, theoretical works for different interaction types lack multiple tasks in the single interaction strategy (Kopp & Gavrilets, 2006), or lack mechanistic perspective (Eklöf *et al.*, 2013; Bastazini *et al.*, 2017; Ovaskainen *et al.*, 2017). To our knowledge, only two frameworks for the occurrence of interactions appear able to incorporate all four features, although they lack an explicit reference to alternative interaction strategies (Poisot *et al.*, 2015; Bartomeus *et al.*, 2016).

Our work aimed to develop a generalised description of how interactions occur. We present the framework in three stages, encompassing all four features in the description of interactions outlined by empirical studies (Fig. 1). Direct interactions of various types: (1) appear directed by goals (first feature in the description of interactions); (2) follow alternative subgoal strategies to goal success (second and third features); and (3) are resolved by trait competition (fourth feature). Following the framework description, two framework applications are provided. First, we summarise our framework by applying it to an empirical plant–pollinator system (Kennedy, 1978), showing the systematic charting of the interactions and traits, e.g. how plant exploitation barriers are involved in the interactions. Second, we create a new dimensionality measure for the minimum number of traits required in the mechanistic explanation of the outcomes in a system. We show that the minimum number of required traits in empirical systems can be underestimated by omitting basic framework concepts. We conclude that our generalised mechanistic description provides a more comprehensive conceptual and mathematical basis for proximate and evolutionary questions in direct biotic interactions.

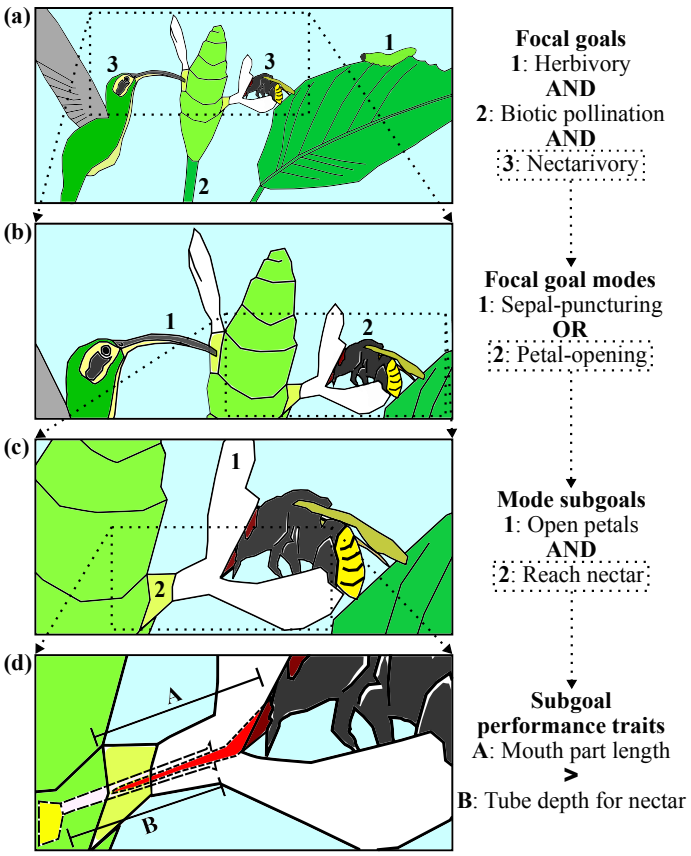

Figure 1: Summary of the four features in our generalised mechanistic description of direct biotic interactions. In each feature's panel, the illustration of a hypothetical system on the left is accompanied by the main concept and logical operator associated with that feature on the right. Dotted boxes and arrows indicate focusing in to the next feature. The four features are: (a) interactions in a system appear to be directed by multiple 'focal goals'; (b) for each focal goal, there can be alternative strategies ('modes') leading to success; (c) in each mode, there can be multiple 'subgoals' that all must be achieved; and (d) for each subgoal success in a mode, the performance in a 'trait' of one interacting individual must be higher than the performance in a trait of the other interacting individual.

FRAMEWORK

Before presenting the framework, we raise three points. First, the framework is applicable to individuals, but also to other levels of biological organisation, e.g. populations, species, or other taxonomic or functional groups, assuming it is sensible from a trait-based viewpoint (Ings *et al.*, 2009). Therefore, we broadly refer to interacting 'players' throughout. Second, the framework concerns direct interactions. Indirect interactions are out of scope, requiring intermediary players, or environmental variables (Abrams, 1987; Wootton, 1994). Third, we limit this first account of the framework to only pairwise interactions. The pairwise interaction is the simplest case, with the minimum number of players for an interaction to occur. Thus, our systems range from a pair of interacting players, to networks of pairwise interactions (see Box 1 for definitions of network terms; for a review of network theory, see Newman, 2003).

Stage 1: Defining the study system

Step 1: Player goals

The unifying concept underpinning our framework posits that interactions 'appear' to be directed by goals. We adopt an intentional language of 'goals' in our framework for the sake of directness, recognising that the apparent goal-directedness of interactions (West & Gardner, 2013) arises from the programmed operation of biological 'teleonomic

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Box 1: Definitions of terms in network (graph) theory

Network (graph): A conceptual and mathematical representation of connections among objects (e.g. a food web representing who consumes whom).

Edge (link): A connection among one or more objects of a network. Edges may have direction (e.g. directed from resources to consumers in a food web), can be of various types (e.g. predatory or parasitic interactions in a food web), and may have qualitative and quantitative attributes (e.g. consumer exploitation strategy and biomass consumed from each particular resource).

Vertex (node): An object of a network. Vertices can be of various types (e.g. plant or herbivore), and may have qualitative and quantitative attributes (e.g. life stage and body mass of each individual or species).

Part: A set of vertices of the same type (e.g. the part of the plants, and the part of the herbivores).

Multilayer network: A network composed of multiple layers. Various aspects determine the network layers. Examples of aspects are the type of edges, the season that the data were collected, and the identity of the observer. Thus, we would create a layer for each combination of edge type, season, and observer. A layer can host a subset of the vertices, and edges can connect vertices in different layers.

Unipartite graph: A network with all vertices belonging to one part. Edges are allowed between any vertices (e.g. in a food web with potential consumption of an individual or species by any other individual or species).

Bipartite graph: A network with the vertices allocated in two parts. Each vertex can have edges only with vertices from the other part (e.g. in a plant–herbivore network, representing consumption of plants by herbivores).

Weighted network: A network with weighted edges, i.e. edges with quantitative attributes (e.g. a weighted food web can show not only who consumes whom, but also how much).

processes' and 'purposive behavior' sensu Mayr (1992, 1998). Common examples of player focal goals are consumption, dominance, replacement, capturing of territory, defeat, and parasitism of others; or attraction of their provisioning, protection, cleaning, dispersal, and pollination services. We expect at least one focal goal to underlie a study system, and multiple goals can be implemented in an integrated system, i.e. as a multilayer network (Ings *et al.*, 2009; Fontaine *et al.*, 2011; Kivelä *et al.*, 2014; Pilosof *et al.*, 2017). In a multilayer network, each layer relates to one focal goal, i.e. one type of interaction (Fig. 1a). Commonly studied systems appear to be governed by one or two focal goals (Fig. 2), for example, the food webs with the single goal of consumption of the other players, and the phage–bacterium systems with the phages' goal to exploit the bacteria. Examples with two goals are plant–animal systems with the plants' goal of receiving an animal service (e.g. pollination), and with the animals' goal of exploiting a plant resource (e.g. nectar or pollen). Hence, we represent such plant–animal systems with bilayer networks, with one layer for the plants' goal, and one layer for the animals' goal.

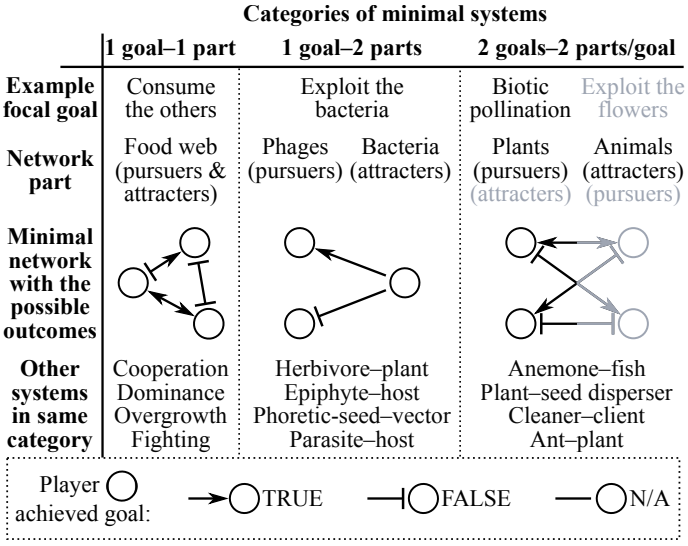

Figure 2: Framework stage 1: defining and categorising a study system. We determine player focal goals, partition players to goal pursuers and attracters, and identify the possible goal pursuit outcomes (see Box 2 for definitions of framework terms). A system must have at least one underlying focal goal, and goal failures are also interaction outcomes. Our 'minimal' systems have at most two focal goals, with each player pursuing one goal in maximum. In the third category of 2 goals–2 parts/goal, the two focal goals are shaded differently, distinguishing the outcomes of each goal in the minimal network.

Step 2: Goal pursuers and attracters

An interaction appears to occur due to a goal pursued by one interacting player, the 'pursuer', attracted to the other player, the 'attracter'. A player can be considered only pursuer, only attracter, or both pursuer and attracter of a focal goal (Fig. 2). In the example of food webs, each player is both a potential consumer (pursuer) and a potential resource (attracter). We allocate all players to one group, called 'part', as both pursuers and attracters of consumption, representing food webs as unipartite graphs. In the example of phage–bacterium systems, the phages are only pursuers, and the bacteria are only attracters. In this case, we have two parts, representing phage–bacterium systems as bipartite graphs: the part of pursuers (the potential exploiters), and the part of attracters (the potentially exploited). As in bipartite graphs, we assume no interactions within the pursuers or the attracters of a part, since a goal-directed interaction occurs only between a pursuer and an attracter. In general, there can be only two allocation possibilities in pairwise interactions: (1) unipartite, with players belonging to one part, considered both pursuers and attracters of a focal goal; or (2) bipartite, with players allocated to two parts, the part of pursuers, and the part of attracters. In the example of the bilayer plant–animal system, both network layers are bipartite: in the first layer of the plants pursuing pollination, the plants are pursuers, and the animals are attracters; conversely, in the second layer, the animals are now pursuers of floral exploitation, whereas the plants are attracters.

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Step 3: Possible interaction outcomes

Given the focal goals, and the allocation to parts, we can identify the possible outcomes (Fig. 2). For example, there are three possible outcomes in a unipartite food web: one of the two interacting players consumes the other, neither consumes the other, or they are mutually consumed. Although the latter outcome of mutual consumption might be impossible in trophic interactions, it can be plausible in other unipartite systems (e.g. cooperation after mutual pursuit of help). In the example of a bipartite phage–bacterium system, there are two possible outcomes: a phage exploits a bacterium, or fails to do so. Lastly, in the example of the plant–animal system, we recognise four possible outcomes: the plant is pollinated, and the animal exploits the plant; neither the plant nor the animal succeed in exploiting the other; the plant is not pollinated, but it is exploited; or the plant is pollinated, and it is not exploited. Note that goal failures are also considered interaction outcomes in our framework.

After defining the study system, we can categorise it based on the focal goals, the allocation of players to parts, and the possible outcomes (see Fig. 2 for our categories of minimal systems, i.e. of two goals in maximum, with each player pursuing at most one goal).

Stage 2: Charting the modes of interaction

Step 1: Goal hierarchy

To achieve a focal goal, the pursuers must succeed in subgoals. Achieving these subgoals depends on the success of further subgoals lower in the hierarchy, and so forth, leading to a branching hierarchy of goals (Fig. 3). For example, two of the prerequisites for a phage to exploit a bacterium are the attachment to the bacterial surface, and the ejection of the viral DNA (Dy *et al.*, 2014). Although a phage must attach to a bacterium before ejecting the DNA, our goal hierarchy lists these two subgoals, dismissing any temporal dependencies. Lower in the hierarchy of the attachment subgoal, two different receptors could be used for attachment, i.e. two alternative routes to achieve the attachment subgoal. In general, a goal might require success in all, or in at least one of its subgoals. In other words, subgoal statements are associated with the logical operations of AND (conjunction), and OR (disjunction). Note that goals regarding direct interactions can be understood as embedded in a general hierarchy of goals, with the increase of inclusive fitness as the ultimate goal at the top hierarchical level (Fig. 3). Hence, each individual appears as pursuing the maximisation of its inclusive fitness (Hamilton, 1964; West & Gardner, 2013), by strategically investing in the various subgoals of the whole goal hierarchy.

Step 2: Interaction form

We reorganise the logically associated subgoals from the lowest level of the focal goal hierarchy to the standardised structure of our 'interaction form' (Fig. 3). The interaction form is organised into clauses. We name a clause 'mode', a distinct strategy towards focal goal achievement. The interaction form enables alternative, independent modes for focal goal success (Fig. 1b). Success via even one mode is sufficient for the success of the focal goal, due to the disjunctive OR connecting the modes (Fig. 3).

Each mode contains subgoals that must be achieved for a success in the focal goal (Fig. 1c). If a pursuer fails in even one subgoal of a mode, the focal goal is not achieved via that mode, illustrated by the conjunctive AND connecting the subgoals. In general, the clauses of the interaction form give priority to the conjunctive operations inside each mode, first checking for success via each mode, and then across modes.

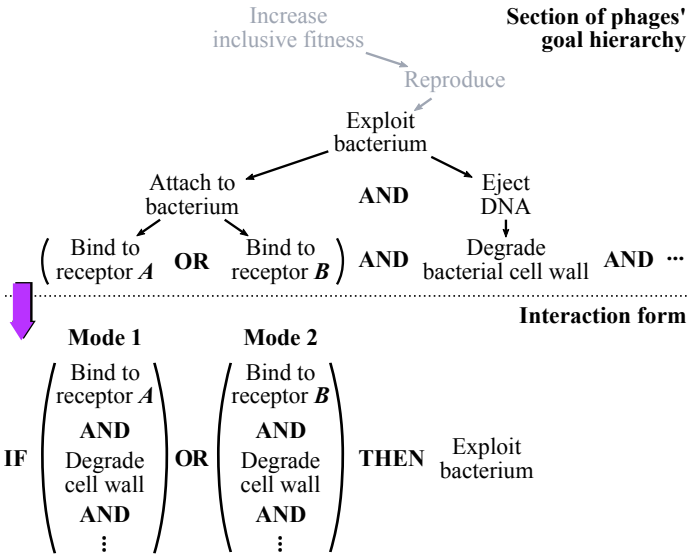

Figure 3: Framework stage 2: charting the modes of interaction. With a hypothetical phage–bacterium system, we illustrate the conversion of a section of a focal goal hierarchy (to 'exploit bacterium') to the interaction form. In our goal hierarchy, we list the subgoals upon which the achievement of a goal depends, without limiting the list because of temporal dependencies, e.g. although a phage must attach to a bacterium before ejecting the DNA, we list these two prerequisites as subgoals of the goal to exploit bacterium. Either all the listed subgoals must be achieved (branching subgoals associated with the logical operator 'AND'), or at least one of them (operator 'OR'). The lowest hierarchical level subgoals, with their logical association, are reorganised to the interaction form, a standardised way to describe the interactions regarding a focal goal in a system. The interaction form posits that there can be alternative modes for focal goal accomplishment (mode 1 and 2 in the phages' example), whereas all mode subgoals must be achieved for a success via a mode. Logic assures that any logical structure (i.e. any logically associated, lowest hierarchical level subgoals) can be reorganised to the standardised structure of the so-called 'disjunctive normal form' (i.e. our interaction form).

Essentially, our interaction form is the 'disjunctive normal form' in logic. Any structure of logical statements can be equivalently expressed in disjunctive normal form (Cohn, 2003). Similarly, any logical association of the subgoals in the lowest level of the goal hierarchy can be equivalently charted in a standardised and comparable way by the interaction form.

Stage 3: Explaining the subgoal outcomes

Step 1: Power–toughness subgoal performance traits

Conceptually, any outcome arises from a goal. Mechanistically, an outcome is determined by the performance of the interacting players (Fig. 1d). In the card game *Magic: The Gathering*®, a creature has two traits ('power' and 'tough-

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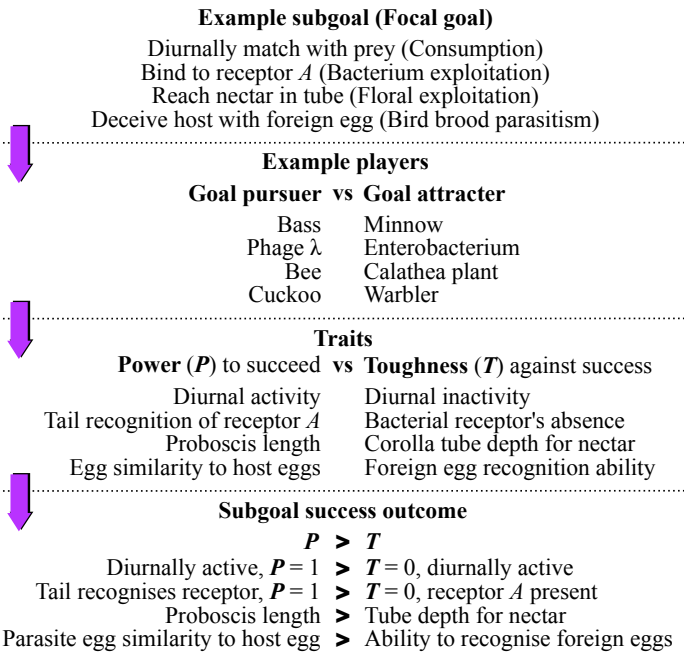

Figure 4: Framework stage 3: explaining the subgoal outcomes. Four examples are given, passing from the subgoal (of a focal goal), to the respective players, subgoal performance traits, and subgoal success outcome in each example. For a subgoal in the interaction form, a goal pursuer trait competes with a goal attracter trait. We call the pursuer trait 'power', and the attracter trait 'toughness', from the power–toughness creature traits of the card game *Magic: The Gathering*® (Garfield, 2017). To determine the subgoal outcome, we compare the power and the toughness trait values with an inequality (taken from the creature combat rules of *Magic: The Gathering*®).

ness') indicating respectively the power to inflict damage, and the toughness against enemy attacks (Garfield, 2017). Correspondingly in our framework, we identify a pursuer trait working towards subgoal success, and an attracter trait preventing subgoal success (Fig. 4). Whereas creatures in the card game interact with a single power–toughness pair of traits, real players can possess multiple pairs for the potentially multiple subgoals in the interaction form. We consider that pursuer and attracter are challenged in one trait 'dimension' of their phenotype space for each subgoal performance competition.

Step 2: Inequality rule of performance competition

The pursuer's subgoal success follows from the pursuer's power superiority over the attracter's toughness (Fig. 4). Simply, if the power of the pursuer is greater than the toughness of the attracter, the pursuer succeeds in the subgoal, which is the creature combat rule in *Magic: The Gathering*® (Garfield, 2017). The inequality rule can demand more than the marginal superiority of the pursuer's power. For example, to explain weighted subgoal successes, the inequality rule can require power superiority proportional to the subgoal success weight, instead of only marginal superiority for explaining qualitatively the successes.

Box 2: Definitions of terms in the framework

Focal goal: A goal that appears to direct one type of interaction. Multiple focal goals can be studied with a multilayer network, where each focal goal underlies a type of interaction (edge) in a layer.
Players: The interacting objects in a system. The players are the vertices in a network representation of a system.
Pursuers: Players regarded as pursuing a focal goal (e.g. predators pursuing consumption of prey).
Attracters: Players regarded as attracting pursuers (e.g. prey attracting their consumption by predators).
Part: A group of only pursuers, only attracters, or both pursuers and attracters. Such a group is a network part in a network representation.
Possible outcomes: A goal success or failure of a pursuer. In multiple focal goals, the overall possible outcomes are the combination of successes and failures in all focal goals.
Goal hierarchy: Goal achievement can depend on the achievement of other goals, creating a hierarchy of goals.
Subgoal: A goal lower than a focal goal in the goal hierarchy.
Interaction form: A standardised and generalised description of how direct interactions occur for a focal goal: alternative strategies to focal goal success.
Mode: A strategy based on subgoals via which a focal goal can be reached.
Power: The pursuer trait acting towards success in a subgoal of a mode.
Toughness: The attracter trait acting against pursuer success in a subgoal of a mode.
Dimension: The pursuer or attracter phenotype space trait dimension which is challenged in a power–toughness performance competition for a mode subgoal.
Inequality rule: If the pursuer power is sufficiently larger than the attracter toughness, the pursuer wins in the subgoal performance competition of a mode.

APPLICATIONS

Framework overview with an empirical system

We illustrate the use of our framework by applying it to an empirical plant–animal system from a lowland wet forest near Puerto Viejo, Heredia, Costa Rica (Kennedy, 1978). The first occurrence of a framework term is given in italics (see Box 2 for definitions). The *players* are representative individuals of species reported for that site (Fig. 5): three Euglossine bees (*Eulaema speciosa*, *E. seabrai*, and *E. meriana*), a hummingbird (*Phaethornis longirostris*), and a closed-flowered plant (*Calathea marantifolia*).

Stage 1: Defining the study system

We define a system in three steps: determining the player *focal goals*, allocating the players to *parts*, and identifying the types of *possible outcomes*. We determine two focal goals (Fig. 5): the animals' goal of consuming nectar, and the plant's goal of receiving animal pollination services. In the animals' focal goal, the animals are assigned to the part of *pursuers*, and the plant to the part of *attracters*; in the plant's focal goal, the plant is now the pursuer, and the animals are the attracters. Thus, we have one bipartite graph

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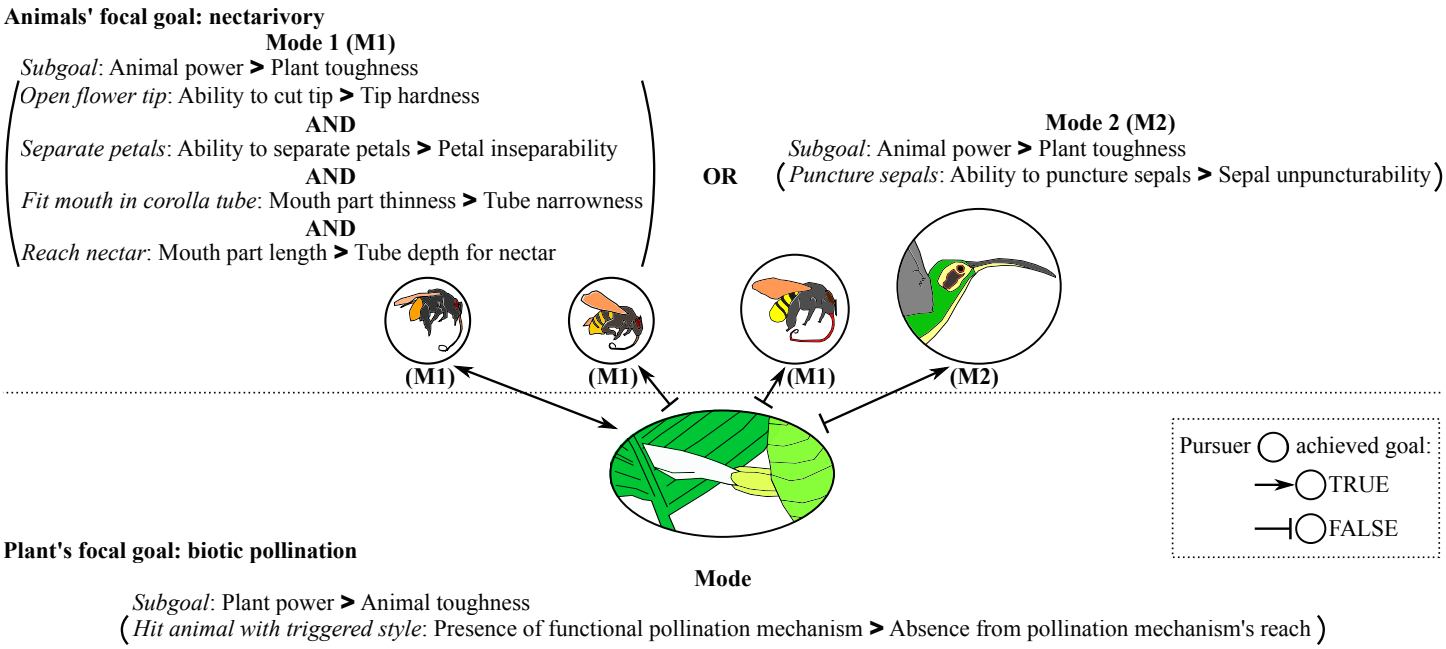

Figure 5: A summary application of the framework for an empirical system (lowland wet forest near Puerto Viejo, Heredia, Costa Rica, in Kennedy, 1978). We show selected subgoals, for the sake of illustration. From left to right, the animals reported are the three Euglossine bees *Eulaema speciosa*, *E. seabrai*, and *E. meriana*, and the hummingbird is *Phaethornis longirostris*. The plant species is the closed-flowered *Calathea marantifolia* (a closed, white flower is shown in the species token). The modes via which animal pursuers succeed are given in parentheses next to the arrowed outcomes. Species token size indicates the relative size of the representative individual.

layer for each focal goal. There are four types of possible outcomes in this category of minimal systems (category of 2 goals–2 parts/goal, in Fig. 2).

Stage 2: Charting the modes of interaction

The first step is to decompose a focal goal to *subgoals* in a *goal hierarchy*. The second step reorganises the goal hierarchy's lowest level subgoals to the standardised *interaction form*. Note that the interaction forms will contain only a few subgoals for the sake of illustration.

For the animals' focal goal of consuming nectar, there are two alternative strategies to success: by opening the petals OR through the calyx. This is translated to two disjunctively associated subgoals branching from the focal goal in the goal hierarchy. The first subgoal of consuming nectar by opening the petals requires success in four subgoals: cutting the flower tip AND separating the petals AND fitting the mouth part in the corolla tube AND reaching nectar down in the holding chamber. Thus, the first subgoal of consuming nectar by opening the petals further branches to the four conjunctively associated subgoals. The second subgoal of accessing nectar directly through the calyx requires the puncturing of the sepals. Passing to the animals' interaction form, the initial disjunctive branching in the goal hierarchy translates to two alternative *modes* to focal goal success (Fig. 5): the first mode includes the four subgoals that all must be achieved for the opening and exploitation of a flower; and the second mode includes only the subgoal of puncturing the sepals.

The plant's focal goal mode of biotic pollination implements a specialised mechanism with a trigger that must be pressed inside the flower, releasing the style to hit the animal for pollination. In the goal hierarchy, the focal goal requires the subgoal achievement of hitting an animal with the triggered style. Thus, the plant's interaction form comprises a single unidimensional mode (Fig. 5).

Stage 3: Explaining the subgoal outcomes

In the first step of identifying traits for the subgoal pursuits (Fig. 5), an animal nectarivory pursuer has to overcome plant toughness traits which are exploitation barriers (Santamaría & Rodríguez-Gironés, 2015). For the plant's focal goal, the power of the plant pollination pursuer is a functional mechanism for the precise transfer of pollen (Santamaría & Rodríguez-Gironés, 2015). The animals might avoid the mechanism by not pressing the trigger, or by not being present on the movement path of the triggered style.

In the second step, we attempt to infer any *inequalities in subgoal performance competition* based on the descriptions of Kennedy (1978). All bees achieve the nectarivory focal goal via the first mode of opening flowers, the hummingbird via the second mode of puncturing flowers, and the plant is pollinated only by the *E. speciosa* bee (Fig. 5). Bees appear unable to puncture the relatively tough calyx, failing via the second nectarivory mode. The hummingbird does not appear to use the first nectarivory mode, perhaps due to expected failure in at least one subgoal (e.g. mouth part cannot fit in the thin corolla tube). For the plant, given the presence of a functional pollination mechanism (the plant power equals one), the animals' toughness depends on the way they handle flowers. The pollinating bee *E. speciosa* forces its head into the flower (the bee's toughness equals zero, inferior to the plant's power), activating the trigger, and the style hits the bee's head. *E. seabrai* has similar proboscis length, but this bee forces the proboscis in by keeping the head outside of the flower (this bee's toughness equals one, equivalent to the plant's power), and out of the style's reach. The larger *E. meriana*, with the lengthier proboscis, does not trigger the mechanism because there is no need to force its head closer to the tube opening to reach nectar (bee's toughness

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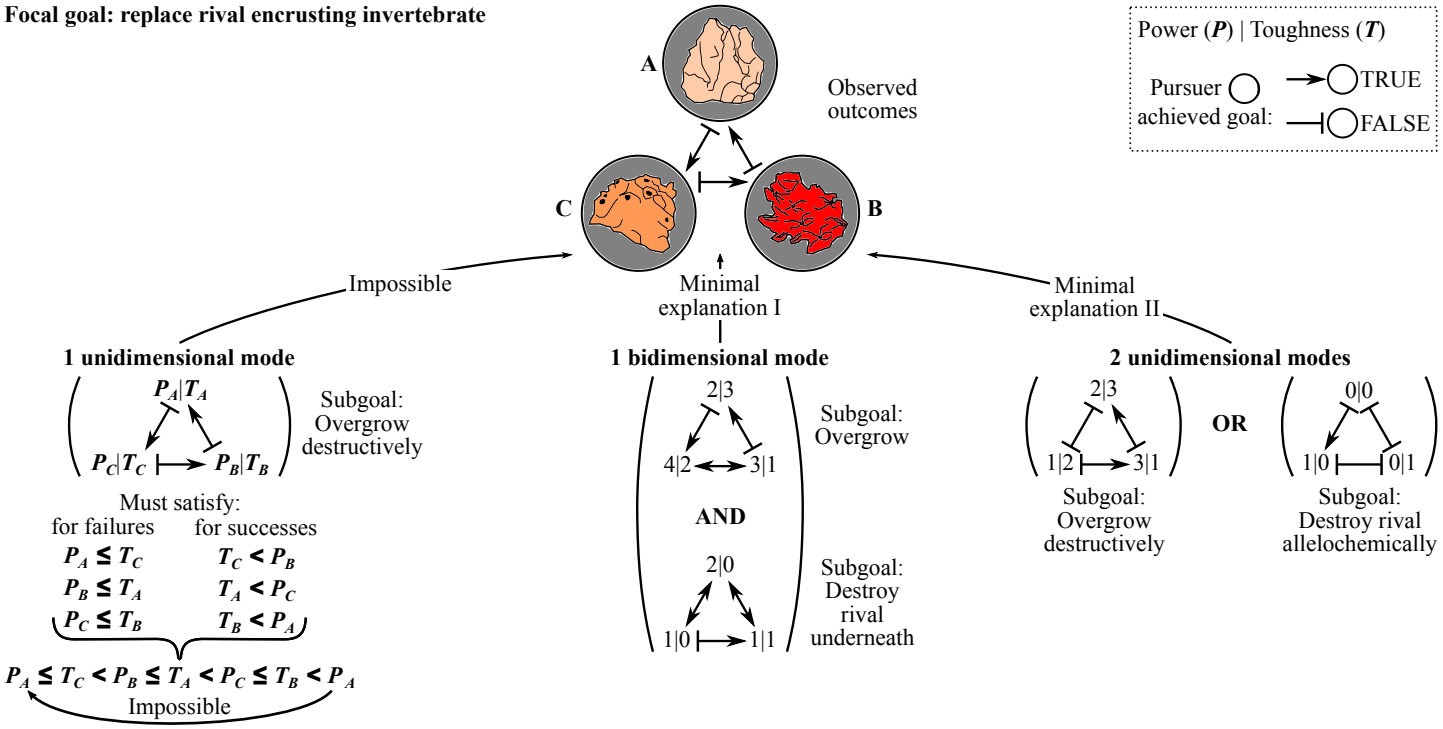

Figure 6: Hidden mechanistic information of at least two dimensions involved in the interactions of an empirical rock–paper–scissors, intransitive network of outcomes. The empirical system is reported in Jackson & Buss (1975), with three species: the ectoproct *Stylopoma spongites* (player A), and the sponges *Tenaciella* sp. and *Toxemna* sp. (players B and C, respectively). We show three attempts to explain minimally the observed outcomes, with the first attempt being mechanistically impossible. Our framework suggests two feasible minimal explanations, the second of which is similar to that suggested by Jackson & Buss (1975): player A replaces B, and B replaces C via destructive overgrowth, whereas C replaces A via an alternative strategy ('mode' in our framework), by toxic effects. We indicate hypothetical subgoals, and power|toughness integer scores in arbitrary units of performance.

equals one). Lastly, the hummingbird does not pollinate because it robs nectar through the calyx (bird's toughness equals one).

Minimum mechanistic dimensionality

In the application described above, the four animals succeeded in their focal goal via two alternative modes, one multidimensional (four dimensions; bees), the other unidimensional (hummingbird). Minimally, we could observe these four successes via one unidimensional mode: all animals could 'easily' consume nectar from a plant with open, wide and short flowers, e.g. pursuing only the first mode's subgoal of reaching nectar in the tube (Fig. 5). In other words, if that system was mechanistically minimal, the same outcomes would have occurred from interactions in one trait dimension. Thus, the idea behind this application is to find a minimal interaction form which is sufficient for the mechanistic explanation of all the observed interaction outcomes of a system. By comparing a theoretically minimal interaction form with the empirically observed one, we can gain insight into the extra strategies, measures, or defences of the players. For instance, the plant attracter imposed five exploitation barriers to the nectar consumers (Fig. 5), challenging these animal pursuers in five dimensions instead of the theoretically required one dimension. Additionally, by computing the minimum number of dimensions involved in the interactions of empirical systems, we can inform mechanistic models about the minimum number of trait dimensions that must be employed to generate realistic ecological networks.

Rock–paper–scissors needs at least two dimensions

The success of the nectarivory pursuers at the empirical plant–animal system in Kennedy (1978) could minimally arise by interactions in one trait dimension. However, one dimension is not sufficient to explain mechanistically the outcomes of an intransitive network of outcomes between three species, such as the cyclic spatial replacement of marine invertebrates studied by Jackson & Buss (1975): ectoproct species *Stylopoma spongites* (player A) replaces sponge species *Tenaciella* sp. (player B), which in turn replaces sponge species *Toxemna* sp. (player C), which in turn replaces the ectoproct species player A (Fig. 6).

It is impossible to explain the observed focal goal outcomes in this unipartite graph with interactions via a unidimensional interaction mode. The pair of power–toughness traits for the single subgoal must satisfy a system of six inequalities for three failures and three successes. For the successful replacements, the power of a winning pursuer must be greater than the toughness of a defeated attracter. For the failures, the power of a losing pursuer must be less than or equal to the toughness of an undefeated attracter. This system of six linear inequalities creates a cyclic sequence of ever-increasing power–toughness scores (impossible attempt in Fig. 6). For example, the single subgoal in the unidimensional mode could be destructive overgrowth, with the offensive and defensive heights of an encrusting invertebrate X taken respectively as power (P_X) and toughness (T_X) subgoal performance traits. If we arrange appropriately the three successes and three failures, we have a cycle of ever-

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increasing, alternating offensive–defensive heights. Initially setting the offensive height of player A to one, $P_A = 1$ in arbitrary units of integer length, then the cyclic relation would be: $P_A = 1 \leq T_C = 1 < P_B = 2 \leq T_A = 2 < P_C = 3 \leq T_B = 3 < P_A = 4$. This is impossible to satisfy, since it returns to P_A requiring a value larger than the initial offensive height.

Our framework provides two alternative minimal mechanistic explanations for the emergence of a rock–paper–scissors system. First, we can find solutions for two pairs of power–toughness traits if we add a second dimension in the same mode (e.g. requiring non-destructive overgrowth AND destruction of rival underneath; minimal explanation I in Fig. 6). We explain the focal goal failure of players A and B as failure in the first dimension (e.g. overgrowth), and the failure of C as failure in the second (e.g. destruction of rival, even if C can overgrow B). Second, we can find solutions for two pairs of power–toughness traits if we add a second dimension in a new unidimensional mode (e.g. requiring destructive overgrowth OR elimination via allelopathy; minimal explanation II in Fig. 6). In that case, we explain the success of A and B as success via the first mode of destructive overgrowth, and the success of C as success via the second mode of allelochemical elimination. Minimal explanation II is described by Jackson & Buss (1975) for this cryptic reef system: ectoproct player A replaces via overgrowth sponge player B, sponge player B replaces via overgrowth sponge player C, but ectoproct player A does not replace sponge player C via overgrowth as well; instead, ectoproct player A is replaced by sponge player C via toxic effects. Hence, our framework can provide alternative minimal mechanistic explanations for intransitive cycles of three or more players.

Solving inequalities for the minimum dimensionality

As we illustrated with the rock–paper–scissors example (Fig. 6), systems might require more than one dimension for the mechanistic explanation of their outcomes. We showed that one method to find the minimum number of dimensions is by attempting to solve a system of linear inequalities. If the system of linear inequalities is impossible, a simple strategy is to increase by one the integer number of dimensions d, and retry. The minimum $d \geq 1$ for a feasible system of inequalities is our minimum mechanistic dimensionality. In the example of Fig. 6, there were two minimal explanations: another dimension belonging to the same mode (minimal explanation I); and another dimension belonging to a new unidimensional mode (minimal explanation II). We will focus on these two extreme explanations, although there could be intermediate minimal interaction forms for more than two dimensions.

Under minimal explanation I (e.g. Fig. 6), the d dimensions must be involved in the same mode. On one hand, an observed focal goal success of pursuer A against attracter B must be the result of success in all subgoals (e.g. a successful parasite has overcome all the host defences). Specifically, the power of pursuer A in any dimension i, $P_{A,i} \geq 0$, must be greater than the toughness of attracter B in that dimension, $T_{B,i} \geq 0$: $P_{A,i} > T_{B,i}$. Since success might require more than the marginal superiority of the pursuer's power (e.g. for explaining weighted subgoal successes with power superiority proportional to the subgoal success weight), we can add a superiority threshold, $t_{A,B,i} > 0$, making the subgoal success requirement $P_{A,i} \geq T_{B,i} + t_{A,B,i}$. On the other hand, an observed focal goal failure of pursuer A against attracter B must be the result of failure in at least one subgoal (e.g. a parasite fails against at least one host defence). We can use a binary variable as an indicator of failure in dimension i, $f_{A,B,i}$ (Williams, 2013). If $f_{A,B,i} = 1$, then pursuer A fails against attracter B in subgoal dimension i; otherwise, $f_{A,B,i} = 0$, a subgoal success. The demand for a failure in at least one dimension i can be formulated with the linear inequality $\sum_{i=1}^{d} f_{A,B,i} \geq 1$. Finally, we include bounds for the power–toughness differences (Williams, 2013): the sufficiently negative lower bound of the pursuer's power inferiority in case of subgoal failure, m; and the sufficiently positive upper bound of the pursuer's power superiority in case of subgoal success, M. Thus, for an observed focal goal failure, the following couple of inequalities must be satisfied in any dimension i:

$$P_{A,i} + M f_{A,B,i} \leq T_{B,i} + M, \quad (1)$$

$$P_{A,i} - m f_{A,B,i} \geq T_{B,i} + t_{A,B,i}. \quad (2)$$

The extra inequality $\sum_{i=1}^{d} f_{A,B,i} \geq 1$ forces at least one of the indicator variables to equal one, i.e. failure in at least one subgoal. In the case of a subgoal failure in dimension i, $f_{A,B,i} = 1$, Inequality 1 is the subgoal failure requirement, and Inequality 2 is the lower bound for the pursuer's power inferiority. In case of a subgoal success, $f_{A,B,i} = 0$, Inequality 1 gives the upper bound for the pursuer's power superiority, and Inequality 2 becomes a success requirement.

Under minimal explanation II (e.g. Fig. 6), each one of the d dimensions must be involved in a different unidimensional mode. On one hand, an observed focal goal failure of any pursuer A against any attracter B must be the result of failure in all d modes, $P_{A,i} \leq T_{B,i}$ in any mode i (e.g. a parasite cannot invade via any of the alternative host entrances). On the other hand, an observed focal goal success of pursuer A against attracter B must come from success via at least one mode (e.g. a parasite successfully invaded via at least one host entrance). We now use a binary variable to indicate success via mode i, $s_{A,B,i}$. Given the same bounds as in minimal explanation I, the following couple of inequalities must be satisfied in any mode i:

$$P_{A,i} + m s_{A,B,i} \geq T_{B,i} + t_{A,B,i} + m, \quad (3)$$

$$P_{A,i} - M s_{A,B,i} \leq T_{B,i}. \quad (4)$$

With the extra inequality $\sum_{i=1}^{d} s_{A,B,i} \geq 1$, we force at least one of the indicator variables to equal one, i.e. success via at least one mode.

A complete system of linear inequalities incorporates all focal goal successes and failures of all possible pursuer–attracter pairs (see Appendix S1 in the Supporting Information for examples of complete systems of linear inequalities under minimal explanations I and II). Such systems of linear inequalities, with continuous traits and integer indicator variables, can be formulated and solved as mixed integer programming problems (Williams, 2013).

Minimum dimensionality of empirical systems

We applied the linear inequalities method to 658 empirical systems, covering six different types of ecological networks: animal social networks, food webs with basal species excluded, basal species–consumers, plant–pollinator, host–parasite, and seed dispersal networks. Considering a single

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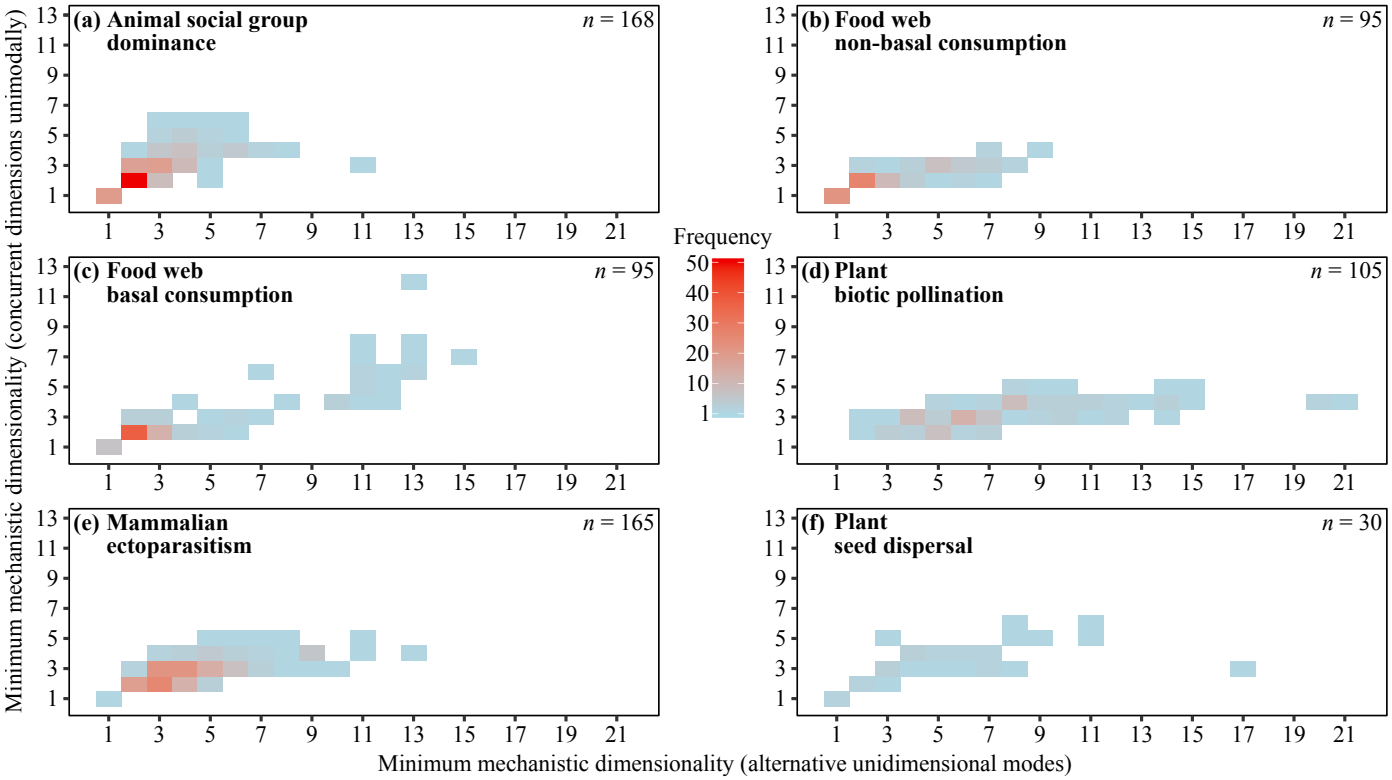

Figure 7: Minimum mechanistic dimensionality of 658 empirical systems. Each shaded cell shows the frequency of systems having the specific pair of values in our two minimum dimensionalities, that is: alternative modes of one dimension each (x-axis), and concurrent dimensions in a single interaction mode (y-axis). One focal goal was underlying each empirical system: (a) animal dominance in unipartite graphs (size range 6–31 individuals); (b) consumption of non-basal species in unipartite graphs (size range 6–57 species, basal species excluded from the original food webs); (c) consumption of basal species from consumers exclusively feeding on them in the same original food webs of (b), in bipartite graphs (size range 11–91 species); (d) plant biotic pollination in bipartite graphs (size range 8–114 species); (e) ectoparasitism of small mammals in bipartite graphs (size range 8–92 species); and (f) plant seed dispersal in bipartite graphs (size range 6–86 species). Parameters in the linear inequalities method for all systems of linear inequalities: $m = -200$; $M = 200$; $t_{A,B,i} = 1$, for all pairs of pursuer A with attracter B, in any dimension i. See Appendix S1 for methods, and Table S1 for empirical network sources, references, characteristics, and raw data for the plots.

focal goal underlying each system, and assuming adequate sampling effort (e.g. no focal goal failures due to rarity) we asked three questions about our minimum mechanistic dimensionality: (1) Is it higher under the assumption of alternative unidimensional modes, compared to the assumption of a single multidimensional mode? (2) Is it higher with goal failures included instead of excluded? (3) Is it higher than the phenomenological dimensionality developed by Eklöf *et al.* (2013)? Finding our minimum dimensionality higher for any of the three questions means that the minimum number of traits involved is underestimated when ignoring any of the three corresponding framework concepts: (1) the alternative interaction modes; (2) the trait-mediated goal failures; and (3) the mechanistic description of interactions. Our linear inequalities method incorporates to the system of linear inequalities the power–toughness constraints from all focal goal successes and failures of a network. Hence, it provides a lower bound to the number of dimensions for reproducing mechanistically all outcomes of a network under our framework. Any underestimation of the lower bound can therefore prevent network models from mechanistically generating or predicting ecological networks at the level of the individual interaction outcomes (Petchey *et al.*, 2008; Vázquez *et al.*, 2009b; Olito & Fox, 2015).

For this analysis, we computed five minimum dimensionalities in each system (see Appendix S1 for methods). Four of the dimensionalities were based on our framework, and the fifth was the phenomenological dimensionality of Eklöf *et al.* (2013). The systems of linear inequalities for our four minimum mechanistic dimensionalities were formulated and solved with the Gurobi Optimizer (Gurobi Optimization and Inc., 2017) as mixed integer programming problems (Williams, 2013). We computed the fifth dimensionality with C code (Kernighan & Ritchie, 1978) provided in the Supporting Information of Eklöf *et al.* (2013). Sources, references, characteristics, and the five minimum dimensionalities of each empirical system for Fig. 7 and Fig. 8 are provided in Table S1.

For the first question, the minimum mechanistic dimensionality was generally higher under the alternative modes explanation, shown by the overall pattern of the two minimum mechanistic dimensionalities (Fig. 7). The dimensionality assuming alternative modes (x-axes in Fig. 7) increased faster than the dimensionality assuming a single interaction mode (y-axes), especially in the systems of non-basal consumption, biotic pollination, ectoparasitism, and seed dispersal (Fig. 7b, d–f). 54% of the empirical systems had higher dimensionality assuming alternative modes, with only 7% of the systems having higher unimodal dimensionality (Fig. 8a).

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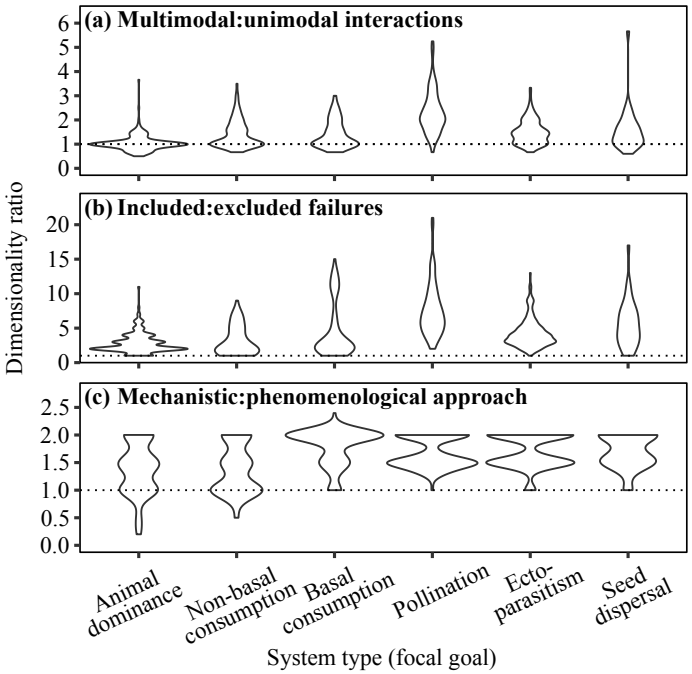

Figure 8: Three minimum dimensionality comparisons in the 658 empirical systems of our dataset (Fig. 7). For each empirical network, we calculated the ratio of: (a) our minimum mechanistic dimensionality under minimal explanation II (alternative unidimensional modes), to our minimum mechanistic dimensionality under minimal explanation I (a single multidimensional mode); (b) our minimum mechanistic dimensionality under minimal explanation II, to the same dimensionality with the failures excluded from the system of linear inequalities; and (c) our minimum mechanistic dimensionality under minimal explanation I, to the comparable minimum phenomenological dimensionality of Eklöf *et al.* (2013). Violin plots show the normalised distributions of the dimensionality ratio for the systems of each type (focal goal). The intercept of the dotted horizontal lines equals one. See Appendix S1 for methods, and Table S1 for empirical network sources, references, characteristics, and raw data for the plots.

For the second question, 92% of the empirical systems had higher minimum dimensionality with goals failures included instead of excluded (Fig. 8b). For this question, we compared our minimum multimodal dimensionality with the same dimensionality but with goal failure inequalities excluded from the linear inequalities system (Inequality 4 for subgoal failure requirements in the case of an otherwise focal goal success via at least one mode, and the subgoal failure requirements via all modes in the case of a focal goal failure). The minimum dimensionality with goal failures excluded always equals one because all pursuers can have power greater than toughness in one dimension, hence explaining any structure of only observed successes unimodally. We further restricted the formulation by requiring pursuers and attracters to compete over one trait per dimension, instead of the default power–toughness pair. In that way, the unipartite systems of animal dominance and non-basal consumption could require more than one dimension with failures excluded, but again the minimum dimensionality of bipartite systems is always equal to one. Even after the restriction to common trait competition, 84% of the unipartite systems had higher minimum dimensionality with failures included rather than excluded.

For the third question, 80% of the empirical systems had higher minimum mechanistic dimensionality compared to the phenomenological dimensionality of Eklöf *et al.* (2013). We used our minimum dimensionality under the assumption of a single mode (minimal explanation I), which is comparable to the niche approach of Eklöf *et al.* (2013). Only 6% of the unipartite systems of dominance and non-basal consumption had higher minimum dimensionality under the phenomenological approach (Fig. 8c), and none of the bipartite systems had higher minimum phenomenological dimensionality (with 95% of them having higher minimum mechanistic dimensionality).

DISCUSSION

We introduced a novel framework describing how interaction modes and traits of individuals contribute to success or failure in direct biotic interactions, organised in three stages: (1) determination of focal goals that appear to direct the interactions; (2) hierarchical decomposition of the focal goals in strategies (modes) of subgoals for success; and (3) explanation of the subgoal outcomes by the pairwise comparison of traits. Each stage has a main corresponding consequence: (1) a focal goal failure is an outcome of interaction; (2) there can be alternative modes for focal goal success; and (3) the inequality rule can handle difference, and matching traits—after reformulating them to difference traits—as described below. We thereafter discuss the plausibility of the stages and their conceptual consequences.

The foundational concept of the framework is the 'goal', and we explicitly incorporate failure to obtain goals. The 'focal goal success' outcomes in our framework are the 'interactions' typically described in the literature (Vázquez *et al.*, 2009a; Poisot *et al.*, 2015; Bartomeus *et al.*, 2016); and our 'focal goal failure' outcomes are synonymous to the 'forbidden links' or 'forbidden interactions' of some authors (Jordano *et al.*, 2003; Morales-Castilla *et al.*, 2015). Under our framework, players interact given their mere inclusion in the study system, even if they never actually meet. Commonly, behavioural studies employ a few predictor traits for the explanation of only the observed dominance events in a system (Chase & Seitz, 2011), i.e. explanation of only the focal goal successes. In contrast, we found that three to six pairs of competing traits must be involved in several dominance systems (Fig. 7a). For example, in the elephant family named 'AA' in Archie *et al.* (2006), almost all observed dominance events are towards younger elephants, and the authors conclude the system is a unidimensional (age-ordered) dominance hierarchy based only on the successes, in agreement with our result of one required dimension when goal failures are excluded (Fig. 8b). Our minimum mechanistic dimensionality, explicitly incorporating focal goal failures, suggests three dimensions for this system under both minimal explanations, because there are several older–younger pairs where no dominance or aggression was observed, i.e. focal goal failures unexplained by Archie *et al.* (2006). In other words, our framework predicts mechanisms preventing these older elephants from dominating the specific younger family members. Most elephants dominated only younger members of their matriline, and of two specific matrilines (Archie *et al.*, 2006). These two preferences are candidates for the two extra dimensions that we expect under our framework, which are lost when ignoring focal

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goal failures.

A potential issue in the second framework stage (mapping the interactions to a standardised form) is the seemingly arbitrary creation of the goal hierarchy. Our goal hierarchy concept comes from Wainwright's 'hierarchical nature of performance' (Wainwright, 2007). Higher performance breaks down to lower level performance subtraits, breaking down further to morphological, physiological, behavioural, and phenological performance subtraits. For example, a phage's higher performance in exploiting a bacterium depends on its ability to attach on a bacterium, which depends on the phage's possession of tail proteins able to bind to specific bacterial receptors (Dy *et al.*, 2014). In each level, performance corresponds to a task, function, goal in our terms (e.g. 'performance in exploiting a bacterium'). Consequently, there must be a correspondence between the traits and subtraits of a performance trait hierarchy, and the goals and subgoals of a goal hierarchy. Studied traits are chosen based on the question, the biological level of interest, and the methods and resources at hand (Wagner, 2001). The corresponding goals and subgoals can be chosen similarly, for the creation of the underlying goal hierarchy.

With the conversion of the goal hierarchy to the interaction form, we were able to incorporate explicitly the feature of alternative interaction modes observed empirically (Fig. 1b). In previous theoretical trait-based works, an exploiter has to overcome all the barriers or defences of a potential resource to consume or parasitise (Santamaría & Rodríguez-Gironés, 2007; Gilman *et al.*, 2012; Débarre *et al.*, 2014; Speed *et al.*, 2015). Other theoretical works adopt one of the four principal versions of the 'ecological niche' concept (Schoener, 1989), i.e. its 'resource-utilisation' approach (MacArthur & Levins, 1967). In the niche approach, the niche dimensions act in conjunction to determine the characteristics of the exploited resources (Stouffer *et al.*, 2006; Allesina *et al.*, 2008; Eklöf *et al.*, 2013). The 'mode' in our framework is equivalent to these two approaches, since a pursuer's performance must be sufficiently high in all the subgoals of a mode. Based on this equivalence, we found that our minimum mechanistic dimensionality was frequently higher than the phenomenological dimensionality in the niche approach of Eklöf *et al.* (2013) (Fig. 8c). Thus, we showed that a phenomenological approach assuming a single mode can frequently underestimate the minimum dimensionality of ecological networks. With our generalisation to alternative modes, we furthermore showed that minimum dimensionality can be underestimated even mechanistically under the assumption of a single instead of multiple interaction modes (Fig. 8a). In general, our framework introduces the possibility of alternative explanations for the outcomes in a system depending on how modes are assumed to be involved in the interactions. As in Fig. 6, this idea of alternative assumptions and explanations could offer a new mechanistic perspective in the study of intransitive networks (Durrett & Levin, 1997; Frean & Abraham, 2001; Czárán *et al.*, 2002; Kerr *et al.*, 2002; Reichenbach *et al.*, 2007; Szolnoki *et al.*, 2014; Kelsic *et al.*, 2015).

For the third framework stage (of explaining the subgoal outcomes), we adopted a phenotype space instead of a niche space approach. One problem with the niche approach is the loss of mechanistic information (as shown in Fig. 8c), when dimensions originate phenomenologically, or abstractly from multiple trait-axes ordination (Eklöf *et al.*, 2013). For example, body size is a trait with high explanatory power in food webs (Stouffer *et al.*, 2011). However, more traits allometrically scaling with body size are mechanistically involved in trophic interactions (Woodward *et al.*, 2005). Even mechanistically, realised niches commonly span a range of the resource gradient (MacArthur & Levins, 1967; Levins, 1968), hiding two traits per niche dimension (one for each extreme of the niche range). For example, with the maximum of the prey size range limited by the predator's mouth gape, the niche range minimum must be limited by a second predator trait, like the predator's inability to capture or handle smaller prey. Another problem is that exploiters might have no place in the niche space because it is created by trait dimensions of the resources (MacArthur & Levins, 1967; Schoener, 1989), and resource traits can be irrelevant for exploiters (e.g. plant traits for herbivores). Our framework takes into account the traits of both interacting players simultaneously, and a dimension is simply a challenged trait-axis in the phenotype space of pursuers or attracters. Apart from its simplicity, the established phenotype space approach (Dietrich & Skipper Jr., 2012; Pigliucci, 2013) can be adopted to study, for instance, trade-offs in traits used in different subgoals, interaction modes, or focal goals (Arnold, 1983; Ghalambor *et al.*, 2003; Fontaine *et al.*, 2011; Shoval *et al.*, 2012; Pilosof *et al.*, 2017).

The inequality rule at the third framework stage is applicable to various types of traits. Continuous-valued quantitative traits can be modelled directly (e.g. the animal reaching nectar in Fig. 4). Comparison of traits with ordered levels (binary, semiquantitative, and quantitative but discontinuous, Legendre & Legendre, 1998) can be modelled with appropriate scaling (e.g. degree of egg similarity versus degree of discrimination ability for the bird brood parasitism example in Fig. 4). Categorical qualitative traits can be redefined to binary traits (e.g. the prey qualitative trait with categories 'diurnal' or 'nocturnal' was redefined to a binary trait for presence–absence of activity during the day in Fig. 4). Moreover, the inequality rule can model both cases of competing traits (Abrams, 2000; Santamaría & Rodríguez-Gironés, 2007; Nuismer *et al.*, 2013): difference traits (also called barrier traits, or unidirectional axes of vulnerability), and matching traits (complementarity traits, or bidirectional axes of vulnerability). The natural case in our framework is the difference traits, since larger power–toughness difference contributes to success. However, if we state the subgoals appropriately, matching traits can be reformulated as difference traits. In the brood parasitism example of Fig. 4, we could have compared the eggs of parasite and host as matching traits, because parasite eggs more similar to the host eggs contribute to parasitism success. Instead, we compared as difference traits the similarity of parasite eggs to the ability of the host to recognise them. Another example is the difference traits formulation for the temporal match of predator and prey during the day (Fig. 4).

Hence, the three framework stages and their main conceptual consequences exhibit generality and plausibility: from the focal goals and the trait-mediated failures, to the goal hierarchy and the alternative interaction modes, to the pursuer–attracter phenotype spaces and the modelling of different types of competing traits.

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CONCLUSION AND FUTURE DIRECTIONS

By incorporating all four features of the empirical description of interactions explicitly (Fig. 1), our framework can support more comprehensive and mechanistic trait-based approaches to proximate and evolutionary questions. For proximate questions, it encourages the systematic description of empirical systems as networks, in a standardised and hence comparable form. Theoretical investigations could benefit from the novel conceptual consequences, e.g. including alternative interaction modes in trait-based models of animal social network dynamics (Pinter-Wollman *et al.*, 2014). For evolutionary questions, it can inspire new hypotheses, e.g. about the reasons for redundancy in strategies, defences, or performance in empirical systems, compared to alternative minimal systems from our theoretical application of minimum mechanistic dimensionality.

We introduced this framework assuming constant performance, determinism in the power–toughness competition, and qualitative (success–failure) trait competition outcomes. In future extensions, power and toughness performance could be variable, e.g. function of climatic or other environmental variables (Ockendon *et al.*, 2014; Poisot *et al.*, 2015), goal success could follow probabilistically (Poisot *et al.*, 2016), e.g. as an increasing function of the power–toughness difference, and quantitative outcomes in weighted networks could be explained by power–toughness differences. Assuming adequate sampling effort, our mechanistic description has not considered in this first account the effects of: interactions on individual fitness or population growth (Burkholder, 1952; Hamilton, 1964); phylogenetic relationship (Rohr & Bascompte, 2014; Eklöf & Stouffer, 2016); and abundance (Vázquez & Aizen, 2003; Vázquez *et al.*, 2009a; Cagnolo *et al.*, 2011). However, it can dictate how players interact mechanistically, for example: in game theoretical models with interaction payoffs (Archetti *et al.*, 2011); in coevolutionary models with phylogenetic history (Manceau *et al.*, 2017); and in spatial models with interacting dispersers or foragers, for the effect of neutrality on community assembly or invasion (Morales & Vázquez, 2008). We hope further development and testing of this framework will open new research paths, and give fresh insight into previous work dealing with ecological systems in a trait-based approach.

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