TITLE

Incorporating trait-based mechanisms, alternative interaction modes and forbidden links increases the minimum dimensionality of ecological networks

RUNNING TITLE

Networks' minimum mechanistic dimensionality

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ABSTRACT

1. Multiple traits are involved in intra- and interspecific interactions, influencing interaction outcomes and community structure. Knowing the minimum number of traits required to explain observed network structures, i.e. the 'minimum dimensionality', can help us to focus on key biological questions. Existing theoretical methods for estimating minimum dimensionality are often simplified in three ways: (*i*) they are phenomenological, (*ii*) they lack the ubiquitous feature of alternative interaction (e.g. feeding) modes, (*iii*) they do not consider phenological and/or phenotypic mismatches, known as 'forbidden links'. Here we develop a method to estimate the 'minimum mechanistic dimensionality' of ecological networks, which can assume alternative interaction modes and account for forbidden links.

2. Our method compares the performance of traits, e.g. predator mouth gape versus prey body size. A system of linear inequalities—making assumptions of how traits are involved in alternative interaction modes—is constructed to explain the observed interaction outcomes. We attempt to solve these inequalities with mixed integer linear programming. Minimum mechanistic dimensionality is the minimum number of traits required for a feasible system of inequalities. We illustrate how the inclusion of alternative interaction modes alters the explanation of an intransitive 'rock–paper–scissors' system of competing marine invertebrates. We apply our method to 658 published empirical ecological networks—including animal dominance, predator–prey, primary consumption, pollination, parasitism and seed dispersal networks—to determine whether minimum dimensionality estimates change following the inclusion of concepts emerging from our framework, i.e., alternative interaction modes, trait-mediated 'forbidden links' and a mechanistic approach to describing trait-based interactions.

3. The minimum mechanistic dimensionality was typically higher in ecological networks when including alternative interaction modes (54% of empirical networks),

‘forbidden interactions’ as trait-mediated interaction outcomes (92%), or a mechanistic perspective (81%), compared to dimensionality estimates in the absence of these features.

4. Our method can inform us about how many traits are mechanistically involved in pairwise interactions, to generate theoretical networks of more accurate structure at the interaction outcome level. In general, it can reduce the risk of omitting essential traits, for improved understanding, explanation, and prediction of community structures, and structure-dependent community, ecosystem, and evolutionary processes.

KEYWORDS

Species interactions, trait-based mechanisms, niche space, phenotype space, food web intervality, multilayer ecological networks, mutualism, trophic interactions, social networks, cyclic rock–paper–scissors intransitive game.

1 INTRODUCTION

Understanding community structure can improve our predictions of structure-dependent population dynamics (Berlow et al., 2009), evolution (Becerra, 2003), ecosystem processes (Woodward, Papantoniou, Edwards, & Lauridsen, 2008), and conservation (Mello et al., 2015). Communities are structured by different forces, including evolution; spatio-temporal distribution of species due to neutral, historical, dispersal, or habitat filtering processes; interaction neutrality; and traits (Bartomeus et al., 2016; Poisot, Stouffer, & Gravel, 2015; Vázquez, Chacoff, & Cagnolo, 2009). A useful representation of the structure of interactions is through network approaches (Delmas et al., 2019; Newman, 2003). Focusing on the contribution of traits in interaction networks, i.e. of how individuals interact via a subset of their phenotypic characters, allows us to ask what the minimum number of traits is that must be involved given the interaction outcomes we observe, hereafter called 'minimum dimensionality'. The minimum dimensionality of a system can concentrate our efforts on investigating which traits underpin community structure (Eklöf et al., 2013).

A mechanistic method for estimating the minimum dimensionality of an interaction network must make assumptions about how interactions are expected to occur. Interactions in different systems appear to share four common features: (1) interactions can be of various types within a system, from cooperative and mutualistic, to antagonistic or victim–exploiter interactions, within or between species; (2) alternative modes can lead to a successful outcome in a given type of interaction, such as the different signals which plants use to attract pollinators (Schiestl & Johnson, 2013), novel pathways to bacterial infection (Meyer et al., 2012), alternative combative mechanisms employed in fungal competition for space (Boddy, 2000), and different feeding modes (Kiørboe, 2011); (3) multiple tasks may need to be completed for success via a given interaction mode, e.g., the encounter–detection–identification–approach–subjugation–consumption steps of a typical predation sequence (Endler, 1991); and (4) for a specific task, the traits involved are measurable, competing features of the interacting players

(McGill, Enquist, Weiher, & Westoby, 2006): physiological (e.g. plant–herbivore toxin versus detoxification enzyme concentrations), morphological (e.g. animal–plant proboscis length versus depth of nectar in floral tube), behavioural (e.g. cheating versus punishment in cleaner–client fish), and phenological (e.g. predator–prey temporal presence versus absence). Here, we attempt to combine all four of these features in a single framework for the first time.

Despite the accumulated empirical knowledge about how interactions occur, the two available methods to estimate minimum dimensionality lack a mechanistic perspective, or an explicit incorporation of the widespread feature of alternative interaction modes. Eklöf et al. (2013) developed a method for estimating minimum dimensionality in different interaction types, rooted in the theory of food web intervality in niche space (Cohen, 1977). In this method, dimensions originate phenomenologically, each dimension potentially accounting for multiple traits. Dalla Riva and Stouffer's (2016) minimum dimensionality method avoids this approach by adopting a simple trait space representation for trophic interactions. Network structure is explained mechanistically here by explicitly modelling exploiter–resource interactions via trait matching. However, Dalla Riva and Stouffer (2016) model interactions via a single interaction mode, since the contributions act additively from each exploiter–resource trait pair. The same focus on a single interaction mode appears in Eklöf et al. (2013), because niche dimensions act in conjunction to determine the niche of the exploiter (resource).

Here, we aimed to develop a new method for estimating the minimum number of traits required to explain the interaction outcomes across a broad range of ecological networks. This 'minimum mechanistic dimensionality' method encompasses all four features of interactions outlined by empirical studies, within a simple phenotypic trait space representation. We ask if our minimum dimensionality estimate is higher than other approaches across a range of different empirical ecological network types: under the assumption of alternative interaction modes compared to a single mode; with failure outcomes taken into account instead of omitted; and under its mechanistic perspective compared to the minimum dimensionality

under the phenomenological, niche approach of Eklöf et al. (2013). We show that essential traits can be missed from ecological networks because the lower bound of the number of traits involved in 658 empirical systems we interrogated was frequently underestimated by omitting the presence of alternative interaction modes, the trait-mediated failure outcomes, and the mechanistic involvement of traits competing in pairs.

2 METHODS

Here, we outline our general approach using empirical examples based on a nectarivory network and an intransitive system of competing marine invertebrates. We describe the interactions among species in the context of exploiter and resource roles, before going on to define and calculate the minimum mechanistic dimensionality of these networks using a linear inequalities method. We then describe how we compared competing minimum dimensionality estimates across 658 empirical examples, ranging from social hierarchies, to mutualistic networks, to food webs.

2.1 A generalised mechanistic description of how interactions occur

We illustrate our mechanistic description with an empirical plant–animal system of two interaction types, reported in Kennedy (1978): nectarivory pursued by four animal species, and biotic pollination pursued by a plant species (Fig. 1). For nectarivory, the animals are the exploiters, and the plant the resource; for pollination, the plant is now considered the exploiter, and the animals the resources. This system can be represented by two bipartite exploiter–resource graphs, regarded as two layers of a multilayer network (Kivelä et al., 2014). There are four possible pairwise interaction outcomes: the plant is pollinated and an animal exploits the plant's nectar; neither the plant nor an animal succeed in exploiting the other; the plant is not pollinated, but its nectar is exploited; or the plant is pollinated, and its

nectar is not exploited. Note that nectarivory and pollination failures are also considered interaction outcomes in our description.

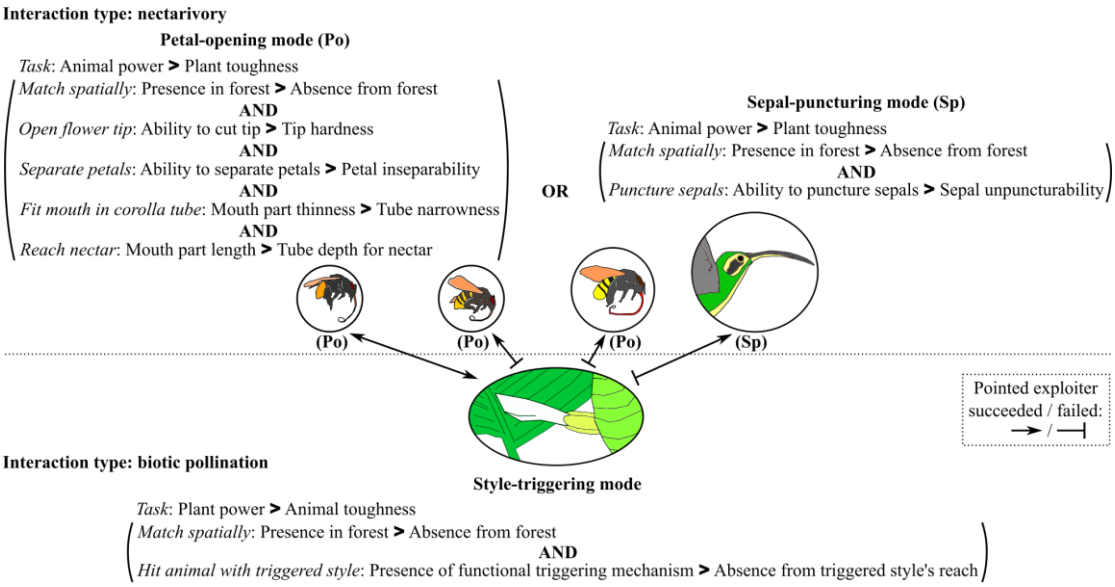

FIGURE 1 The mechanistic description of interactions applied to an empirical system (lowland wet forest near Puerto Viejo, Heredia, Costa Rica, described in Kennedy, 1978). From left to right, the animals reported are the three Euglossine bees *Eulaema speciosa*, *E. seabrai*, and *E. meriana*, and the hummingbird is *Phaethornis longirostris*. The plant species is the closed-flowered *Calathea marantifolia* (a closed, white flower is shown in the species token). The interaction modes via which animals succeed are given in parentheses next to the outcomes indicated by arrows. We show only some indicative tasks in the modes, for the sake of illustration. Species token size indicates the relative size of the representative individual.

Successful nectarivory or pollination outcomes could occur via alternative modes. For instance, the animals adopt two alternative modes of achieving nectarivory: accessing nectar either by opening petals or puncturing sepals (Fig. 1). Success in a given mode may require success in multiple tasks. For example, the petal-opening nectarivory mode requires success in at least five tasks (Fig. 1). For a success in a task, an exploiter's performance in a trait, termed 'power', must be sufficiently higher than the resource's performance in a corresponding trait called 'toughness' (taken from the creature combat rules of the card game *Magic: The Gathering*® in Garfield, 2017). We consider that exploiter and resource are

challenged in one trait ‘dimension’ of their phenotype space, where the performance of the corresponding power–toughness traits compete to determine who succeeds in that task. Using Boolean logic terms, modes can be represented as OR-associated clauses of AND-associated tasks. Any structure of logical statements can be equivalently expressed in this ‘disjunctive normal form’ (Cohn, 2003), herein termed ‘interaction form’.

2.2 The minimum mechanistic dimensionality of ecological networks

In the nectarivory example above, the animals succeeded via two alternative modes, one five-dimensional (one spatial and four morphological traits for the bees), the other two-dimensional (one spatial and one morphological trait for the hummingbird) (Fig. 1). Minimally, we could observe these four animal successes in nectarivory via a one-dimensional mode: all animals could ‘easily’ consume nectar from a plant with open, wide and short flowers just because of spatial matching with the flowered plant. In other words, if this system was mechanistically minimal, the same outcomes would have occurred only because of interactions in one exploiter–resource dimension. Thus, the idea behind our method 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 employed by the players. In the example illustrated in Fig. 1, the plant imposed six exploitation barriers (*sensu* Santamaría & Rodríguez-Gironés, 2015), challenging the animals in six dimensions instead of the theoretically required one dimension.

2.2.1 Rock–paper–scissors: an intransitive network with marine invertebrates

The success of the animals at the empirical plant–animal system in Kennedy (1978) could minimally arise by interactions in one pair of exploiter–resource trait dimensions. However,

one dimension is not sufficient to mechanistically explain the outcomes of an intransitive network of outcomes between three (or more) species, such as the cyclic spatial replacement of marine invertebrates studied by Jackson and Buss (1975): an ectoproct species *Stylopoma spongites* (player *A*) replaces a sponge species *Tenaciella* sp. (player *B*), which in turn replaces sponge species *Toxemna* sp. (player *C*), and which in turn replaces the ectoproct species player A. We consider all three species both exploiters and resources in spatial replacement (Fig. 2).

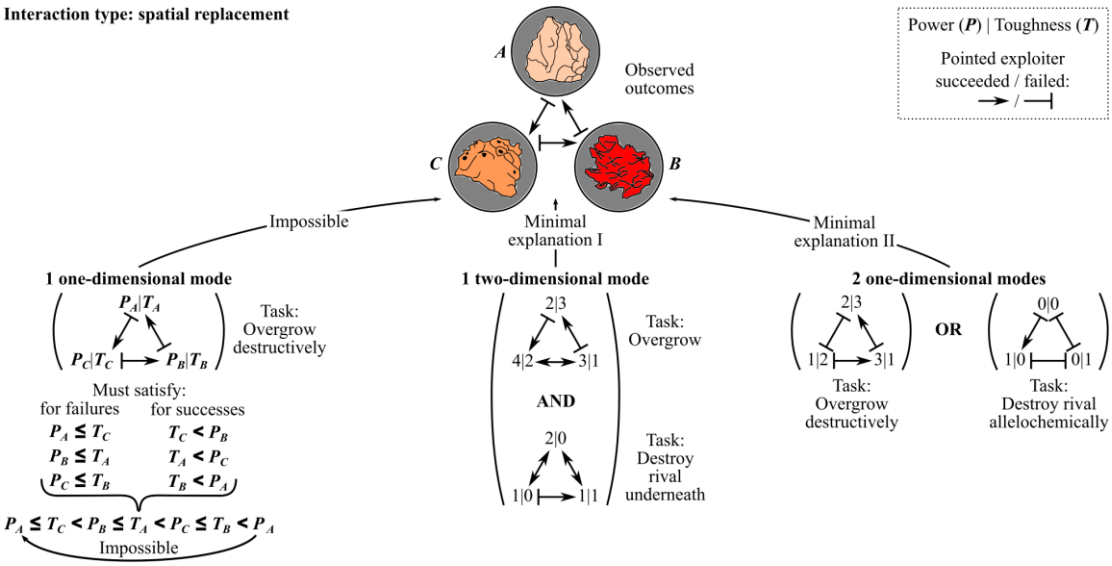

FIGURE 2 The mechanistic explanation of outcomes of an intransitive three-player interaction in a rock–paper–scissors empirical system requires at least two exploiter–resource trait pairs, i.e. two dimensions. The empirical system is reported in Jackson and Buss (1975), with three encrusting invertebrate 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 minimally explain the observed outcomes, with the first attempt being mechanistically impossible. We indicate hypothetical tasks, and power | toughness trait scores in arbitrary units of performance.

It is impossible to explain the observed outcomes in this unipartite graph with interactions via a one-dimensional interaction mode. The single pair of exploiter–resource power–toughness traits is involved in a system of six inequalities, to satisfy the observed successes and failures. For the successful replacements, the power of a winning exploiter must be greater than the

toughness of a defeated resource. For the failures, the power of a losing exploiter must be less than or equal to the toughness of an undefeated resource. This system of six linear inequalities creates a cyclic sequence of ever-increasing power–toughness scores (the impossible '1 one-dimensional mode' in Fig. 2).

Our framework provides two alternative minimal mechanistic explanations for the emergence of a rock–paper–scissors system. First, we can find solutions if we add a second pair of power–toughness traits in the same mode (Fig. 2). We explain the 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 dimension (e.g. destruction of rival, even if *C* can overgrow *B*). Second, we can find solutions if we add a second pair of power–toughness traits in a new one-dimensional mode (Fig. 2). In that case, we explain the success of *A* and *B* as success via the first mode (e.g. destructive overgrowth), and the success of *C* as success via a second mode (e.g. allelochemical elimination). Minimal explanation II is described by Jackson and Buss (1975) for this cryptic reef system: player *A* replaces *B* via overgrowth, player *B* replaces *C* via overgrowth, but player *A* is replaced by *C* due to toxic effects. Appendix S1 in the Supporting Information includes the complete systems of linear inequalities for rock–paper–scissors under minimal explanations I and II.

2.2.2 The linear inequalities method for calculating the minimum mechanistic dimensionality

As illustrated with the rock–paper–scissors example (Fig. 2), systems might require more than one pair of exploiter–resource competing traits for their outcomes to be explained mechanistically. One method to find this 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 the number of dimensions (d) by one, and retry. The minimum $d \geq 1$ for a feasible system of inequalities is our minimum mechanistic dimensionality. In the marine invertebrates example of Fig. 2, there were two minimal explanations: an additional

trait pair belonging to the same mode (minimal explanation I); or belonging to a new one-dimensional 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.

When a new task is added to a single mode, that permits feasibility of the system of linear equalities, the *d* exploiter–resource trait pairs (dimensions) must be involved in the same mode (minimal explanation I, Fig. 2). On one hand, an observed success of exploiter *A* against resource *B* must be the result of success in all tasks (e.g. a successful parasite has overcome all the host defences). Specifically, the power of exploiter *A* in any trait pair *i*, $P_{A,i} \geq 0$, must be greater than the toughness of resource *B* in that trait pair, $T_{B,i} \geq 0$: $P_{A,i} > T_{B,i}$. Since success might require more than the marginal superiority of the exploiter's power, we can add a superiority threshold, $t_{A,B,i} > 0$, making the task success requirement $P_{A,i} \geq T_{B,i} + t_{A,B,i}$. On the other hand, an observed failure of exploiter *A* against resource *B* must be the result of failure in at least one task (e.g. a parasite fails against at least one host defence). We can use a binary variable as an indicator of failure in trait pair *i*, $f_{A,B,i}$ (Williams, 2013). If $f_{A,B,i} = 1$, then exploiter *A* fails against resource *B* in trait pair *i*; otherwise, $f_{A,B,i} = 0$, representing exploiter success in the task. The demand for a failure in at least one trait pair *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 for computational efficiency (Williams, 2013): a sufficiently negative lower bound of the exploiter's power inferiority in case of task failure, *m*; and a sufficiently positive upper bound of the exploiter's power superiority in case of task success, *M*. Thus, for an observed failure, the following pair of inequalities must be satisfied in any trait pair *i*:

$$P_{A,i} + M\, f_{A,B,i} \leq T_{B,i} + M, \tag{1}$$

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

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

When a new one-dimensional mode is added, permitting a feasible system (minimal explanation II, Fig. 2), each of the d pairs of competing exploiter–resource traits must be involved in a different mode. On one hand, the observed failure of any exploiter A against any resource 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, the observed success of exploiter A against resource B must come from success via at least one mode (e.g. a parasite invades via at least one host entrance). We now use a binary variable, $s_{A,B,i}$, to indicate success via mode i. Given the same bounds as in minimal explanation I, the following pair of inequalities must be satisfied to indicate exploiter success in any mode i:

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

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

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. exploiter success occurs via at least one mode.

A complete system of linear inequalities incorporates all observed successes and failures of all possible exploiter–resource 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 trait values and integer indicator variables, can be formulated and attempted to be solved as mixed integer linear programming

problems (Williams, 2013). In both minimal explanations (I and II), minimum mechanistic dimensionality is the minimum *d* leading to a feasible system of inequalities.

2.3 Comparing the minimum dimensionality of empirical networks

We applied our method to 658 empirical systems, covering six different types of ecological networks: animal social dominance networks, food webs with basal species excluded, basal–consumer, plant–pollinator, host–parasite, and seed dispersal networks (see Appendix S1 for details). Considering a single interaction type in each system, and assuming adequate sampling effort (e.g. no observed failures due to rarity), we computed five dimensionality measures (Appendix S1). Four minimum mechanistic dimensionality measures were based on our framework: (*a*) a single, potentially multidimensional mode; (*b*) potentially multiple, one-dimensional modes; (*c*) as measure (*b*), but excluding observed failures; (*d*) as measure (*c*) but with players interacting via a common trait per dimension, rather than a power against toughness trait. The fifth dimensionality measure we considered (*e*) was the phenomenological measure of Eklöf et al. (2013). We used these five dimensionality measures to answer three questions about minimum mechanistic dimensionality (MMD): (1) Is MMD higher under the assumption of alternative one-dimensional modes (dimensionality measure *b*), compared to the assumption of a single multidimensional mode (dimensionality measure *a*)? (2) Is MMD higher with observed failures taken into account (dimensionality *b*), or excluded (dimensionality *c* or *d*)? (3) Is MMD higher than the phenomenological dimensionality measure developed by Eklöf et al. (2013) (dimensionality *a* versus *e*)?

The systems of linear inequalities for our four minimum mechanistic dimensionality measures were formulated and solved with the Gurobi Optimizer (Gurobi Optimization and Inc., 2017) as mixed integer linear programming problems (Williams, 2013). R and Python code for formulating and solving for these four minimum mechanistic dimensionalities are provided (DATA ACCESSIBILITY). We computed the fifth dimensionality with code provided in the

Supporting Information of Eklöf et al. (2013). The references we provide for the empirical networks (DATA ACCESSIBILITY) were retrieved from five data sources (Cohen, 2010; Ortega, Fortuna, & Bascompte, 2017; Shizuka & McDonald, 2015; Stanko & Miklisova, 2014; Thompson & Townsend, 2004). Additionally, we provide characteristics, and raw data from the five computed dimensionality measures, for each of the 658 empirical systems (DATA ACCESSIBILITY).

3 RESULTS

For the five dimensionality measures we considered, the inclusion of alternative interaction modes, forbidden links and a mechanistic approach to describing interactions consistently increased the minimum dimensionality estimate across a wide range of empirical ecological networks.

3.1 Multimodal versus unimodal minimum mechanistic dimensionality

Our minimum mechanistic dimensionality was frequently higher under the alternative modes explanation than under the single mode explanation (Fig. 3). The dimensionality assuming alternative modes (horizontal axes in Fig. 3) increased faster than the dimensionality assuming a single interaction mode (vertical axes in Fig. 3), especially in the systems of non-basal consumption, biotic pollination, ectoparasitism, and seed dispersal (Fig. 3b,d–f). 54% of the empirical systems had higher dimensionality if alternative modes were assumed, with only 7% of the systems having higher unimodal dimensionality (Fig. 4a).

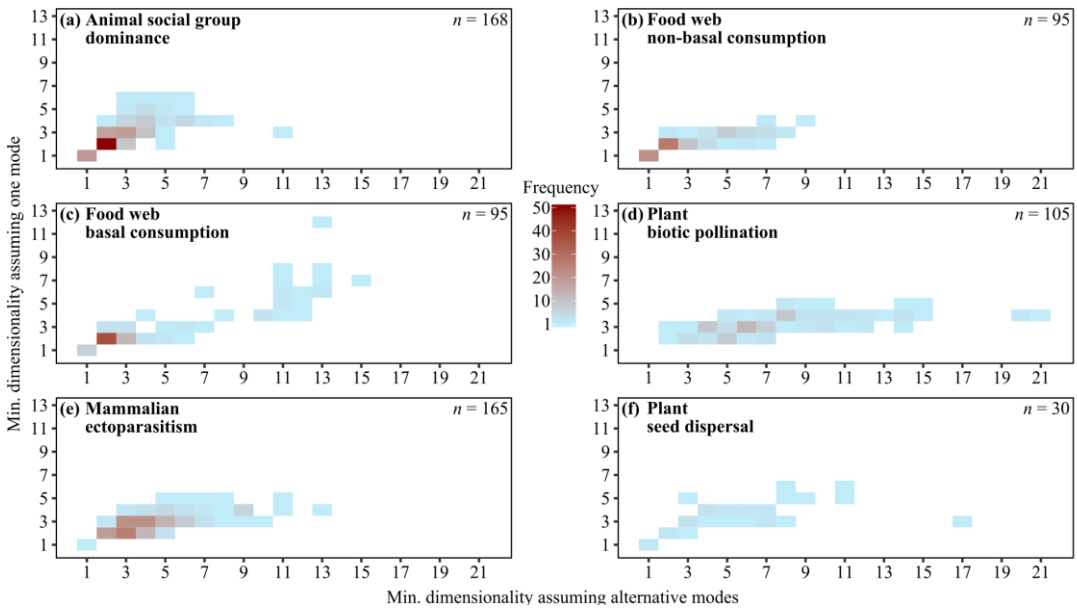

FIGURE 3 Minimum mechanistic dimensionality estimates from 658 empirical systems. Cell shading shows how many of the *n* systems had the specific pair of values in our two minimum dimensionality measures, i.e. number of exploiter–resource trait pairs in: alternative one-dimensional modes (x-axis; minimal explanation II); a single mode (y-axis; minimal explanation I). We focused on one interaction type in each empirical system: (a) animal dominance in unipartite graphs (6–31 individuals); (b) consumption of non-basal species in unipartite food web graphs (6–57 species, basal species excluded from the original food webs); (c) consumption of basal species by consumers exclusively feeding on them in bipartite graphs (11–91 species; from the same food webs used in (b)); (d) plant biotic pollination in bipartite graphs (8–114 species); (e) ectoparasitism of small mammals in bipartite graphs (8–92 species); and (f) plant seed dispersal in bipartite graphs (6–86 species). Parameter values in the linear inequalities method: $m = -200$; $M = 200$; $t_{A,B,i} = 1$, for all pairs of exploiter *A* with resource *B*, in any trait pair *i*.

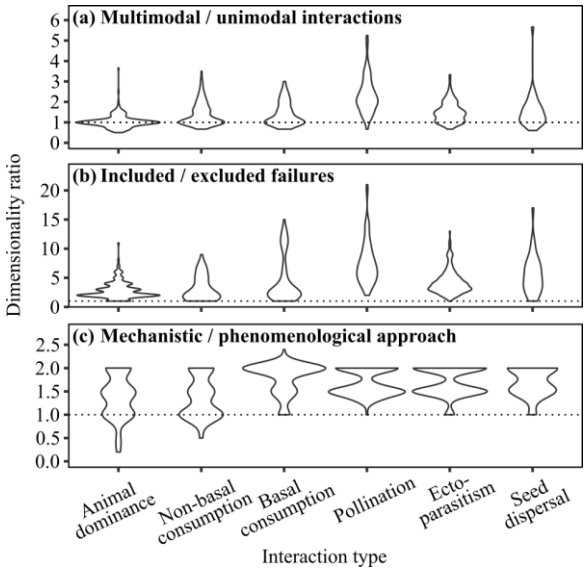

FIGURE 4 Comparisons of three minimum dimensionality measures estimated from 658 empirical systems. For each empirical network, we calculated the ratio of: (a) our minimum mechanistic dimensionality under minimal explanation II (alternative one-dimensional modes), to our minimum mechanistic dimensionality under minimal explanation I (a single 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 phenomenological dimensionality of Eklöf et al. (2013). Violin plots show the normalised distributions of the dimensionality ratios. The dotted horizontal lines give the ratio of one.

3.2 Minimum mechanistic dimensionality with failure outcomes taken into account versus excluded

Minimum mechanistic dimensionality was higher in 92% of the empirical systems when failure outcomes were included, instead of excluded (Fig. 4b). In the rest of the empirical systems, the two dimensionality estimates were equal. Here, we compared our minimum multimodal dimensionality with the same dimensionality but with any failure inequalities excluded from the inequalities system. The minimum dimensionality with failures excluded always equals one because all exploiters can have a single power trait with value greater than the value of the single toughness trait of any resource, in the absence of any inequalities constraining the power scores, hence explaining any structure of only observed successes

unimodally. We further required that exploiters and resources possess the same trait for power and toughness in the unipartite systems of animal dominance and non-basal consumption, instead of the default power–toughness trait pair. In that way, the unipartite systems could require more than one dimension with failures excluded. Even in this case of modelling trait competition with a single, common trait per dimension, 79% of the unipartite systems had higher minimum dimensionality with failures included rather than excluded.

3.3 Mechanistic versus phenomenological minimum dimensionality

In 81% of the empirical systems, our minimum mechanistic dimensionality was higher than the phenomenological dimensionality estimate of Eklöf et al. (2013). We assumed a single mode (minimal explanation I), which is comparable to the niche approach of Eklöf et al. (2013). Only 2% of the networks had higher minimum dimensionality under the phenomenological approach, with no bipartite networks among them (Fig. 4c).The minimum number of trait pairs for the explanation of all outcomes in our approach, was 1.5 times larger (median) than with the phenomenological dimensionality across all networks. Note that since our dimensionality refers to exploiter–resource trait pairs, the actual number of necessary traits is double our dimensionality, i.e. the present approach suggested a median of 3 times more traits required for the explanation of the observed outcomes than the Eklöf et al. (2013) approach.

4 DISCUSSION

We introduced a method for calculating the minimum number of traits required to explain all observed interaction outcomes of an ecological network mechanistically, using a general framework which is applicable to different interaction types, modes, tasks, and types of traits. Applying our method to 658 empirical systems, we showed that the minimum number of traits involved is typically underestimated when ignoring any of the three framework features

we combined here for the first time: (1) alternative interaction modes; (2) trait-mediated failure outcomes; and (3) a mechanistic description of interactions.

With our generalised framework, minimum mechanistic dimensionality can explicitly incorporate the alternative interaction modes observed empirically, e.g. alternative feeding modes. In previous theoretical trait-based works, an exploiter has to overcome all the barriers or defences of a potential resource to consume or parasitise the resource (Gilman, Nuismer, & Jhwueng, 2012; Santamaría & Rodríguez-Gironés, 2007); similarly, in other theoretical works adopting a niche approach, a niche arises from the intersection of all niche dimension intervals (Eklöf et al., 2013; Stouffer, Camacho, & Amaral, 2006). The interaction mode in our framework is equivalent to these two approaches, since an exploiter's performance must be sufficiently high in all the mode's tasks. By additionally generalising to alternative interaction modes, we showed that minimum mechanistic dimensionality can differ, frequently being larger under alternative interaction modes than in a single mode (Fig. 4a). Additionally, different assumptions about the interaction form can lead to alternative minimal explanations of the outcomes, as in rock–paper–scissors systems (Fig. 2), offering a new mechanistic perspective in the study of intransitive networks (Szolnoki et al., 2014).

We adopted a phenotype rather than a niche space representation of traits. Studies of interactions commonly use the 'resource-utilization' approach to representing the 'ecological niche' concept (MacArthur & Levins, 1967, Schoener, 1989). Despite its operational advantage (Schoener, 1989), dimensions usually arise phenomenologically, as in the minimum dimensionality of Eklöf et al. (2013). For example, body size is a trait with high explanatory power in food webs (Stouffer, Rezende, & Amaral, 2011). However, more traits allometrically scaling with body size are mechanistically involved in trophic interactions (Woodward et al., 2005). Even if taken mechanistically, realised niches commonly span a range of the resource gradient (MacArthur & Levins, 1967), implying two traits per niche dimension. For instance, with the maximum prey size range limited by a predator's mouth

gape, the niche range minimum must be delimited due to a second trait, like the predator's inability to handle smaller prey. Another problem is that exploiters are excluded from the niche space because it is created by trait dimensions of the resources (MacArthur & Levins, 1967; Schoener, 1989). Our framework accounts for the traits of both interacting players simultaneously, and a dimension is simply a challenged trait-axis in the phenotype space of exploiters and resources, as in the approach of Dalla Riva and Stouffer (2016). In that way, we found that our minimum mechanistic dimensionality assuming a single interaction mode was frequently higher than the comparable phenomenological dimensionality of Eklöf et al's (2013) niche-based approach (Fig. 4c).

We regarded failures as trait-mediated outcomes of an interaction, meaning more traits are expected to be involved in the interactions (Fig. 4b). The 'success' outcomes in our framework are the 'interactions' typically described in the literature (Bartomeus et al., 2016); and our 'failure' outcomes are synonymous to the 'forbidden links' or 'forbidden interactions' of some authors (Jordano, Bascompte, & Olesen, 2003; Morales-Castilla, Matias, Gravel, & Araújo, 2015). Under our framework, players interact given their mere inclusion in the study system, even if they never actually meet, e.g. through spatio-temporal mismatch. Behavioural studies commonly employ a few predictor traits to explain only the observed dominance events in a system (Chase & Seitz, 2011), i.e. only the successes. In contrast, we found that three to six pairs of competing traits must be involved in several dominance systems (Fig. 3a). For example, in the elephant family named 'AA' in Archie et al. (2006), almost all observed dominance events are directed towards younger elephants, and the authors conclude the system is an age-ordered dominance hierarchy based only on the successes, in agreement with our one dimension with failures-excluded analysis (Fig. 4b). Our minimum mechanistic dimensionality though, explicitly incorporating failures, suggests three trait pairs here under both minimal explanations, because there are several older–younger pairs where no dominance or aggression was observed, i.e. failures unaccounted for by Archie et al. (2006).

In other words, our framework predicts mechanisms preventing the occurrence of dominance between these older–younger pairs. 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 overlooked when ignoring failure outcomes.

Our framework is applicable to various types of traits. Continuous-valued quantitative traits can be modelled directly (e.g. for animal reaching nectar in Fig. 1). Comparison of traits with ordered levels (binary, semiquantitative, and quantitative but discontinuous; Legendre & Legendre, 1998) can be modelled with appropriate scaling (e.g. for animals separating petals in Fig. 1). Categorical qualitative traits can be redefined as binary traits (e.g. a qualitative trait for inhabiting a forest can be redefined to a binary presence–absence trait as in Fig. 1). Moreover, the inequality rule can model both cases of competing traits (Abrams, 2000; Santamaría & Rodríguez-Gironés, 2007): 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 a larger power–toughness difference contributes to success. However, if we state the tasks appropriately, matching traits can be reformulated as difference traits (e.g. the difference traits formulation for the animal–plant spatial matching in Fig. 1).

The proposed method for calculating the minimum dimensionality is mechanistic, based on biologically plausible features of interactions; yet, it is simple with its phenotype space representation, and easy to adjust and extend. In this first account, we assumed two simple and extreme minimal interaction forms (minimal explanations I and II), but the user can input any minimum number of traits and trait values, in any interaction form. Additionally, we presented a deterministic version, but future versions could be probabilistic (Dalla Riva & Stouffer, 2016; Poisot et al., 2016), e.g. with more probable outcomes explained by larger power–toughness differences. Assuming adequate sampling effort, our mechanistic

description has not considered the effects of phylogenetic relationship (Rohr & Bascompte, 2014), and abundance (Vázquez & Aizen, 2003), which could also be incorporated in future extensions.

In conclusion, we have outlined a novel method of estimating the minimum dimensionality of ecological networks, which is relatively straightforward to adopt and calculate. Studies can rely on network models reproducing community structure more accurately at the interaction outcome level (Olito & Fox, 2015), and can reduce the risk of missing important traits that are involved mechanistically, in alternative interaction modes, or only in failure outcomes. In that way, our method could contribute to a better understanding, explanation, and prediction of community structure and structure-dependent processes.

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AUTHORS' CONTRIBUTIONS

DAK developed the method and the required code, compiled the empirical networks dataset, computed the dimensionalities of the networks, analysed the data, and wrote the first draft of the manuscript. All authors contributed to the development of the method, data analysis, and to the writing of the manuscript.

DATA ACCESSIBILITY

Data and code will be made available at the Dryad Digital Repository.

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