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

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ABSTRACT

1.   Individual-level traits mediate interaction outcomes and community structure. It is important, therefore, to identify the minimum number of traits that characterise ecological networks, i.e. their 'minimum dimensionality'. Existing methods for estimating minimum dimensionality often lack three features associated with increased trait numbers: alternative interaction modes (e.g. feeding strategies such as active *vs*. sit-and-wait feeding), trait-mediated 'forbidden links' and a mechanistic description of interactions. Omitting these features can underestimate the trait numbers involved, and therefore, minimum dimensionality. We develop a 'minimum mechanistic dimensionality' measure, accounting for these three features.

2.   The only input our method requires is the network of interaction outcomes. We assume how traits are mechanistically involved in alternative interaction modes. These unidentified traits are contrasted using pairwise performance inequalities between interacting species. For example, if a predator feeds upon a prey species via a typical predation mode, in each step of the predation sequence the predator's performance must be greater than the prey's. We construct a system of inequalities from all observed outcomes, which we attempt to solve with mixed integer linear programming. The number of traits required for a feasible system of inequalities provides our minimum dimensionality estimate.

3.   We applied our method to 658 published empirical ecological networks including primary consumption, predator–prey, parasitism, pollination, seed dispersal and animal dominance networks, to compare with minimum dimensionality estimates when the three focal features are missing. Minimum dimensionality was typically higher when including alternative interaction modes (54% of empirical networks), 'forbidden interactions' as trait-mediated interaction outcomes (92%), or a mechanistic perspective (81%), compared to estimates missing these features. Additionally, we tested minimum dimensionality estimates on simulated networks with known dimensionality. Our method typically estimated a higher minimum dimensionality, closer to the actual dimensionality, while avoiding the overestimation associated with a previous method.

4.   Our method can reduce the risk of omitting traits involved in different interaction modes, in failure outcomes, or mechanistically. More accurate estimates will allow us to parameterise models of theoretical networks with more realistic structure at the interaction outcome level. Thus, we hope our method can improve predictions of community structure and structure-dependent dynamics.

ΠΕΡΙΛΗΨΗ (Abstract in Greek)

1.   Τα φαινοτυπικά χαρακτηριστικά των οργανισμών συνεισφέρουν στις εκβάσεις των οικολογικών αλληλεπιδράσεων και στη δομή των οικολογικών κοινοτήτων. Είναι επομένως σημαντικό να προσδιοριστεί ο ελάχιστος αριθμός χαρακτηριστικών που εμπλέκονται σε ένα οικολογικό δίκτυο, δηλαδή η «ελάχιστη διαστασιμότητα». Οι υπάρχουσες μέθοδοι για την εκτίμηση της ελάχιστης διαστασιμότητας δεν διαθέτουν κοινώς τρεις ιδιότητες που σχετίζονται με περισσότερα χαρακτηριστικά: εναλλακτικούς τρόπους αλληλεπίδρασης (π.χ. στρατηγικές θήρευσης μέσω ενεργής αναζήτησης ή ενέδρας), «απαγορευμένες συνδέσεις» εξαιτίας χαρακτηριστικών, και μηχανιστική περιγραφή των αλληλεπιδράσεων. Η παράλειψη αυτών των ιδιοτήτων μπορεί να υποτιμήσει τον αριθμό των συμμετεχόντων χαρακτηριστικών, και συνεπώς την ελάχιστη διαστασιμότητα. Στην παρούσα εργασία, αναπτύσσουμε μια μετρική «ελάχιστης μηχανιστικής διαστασιμότητας», η οποία λαμβάνει υπόψιν αυτές τις τρεις ιδιότητες.

2.   Τα μόνα δεδομένα που χρειάζεται η μέθοδός μας είναι οι εκβάσεις αλληλεπιδράσεων ενός δικτύου. Κάνουμε μια παραδοχή για το πώς τα χαρακτηριστικά εμπλέκονται μηχανιστικά μέσω εναλλακτικών τρόπων αλληλεπίδρασης. Αυτά τα αφηρημένα χαρακτηριστικά συγκρίνονται κατά ζεύγη μέσω ανισοτήτων στην επίδοση των αλληλεπιδρόντων οργανισμών. Για παράδειγμα, εάν κάποιος θηρευτής τρέφεται με κάποια λεία μέσω ενός τυπικού τρόπου θήρευσης, σε κάθε βήμα της θηρευτικής διαδικασίας η επίδοση του θηρευτή πρέπει να είναι μεγαλύτερη από της λείας. Κατασκευάζουμε ένα σύστημα ανισοτήτων από όλες τις παρατηρηθείσες εκβάσεις, το οποίο προσπαθούμε να λύσουμε με μικτό ακέραιο γραμμικό προγραμματισμό. Ο αριθμός των χαρακτηριστικών που

απαιτούνται για ένα επιλύσιμο σύστημα ανισοτήτων είναι η εκτίμησή μας για την ελάχιστη διαστασιμότητα.

3.   Εφαρμόσαμε τη μέθοδό μας σε 658 δημοσιευμένα εμπειρικά οικολογικά δίκτυα, συμπεριλαμβανομένων δικτύων κατανάλωσης παραγωγών, λείας–θηρευτή, παρασιτισμού, επικονίασης, διασποράς σπερμάτων και κυριαρχικότητας σε ομάδες ζώων, για να συγκριθεί με εκτιμήσεις ελάχιστης διαστασιμότητας όταν παραλείπονται οι τρεις σχετικές ιδιότητες. Η ελάχιστη διαστασιμότητα ήταν τυπικώς υψηλότερη όταν ενσωματώσαμε εναλλακτικούς τρόπους αλληλεπίδρασης (54% των εμπειρικών δικτύων), «απαγορευμένες αλληλεπιδράσεις» εξαιτίας χαρακτηριστικών (92%) ή μια μηχανιστική προσέγγιση (81%), σε σύγκριση με εκτιμήσεις από τις οποίες έλειπαν αυτές οι ιδιότητες. Επιπλέον, ελέγξαμε εκτιμήσεις ελάχιστης διαστασιμότητας σε προσομοιωμένα δίκτυα γνωστής διαστασιμότητας. Η μέθοδός μας τυπικώς εκτίμησε μια υψηλότερη ελάχιστη διαστασιμότητα, πιο κοντά στην πραγματική διαστασιμότητα, αποφεύγοντας παράλληλα υπερεκτιμήσεις χαρακτηριστικές μιας προηγούμενης μεθόδου.

4.   Η μέθοδός μας μπορεί να μειώσει τον κίνδυνο παράλειψης χαρακτηριστικών που εμπλέκονται σε διαφορετικούς τρόπους αλληλεπίδρασης, σε αποτυχημένες εκβάσεις αλληλεπίδρασης ή μηχανιστικά. Οι πιο ακριβείς εκτιμήσεις θα μας επιτρέψουν να παραμετροποιήσουμε μοντέλα θεωρητικών δικτύων πιο εύλογης δομής στο επίπεδο των εκβάσεων. Έτσι, ελπίζουμε ότι η μέθοδός μας μπορεί να συνεισφέρει σε βελτιωμένες προβλέψεις της δομής και δυναμικής των οικολογικών κοινοτήτων.

1 INTRODUCTION

Ecological networks are structured by different forces, including dispersal, habitat filtering processes and species interactions (Bartomeus et al., 2016). Interaction outcomes are determined by the relative performance of each organism's traits, i.e. whether one individual successfully exploits another (Bartomeus et al., 2016; Pichler et al., 2020). For example, a nectarivory outcome can depend on the length of a nectarivore's mouth part compared to the depth of the plant's corolla tube. Thus, the comparison of trait-mediated performance between interacting exploiters and resources underlies interaction outcomes and, subsequently, community structure (Arnold, 1983). Here, we develop a method which leads backwards from the observed interaction outcomes to an estimate of the minimum number of traits involved in that type of interaction, which we term 'minimum dimensionality'.

Knowing the minimum dimensionality for a set of interaction outcomes focusses our investigations on which traits underpin community structure (Eklöf et al., 2013). A set of interaction outcomes can be represented by a network (Delmas et al., 2019), illustrating which organisms achieve success in their interactions. They can be represented as unipartite networks, where all participants are included in a single group, and interactions occur between any group member, e.g. a food web; or bipartite networks, where participants are assigned to either of two groups, and interactions can occur between different groups, e.g. a plant–pollinator network. Estimating the minimum dimensionality of such networks before deciding how many traits to investigate can prevent the omission of important traits. More accurate prediction of interaction outcomes can then be made by combining information on the minimum number of necessary traits with appropriate biological knowledge and methods to investigate the contribution of specific traits (Pichler et al, 2020). Minimum dimensionality can also inform theoretical network models about the minimum number of trait axes which have to be included for the reproduction of realistic networks.

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Since interaction networks are often characterised by traits, accurately estimating minimum dimensionality will improve our understanding of interaction outcomes. Here, we combine three relevant features for the first time, which we predict will increase the estimated minimum number of traits involved in interactions. First, resources can be successfully exploited via alternative strategies, which we term 'interaction modes'. For example, flowering plants use visual or olfactory signals to achieve pollination (Schiestl & Johnson, 2013), and zooplankton species exhibit feeding modes such as active predation and filter feeding (Kiørboe, 2011). These different trait combinations can modify the minimum dimensionality. Second, failure to exploit a resource can be considered a trait-mediated outcome of interaction, i.e. a 'forbidden link' or 'forbidden interaction' (Jordano, Bascompte, & Olesen, 2003). Here, we assume that two organisms interact given their inclusion in the network, even if they never actually meet, e.g. through temporal mismatch. Thus, traits involved in failures can also be included, which may differ from traits involved in successes. Third, to successfully exploit a resource via a given mode, an exploiter may have to succeed in different 'tasks', each employing different traits. For instance, a predator must succeed in all tasks of the predation sequence: encounter, detect, identify, approach, subjugate and consume a prey (Endler, 1991).

Existing methods for estimating minimum dimensionality lack at least one of these three features. The minimum dimensionality method of Eklöf et al. (2013) estimates the minimum number d of dimensions such that the trait values of each exploiter's resources lie in a contiguous volume of a d-dimensional space (also applied to each resource's exploiters). Alternative interaction modes are not considered because all d dimensions act in conjunction to determine exploitation. Additionally, each dimension potentially accounts for multiple traits. Thus, although their method tells about the niches of the exploiters and resources, it does not address the issues of alternative interaction modes and tasks (see an illustrative example in Fig. 1). Ignoring interaction modes and tasks places this method towards the phenomenological end of a phenomenological–mechanistic continuum, where we consider

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mechanistic approaches in a proximate (ecologically motivated) rather than an ultimate (evolutionarily motivated) sense. Dalla Riva and Stouffer (2016) adopted a more mechanistic approach to minimum dimensionality, with a simple trait space representation for trophic interactions. They explicitly modelled interaction network structure, comparing paired exploiter–resource trait values. However, Dalla Riva and Stouffer (2016) model interactions via a single interaction mode; the task outcomes act additively from each corresponding exploiter–resource trait pair comparison. Finally, corresponding to forbidden links, it is common for behavioural studies to employ predictor traits to explain only the observed dominance events in a system, i.e. only the success outcomes (Chase & Seitz, 2011). Such attempts can overlook relevant traits which might contribute only to the interaction failure outcomes.

We developed a novel method providing a different view on interaction networks by combining alternative interaction modes, trait-mediated failures and mechanistically-based tasks, in a minimum dimensionality measure. Our 'minimum mechanistic dimensionality' measure can be applied to a broad range of ecological networks, including animal dominance, predator–prey, primary consumption, pollination, parasitism and seed dispersal networks. We investigated how our minimum dimensionality estimate compares with previous approaches across a range of empirical networks: under the assumption of alternative interaction modes compared to a single mode; with failure outcomes taken into account instead of omitted; and under a more mechanistic perspective compared to the minimum dimensionality under the more phenomenological, niche approach of Eklöf et al. (2013). We go on to estimate minimum dimensionality on simulated networks with a known underlying number of dimensions. Therefore, we test for potential underestimation of minimum dimensionality across different scenarios which could lead to the omission of key traits and mechanisms underlying interactions and community structure.

2 METHODS

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We illustrate our approach with an empirical example of cyclic spatial replacement among three competing marine invertebrates. While the minimum dimensionality of this intransitive network equals one dimension following Eklöf et al.'s (2013) method, since each exploiter (resource) has a single resource (exploiter), our method estimates two dimensions, providing a useful illustrative example. We describe the interactions in the context of exploiter and resource roles, going on to define and calculate the minimum mechanistic dimensionality of the network using inequalities. We then describe how we compared competing minimum dimensionality estimates across 658 empirical networks—including social hierarchies, mutualistic networks and food webs—and on simulated networks of known dimensionality.

2.1 Minimum mechanistic dimensionality: an overview

Jackson and Buss (1975) described the cyclic spatial replacement of three encrusting marine invertebrates: ectoproct species *Stylopoma spongites* (player *A*) replaces sponge species *Tenaciella* sp. (player *B*); *Tenaciella* replaces the sponge *Toxemna* sp. (player *C*), which in turn replaces the ectoproct player *A*. In our framework, a player (individual or species) can adopt the role of an exploiter, a resource, or both. In the marine invertebrates example, we consider any species both exploiter-and-resource of the other species, representing the observed replacement outcomes of spatial competition with a unipartite network (Fig. 1). Exploiters possess traits involved in achieving exploitation, whereas resources possess traits working against exploitation. For task success, an exploiter's performance in a given trait, termed 'power', must be 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). Exploiter and resource are challenged in one trait 'dimension' of their phenotype space, where the corresponding power–toughness trait performance is directly compared to determine who succeeds in that task. Using Boolean

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logic terms, interaction modes can be represented as OR-associated clauses of AND-associated tasks (see examples of one 2-dimensional mode and two 1-dimensional modes in Fig.1). In logic, any structure of logical statements can be expressed in this 'disjunctive normal form', which we term the 'interaction form', providing a systematic description of how interactions occur.
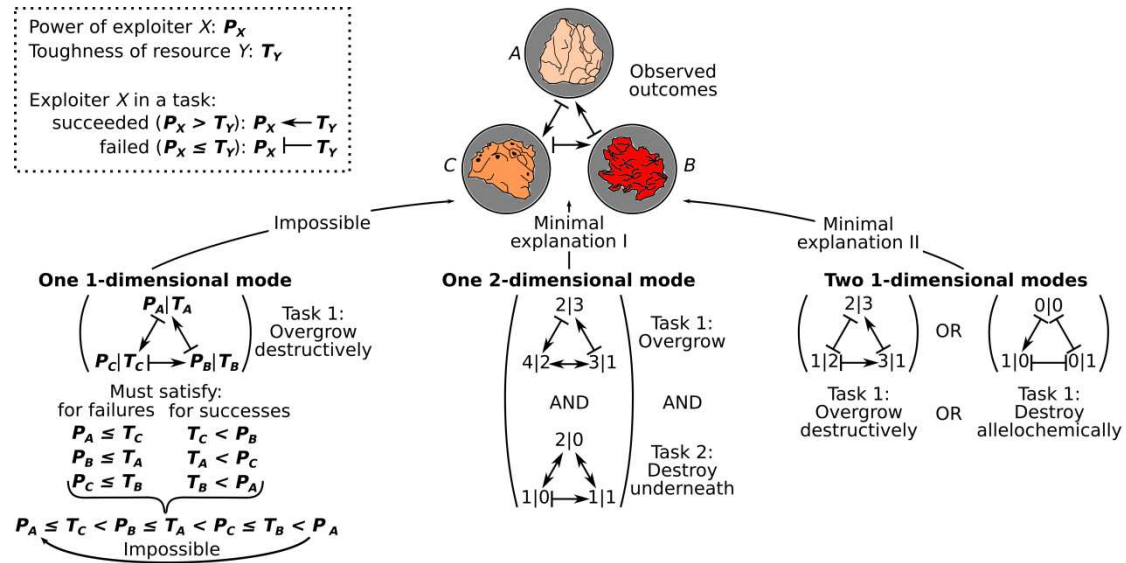

FIGURE 1 Explaining the observed competitive outcomes in an empirical rock–paper–scissors system of spatial replacement in three marine invertebrates. Each species was considered exploiter-and-resource of the others, possessing a power|toughness trait pair per task. We illustrate three minimal explanations for the observed outcomes: a 1-dimensional mode is mechanistically impossible, presuming a single trait pair for a single task, i.e. one dimension; the other two attempts are feasible, requiring two trait pairs in two tasks, i.e. two dimensions. We indicate hypothetical tasks, and power|toughness trait scores in arbitrary units of performance. The indicative power|toughness values demonstrate that only the 2-dimensional minimal explanations are mathematically feasible.

The only input our method requires is the set of observed interaction outcomes. We then define an interaction form describing the number of interaction modes which produced these outcomes, with each mode having a specific number of tasks. Since our aim is a minimum dimensionality estimate, we start with the simplest interaction form of a single task. In our example, we assumed that interactions occurred via the destructive overgrowth of a

rival invertebrate. For this task, a single pair of opposed, exploiter–resource power–toughness traits is assumed for all species. For example, the body height of the invertebrates when extending to an adjacent rival could be a trait for the power to overgrow destructively; and their body height when defending against overgrowth by rivals could be a trait for the toughness against destructive overgrowth. We then confront this trait pair in a system of inequalities, to satisfy the observed task successes and failures which correspond to the observed outcomes for this single-task interaction form. For task successes, the power of a winning exploiter must be greater than the toughness of a defeated resource, e.g. the exploiter's body height must be higher than the defender's. For task failures, the power of a losing exploiter must be less than or equal to the toughness of an undefeated resource. In our example, the resulting system of six inequalities creates a cyclic sequence of ever-increasing power–toughness scores (the impossible 'one 1-dimensional mode' in Fig. 1). Thus, it is impossible to explain the observed outcomes in this unipartite graph if we presume that interactions occurred via a 1-dimensional interaction mode of a single task.

Our framework provides two alternative minimal mechanistic explanations for the emergence of this rock–paper–scissors network. First, we can find feasible power–toughness scores if we add a second task, i.e. another pair of power–toughness traits in the same mode (minimal explanation I in Fig. 1). We explain the failure of players *A* and *B* as failure in the first task (failure in overgrowth), and the failure of *C* as failure in the second task (failure to destroy the rival, even if *C* can overgrow *B*). Alternatively, we can find solutions if we add a second interaction mode with one task, i.e. another pair of power–toughness traits in a new 1-dimensional mode (minimal explanation II in Fig. 1). In that case, *A* and *B* achieve success via the first mode (destructive overgrowth), and *C* achieves success via a second mode (allelochemical elimination). Since the addition of a second task (power–toughness trait pair) leads to feasible power–toughness scores under both minimal explanations, the minimum mechanistic dimensionality of the empirical network equals two dimensions in both cases. This result, combined with biological insight from Jackson and Buss (1975), suggests that

minimal explanation II is the more plausible one, since: player A replaces B via overgrowth, player B replaces C via overgrowth, but player C replaces A via toxic effects. Appendix S1 presents the complete systems of inequalities for this network under minimal explanations I and II, following the details presented next.

2.2 Minimum mechanistic dimensionality: formulating the inequalities

As illustrated above (Fig. 1), the mechanistic explanation of the interaction outcomes in a network might require more than one pair of opposed exploiter–resource trait dimensions. One method to find this minimum number of trait dimensions is by attempting to solve a system of inequalities. If the system of inequalities is impossible, a simple strategy is to increase the number d of dimensions by one, and retry (illustrated with pseudocode in Fig. 2). Our minimum mechanistic dimensionality estimate is, therefore, the minimum $d \geq 1$ for a feasible system of inequalities. In the marine invertebrates example, there were two types of minimal explanation: additional trait pairs belonging to the same interaction mode (minimal explanation I); or belonging to other, independent, 1-dimensional modes (minimal explanation II). We will illustrate these two extreme explanations, although tasks could be distributed to interaction modes in other ways for cases requiring more than two tasks.

```
obs_outc = read_observed_outcomes() # input from a network
min_expl_type = read_type() # input minimal explanation 1 or 2

d = 0 # the min. mechanistic dimensionality of the network
system_feas = FALSE # assume infeasible inequalities system
while(system_feas == FALSE):
  d = d + 1 # will increment d until reaching system feasibility

  if(min_expl_type == 1): # tasks in a single mode
    for each success of exploiter A vs. resource B in obs_outc:
      for each task i from 1 to d:
        formulate inequality (1) # success in all mode tasks
    for each failure of exploiter A vs. resource B in obs_outc:
      for each task i from 1 to d:
        formulate inequalities (2) and (3)
      formulate inequality (4) # failure in at least one mode task

  elseif(min_expl_type == 2): # alternative 1-task modes
    for each failure of exploiter A vs. resource B in obs_outc:
      for each mode j from 1 to d:
        formulate inequality (5) # failure via all modes
    for each success of exploiter A vs. resource B in obs_outc:
      for each mode j from 1 to d:
        formulate inequalities (6) and (7)
      formulate inequality (8) # success via at least one mode

  system_feas = solve_formulated_system() # update if feasible
```

FIGURE 2 Pseudocode for estimating the minimum mechanistic dimensionality of an ecological network, from the observed outcomes under minimal explanations I and II.

When a new task is added to a single mode, permitting feasibility of the system of equalities, the d exploiter–resource trait pairs (dimensions) must be involved in the same mode (minimal explanation I, Fig. 1). On one hand, an observed success of exploiter A against resource B must be the result of success in all tasks (e.g. player A succeeds in both overgrowing and destroying B in Fig. 1). Specifically, the power $P_{A,i} \geq 0$ of exploiter A in any trait pair i must be greater than the toughness $T_{B,i} \geq 0$ of resource B in that trait pair: $P_{A,i} > T_{B,i}$. Since each trait pair i appears only in one task in our current formulation, we use the same index i for both trait pairs and tasks. If success requires more than the marginal superiority of the exploiter's power, a superiority threshold can be added, $t_{A,B,i} > 0$, making the task success requirement:

$$P_{A,i} \geq T_{B,i} + t_{A,B,i}. \tag{1}$$

On the other hand, the observed failure of exploiter A against resource B must be the result of failure in at least one task (e.g. player C failing at task 2 against B in Fig. 1). 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

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success in the task. Finally, we include bounds for the power–toughness differences for computational efficiency (Williams, 2013): a sufficiently negative lower bound m of the exploiter's power inferiority in case of task failure; and a sufficiently positive upper bound M, of the exploiter's power superiority in case of task success. Here, we set $m = -200$ and $M = 200$, but these limits were not reached in any of the empirical and simulated networks we considered. Thus, for an observed failure, the following pair of inequalities must be satisfied in any trait pair i:

$$P_{A,i} + M f_{A,B,i} \leq T_{B,i} + M, \qquad (2)$$

$$P_{A,i} - m f_{A,B,i} \geq T_{B,i} + t_{A,B,i}. \qquad (3)$$

With an extra inequality for the observed failure, we can force at least one of the binary indicator variables to equal one, i.e. failure in at least one task:

$$\sum_{i=1}^{d} f_{A,B,i} \geq 1. \qquad (4)$$

With a task failure in trait pair i ($f_{A,B,i} = 1$), inequality (2) is the task failure requirement and inequality (3) is the lower bound for the exploiter's power inferiority. With a task success ($f_{A,B,i} = 0$), inequality (2) gives the upper bound for the exploiter's power superiority and inequality (3) becomes a success requirement.

Adding a new 1-dimensional mode that creates a feasible system of inequalities (minimal explanation II, Fig. 1), each of the d pairs of opposed exploiter–resource traits must be involved in a different mode. Again here, each trait pair appears only in one mode j, so we use the same index j for both trait pairs and modes. On one hand, the observed failure of any exploiter A against any resource B must be the result of failure in any mode j of the d modes (e.g. player A failing via both overgrowth and allelopathy against C in Fig. 1):

$$P_{A,j} \leq T_{B,j}. \qquad (5)$$

On the other hand, the observed success of exploiter A against resource B must come from success via at least one mode (e.g. player C replacing A via allelopathy in Fig. 1). We now use a binary variable, $s_{A,B,j}$, to indicate success via mode j. Given the same bounds as in minimal

explanation I, the following pair of inequalities must be satisfied to indicate exploiter success in any mode j:

$$P_{A,j} + m\, s_{A,B,j} \geq T_{B,j} + t_{A,B,j} + m, \tag{6}$$

$$P_{A,j} - M\, s_{A,B,j} \leq T_{B,j}. \tag{7}$$

With an extra inequality for the observed success, we can force at least one of the binary indicator variables to equal one, i.e. exploiter success occurs via at least one interaction mode:

$$\sum_{j=1}^{d} s_{A,B,j} \geq 1. \tag{8}$$

A complete system of inequalities takes into account all observed successes and failures for all possible exploiter–resource pairs (Fig. 2). 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 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 excluding basal species, basal–consumer interactions, plant–pollinator, host–parasite and seed dispersal networks (Appendix S1). By assuming adequate sampling effort (e.g. no observed failures due to rarity), we computed five dimensionality measures (Appendix S1). Four of the measures were based on our framework: (*a*) a single, potentially multidimensional mode; (*b*) one-or-more 1-dimensional modes; (*c*) as *b*, but excluding observed failures; (*d*) as *c*, but with players interacting via a common trait per dimension, rather than a power against toughness trait. To compare our approach with another established dimensionality estimate in this first account, we considered (*e*) Eklöf et al.'s (2013) niche-based method. We asked three questions about

our minimum mechanistic dimensionality (MMD) estimates; does MMD change: (1) under the assumption of alternative 1-dimensional modes (dimensionality estimate b), compared to the assumption of a single multidimensional mode (dimensionality a)? (2) with observed failures taken into account (dimensionality b), or excluded (dimensionality c or d)? (3) compared to the measure developed by Eklöf et al. (2013) (dimensionality a versus e)?

The systems of inequalities for our four minimum mechanistic dimensionality measures a–d were formulated and solved as mixed integer linear programming problems with the Gurobi Optimizer (Gurobi Optimization and Inc., 2020). R and Python codes for formulating and solving these are provided (see 'DATA ACCESSIBILITY'). We computed the fifth dimensionality estimate with code available in Eklöf et al. (2013). The empirical networks were retrieved from five data sources (Cohen, 2010; Ortega, Fortuna, & Bascompte, 2017; Shizuka & McDonald, 2015; Stanko & Miklisova, 2014; Thompson & Townsend, 2004). We provide the network characteristics and references, raw data from the five computed dimensionality measures for each of the 658 empirical systems, and R code for plotting the results (see 'DATA ACCESSIBILITY').

2.4 Minimum dimensionality of simulated networks with known dimensionality

We generated networks where we knew how many dimensions contributed to the interaction outcomes, based on Santamaría & Rodríguez-Gironés' (2007) 'barrier' traits model with differences in exploiter–resource performance traits, in this first evaluation of our method. We then estimated minimum dimensionality in these networks with our MMD method and that of Eklöf et al. (2013), testing which method performed better by comparing minimum dimensionality estimates with the actual number of dimensions involved. We note that a minimum dimensionality method does not estimate the actual dimensionality of a network, but only the lower bound required to generate such a structure. For simplicity, we generated each simulated network with species traits involved either in a single interaction

mode, or with each trait dimension belonging to an alternative, single-task mode. We generated unipartite and bipartite networks, to give four scenarios: single-mode unipartite, or bipartite; multi-mode unipartite, or bipartite.

We generated unipartite networks with $S = \{3, 5, 10, 15, 20 \text{ or } 25\}$ species. This was doubled for bipartite networks, where the number of exploiters was chosen randomly from a uniform distribution in the range 1 to $S - 1$, and the remaining species were resources. Each uni- or bipartite network had D dimensions, $D = \{2, 5, 10, 15 \text{ or } 20\}$. The S–D combinations were chosen in a fully factorial design, giving 30 unique combinations. For each combination, we generated ten replicate networks, leading to 300 networks for each of the four scenarios.

Random values for power and toughness traits were drawn independently from distinct normal distributions of equal variance ($\sigma^2 = 0.01$) for each replicated S–D combination. We set the distance between the means of the two distributions such that networks of size S had a wide range of connectance given the range of D (Appendix S1). R codes for simulating these networks and plotting results are provided (see 'DATA ACCESSIBILITY').

3 RESULTS

3.1 Minimum dimensionality of empirical networks

For the five dimensionality measures we considered, the inclusion of alternative interaction modes, forbidden links, and a more mechanistic approach describing interaction tasks, consistently increased the minimum dimensionality estimate across a wide range of empirical networks (Fig. 3 and Fig. 4).

We frequently estimated higher minimum mechanistic dimensionality under the alternative rather than the single mode explanation (Fig. 3), especially in 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).
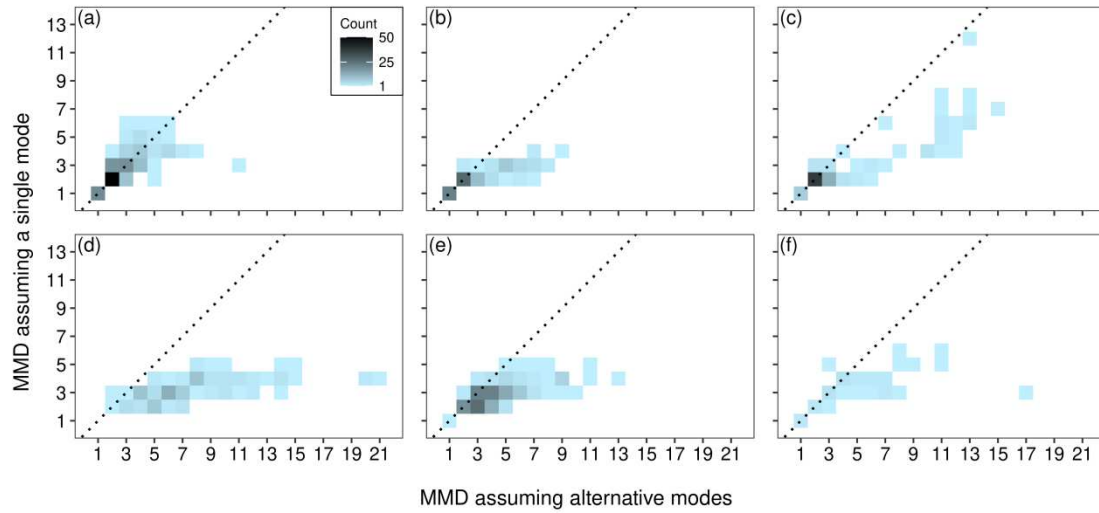

FIGURE 3 Minimum mechanistic dimensionality estimates from 658 empirical systems. Cell colour indicates frequency of the n systems with the corresponding pair of values in our two minimum mechanistic dimensionalities (MMD), i.e. number of exploiter–resource trait pairs assuming: alternative 1-dimensional modes (x-axis; minimal explanation II); and tasks in a single mode (y-axis; minimal explanation I). Panels represent: (a) animal dominance in $n = 168$ unipartite graphs (6–31 individuals); (b) consumption of non-basal species in $n = 95$ unipartite food webs (6–57 species; basal species excluded from the original food webs); (c) consumption by consumers exclusively feeding on basal species in $n = 95$ bipartite graphs (11–91 species; same food webs used in panel b); (d) biotic plant pollination in $n = 105$ bipartite graphs (8–114 species); (e) ectoparasitism of small mammals in $n = 165$ bipartite graphs (8–92 species); and (f) plant seed dispersal in $n = 30$ bipartite graphs (6–86 species). Parameter values in the inequalities method: $m = -200$, $M = 200$, $t_{A,B,i} = 1$, for all pairs of exploiter A with resource B, and in any trait pair i.
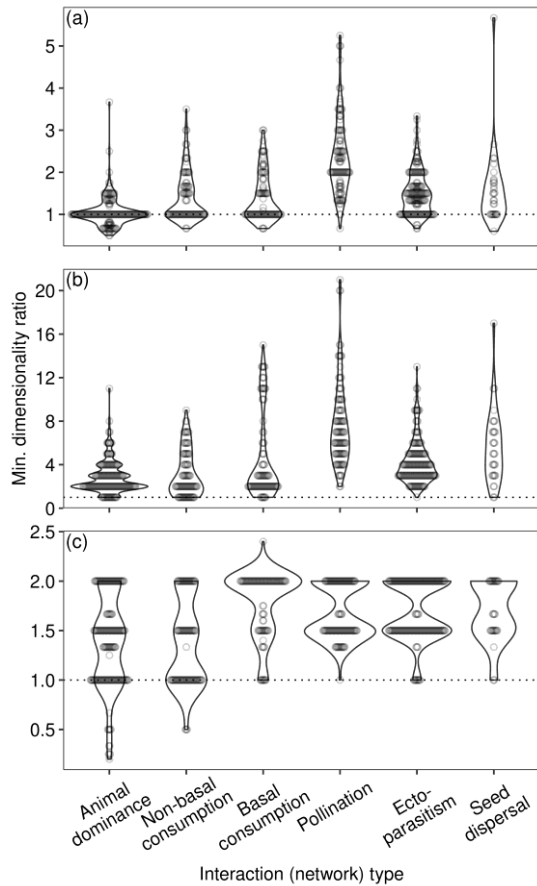
FIGURE 4 Comparisons of minimum dimensionality measures estimated from 658 empirical systems. Violin plots show the normalised distributions of the dimensionality ratios (see Section 2.3 for details) of: (a) our minimum mechanistic dimensionality under minimal explanation II (alternative 1-dimensional modes), to our minimum mechanistic dimensionality under minimal explanation I (tasks in a single mode); (b) our minimum mechanistic dimensionality under minimal explanation II, to the same dimensionality estimate with the failures ignored; and (c) our minimum mechanistic dimensionality under minimal explanation I, to the comparable dimensionality of Eklöf et al. (2013). The raw data are displayed as semi-transparent points which, for the same x–y value, are spread regularly among the x-axis to avoid overplotting. Dotted horizontal lines mark a ratio of one, with values above the line indicating higher minimum dimensionality when assuming: alternative modes (a), failures as trait-mediated outcomes (b), and a more mechanistic perspective (c).

Comparing our minimum multimodal dimensionality with the same dimensionality estimate excluding failure inequalities from the system of inequalities, showed that minimum mechanistic dimensionality was higher in 92% of the empirical systems when including failure outcomes (Fig. 4b). In the remaining 8% of empirical systems, both dimensionality estimates were equal. With failures excluded, minimum dimensionality was always one

dimension. In this case, the structure of observed successes can be explained unimodally, as exploiters can have a single power trait with a greater value than the single toughness trait of any resource (in the absence of any inequalities constraining the power scores). 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. Thus, the unipartite systems could require more than one dimension with failures excluded. Even when modelling trait opposition with a common trait per dimension, 79% of the unipartite systems had higher minimum dimensionality with failures included rather than excluded (Fig. 4b).

In 81% of the empirical systems, our minimum mechanistic dimensionality was higher than the dimensionality estimate of Eklöf et al. (2013) (Fig. 4c). We assumed a single mode (minimal explanation I), comparable to the niche approach of Eklöf et al. (2013). Only 2% of the networks had higher minimum dimensionality under Eklöf et al.'s (2013) more 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 (median) 1.5 times larger than with the more phenomenological dimensionality estimate 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. our approach suggested a median of 3 times more trait axes required for the explanation of the observed outcomes.

3.2 Minimum dimensionality of simulated networks with known dimensionality

In simulated networks built with a single mode of multiple tasks, our MMD method (also assuming a single mode) typically estimated a higher minimum dimensionality—i.e. closer to the actual number of dimensions involved—than the comparable Eklöf et al. (2013) method (Fig. 5a,c), particularly in larger networks (Appendix S1). The Eklöf et al. (2013) method sometimes erroneously estimated a minimum dimensionality which was higher than

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the actual dimensionality for some large, two-dimensional unipartite networks (Fig. 5c; Appendix S1).

As Eklöf et al. (2013) essentially assumed a single interaction mode, applying their approach to theoretical networks with multiple modes is not straightforward. Nevertheless, we experimented by using the Eklöf et al. (2013) and our method by assuming the opposite interaction form than the one used for building the networks, to identify any characteristic trend in minimum dimensionality estimates when an incorrect assumption is used. Applying our MMD assuming multiple modes to networks built with a single mode, resulted in higher estimates compared to those assuming a single mode (Fig. 5a,b). Similarly, when applying our MMD and the Eklöf et al. (2013) method, both assuming a single mode, to networks built with multiple modes, the minimum dimensionality estimate was higher than with our MMD correctly assuming multiple modes (Fig. 5d,f versus Fig. 5e, respectively).
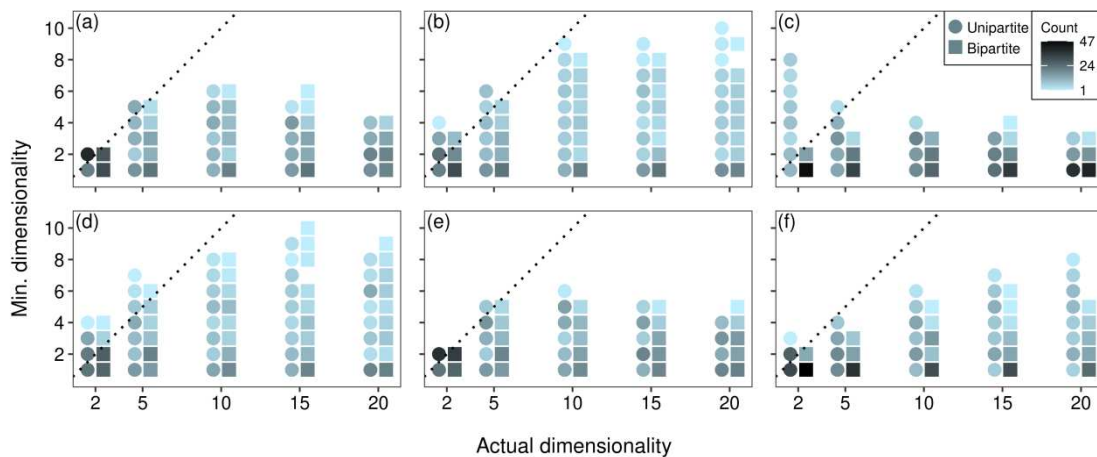

FIGURE 5 The minimum dimensionality estimates for simulated networks with known dimensionality. The top row shows networks built with one multi-task mode, the bottom row shows networks with multiple, single-task modes. For each value of actual dimensionality (x-axis), there are 60 unipartite (circles) and 60 bipartite networks (squares), with all panels on the same row with the same x-value hosting the same networks. Symbol colour indicates the frequency that networks had the corresponding pair of actual and minimum dimensionality values. Panels show: (a) MMD assuming a single mode with multiple tasks (minimal explanation I); (b) MMD assuming multiple, single-task modes (minimal explanation II); (c) Eklöf et al. (2013) method; (d) MMD under minimal explanation I; (e) MMD under minimal explanation II; and (f) Eklöf et al. (2013) method. Dotted lines show $y = x$.

4 DISCUSSION

We introduced a novel method for calculating the minimum number of traits required
to explain all observed interaction outcomes of ecological networks more mechanistically,
using a general framework applicable to different interaction (network) types, modes, tasks,
and types of traits. Applying this to 658 empirical systems, and simulated networks of known
dimensionality, 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
more mechanistic description of interactions broken down to tasks. This underestimation risks
omitting important traits in empirical investigations, and generating less realistic theoretical
networks at the level of interaction outcomes.

Our minimum mechanistic dimensionality framework can explicitly incorporate the
alternative interaction modes frequently observed empirically, e.g. alternative feeding modes.
In previous theoretical trait-based works, an exploiter has to overcome all barriers or defences
of a potential resource to exploit the resource (Gilman, Nuismer, & Jhwueng, 2012;
Santamaría & Rodríguez-Gironés, 2007). Similarly, in other 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—an exploiter's performance must be sufficiently high in
all the mode's tasks. Generalising to alternative modes, we also showed that minimum
mechanistic dimensionality was frequently higher under alternative modes than under a single
mode (Fig. 4a). By simulating networks of known dimensionality and interaction form, we
showed that applying a method assuming the incorrect interaction form frequently increased
minimum dimensionality estimates (Fig. 5). Thus, we suggest that many of the empirical
networks we tested may be built using fewer modes of multiple tasks, a hypothesis that can be

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investigated further in future work. Our framework's generalization to alternative modes can offer a new mechanistic perspective to the study of interactions, for example, offering alternative minimal explanations for the emergence of intransitive networks (Fig. 1), or for the emergence of pollination syndromes and floral mimicry (Schiestl & Johnson, 2013).

We regarded failures as trait-mediated outcomes of interaction, meaning more traits were expected to be involved in the interactions (Fig. 4b). We found that three to six pairs of opposed traits must be involved in several behavioural dominance systems (Fig. 3a), whereas only a few traits are commonly employed in behavioural studies for the explanation of only the successful dominance outcomes (Chase & Seitz, 2011). For example, in the elephant family named 'AA' in Archie et al. (2006), almost all observed dominance events were directed towards younger elephants, and the authors conclude the system is an age-ordered dominance hierarchy based only on the successes, agreeing with the one dimension estimated in our failures-excluded analysis (Fig. 4b). However, incorporating failures in our minimum mechanistic dimensionality estimates suggests three trait pairs 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 fact, most elephants dominated younger members within their matriline, but also younger members of two specific matrilines (Archie et al., 2006). These two behavioural tendencies are candidates for the two extra dimensions predicted by our method, overlooked when ignoring failure outcomes. Again, we recommend combining our approach—incorporating interaction failures with trait-based methods—with system-specific biological knowledge, to improve estimates when other approaches perform poorly; e.g. our MMD can indicate a minimum bound for the number of traits that might be represented by phylogeny when missing traits may be difficult to ascertain (e.g. Brousseau et al., 2018).

We adopted a phenotype rather than a niche space representation for traits. Studies of interactions commonly use the 'resource-utilization' approach to represent the 'ecological

niche' concept (Schoener, 1989). Despite its operational advantage, dimensions usually arise more 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, other traits scaling allometrically 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, implying two traits per niche dimension. For instance, in systems where the maximum prey size is limited by a predator's mouth gape, the size range minimum must be limited by a second trait, like the predator's inability to handle smaller prey. The resource-utilization approach also excludes exploiters from the niche space, as it is created by resource trait dimensions (Schoener, 1989). Our framework accounts for the traits of both interacting players simultaneously; a dimension is simply a challenged trait-axis in the phenotype space of exploiters and resources, as in Dalla Riva and Stouffer (2016). Thus, our minimum dimensionality assuming a single interaction mode was frequently higher than the comparable dimensionality of Eklöf et al's (2013) niche-based approach in empirical networks of unknown dimensionality (Fig. 4c). Comparing the two methods on simulated networks with known dimensionality confirmed that minimum dimensionality can often be underestimated when using this more phenomenological, niche-based approach (Fig. 5a,c).

In this first account, we assumed two simple and extreme minimal interaction forms, but users can input any number of traits and values, in any interaction form. While we presented a deterministic version, future versions could incorporate stochasticity (Dalla Riva & Stouffer, 2016), e.g. more probable successes explained by larger power–toughness differences. Further extensions could consider the effects of abundance, and indirect interactions in the estimation of minimum dimensionality. Additionally, we tested our method in simulated networks only generated with a 'barrier' traits mechanism (Santamaría & Rodríguez-Gironés, 2007), but future work can address the effect of other mechanisms, such as 'complementarity' or 'mixed' barrier–complementarity traits. Lastly, we assumed that

performance is independent in the different tasks, i.e. a unique trait per task per player in our formulation of the inequalities. In reality, several traits can contribute to performance in the same task, and the same trait can contribute to performance in several tasks (Arnold, 1983). Since our aim was a minimum dimensionality measure, we assumed independence in task performance, to impose fewer constraints in the linear inequalities system, allowing the estimation of a lower minimum. We expect that trait correlations will increase the minimum number of dimensions required to explain a specific network, given the associated restrictions on possible trait values.

In conclusion, we have outlined a novel method under a different perspective on how interactions occur, for estimating the minimum dimensionality of ecological networks. Informed by a more accurate minimum dimensionality estimate, future studies can rely on network models reproducing community structure more accurately at the interaction outcome level, reducing the risk of omitting important traits that are involved in alternative interaction modes, only in failure outcomes, and mechanistically in tasks. In that way, our method, combined with appropriate biological insight and other methods, could improve understanding, explanation, and prediction of community structure and structure-dependent processes.

AUTHORS' CONTRIBUTIONS

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

DATA ACCESSIBILITY

Data and code are deposited in the Dryad repository:
https://doi.org/10.5061/dryad.dfn2z34zp (Kiziridis et al., 2020).

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