

# Interaction Matrices as Unifying Tools for Navigating Ecological Complexity

J. Christopher D. Terry<sup>1\*</sup> 0000-0002-0626-9938  
Andrea Tabi<sup>2</sup> 0000-0002-5028-1117  
David García-Callejas<sup>3</sup> 0000-0001-6982-476X  
Virginia Domínguez-García<sup>4</sup> 0000-0002-4591-4186

1: Department of Biology, University of Oxford, Oxford, UK

2: Computational Science Lab, Informatics Institute, University of Amsterdam, Amsterdam, The Netherlands

3: Institute of Biology, University of Graz, Holteigasse 6, 8010 Graz, Austria

4: Estación Biológica de Doñana (EBD-CSIC), Seville, Spain

\*: Corresponding Author: christopher.terry@biology.ox.ac.uk

**Key words:** interaction matrix, community ecology, complexity, uncertainty, reductionism, ecological network

## Abstract

Interaction matrices summarise pairwise species impacts within ecological communities into an analytically tractable format and have been central to advancing our understanding of ecosystem dynamics. However, despite their ubiquity, they have faced constant, recurring, criticism for oversimplifying ecological complexity. While suggested extensions address specific shortcomings, they often come with significant trade-offs, including increased data demands and analytical complexity. Despite their challenges, interaction matrices have been a nexus of fundamental ecology connecting many subdisciplines, representing both cause and consequence of ecological dynamics. Here we overview the fundamental definitional, dynamism and data challenges confronting the interaction matrix framework and critically examine the current state-of-the-art of approaches developed to tackle them. We contend that the centrality of interaction matrices within academic ecology is set to continue. Nonetheless, their role as a unifying and focus of synthesis could be markedly improved by refreshing how they are considered. We argue that by fully embracing, rather than fighting, their inherent nature as uncertain, transient abstractions, ecology can better maximise their potential as a unifying nexus of ecological research and incorporate advances in wider complexity sciences. As we enter the second century of their use within ecology, such a shift will reinforce interaction matrices as a valuable tool to unlock the complex dynamics of ecological communities.

## 39 The centrality of interaction matrices in ecology

40 A fundamental goal of ecology is to understand the consequences of the relationships between  
 41 species. A common approach to addressing the complexity of natural ecosystems has been to  
 42 distil species interactions into a discrete 'interaction matrix' that summarises the pairwise  
 43 effects organisms have on one another given a specific environmental context. The  
 44 mathematical construct brings tractability to entangled webs of linkages within communities  
 45 and allows researchers to study the emergent properties of ecological systems as a complex  
 46 system<sup>1</sup>. As such, interaction matrices have been described as “*among ecology's most*  
 47 *important mathematical abstractions*”<sup>2</sup> and are a foundational staple of ecological research,  
 48 forming a key connecting bridge between theory and observation.

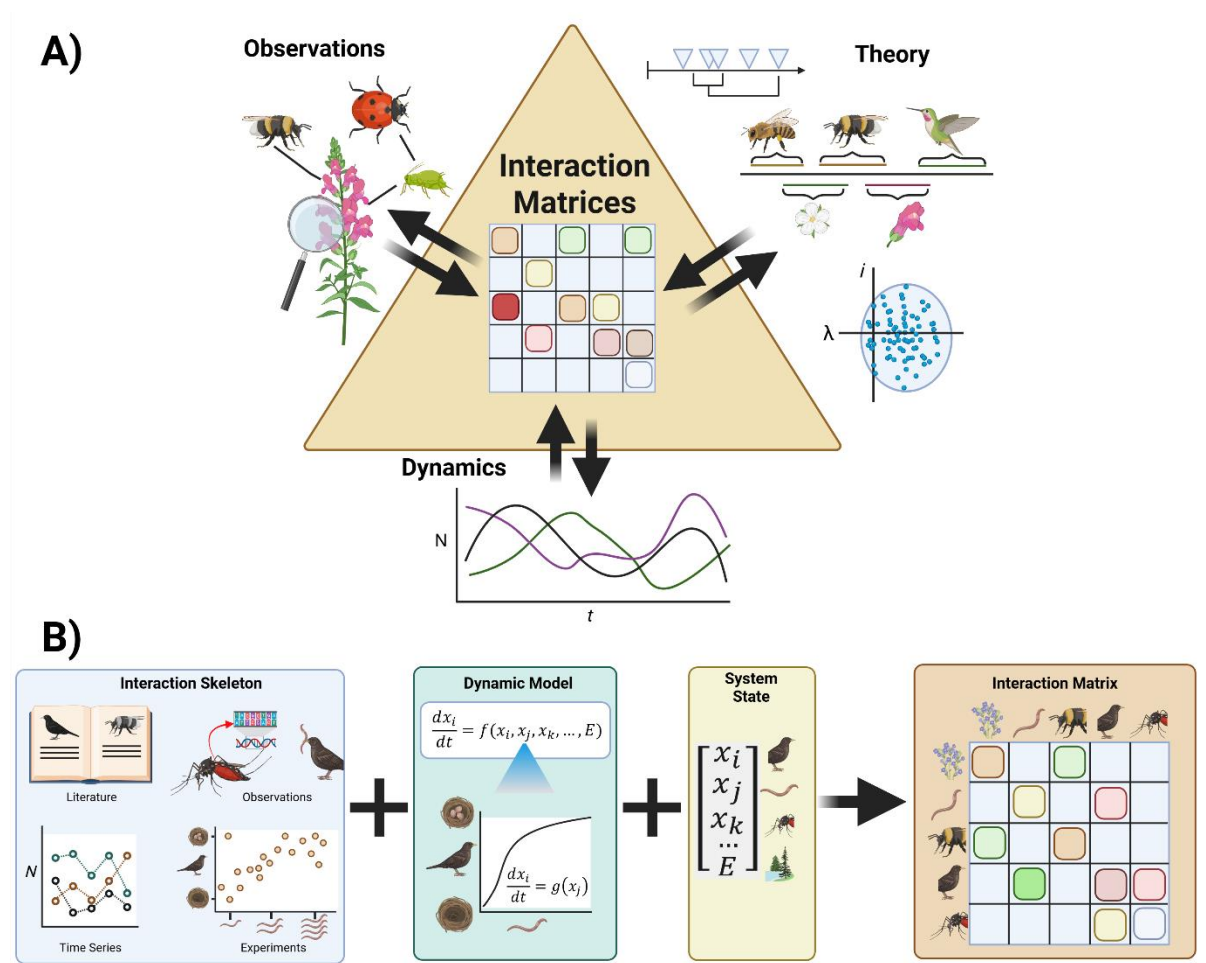
49 Recognition of the interconnectedness of ecosystems dates back to the earliest pioneers of  
 50 ecology<sup>3-5</sup>, but it took the influence of physical scientists such as Alfred Lotka<sup>6</sup> and Vito Volterra<sup>7</sup>  
 51 to bring into ecology the fundamental ‘mass action’ abstraction of distilling interspecific  
 52 interactions into a single rate term<sup>8,9</sup>. Since then, a multitude of distinct approaches to defining  
 53 the elements of interaction matrices have developed<sup>2,10-12</sup>, ranging from two-by-two systems up  
 54 to mathematically-large abstractions<sup>13</sup>, but all share the aim of capturing direct impacts  
 55 between a set of species populations with a two-dimensional grid of values (Box 1).

56 Both the opportunities and limitations that such mean-field approximations represent in an  
 57 ecological context were rapidly recognised<sup>14</sup> and their value has been much discussed ever  
 58 since<sup>15</sup>. Fundamentally, while mean-field approaches rooted in statistical physics unlock  
 59 tractable solutions for high-dimensional biological systems<sup>16</sup>, the level of abstraction and  
 60 reductionism embedded into the construction of interaction matrices frequently conflicts with  
 61 desires to explicitly account for known ecological processes and fine-grain detail<sup>17</sup>. Despite  
 62 these reservations, the potential of interaction matrices to link ecological frameworks and data  
 63 is evident (Figure 1), for example, translating resource use overlap between pairs of species into  
 64 community-level dynamics<sup>18</sup>. This utility of interaction matrices has repeatedly been sufficient  
 65 to override, at least temporarily, misgivings about their ‘realism’, and their use today is  
 66 widespread. As an illustration, 35 of the 210 articles published in *Ecology Letters* during 2023  
 67 (16%) use interaction matrices in some way, rising to 36% when considering only community  
 68 ecology papers (SI 1).

69 The use of interaction matrices and the wider concept of interaction networks<sup>19,20</sup> extends to  
 70 nearly every corner of ecology from biogeography<sup>21</sup> to conservation<sup>22,23</sup>. A totemic example of  
 71 the use of interaction matrices has been the relationship between stability and complexity of  
 72 ecosystems: early results using the simplest possible models<sup>24</sup> were followed by a succession  
 73 of studies that included additional ‘realistic’ structuring, while still retaining the fundamental  
 74 interaction matrix approach<sup>13,25,26</sup>. Interaction matrix based analyses have shown that stabilising  
 75 structures appear to be overrepresented in real networks<sup>28-31</sup> and allow the identification of  
 76 community level responses to changing environments that could not be identified from pairwise  
 77 analyses<sup>32</sup>. Despite the diversity of metrics that can be used to quantify ecological stability,  
 78 most fundamentally depend on interaction matrices in one way or another<sup>27</sup>.

79 In recent years, new data streams, increased appreciation of feedback, and growing ambitions  
 80 to represent increasingly complex systems are posing significant questions for how the  
 81 venerable interaction matrix can be best used to accelerate ecological understanding. In this  
 82 perspective, we collate and examine the diverse recurring challenges for the interaction matrix  
 83 framework within ecology, grouped into questions of definition, dynamism and data. We argue  
 84 that although some of these are fundamentally ‘unsolvable’, quantitative interaction matrices  
 85 will continue to provide a distinct and valuable convergence point for different subfields within  
 86 ecology where theoretical and empirical work can meet to maximise each other’s utility through

mechanistic predictions. Despite their issues, these perennially controversial abstractions are still rich in underexploited promise. However, this will require the active acknowledgement and engagement with both their strengths and deficiencies. We propose four directions that can maximise their potential to drive forward community ecology.



**Figure 1** A) Interaction matrices are the central uniting feature of community ecology. They are uniquely placed to unite observations of interspecific interactions, trajectories of populations and theoretical understanding of the structure and dynamics of communities (here illustrated with niche models and random matrix theory). B) Interaction matrices are specified by three components: an underlying skeleton of interactions, a dynamic modelling framework and a system state. The dynamics and state are often implicit but are crucial to interpreting the interaction matrix appropriately. The interaction skeleton can derive from many alternative sources (Box 2): illustrated here (clockwise from top left) are extrapolation from literature records, observation of interaction frequency from DNA barcoding or by observation of feeding, experiments where functional responses of performance (here egg number) is measured in response to varying density of another species (here worms), and time series reporting the dynamics of multiple populations. Created in BioRender. Terry, C. (2025) <https://BioRender.com/2425ztg>

### Box 1. Mathematical formulation of interaction matrices.

For the purposes of this perspective, we are defining ‘*interaction matrices*’ broadly as arrays of numbers that define the impact of one population on another. Mathematically, this can make interaction matrices Jacobian matrices, whose elements in row  $i$  and column  $j$  describe the first-order partial derivatives of the  $i$ th function with respect to the  $j$ th variable. As such, they are a distinct, more specific, concept to ‘*interaction networks*’ that only graph links (possibly quantified) between components of the ecological community.

Importantly, there are several distinct approaches to formally mathematically defining the elements of an interaction matrix<sup>2</sup>, that are often referred to with overlapping names. All are only defined for a particular set of species abundances  $\mathbf{N}$  (and implicitly particular environmental conditions) and as such are short-term responses where all populations are assumed to be held constant. Assuming a Lotka-Volterra model:

$$\frac{dN_i}{dt} = r_i N_i + \sum_j^s \alpha_{ij} N_i N_j$$

an apparently direct approach is to specify the interaction matrix  $\mathbf{A}$  as being made up of the  $\alpha$  coefficients. This corresponds to the effect on each species’ per-capita growth rate:

$$A_{ij}^{\text{interaction}} = \alpha_{ij} = \frac{\partial}{\partial N_j} \frac{1}{N_i} \frac{dN_i}{dt}$$

and is hence distinct to approaches that use the effects on each *population*, which at equilibrium can be defined<sup>33</sup> as:

$$A_{ij}^{\text{community}} = \alpha_{ij} N_i = \frac{\partial}{\partial N_j} \frac{dN_i}{dt}$$

Other approaches take other formulations such as the ‘alpha matrix’ that scales the population growth rate relative to both self-effects and intrinsic growth (the original ‘community matrix’<sup>18</sup>) or different underlying dynamic models. However, given information on other parameters and system state<sup>2</sup> these classes of ‘interaction matrix’ are interchangeable and most of our points apply equally to them all.

## Box 2. Approaches to building an interaction matrix:

We can differentiate three principal approaches to specifying interaction matrices across ecology. While different research fields have distinct traditions driven by availability of data they are ultimately converging on a similar goal. A further approach, the inference of interactions from spatial cooccurrence data, does not meet our definition of dynamic interaction matrices and has significant challenges<sup>34</sup>. In all cases the interaction matrix assumes a particular (often implicit) model of population dynamics.

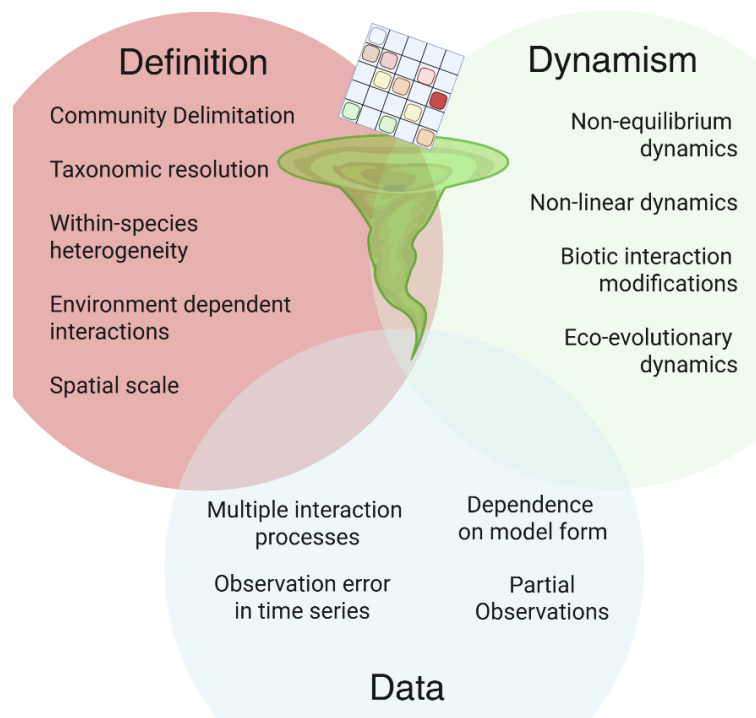
1. *Direct specification based on theoretical expectations*. Mostly associated with theoretical analyses, in this approach the elements of the interaction matrices are directly specified from distributions determined by the researcher. This can range from randomly generated Jacobian matrices<sup>35,36</sup>, through to more ecologically informed models such as the niche model<sup>38</sup> including allometric relationships<sup>39</sup> and include a variety of dynamical forms using generalised niche modelling<sup>37</sup>.

2. *Reconstruction from observations of population counts*. With this approach, comparisons of populations of multiple species within the community through time are used to identify the elements of the interaction matrix. The raw data can be purely observational, include deliberate perturbations in the style of ‘Press’ or ‘Pulse’ experiments<sup>40</sup>, or structured experiments<sup>41</sup>. The method used can be purely correlative, for example S-maps and causal discovery algorithms<sup>42–44</sup> or can embed assumptions about the underlying functional form of the interactions between species with auto-regressive models<sup>45</sup>. The input data can be long-term time series, or multiple short or single-generation transitions<sup>46,47</sup> and can also imbed other extraneous variables such as climate variables.

3. *From observations of underlying interaction processes*. Records of the frequency of observable interactions such as pollination visits or parasitism can be converted into interaction matrices. Translating such sets of observations into a quantitative interaction matrix describing the impact of populations on each other requires additional assumptions, for example body-size based parameterisation<sup>10</sup> or inferring interaction strength from resource use overlap<sup>48</sup>. The estimation of interactions not directly observed is also an increasing line of research, whereby unobserved interactions can be approximated from variables such as functional traits, species abundances, or environmental factors<sup>49,50</sup>. Likely interactions can be inferred from larger-scale ‘metawebs’ of observed interactions tabulating which species have been seen to interact in that region<sup>51</sup>.

# Fundamental Challenges to The Interaction Matrix Approach

Throughout their history, the use of interaction matrices has been subject to numerous criticisms and suggested developments. These challenges are tightly interlinked but can be grouped into three themes related to their definition, dynamism and data (Figure 2). Here we briefly scan the diversity of challenges and criticisms of interaction matrices. In each case, while some suggested ‘solutions’ exist, these are often incompatible with each other and can in turn generate further challenges.



**Figure 2.** Multiple interacting challenges assail the interaction matrix approach. Created in BioRender. Terry, C. (2025) <https://BioRender.com/0yzqn3h>

## Definition: problems of resolution and scale

Natural ecosystems are manifestly not the tidy, bounded, discretisable and well-mixed systems that an interaction matrix presents. Communities have internal structure, ranging from spatial heterogeneities or intra-specific genetic variation, to matters of animal behaviour and life stages:

**Spatial scale and structuring.** The first challenge when creating an interaction matrix is defining the spatial boundaries of the community in question. This seemingly innocuous step continues to pose difficulties since it is vanishingly rare for natural communities to have discrete boundaries. Even within apparently bounded habitats (e.g. ponds) species with high movement capacity can link the dynamics of other species across natural boundaries<sup>52</sup>. Interaction network structure frequently scales with the area under consideration<sup>53–55</sup>, and once an outer boundary is defined, there is frequently significant heterogeneity and spatial structuring, both of which can have dynamic consequences. While this can be partially addressed by explicitly building space into a metacommunity modelling approach<sup>56,57</sup>, these models bring the additional challenge of integrating spatial interactions in metacommunity matrices. Dispersal between spatially distinct populations is frequently modelled as a diffusive term that positively influences local dynamics<sup>57</sup>, but empirical validations remain scarce<sup>58</sup>.

**Selection and resolution of state variables.** An interrelated challenge is to determine what the rows and columns of the matrix should represent, i.e. defining the state variables of the system.

There has been considerable progress in moving on from early empirical matrices whose components were frequently very loosely taxonomically defined<sup>59</sup>, towards quantitative networks of more tightly defined state variables<sup>60,61</sup>, and more recently expansions to hundreds of species and multiple interaction types (e.g. <sup>62–65</sup>). However, although the size and resolution of empirical networks has increased dramatically, there isn't a clear endpoint<sup>66,67</sup>. While the population appears to be a natural unit, the assumption of species populations as discrete, homogenous sets with ecological relevance is severely challenged by multiple forms of intra-specific variation, whether driven by genetic, micro-environment, behavioural or life-stage differences<sup>68–71</sup>. Regardless of recent improvements in the detail of description, summarising the impacts of a species on another with a single 'average' parameter is unavoidable within the standard interaction matrix formulation. Although such parameters should be interpreted as long-term average effects reflecting the effective dynamics of the system this simplification inevitably still discards whole classes of information.

**Dependence on temporally variable environmental conditions.** Interaction strength between species strongly depends on abiotic conditions that fluctuate through space and time<sup>54,72,73</sup>. To resolve this variability into a fixed matrix it is necessary to define and measure an average over a meaningful timescale for the community. However, it is widely appreciated both that key timescales may vary dramatically for different components of the system<sup>74</sup> and that fluctuating interaction strength under different variable environments is itself a key determinant of key dynamics such as coexistence<sup>75</sup>. While there are multiple proposed frameworks to embed environmental dependence into interaction matrix specification<sup>76</sup> or extend to multi-dimensional arrays across a gradient<sup>77</sup>, these move away from the fundamental concept of the interaction matrix, and their implementation in dynamical models is still not fully developed.

## Dynamism: non-linearities, higher order interactions and evolution

Even in a perfectly defined ecosystem, internal community dynamics generate fundamental challenges to the interaction matrix approach<sup>12,17</sup>. The purpose of an interaction matrix is to summarise the effect of one species onto another with a single number, which necessarily involves linearisation. However, effects between species are frequently observed to be non-linearly dependent on the state of the system<sup>78,79</sup>. Interactions are therefore poorly captured unless they are strongly constrained to a fixed point.

**Non-linearities in pairwise interactions.** Non-linear, density-dependent interactions between species are the norm, rather than an exception. The impact has been thoroughly investigated in small modules<sup>80</sup>, but analysis of extensions beyond linear cases for wider communities remains a challenge. This linearisation issue is particularly acute for the assessment of the stability where apparently small differences in the form of density dependence can have substantial impacts<sup>81</sup>. Suggested remedies include generalized modelling frameworks<sup>37</sup> to explore the effects of nonlinearities on stability by fixing only a few key parameters, or structural methods<sup>48,82</sup> that sidestep detailed parameterization by focusing instead on persistence probabilities as a function of general network topology. However, many of these methods remain tied to Lotka-Volterra formulations or closely related dynamics<sup>83</sup>. This reliance on Lotka-Volterra models reflects the core paradox: despite their well-documented limitations, their mathematical tractability and capacity to reproduce almost any dynamical behaviour<sup>84</sup> has made them an indispensable tool. While understanding of these potential complexities has evolved significantly, solutions to integrating complex interactions at the community scale has not yet advanced to the same degree due to these fundamental constraints.

**Higher-order interactions:** Many interactions between species are influenced by the wider ecological community which generates the potential for complex emergent dynamics and feedbacks<sup>85</sup>. The challenge these effects pose for the interaction matrix approach was recognized early<sup>86,87</sup> under the broad umbrella of 'higher-order interactions'. They are expected



to be widespread<sup>88</sup>, although there still exist only a few large-scale parameterised examples<sup>89</sup>. Proposed solutions to the challenge of biotic contextualisation include frameworks for modelling adaptive foraging<sup>90</sup>, interaction modifications<sup>91</sup>, hypergraphs<sup>92</sup>, and rewiring<sup>93</sup>, as well as extending analysis of interaction matrices into successively higher dimensional arrays<sup>94,95</sup>. While models can be built, their analysis is challenging, for example, the significant increase in parameters can create many more fixed points<sup>96</sup>.

**Evolutionary changes:** A further internal source of feedback between the structure and dynamics of communities are evolutionary changes to interactions between species. Rapid evolution is increasingly recognised as having the potential to substantially impact the dynamics of communities<sup>97</sup>. This introduces path dependence to the dynamics of the system, as knowledge of the current state of the system is not necessarily sufficient because interaction strength will depend on the history of the system. As with higher-order interactions, there are a number of modelling frameworks exploring different consequences<sup>98,99</sup>, but very little robust empirical information and strong limits to analytical opportunities.

## Data: Quality of Available Information

Thirdly, but as importantly, the preceding challenges rest on the assumption that there is sufficient information available to confidently infer the entries of the interaction matrix, even when the assumptions made about the dynamics are considered reasonable.

**Converting observed interactions to matrices:** It is widely appreciated that most observed interaction networks are undersampled<sup>100,101</sup>, leading to the so called ‘Eltonian shortfall’ in our knowledge of interactions<sup>102</sup>. While the quality of observed interaction networks has improved greatly (as discussed above), and there is increasing optimism that it will be possible to tackle gaps in partially observed networks<sup>103</sup>, the precision of inferred interaction networks will always be constrained. Furthermore, species impact each other through multiple processes, yet frequently observed interaction networks capture only a single class of interaction (for example trophic, pollination or competition). While increasing efforts are being made to construct multi-layer networks<sup>104,105</sup> the additional empirical effort and challenges comparing interaction types are significant constraints.

Even with a reasonable set of observations, a fundamental challenge is converting from observed interaction networks to interaction matrices that describe the dynamics of the community (Figure 1B). While interaction matrices represent a strong unifying objective, the gap between observed ecological network and inferred interaction matrix is more precarious than may be assumed. For example, translating from observed mutualistic pollination networks to an interaction network requires assumptions of both the benefit of a visit to each partner and intraguild competition<sup>48</sup>. Development of approaches to translate between types of networks began early, for example to translate resource use overlap into competition<sup>106</sup> and refinements are still being developed (e.g.<sup>107</sup>), yet it remains the case that such conversions are sensitive to model form<sup>108,109</sup> and scaling with self-regulation terms<sup>110</sup>.

**Observed dynamics:** Parallel issues arise when inferring interaction matrices from time-series or observation of population responses. The idealised long time-series under steady conditions or the small, short, perturbations from equilibrium envisaged in theoretical frameworks<sup>40</sup> are essentially impossible to empirically observe. Observational error is frequently large and can require careful handling<sup>111</sup>. Unique interaction networks are rarely identifiable without some kind of assumed model structure, however, the specific assumptions of the model functional form that can have significant impact on the inferred structure of the interaction matrix<sup>112</sup>. Highly uncertain interaction strengths have the potential to generate artefactual results in subsequent analyses<sup>113</sup>. Recently developed ‘model-free’ approaches<sup>114,115</sup> can sidestep some challenges by estimating interaction matrix coefficients directly from abundance time series without assuming an underlying model but have considerably greater data demands, often

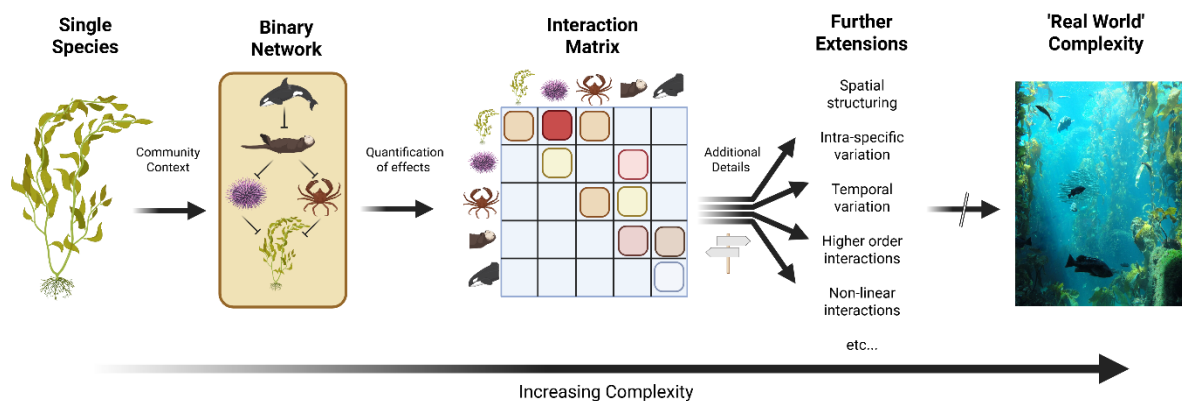


needing more than 35-40 temporal observations even for simplified assemblages<sup>115</sup>. As such, the ability to infer interaction matrices from large, diverse communities remains an open area of research<sup>43</sup> and will reach fundamental limits to inference of network structure from time series<sup>116</sup>.

## Tackling the Challenges

We would expect that the above catalogue of challenges is familiar to most ecologists. However, collating even this undoubtedly incomplete list in one place clarifies that piecemeal solutions simply cannot ‘fix’ interaction matrices. ‘Solving’, or even addressing, one set of issues almost inevitably exacerbates a different category of challenges facing interaction matrices. What should be done?

The interaction matrix is currently a central paradigm within ecology, in the sense that it is a construct that informs and underlies a substantial proportion of research. Is this dominance an impediment, building up tensions and awaiting a Kuhnian paradigm shift to a fundamentally different approach<sup>117</sup>? While the very nature of a paradigm makes it hard to identify alternatives, fundamental challenges and extensions have been raised through most of their 100 year history, yet their popularity remains undimmed. There has been a repeated cycle of problems being identified, a specific solution presented, but a swift reversion back to original interaction matrices. While predictions of the future course of science are inherently risky, it seems likely that interaction matrices are here to stay, despite their deficiencies (Figure 3).

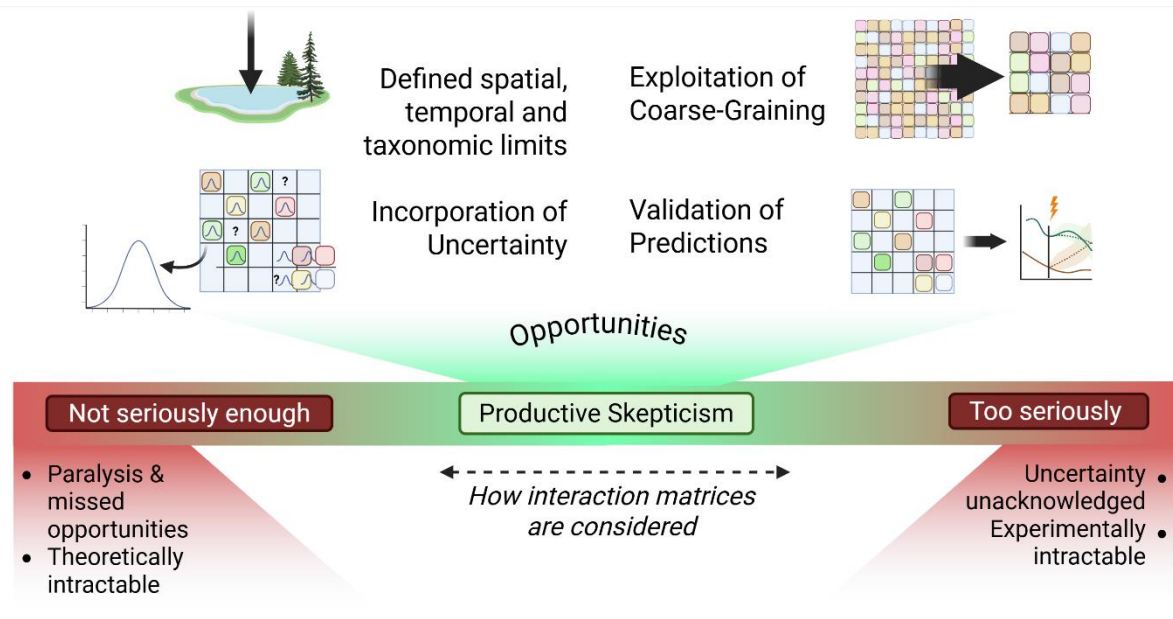


**Figure 3:** Quantitative interaction matrices represent a useful trade-off in complexity including quantification of the community context and which can be expected to be attained for a wide variety of communities. Further extensions can further narrow the gap to real-world complexity and capture influential details but are frequently not able to be incorporated concurrently due to analytic and data limitations. The approach to ‘real-world’ complexity is here illustrated by an image of the kelp-forest exhibit from Monterey Bay Aquarium (CC0). Created in BioRender. Terry, C. (2025) <https://BioRender.com/ufbrlcc>

It seems most useful to see interaction matrices as being an inevitable consequence of a reductionist approach to ecology<sup>118</sup>, that unlocks a tractable window into complexity, rather than an outdated framework to continuously press to move beyond. The trade-offs are the price one must acknowledge to get closer to mechanistic understanding and predictions. As such, the real challenge community ecology faces is to make the best value from these imperfect constructs. Given the diversity of limitations to the use of interaction matrices, we contend that there is often more to gain from better *interpreting* interaction matrices, over developing yet more extended frameworks. While it will always be a case of matching the tool to the specific question, as a field we need to need to get better at reading across systems to accelerate progress, and this requires a more consistent and comparable approach.

Instead of caveating results after they are presented as a defence against critique, we suggest the fastest progress from both theoretical and empirical poles can be made by treating interaction matrices with appropriate *productive scepticism* throughout the scientific process

(Figure 4). By consciously letting go of the idea of a ‘perfect’ interaction matrix, this can facilitate the best use of the information that is both available. We suggest four focuses to aid this goal:



**Figure 4.** How should interaction matrices be most productively considered? Between dismissal as artificial constructs and over-emphasis, there is a productive middleground of productive skepticism with significant scope for future developments. Created in BioRender. Terry, C. (2025) <https://BioRender.com/wbhx7z5>

### 1) Clearly defining the focus and bounds of applicability to allow cross-system comparison

More rigorously and explicitly defining the taxonomic, spatial and temporal bounds of applicability that a particular interaction matrix is intended to represent is an achievable goal with great potential benefits. This can substantially reduce the risk of misinterpretation of any conclusions but also offers the prospect to build towards stronger, wider generalisations. While currently a distant prospect, interaction matrices specifying the relationships between populations have the potential to better link many disparate areas of ecology by acting as a common currency. While databases for interaction networks have existed for some time<sup>59,119</sup> and form the basis for many meta-analyses<sup>120</sup>, comparable frameworks for the standardisation and publication of interaction matrix metadata are still lacking. Improving interoperability between studies by more clearly defining scope of published interaction matrices and the assumptions embedded within them will be a key first step to this goal.

### 2) Actively acknowledging inevitable uncertainty and testing the robustness of conclusions

Methods to account for the diverse sources of uncertainty in empirical interaction matrices have rapidly developed in recent years. They have the potential to address many of the fundamental data-challenges, yet their use is still the exception rather than a rule. The existence of particular interactions can be treated probabilistically<sup>121–124</sup> or as a fuzzy interaction web<sup>125</sup>, the sensitivity of results to inclusion of most-likely missing links<sup>126</sup> can be tested, and uncertainty in interaction strength parameter estimates can be directly propagated<sup>127</sup>. The uncertainty in interaction estimates derived from the unknown form of the relationship between variables (model selection error) poses a more fundamental challenge<sup>112</sup>, but can still be explored and the robustness or otherwise of results to alternative plausible assumptions can be confirmed<sup>128</sup>. Model-averaging and MCMC approaches are potential methods to quantify the uncertainty associated to interaction strength estimates, albeit at the cost of potentially high computational requirements. As well as technical methods, this is as much a psychological shift towards being ready to acknowledge limitations to build stronger foundations. Inevitably,

this process may well identify that certain properties are practically unidentifiable due to sensitivities in the specification of the interaction matrix<sup>129</sup>. This may necessitate a move towards responses that are more robust to uncertainties in individual terms<sup>130–132</sup>, but will strengthen the field as a whole.

### **3) Embracing advances across complexity sciences, especially coarse-graining.**

The wider field of complexity science offers rapidly expanding opportunities to address new ecological questions using interaction matrices<sup>133</sup>. For instance, new developments have used interaction matrices to understand ecosystem learning<sup>134</sup>, ecological memory<sup>135</sup> and information processing<sup>136</sup>. Of particular interest to ecology are complexity science developments within ‘coarse-graining’ to deal with scaling challenges<sup>137</sup>. This refers to simplifying complex data to reduce dimensionality while preserving general patterns and system behaviour properties.

Ecosystems are highly structured<sup>138</sup> due to continuous community assembly leading to non-random trait distributions<sup>139</sup>, which have important implications for dynamics, coexistence, and resilience. Thus, species are typically able to be coarse-grained into functional groups<sup>140</sup>, taxonomic and phylogenetic groups<sup>141,142</sup>, or aggregated based on statistical patterns. For instance, using techniques borrowed from statistical physics such as Renormalization Group (RG) theory<sup>143</sup> we can understand scale-invariant patterns, critical transitions, and emergent properties by systematically coarse-graining a system and studying how its parameters evolve. Validating such methods is typically conducted by predicting target metrics such as richness and diversity indices within a coarse-grained scale<sup>142</sup> or testing for scale invariance indicating successful dimension reduction<sup>143</sup>.

Emergent systems can be defined as self-contained processes that evolve over time<sup>144</sup>. In this framework, a coarse-grained process becomes an autonomous computational entity when it has a distinct function, informational self-sufficiency and its own causal dynamics. In ecology, this perspective aligns with ecosystems’ hierarchical structure where macro-patterns such as population dynamics emerge from micro-processes such as individual behaviour, metabolism, or species interactions. While coarse-graining is often applied intuitively in ecology, computational science advances offer a rigorous route to determine when a coarse-grained level genuinely captures an emergent process, and identify appropriate resolution and scale of interaction matrices.

### **4) Validation of higher-level predictions from interaction matrices.**

Systems theory<sup>145</sup> suggests that the usefulness of a model lies not in its ability to replicate every detail, but in its capacity to reveal general patterns and consistent system-level behaviours. Interaction matrices, as structured representations of ecological organisation, are particularly well-suited for this kind of systems-level reasoning. When treated as a mesoscopic layer between individual mechanisms and macroscopic community behaviour, these matrices allow us to formulate testable hypotheses about the stability, resilience, and functioning of these communities and the species that compose them. While they rely on simplifying assumptions, their mechanistic structure enables predictions that remain linked to ecological processes and supports multiple avenues of empirical and theoretical validation. Rather than seeking precise forecasts of individual species’ trajectories, validation can often more usefully focus on reproducible ensemble properties—such as coexistence thresholds, stability regimes, or responses to perturbations—that emerge across replicates or parameterisations. This can be achieved through microcosm experiments<sup>32,43,146</sup> or tracking of field communities<sup>148,149</sup>. These strategies are especially valuable when full mechanistic detail is unknown or unknowable, allowing progress through the identification of statistical regularities and structural constraints<sup>131</sup>. By adopting a systems-theoretic approach that emphasizes both structure and function, interaction matrices can be used not just to describe, but to explain and predict

ecological phenomena—transforming them from theoretical constructs into empirically grounded components of a unified ecological science.

## Conclusion

Interaction matrices represent a major step towards a holistic analysis of a community, perhaps the last universally applicable stepping-stone building up from analysing populations separately. Matrices offer the mathematical foundation to pursue a systems approach and to make predictions at the community scale. Despite their simplicity, the fact that interaction matrices have frequently demonstrated their usefulness implies they are capable of capturing fundamental information about communities. They continue to represent one of the best chances to bring unity to community ecology across systems from small microbial systems to whole oceans.

In his last book, Robert MacArthur described linear interaction matrices as possibly being ‘*hopelessly far from the truth and [so] should not be used*’<sup>150</sup>, pg. 33). The still relevant challenge identified then is to exercise judgment on the extent that we can rely on their answers. This process will be greatly helped by a more careful treatment of interaction matrices, as uncertain, but powerful, constructs.

## Acknowledgments

All figures are made with BioRender (BioRender.com). JCDDT was funded by the Leverhulme Trust ECF-2022-666. DGC was funded by the Austrian Science Fund grant ESP-671 (Project *Horos*). Adam Clark and Talya Hackett provided constructive feedback on earlier manuscript drafts.

**Author Contributions:** All authors contributed equally.

## Supplementary Information

### SI 1

Estimating prevalence of interaction matrices in the literature.

VDG recovered from Web-of-Science all articles published in the journal *Ecology Letters* during 2023 (210 records). From those, we subset articles containing “*interaction matrix OR interaction matrices OR matrix OR matrices OR ecological network OR community ecology*” in any field (98 articles), and read the papers to identify those that directly used interaction matrices (either between different species or within the same species) resulting in 35 entries.

## References

1. Levin, S. A. Ecosystems and the Biosphere as Complex Adaptive Systems. *Ecosystems* **1**, 431–436 (1998).
2. Novak, M. *et al.* Characterizing Species Interactions to Understand Press Perturbations: What Is the Community Matrix? *Annual Review of Ecology, Evolution, and Systematics* **47**, 409–432 (2016).
3. Darwin, C. R. *On the Origin of Species by Means of Natural Selection; or the Preservation of Favoured Races in the Struggle for Life*. (John Murray, London, 1859). doi:10.1038/005318a0.
4. Egerton, F. N. Understanding Food Chains and Food Webs, 1700–1970. *Bulletin of the Ecological Society of America* **88**, 50–68 (2007).
5. Forbes, S. A. The Lake as a Microcosm. *Bulletin of the Scientific Association (Peoria, Illinois)* 77–87 (1887).
6. Lotka, A. J. *Elements of Physical Biology*. (Williams and Watkins, Baltimore, 1926).
7. Volterra, V. Fluctuations in the Abundance of a Species considered Mathematically. *Nature* **118**, 558–560 (1926).

8. Kingsland, S. Alfred J. Lotka and the origins of theoretical population ecology. *Proceedings of the National Academy of Sciences* **112**, 9493–9495 (2015).
9. Kingsland, Sharon. E. *Modelling Nature: Episodes in the History of Population Ecology*. (University of Chicago Press, London, 1995).
10. Berlow, E. L. et al. Simple prediction of interaction strengths in complex food webs. *Proceedings of the National Academy of Sciences* **106**, 187–191 (2009).
11. Laska, M. S. & Wootton, J. T. Theoretical Concepts and Empirical Approaches to Measuring Interaction Strength. *Ecology* **79**, 461–476 (1998).
12. Wootton, J. T. & Emmerson, M. Measurement of Interaction Strength in Nature. *Annual Review of Ecology, Evolution, and Systematics* **36**, 419–444 (2005).
13. Allesina, S. & Tang, S. The stability–complexity relationship at age 40: a random matrix perspective. *Population Ecology* **57**, 63–75 (2015).
14. Kerner, E. H. A statistical mechanics of interacting biological species. *Bulletin of Mathematical Biophysics* **19**, 121–146 (1957).
15. Halperin, T. Georgii F. Gause’s The Struggle for Existence and the Integration of Natural History and Mathematical Models. *The American Naturalist* 000–000 (2024) doi:10.1086/734003.
16. Solé, R. V. *Phase Transitions*. vol. 3 (Princeton University Press, 2011).
17. Paine, R. T. Road Maps of Interactions or Grist for Theoretical Development? *Ecology* **69**, 1648–1654 (1988).
18. Levins, R. *Evolution in Changing Environments: Some Theoretical Explorations*. (Princeton University Press, 1968).
19. Delmas, E. et al. Analysing ecological networks of species interactions. *Biological Reviews* **94**, 16–36 (2019).
20. Dunne, J. A. & Pascual, M. *Ecological Networks: Linking Structure to Dynamics in Food Webs*. (Oxford University Press, Oxford, 2006).
21. Windsor, F. M., van den Hoogen, J., Crowther, T. W. & Evans, D. M. Using ecological networks to answer questions in global biogeography and ecology. *Journal of Biogeography* **50**, 57–69 (2023).
22. Dansereau, G. et al. Overcoming the disconnect between interaction networks and biodiversity conservation and management. *Trends in Ecology & Evolution* (2025).
23. Harvey, E., Gounand, I., Ward, C. L. & Altermatt, F. Bridging ecology and conservation: from ecological networks to ecosystem function. *Journal of Applied Ecology* **54**, 371–379 (2017).
24. May, R. M. *Stability and Complexity in Model Ecosystems*. (Princeton University Press, Princeton, 1973).
25. Akjouj, I. et al. Complex systems in ecology: a guided tour with large Lotka–Volterra models and random matrices. *Proceedings of the Royal Society A: Mathematical, Physical and Engineering Sciences* **480**, 20230284 (2024).
26. Rooney, N. & McCann, K. S. Integrating food web diversity, structure and stability. *Trends in Ecology & Evolution* **27**, 40–6 (2012).
27. Domínguez-García, V., Dakos, V. & Kéfi, S. Unveiling dimensions of stability in complex ecological networks. *Proceedings of the National Academy of Sciences of the United States of America* **116**, 25714–25720 (2019).
28. Bascompte, J. & Jordano, P. *Mutualistic Networks*. (Princeton University Press, Princeton, 2013).
29. Dormann, C. F., Fründ, J. & Schaefer, H. M. Identifying Causes of Patterns in Ecological Networks: Opportunities and Limitations. *Annual Review of Ecology, Evolution, and Systematics* **48**, 559–584 (2017).
30. García-Callejas, D. et al. Non-random interactions within and across guilds shape the potential to coexist in multi-trophic ecological

- communities. *Ecology Letters* **26**, 831–842 (2023).
31. Johnson, S., Domínguez-García, V., Donetti, L. & Muñoz, M. A. Trophic coherence determines food-web stability. *Proceedings of the National Academy of Sciences* **111**, 17923–17928 (2014).
32. Tabi, A. *et al.* Species multidimensional effects explain idiosyncratic responses of communities to environmental change. *Nat Ecol Evol* **4**, 1036–1043 (2020).
33. Case, T. J. *An Illustrated Guide to Theoretical Ecology*. (New York ; Oxford : Oxford University Press, 2000).
34. Blanchet, F. G., Cazelles, K. & Gravel, D. Co-occurrence is not evidence of ecological interactions. *Ecology Letters* **23**, 1050–1063 (2020).
35. Allesina, S. & Tang, S. Stability criteria for complex ecosystems. *Nature* **483**, 205–208 (2012).
36. May, R. M. Will a large complex system be stable? *Nature* **238**, 413–414 (1972).
37. Gross, T., Rudolf, L., Levin, S. A. & Dieckmann, U. Generalized Models Reveal Stabilizing Factors in Food Webs. *Science* **325**, 747–750 (2009).
38. Williams, R. J. & Martinez, N. D. Simple rules yield complex food webs. *Nature* **404**, 180–183 (2000).
39. Brose, U., Williams, R. J. & Martinez, N. D. Allometric scaling enhances stability in complex food webs. *Ecology Letters* **9**, 1228–1236 (2006).
40. Bender, E. A., Case, T. J. & Gilpin, M. E. Perturbation Experiments in Community Ecology: Theory and Practice. *Ecology* **65**, 1–13 (1984).
41. Hart, S. P., Freckleton, R. P. & Levine, J. M. How to quantify competitive ability. *Journal of Ecology* **106**, 1902–1909 (2018).
42. Bonnaffé, W., Sheldon, B. C. & Coulson, T. Neural ordinary differential equations for ecological and evolutionary time series analysis. *Methods in Ecology and Evolution* **2**, (2021).
43. Chang, C.-W. *et al.* Reconstructing large interaction networks from empirical time series data. *Ecology Letters* **24**, 2763–2774 (2021).
44. Munch, S. B., Rogers, T. L. & Sugihara, G. Recent developments in empirical dynamic modelling. *Methods in Ecology and Evolution* **14**, 732–745 (2023).
45. Ives, A. R., Dennis, B., Cottingham, K. L. & Carpenter, S. R. Estimating community stability and ecological interactions from time-series data. *Ecological Monographs* **73**, 301–330 (2003).
46. Clark, A. T. *et al.* Spatial convergent cross mapping to detect causal relationships from short time series. *Ecology* **96**, 1174–1181 (2015).
47. García-Callejas, D., Bartomeus, I. & Godoy, O. The spatial configuration of biotic interactions shapes coexistence-area relationships in an annual plant community. *Nat Commun* **12**, 6192 (2021).
48. Rohr, R. P., Saavedra, S. & Bascompte, J. On the structural stability of mutualistic systems. *Science* **345**, 1253497–1253497 (2014).
49. Martinez, A. & Pires, M. Estimated missing interactions change the structure and alter species roles in one of the world’s largest seed-dispersal networks. *Oikos* **2024**, e10521 (2024).
50. Wootton, K. L. *et al.* Layer-specific imprints of traits within a plant–herbivore–predator network – complementary insights from complementary methods. *Ecography* **2024**, e07028 (2024).
51. Maiorano, L., Montemaggiore, A., Ficetola, G. F., O’Connor, L. & Thuiller, W. TETRA-EU 1.0: A species-level trophic metaweb of European tetrapods. *Global Ecology and Biogeography* **29**, 1452–1457 (2020).
52. Knight, T. M., McCoy, M. W., Chase, J. M., McCoy, K. A. & Holt, R. D. Trophic cascades across ecosystems. *Nature* **437**, 880–883 (2005).

53. Galiana, N. *et al.* Ecological network complexity scales with area. *Nat Ecol Evol* **6**, 307–314 (2022).
54. Poisot, T., Stouffer, D. B. & Gravel, D. Beyond species: why ecological interaction networks vary through space and time. *Oikos* **124**, 243–251 (2015).
55. Trøjelsgaard, K. & Olesen, J. M. Ecological networks in motion: micro- and macroscopic variability across scales. *Functional Ecology* **30**, 1926–1935 (2016).
56. Gravel, D., Massol, F. & Leibold, M. A. Stability and complexity in model meta-ecosystems. *Nature Communications* **7**, (2016).
57. Thompson, P. L. *et al.* A process-based metacommunity framework linking local and regional scale community ecology. *Ecology Letters* **23**, 1314–1329 (2020).
58. Resasco, J. & Fletcher, R. J. Accounting for connectivity alters the apparent roles of spatial and environmental processes on metacommunity assembly. *Landscape Ecol* **36**, 1089–1099 (2021).
59. Cohen, J. E. *Food Webs and Niche Space*. (Princeton University Press, Princeton, 1978).
60. Pimm, S. L. *et al.* Food web patterns and their consequences. *Nature* **350**, 669–674 (1991).
61. Polis, G. A. Complex Trophic Interactions in Deserts: An Empirical Critique of Food-Web Theory. *The American Naturalist* **138**, 123–155 (1991).
62. Gripenberg, S. *et al.* A highly resolved food web for insect seed predators in a species-rich tropical forest. *Ecology Letters* **22**, 1638–1649 (2019).
63. Jacob, U. *et al.* The Role of Body Size in Complex Food Webs. in *Advances in Ecological Research* vol. 45 181–223 (Elsevier, 2011).
64. Kéfi, S. *et al.* Network structure beyond food webs : mapping non-trophic and trophic interactions on Chilean rocky shores. *Ecology* **96**, 291–303 (2015).
65. Pocock, M. J. O., Evans, D. M. & Memmott, J. The robustness and restoration of a network of ecological networks. *Science* **335**, 973–7 (2012).
66. Gauzens, B. *et al.* Tailoring interaction network types to answer different ecological questions. *Nat. Rev. Biodivers.* 1–10 (2025) doi:10.1038/s44358-025-00056-7.
67. Guimarães, P. R. The Structure of Ecological Networks Across Levels of Organization. *Annual Review of Ecology, Evolution, and Systematics* **51**, 433–460 (2020).
68. Arroyo-Correa, B., Jordano, P. & Bartomeus, I. Intraspecific variation in species interactions promotes the feasibility of mutualistic assemblages. *Ecology Letters* **26**, 448–459 (2023).
69. Bolnick, D. I. *et al.* Why intraspecific trait variation matters in community ecology. *Trends in Ecology and Evolution* **26**, 183–192 (2011).
70. Paniw, M. *et al.* Pathways to global-change effects on biodiversity: new opportunities for dynamically forecasting demography and species interactions. *Proceedings of the Royal Society B: Biological Sciences* **290**, 20221494 (2023).
71. Tur, C., Vigalondo, B., Trøjelsgaard, K., Olesen, J. M. & Traveset, A. Downscaling pollen-transport networks to the level of individuals. *Journal of Animal Ecology* **83**, 306–317 (2014).
72. Chamberlain, S. A., Bronstein, J. L. & Rudgers, J. A. How context dependent are species interactions? *Ecology Letters* **17**, 881–890 (2014).
73. Tylianakis, J. M. & Morris, R. J. Ecological Networks Across Environmental Gradients. *Annual Review of Ecology, Evolution, and Systematics* **48**, 25–48 (2017).
74. Hastings, A. Timescales, dynamics, and ecological understanding. *Ecology* **91**, 3471–3480 (2010).
75. Chesson, P. Mechanisms of Maintenance of Species Diversity. *Annual Review of Ecology, Evolution, and Systematics* **31**, 343–366 (2000).
76. Gilbert, B. *et al.* A bioenergetic framework for the temperature



- dependence of trophic interactions. *Ecology Letters* **17**, 902–914 (2014).
77. Kissling, W. D. *et al.* Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents. *Journal of Biogeography* **39**, 2163–2178 (2012).
  78. Clark, T. J. & Luis, A. D. Nonlinear population dynamics are ubiquitous in animals. *Nature Ecology and Evolution* **4**, 75–81 (2020).
  79. Scheffer, M., Carpenter, S., Foley, J. A., Folke, C. & Walker, B. Catastrophic shifts in ecosystems. *Nature* **413**, 591–596 (2001).
  80. Rosenzweig, M. L. & MacArthur, R. H. Graphical Representation and Stability Conditions of Predator-Prey Interactions. *The American Naturalist* **97**, 209–223 (1963).
  81. Hatton, I. A., Mazzarisi, O., Altieri, A. & Smerlak, M. Diversity begets stability: Sublinear growth and competitive coexistence across ecosystems. *Science* **383**, eadg8488 (2024).
  82. Saavedra, S. *et al.* A structural approach for understanding multispecies coexistence. *Ecological Monographs* **87**, 470–486 (2017).
  83. Cenci, S. & Saavedra, S. Structural stability of nonlinear population dynamics. *Physical Review E* **97**, (2018).
  84. Takeuchi, Y. *Global Dynamical Properties of Lotka-Volterra Systems*. (World Scientific, 1996).
  85. Abrams, P. A. Arguments in Favor of Higher Order Interactions. *The American Naturalist* **121**, 887–891 (1983).
  86. Neill, W. E. The Community Matrix and Interdependence of the Competition Coefficients. *The American Naturalist* **108**, 399–408 (1974).
  87. Vandermeer, J. H. The competitive structure of communities: an experimental approach with protozoa. *Ecology* **50**, 362–371 (1969).
  88. Letten, A. D. & Stouffer, D. B. The mechanistic basis for higher-order interactions and non-additivity in competitive communities. *Ecology Letters* **22**, 423–436 (2019).
  89. Mayfield, M. M. & Stouffer, D. B. Higher-order interactions capture unexplained complexity in diverse communities. *Nature Ecology & Evolution* **1**, 0062 (2017).
  90. Beckerman, A., Petchey, O. L. & Morin, P. J. Adaptive foragers and community ecology: linking individuals to communities and ecosystems. *Functional Ecology* **24**, 1–6 (2010).
  91. Terry, J. C. D., Morris, R. J. & Bonsall, M. B. Trophic interaction modifications: an empirical and theoretical framework. *Ecology Letters* **20**, 1219–1230 (2017).
  92. Golubski, A. J., Westlund, E. E., Vandermeer, J. & Pascual, M. Ecological Networks over the Edge: Hypergraph Trait-Mediated Indirect Interaction (TMII) Structure. *Trends in Ecology & Evolution* **31**, 344–354 (2016).
  93. Gilljam, D., Curtsdotter, A. & Ebenman, B. Adaptive rewiring aggravates the effects of species loss in ecosystems. *Nature Communications* **6**, 8412 (2015).
  94. Bairey, E., Kelsic, E. D. & Kishony, R. High-order species interactions shape ecosystem diversity. *Nature Communications* **7**, 12285 (2016).
  95. Gibbs, T., Levin, S. A. & Levine, J. M. Coexistence in diverse communities with higher-order interactions. *Proceedings of the National Academy of Sciences* **119**, e2205063119 (2022).
  96. AlAdwani, M. & Saavedra, S. Ecological models: higher complexity in, higher feasibility out. *Journal of The Royal Society Interface* **17**, 20200607 (2020).
  97. Fussmann, G. F., Loreau, M. & Abrams, P. A. Eco-evolutionary dynamics of communities and ecosystems. *Functional Ecology* **21**, 465–477 (2007).
  98. Guimarães, P. R., Pires, M. M., Jordano, P., Bascompte, J. & Thompson, J. N. Indirect effects drive coevolution in mutualistic networks. *Nature* **550**, 511–514 (2017).

99. Segar, S. T. *et al.* The Role of Evolution in Shaping Ecological Networks. *Trends in Ecology & Evolution* **35**, 454–466 (2020).
100. Blüthgen, N. & Staab, M. A Critical Evaluation of Network Approaches for Studying Species Interactions. *Annual Review of Ecology, Evolution, and Systematics* **55**, 65–88 (2024).
101. Jordano, P. Sampling networks of ecological interactions. *Functional Ecology* **30**, 1883–1893 (2016).
102. Hortal, J. *et al.* Seven Shortfalls that Beset Large-Scale Knowledge of Biodiversity. *Annual Review of Ecology, Evolution, and Systematics* **46**, 523–549 (2015).
103. Strydom, T. *et al.* A roadmap towards predicting species interaction networks (across space and time). *Phil. Trans. R. Soc. B* **376**, 20210063 (2021).
104. García-Callejas, D., Molowny-Horas, R. & Araújo, M. B. Multiple interactions networks: towards more realistic descriptions of the web of life. *Oikos* **127**, 5–22 (2018).
105. Kéfi, S. *et al.* More than a meal... integrating non-feeding interactions into food webs. *Ecology Letters* **15**, 291–300 (2012).
106. MacArthur, R. Species packing and competitive equilibrium for many species. *Theoretical Population Biology* **1**, 1–11 (1970).
107. Letten, A. D., Ke, P. J. & Fukami, T. Linking modern coexistence theory and contemporary niche theory. *Ecological Monographs* **87**, 161–177 (2017).
108. McPeck, M. A. *Coexistence in Ecology: A Mechanistic Perspective*. (Princeton University Press, 2022).
109. O'Dwyer, J. P. Whence Lotka-Volterra? *Theor Ecol* **11**, 441–452 (2018).
110. Barabás, G., Michalska-Smith, M. J. & Allesina, S. Self-regulation and the stability of large ecological networks. *Nature Ecology & Evolution* **1**, 1870–1875 (2017).
111. Clark, J. S. & Bjørnstad, O. N. Population Time Series: Process Variability, Observation Errors, Missing Values, Lags, and Hidden States. *Ecology* **85**, 3140–3150 (2004).
112. Cervantes-Loreto, A. *et al.* Environmental context, parameter sensitivity, and structural sensitivity impact predictions of annual-plant coexistence. *Ecological Monographs* **93**, e1592 (2023).
113. Terry, J. C. D. Uncertain competition coefficients undermine inferences about coexistence. *Nature* **632**, E9–E14 (2024).
114. Cenci, S., Sugihara, G. & Saavedra, S. Regularized S-map for inference and forecasting with noisy ecological time series. *Methods in Ecology and Evolution* **10**, 650–660 (2019).
115. Sugihara, G. *et al.* Detecting Causality in Complex Ecosystems. *Science* **338**, 496–500 (2012).
116. Angulo, M. T., Moreno, J. A., Lippner, G., Barabási, A. L. & Liu, Y. Y. Fundamental limitations of network reconstruction from temporal data. *Journal of the Royal Society Interface* **14**, (2017).
117. Graham, M. H. & Dayton, P. K. On the Evolution of Ecological Ideas: Paradigms and Scientific Progress. *Ecology* **83**, 1481–1489 (2002).
118. Hastings, A. Unstructured Models in Ecology: Past, Present and Future. in *Ecological Paradigms Lost: Routes of Theory Change* (eds Cuddington, K. & Beisner, B. E.) 9–30 (Elsevier Academic Press Inc, 2005).
119. Poisot, T. *et al.* mangal – making ecological network analysis simple. *Ecography* **39**, 384–390 (2016).
120. Xing, S. & Fayle, T. M. The rise of ecological network meta-analyses: Problems and prospects. *Global Ecology and Conservation* **30**, e01805 (2021).
121. Banville, F. *et al.* Deciphering Probabilistic Species Interaction Networks. *Ecology Letters* **28**, e70161 (2025).
122. Cirtwill, A. R., Eklöf, A., Roslin, T., Wootton, K. & Gravel, D. A quantitative framework for investigating the reliability of empirical network construction.

- Methods in Ecology and Evolution* **10**, 902–911 (2019).
123. Poisot, T. *et al.* The structure of probabilistic networks. *Methods in Ecology and Evolution* **7**, 303–312 (2016).
  124. Yeakel, J. D., Guimarães, P. R., Novak, M., Fox-Dobbs, K. & Koch, P. L. Probabilistic patterns of interaction: the effects of link-strength variability on food web structure. *Journal of the Royal Society Interface* **9**, 3219–28 (2012).
  125. Pearson, D. E. & Clark-Wolf, T. J. Predicting ecological outcomes using fuzzy interaction webs. *Ecology* **104**, e4072 (2023).
  126. Terry, J. C. D. & Lewis, O. T. Finding missing links in interaction networks. *Ecology* **101**, 1–13 (2020).
  127. Bowler, C. H., Weiss-Lehman, C., Towers, I. R., Mayfield, M. M. & Shoemaker, L. G. Accounting for demographic uncertainty increases predictions for species coexistence: A case study with annual plants. *Ecology Letters* **25**, 1618–1628 (2022).
  128. Letten, A. D. Making sense of (sublinear) density dependence. *Trends in Ecology & Evolution* **0**, (2025).
  129. Yodzis, P. The Indeterminacy of Ecological Interactions as Perceived Through Perturbation Experiments. *Ecology* **69**, 508–515 (1988).
  130. Barabás, G. & Allesina, S. Predicting global community properties from uncertain estimates of interaction strengths. *Journal of The Royal Society Interface* **12**, 20150218 (2015).
  131. Barbier, M., Arnoldi, J.-F., Bunin, G. & Loreau, M. Generic assembly patterns in complex ecological communities. *Proceedings of the National Academy of Sciences* **115**, 2156–2161 (2018).
  132. Barbier, M., Bunin, G. & Leibold, M. A. Getting More by Asking for Less: Linking Species Interactions to Species Co-Distributions in Metacommunities. 2023.06.04.543606 Preprint at <https://doi.org/10.1101/2023.06.04.543606> (2024).
  133. Riva, F. *et al.* Toward a cohesive understanding of ecological complexity. *Science Advances* **9**, eabq4207 (2023).
  134. Power, D. A. *et al.* What can ecosystems learn? Expanding evolutionary ecology with learning theory. *Biology Direct* **10**, 69 (2015).
  135. Khalighi, M., Sommeria-Klein, G., Gonze, D., Faust, K. & Lahti, L. Quantifying the impact of ecological memory on the dynamics of interacting communities. *PLOS Computational Biology* **18**, e1009396 (2022).
  136. Brose, U. *et al.* Embedding information flows within ecological networks. *Nat Ecol Evol* **9**, 547–558 (2025).
  137. Levin, S. A. The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture. *Ecology* **73**, 1943–1967 (1992).
  138. Long, C. *et al.* Structured community transitions explain the switching capacity of microbial systems. *Proceedings of the National Academy of Sciences* **121**, e2312521121 (2024).
  139. Tabi, A., Siqueira, T. & Tonkin, J. D. Species interactions drive continuous assembly of freshwater communities in stochastic environments. *Sci Rep* **14**, 21747 (2024).
  140. Moran, J. & Tikhonov, M. Defining Coarse-Grainability in a Model of Structured Microbial Ecosystems. *Phys. Rev. X* **12**, 021038 (2022).
  141. Goldford, J. E. *et al.* Emergent simplicity in microbial community assembly. *Science* **361**, 469–474 (2018).
  142. Shoemaker, W. R. & Grilli, J. Investigating macroecological patterns in coarse-grained microbial communities using the stochastic logistic model of growth. *eLife* **12**, RP89650 (2024).
  143. Castro, D. M., Raposo, E. P., Copelli, M. & Santos, F. A. N. Interdependent scaling exponents in the human brain. Preprint at <https://doi.org/10.48550/arXiv.2411.09098> (2025).

144. Rosas, F. E. *et al.* Software in the natural world: A computational approach to hierarchical emergence. Preprint at <https://doi.org/10.48550/arXiv.2402.09090> (2024).
145. von Bertalanffy, L. von. *General System Theory: Foundations, Development, Applications*. (George Braziller, Incorporated, 1968).
146. Hu, J., Amor, D. R., Barbier, M., Bunin, G. & Gore, J. Emergent phases of ecological diversity and dynamics mapped in microcosms. *Science* **378**, 85–89 (2022).
147. Deyle, E. R., May, R. M., Munch, S. B. & Sugihara, G. Tracking and forecasting ecosystem interactions in real time. *Proceedings of the Royal Society B: Biological Sciences* **283**, 20152258 (2016).
148. Bartomeus, I., Saavedra, S., Rohr, R. P. & Godoy, O. Experimental evidence of the importance of multitrophic structure for species persistence. *Proceedings of the National Academy of Sciences* **118**, e2023872118 (2021).
149. Domínguez-García, V., Molina, F. P., Godoy, O. & Bartomeus, I. Interaction network structure explains species' temporal persistence in empirical plant–pollinator communities. *Nat Ecol Evol* **8**, 423–429 (2024).
150. MacArthur, R. H. *Geographical Ecology: Patterns in the Distribution of Species*. (Princeton University Press, 1972).