1 Interaction Matrices as Unifying Tools for Navigating Ecological

2 Complexity

3 J. Christopher D. Terry^{1*} 0000-0002-0626-9938

4 Andrea Tabi² 0000-0002-5028-1117

5 David García-Callejas³ 0000-0001-6982-476X

6 Virginia Domínguez-García 4 0000-0002-4591-4186

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- 8 1: Department of Biology, University of Oxford, Oxford, UK
- 9 2: Computational Science Lab, Informatics Institute, University of Amsterdam, Amsterdam, The Netherlands
- 10 3: Institute of Biology, University of Graz, Holteigasse 6, 8010 Graz, Austria
- 4: Estación Biológica de Doñana (EBD-CSIC), Seville, Spain

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- *: Corresponding Author: christopher.terry@biology.ox.ac.uk
- 14 **Author Contributions:** All authors contributed equally.

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Abstract

20 Interaction matrices summarise pairwise species impacts within ecological communities into 21 an analytically tractable format and have been central to advancing our understanding of 22 ecosystem dynamics. However, despite their ubiquity, they have faced constant, recurring, 23 criticism for oversimplifying ecological complexity. While suggested extensions address 24 specific shortcomings, they often come with significant trade-offs, including increased data 25 demands and analytical complexity. Despite their challenges, interaction matrices have been a 26 nexus of fundamental ecology connecting many subdisciplines, representing both cause and 27 consequence of ecological dynamics. Here we overview the fundamental definitional, 28 dynamism and data challenges confronting the interaction matrix framework and critically 29 examine the current state-of-the-art of approaches developed to tackle them. It is clear that the 30 centrality of interaction matrices within academic ecology is set to continue. Nonetheless, their 31 role as a unifying and focus of synthesis could be markedly improved by refreshing how they are 32 considered. We argue that by fully embracing, rather than fighting, their inherent nature as 33 uncertain, transient abstractions, ecology can better maximise their potential as a unifying 34 nexus of ecological research and incorporate advances in wider complexity sciences. As we 35 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.

The centrality of interaction matrices in ecology

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A fundamental goal of ecology is to understand the consequences of the relationships between species. A common approach to addressing the complexity of natural ecosystems has been to distil species interactions into a discrete 'interaction matrix' that summarises the pairwise effects organisms have on one another given a specific environmental context. This focus on dynamics goes a step further than interaction networks, which seek only to map the links between species by particular processes. The mathematical construct brings tractability to entangled webs of linkages within communities and allows researchers to study the emergent properties of ecological systems as a complex system¹. As such, interaction matrices have been described as "among ecology's most important mathematical abstractions" and are a foundational staple of ecological research, forming a key connecting bridge between theory and observation. Recognition of the interconnectedness of ecosystems dates back to the earliest pioneers of ecology³⁻⁵, but it took the influence of physical scientists such as Alfred Lotka⁶ and Vito Volterra⁷ to bring into ecology the fundamental 'mass action' abstraction of distilling interspecific interactions into a single rate term^{8,9}. Since then, a multitude of distinct approaches to defining the elements of interaction matrices have developed^{2,10-12}, ranging from two-by-two systems up to mathematically-large abstractions 13, but all share the aim of capturing direct impacts between a set of species populations with a two-dimensional grid of values (Box 1). Both the opportunities and limitations that such mean-field approximations represent in an ecological context were rapidly recognised14 and their value has been much discussed ever since¹⁵. Fundamentally, while mean-field approaches rooted in statistical physics unlock tractable solutions for high-dimensional biological systems¹⁶, the level of abstraction and reductionism embedded into the construction of interaction matrices frequently conflicts with desires to explicitly account for known ecological processes and fine-grain detail¹⁷. Despite these reservations, the potential of interaction matrices to link ecological frameworks and data is evident (Figure 1), for example, translating resource use overlap between pairs of species into community-level dynamics¹⁸. This utility of interaction matrices has repeatedly been sufficient to override, at least temporarily, misgivings about their 'realism', and their use today is widespread. As an illustration, 35 of the 210 articles published in Ecology Letters during 2023 (16%) use interaction matrices in some way, rising to 36% when considering only community ecology papers (SI 1). The use of interaction matrices and the wider concept of interaction networks 19,20 extends to nearly every corner of ecology, from biogeography²¹ to conservation^{22,23}. A totemic example of the use of interaction matrices has been the relationship between stability and complexity of ecosystems: early results using the simplest possible models²⁴ were followed by a succession

of studies that included additional 'realistic' structuring, while still retaining the fundamental interaction matrix approach^{13,25,26}. Interaction matrix based analyses have shown that stabilising structures appear to be overrepresented in real networks^{28–31} and allow the identification of community level responses to changing environments that could not be identified from pairwise analyses³². Despite the diversity of metrics that can be used to quantify ecological stability, most fundamentally depend on interaction matrices in one way or another²⁷.

In recent years, new data streams, increased appreciation of feedback, and growing ambitions to represent increasingly complex systems are posing significant questions for how the venerable interaction matrix can be best used to accelerate ecological understanding. Here we collate and examine the diverse recurring challenges for the interaction matrix framework within ecology, grouped into questions of definition, dynamism and data. We argue that although some of these are fundamentally 'unsolvable', quantitative interaction matrices will continue to provide a distinct and valuable convergence point for different subfields within 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 identify four directions that can maximise their potential to drive forward community ecology.

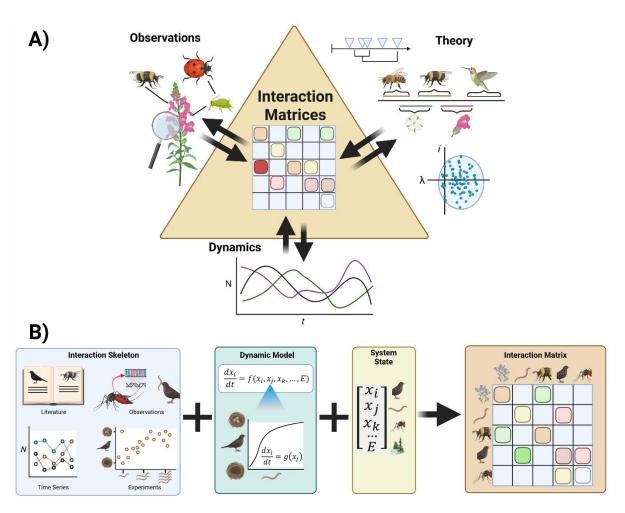


Figure 1 A) Interaction matrices are the central uniting feature of community ecology. They are uniquely placed to unite observations of interspecific interactions, trajectories of populations and theoretical understanding of the structure and dynamics of communities (here illustrated with niche models 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 ith function with respect to the jth 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 matrix², that are often referred to with overlapping names. All are only defined for a particular set of species abundances 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:

$$\frac{dN_i}{dt} = r_i N + \sum_{i}^{S} \alpha_{ij} N_i N_j$$

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

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

and is hence distinct to approaches that use the effects on each *population*, which at equilibrium can be defined³³ as:

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

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' ¹⁸) or different underlying dynamic models. However, given information on other parameters and system state ² 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 challenges³⁴. 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^{35,36}, through to more ecologically informed models such as the niche model³⁸ including allometric relationships³⁹ and include a variety of dynamical forms using generalised niche modelling³⁷.
- 2. Reconstruction from observations of population counts. With this approach, changes in populations as a function of the density of other species within the community through time are used to identify the elements of the interaction matrix. The raw data can be from structured experiments⁴⁰, include deliberate perturbations in the style of 'Press' or 'Pulse' experiments⁴¹ or be simply observational. The method used can be purely correlative, for example S-maps and causal discovery algorithms^{42–44} or can embed assumptions about the underlying functional form of the interactions between species with auto-regressive models⁴⁵. The input data can be long-term time series, or multiple short or single-generation transitions^{46,47} 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 parameterisation¹⁰ or inferring interaction strength from resource use overlap⁴⁸. 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^{49,50}. Likely interactions can be inferred from larger-scale 'metawebs' of observed interactions tabulating which species have been seen to interact in that region⁵¹.

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.

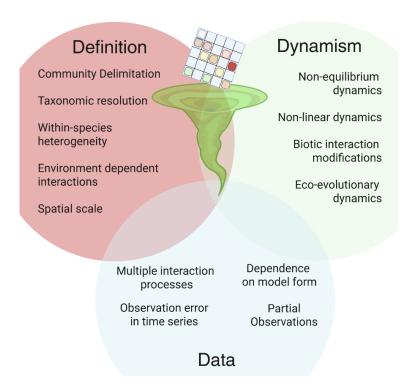


Figure 2. Multiple interacting challenges assail the interaction matrix approach. Created in BioRender. Terry, C. (2025) https://BioRender.com/0yzqn3h

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 boundaries⁵².

Interaction network structure frequently scales with the area under consideration ⁵³⁻⁵⁵, 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 ^{56,57}, 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 ⁵⁷, but empirical validations remain scarce ⁵⁸.

Interaction dependence on temporally variable environmental conditions. Interaction strength between species strongly depends on abiotic conditions that fluctuate through space and time^{54,72,73}. 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 system⁷⁴ and that fluctuating interaction strength under different variable environments is itself a key determinant of key dynamics such as coexistence⁷⁵. While there are multiple proposed frameworks to embed environmental dependence into interaction matrix specification^{76,77} or extend to multi-dimensional arrays across a gradient⁷⁸, 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^{12,17}. 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^{79,80}. Interactions can therefore be poorly captured unless populations are strongly constrained to a fixed point.

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Non-linearities in pairwise interactions. Non-linear, density-dependent interactions between species are the norm, rather than an exception⁸¹. The impact has been thoroughly investigated in small modules⁸² and may be justified within the normal range of species populations⁸³, 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 impacts⁸⁴. Suggested remedies include generalized modelling frameworks³⁷ to explore the effects of nonlinearities on stability by fixing only a few key parameters, or structural methods^{48,85} 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 dynamics⁸⁶. 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 behaviour⁸⁷ 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 feedbacks88. The challenge these effects pose for the interaction matrix approach was recognized early^{89,90} under the broad umbrella of 'higher-order interactions'. They are expected to be widespread⁹¹, although there still exist only a few large-scale parameterised examples⁹². Proposed solutions to the challenge of biotic contextualisation include frameworks for modelling adaptive foraging⁹³, interaction modifications⁹⁴, hypergraphs⁹⁵, and rewiring⁹⁶, as well as extending analysis of interaction matrices into successively higher dimensional arrays 97,98. While models can be built, impacts are dependent on model form and their analysis is challenging, for example, the significant increase in parameters can create many more fixed points⁹⁹. Higher-order interactions have been quantified in controlled settings using synthetic microbial communities 100,101 and certain other model systems 2 and show that incorporating HOI information improve predictions of multispecies community outcomes. However, experimental assays rapidly become combinatorially infeasible and apply only under wellcontrolled conditions. Most approaches provide only an empirical correction91. rather than a mechanistic understanding of the why underlying metabolic, spatial, or ecological processes interactions change.

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 communities¹⁰². 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^{103,104}, 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 ^{105,106}, leading to the so called 'Eltonian shortfall' in our knowledge of interactions ¹⁰⁷. 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 ¹⁰⁸, 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 more abstract 'competition'). While increasing efforts are being made to construct multi-layer networks ^{109,110} 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 competition⁴⁸. Development of approaches to translate between types of networks began early, for example to translate resource use overlap into competition¹¹¹ and refinements are still being developed (e.g. ¹¹²), yet it remains the case that such conversions are sensitive to model form ^{113,114} and scaling with self-regulation terms ¹¹⁵. Validation of whether the dynamics implied by an interaction matrix constructed from the ground-up align with observed population trajectories is very rare.

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 frameworks⁴¹ are essentially impossible to empirically observe. Observational error is frequently large and can require careful handling¹¹⁶. 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 matrix¹¹⁷. Highly uncertain interaction strengths have the potential to generate artefactual results in subsequent analyses¹¹⁸. Recently developed 'model-free' approaches^{119,120} 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 assemblages¹²⁰. As such, the ability to infer interaction matrices from large, diverse communities remains an open area of research⁴³ and will reach fundamental limits to inference of network structure from time series¹²¹.

Tackling Simultaneous 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. In practical terms, this means that addressing different categories of challenges asks for approaches that can be outright incompatible, which makes it impossible to expand the complexity of interaction matrices in different dimensions simultaneously (Figure 3). The increased sophistication and centrality of analyses using interaction matrices can be charted by comparing the contents of a major series of Theoretical Ecology textbooks through time ¹²². Coverage of interspecific interactions within communities has grown from around half a chapter in the first 1976 edition ¹²³, to two chapters in 2007 ¹²⁴, to being embedded in the majority of chapters by the 2020 edition ¹²⁵. However, it is still notably rare for more than a single extension of the core quantitative interaction matrix approach to be used at a time.

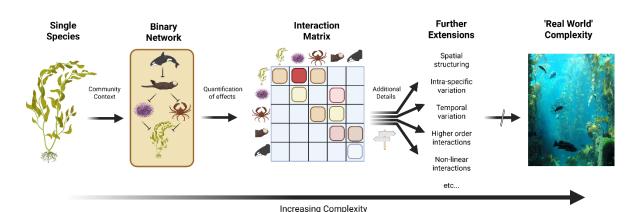


Figure 3: Quantitative interaction matrices represent a useful trade-off in complexity including quantification of the community context and which can be expected to be attained for a wide variety of communities. Further extensions can further narrow the gap to real-world complexity and capture influential 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

 As a specific example, we can consider the well-studied Mediterranean grassland systems within Doñana national park (SW Spain), where interactions between plant, pollinator and herbivore species have been studied from many perspectives to incorporate extensions including non-linear interactions¹²⁶, higher order interactions¹²⁷, and intraspecific variation¹²⁸. However, simultaneous development is still empirically infeasible and often analytically intractable. For example, a recent study assessing the contributions of interactions to plant performance¹²⁷ was able to include pairwise and 3-way HOIs involving 24 plant species, 48 pollinators and 15 herbivores by implementing a sparse modelling approach to reduce the number of parameters from a potential 639. By contrast, a concurrent study of a similar Mediterranean plant-pollinator community¹²⁸, considered the effect of intraspecific variability in on plant-pollinator interactions on community stability, but could not consider other dimensions of interaction matrix complexity. Space poses further challenges: one well-trodden study area in this ecosystem³⁰ comprises 9 plots in which around 15 plant species, 40 pollinators and 10 herbivores can be regularly observed. Incorporating a spatial element to even this quite simple system would require means estimating dispersal coefficients for every mobile species in addition to the 1000 possible pairwise inter-guild interactions and an even larger set of intraguild coefficients responding to the different environments. The amount of field data needed to parameterise such a system is enormously challenging to obtain, making the addition of other extensions prohibitive.

Maximising the Value of Interaction Matrices

Given these prospects, what should be done to strike an appropriate balance between tractability, realism, and breadth of ecological processes considered? 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?¹³⁰ 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 the popularity of the core approach continues to grow. There has been a repeated cycle of particular problems being identified (e.g. ^{17,110,131,132}), a specific solution presented, but a reversion back to original interaction matrices on which are built solutions to other problems. While predictions of the future course of science are inherently risky, it seems likely that interaction matrices are here to stay, despite their deficiencies.

As such, it is most useful to see interaction matrices as being an inevitable consequence of a reductionist approach to ecology¹³³, 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, beyond just 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. Four focuses have particular potential to aid this goal:

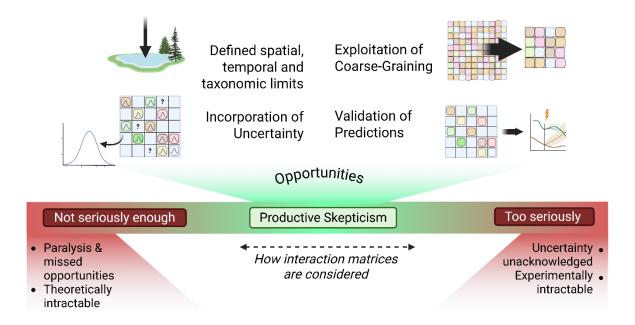


Figure 4. How should interaction matrices be most productively considered? Between dismissal as artificial constructs and over-emphasis, there is a productive middleground of productive skepticism with significant scope for future developments. Created in BioRender. Terry, C. (2025) https://BioRender.com/wbhx7z5

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 because of the diversity of approaches used, interaction matrices specifying the relationships between populations have the potential to better link many disparate areas of ecology by acting as a common currency. Despite differences in construction approach¹³⁴, databases for interaction networks have existed for some time^{59,135} and form the basis for many meta-analyses¹³⁶. 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 137-140 or as a fuzzy interaction web 141, the sensitivity of results to inclusion of most-likely missing links¹⁴² can be tested, and uncertainty in interaction strength parameter estimates can be directly propagated 143. The uncertainty in interaction estimates derived from the unknown form of the relationship between variables (i.e. model selection error) poses a more fundamental challenge¹¹⁷, but can still be explored and the robustness or otherwise of results to alternative plausible assumptions can be confirmed¹⁴⁴. 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 matrix¹⁴⁵. This may necessitate a move towards responses that are more robust to uncertainties in individual terms 146-148, but will strengthen the field as a whole.

3) Embracing advances across complexity sciences such as coarse-graining.

The wider field of complexity science offers rapidly expanding opportunities to address new ecological questions using interaction matrices¹⁴⁹. For instance, new developments have used

interaction matrices to understand ecosystem learning¹⁵⁰, ecological memory¹⁵¹ and information processing¹⁵². Of particular interest to ecology are complexity science developments within 'coarse-graining' to deal with scaling challenges¹⁵³. This refers to simplifying complex data to reduce dimensionality while preserving general patterns and system behaviour properties.

Ecosystems are highly structured to continuous community assembly leading to non-random trait distributions to which have important implications for dynamics, coexistence, and resilience. Thus, species are typically able to be coarse-grained into functional groups to account and phylogenetic groups to a garegated based on statistical patterns. For instance, using techniques borrowed from statistical physics such as Renormalization Group theory 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 to testing for scale invariance indicating successful dimension reduction to the control of the control of the coarse to the coarse

Emergent systems can be defined as self-contained processes that evolve over time¹⁶⁰. 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 theory¹⁶¹ 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 ^{32,43,162} or tracking of field communities ^{129,164}. These strategies are especially valuable when full mechanistic detail is unknown or unknowable, allowing progress through the identification of statistical regularities and structural constraints ¹⁴⁷. 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" ^{165, 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

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Supplementary Information

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- 479 Estimating prevalence of interaction matrices in the literature.
- 480 VDG recovered from Web-of-Science all articles published in the journal Ecology Letters during
- 481 2023 (210 records). From those, we subset articles containing "interaction matrix OR interaction
- 482 matrices OR matrix OR matrices OR ecological network OR community ecology" in any field (98
- 483 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.

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