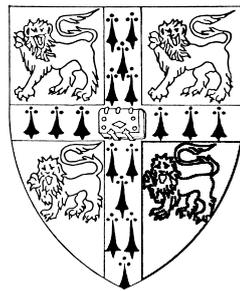


Macroscopic insights from mechanistic ecological network models in a data void

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8 April 2015

Sidney Sussex College, University of Cambridge
A dissertation submitted for the degree of Doctor of Philosophy

在缺乏數據的狀態下
以機械性生產網絡形態
呈現
自觀照見

林揚塵
博士學位論文
新橋大學

to Man

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On the cover: the arms of the University of Cambridge,
gules on a cross ermine between four lions passant gardant a book gules (granted 1573).

PREFATORY NOTE

This work attempts to serve as a dissertation for a degree qualification, but even more importantly it has emerged symphonically from a voyage of exploration and discovery of the world and of myself that involved not only scientific research but also the concurrent pursuit of artistic and spiritual fulfilment. I am indebted to my supervisor, Professor William J. Sutherland, who accompanied and guided me on this exhilarating journey. I am also grateful to Dr. Andrea Manica and Dr. Rufus Johnstone, who helped man the proverbial Apollo mission control ensuring that the trajectory of my voyage into the unknown remained within survivable constraints.

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Parts of this dissertation were published [1–4] but have been brought up to date and improved in the light of subsequent ideas and literature. Insights from here have also been contributed to coauthored publications [5, 6].

Declaration. This dissertation is the result of my own work and includes nothing which is the outcome of work done in collaboration except as declared in the preface and specified in the text. It is not substantially the same as any that I have submitted, or is being concurrently submitted, for a degree or diploma or other qualification at the University of Cambridge or any other university or similar institution except as declared in the preface and specified in the text. I further state that no substantial part of my dissertation has already been submitted, or is being concurrently submitted, for any such degree, diploma or other qualification at the University of Cambridge or any other university of similar institution except as declared in the preface and specified in the text. The dissertation does not exceed the prescribed word limit for the relevant Degree Committee. ©

YANGCHEN LIN
Cambridge, spring 2015

SUMMARY

Complexity science has come into the limelight in recent years as the scientific community begins to grapple with higher-order natural phenomena that cannot be fully explained via the behaviour of components at lower levels of organization. Network modeling and analysis, being a powerful tool that can capture the interconnections that embody complex behaviour, has therefore been at the forefront of complexity science. In ecology, the network paradigm is relatively young and there remain limitations in many ecological network studies, such as modeling only one type of species interaction at a time, lack of realistic network structure, or non-inclusion of community dynamics and environmental stochasticity. I introduce bioenergetic network models that bring together for the first time many of the fundamental structures and mechanisms of species interactions present in real ecological communities. I then use these models to address some outstanding questions that are relevant to understanding ecological networks at the systems level rather than at the level of subsets of interactions. Firstly, I find that realistic red-shifted environmental noise, and synchrony of species responses to noise, are associated with increased variability in ecosystem properties, with implications for predictive ecological modeling which usually assumes white noise. Next, I look at simultaneous species extinction and invasion, finding that as their individual impacts increase, their combined impact becomes decreasingly additive. In addition, the greater the impact of extinction or invasion, the lesser their reversibility via reintroduction or eradication of the species in question. For modifications of pairwise species interactions by third-party species, a phenomenon that has so far been studied one interaction at a time, I find that the many interaction modifications that occur concurrently in a community can collectively have systematic effects on total biomass and species evenness. Finally, examining a higher level of organization in the form of compartmentalized networks, I find that the relationship between intercompartment connectivity and the impacts of species decline depends considerably on network topology and whether the consumer-resource functional response is prey- or ratio-dependent. Over-

all, the results vary considerably across model communities with different parameterizations, underscoring the contingency and context dependence of nature that scientists and policy makers alike should no longer ignore. This work hopes to contribute to a growing multidisciplinary understanding, appreciation and management of complex systems that is fundamentally transforming the modern world and giving us insights on how to live more harmoniously within our environment.

I EXPOSITION

I.1 A COMPLEX SYSTEMS APPROACH TO ECOLOGY

The twenty-first century has been marked by the advent of a new frontier in humanity's scientific enterprise: the so-called complexity science. It arose from the recognition that many locally interacting agents can give rise to a system with unexpected macroscopic properties, and that this system furthermore adapts to changes in its external environment over time and is often far from equilibrium, its trajectory highly dependent on conditions early in its history. Consequently, such systems are not amenable to mathematical analysis, and their future possible states are 'not finitely prestatable' [7]. Despite their real-world prevalence in the guise of financial markets, ecosystems, ant colonies and many others, their interesting and potentially beneficial or destructive behaviours are hardly understood or controllable. In his seminal monograph in 1997, PRIGOGINE [8] called for scientists to move on from traditional deterministic approaches and embrace the indeterminism of complex systems.

I think the next century will be the century of complexity.

Stephen Hawking, *San Jose Mercury News* (2000)

In ecology, it was realized as early as 1994 that research had (and as of today, has) been dominated by the approach of studying at most a few species or interactions at a time [9], inherited from the early days of observation and description of living organisms. This has partly been wrought by the difficulty of collecting detailed field data on more than a few selected components of the system (see §1.3.2), and partly by the popularity of simple mathematical models for finding analytical solutions of ecological equilibria. While exact, tidy and easy to interpret, the reductionistic approach does not encapsulate the complex interactions of nature [9]. Reductionism may be beginning to take its toll on advancement in ecological research. In a 2014 meta-analysis of more than 18000 published articles, LOW-DÉCARIE *et al.* [10]

observed that despite an increasing number of hypotheses being tested per article in ecology, their explanatory power seemed to be declining. One possible cause cited was that the simple questions had mostly been answered, leading ecologists to tackle increasingly complicated questions. Although correspondingly sophisticated statistical procedures were used to attack such questions, it is not unreasonable to suppose that even those procedures will have difficulty explaining and predicting ecological behaviour as long as only a few components of the system are analyzed for extrapolation to the system as a whole. A more fundamental shift from reductionistic to holistic approaches may be needed to bring about the next golden age in ecological research [11].

1.2 THE NETWORK PARADIGM IN ECOLOGY

Network analysis is a powerful framework that has been applied to complex nonlinear systems in many disciplines [12], being flexible to the idiosyncrasies of each. It has been hailed as the tool for addressing the ‘big questions of contemporary science’ [13]. The versatility of the network approach for diverse purposes is illustrated, for example, by SCHICH *et al.* [14], who traced the evolution of cultural history via networks of intellectual mobility reconstructed from birth and death location data of individuals who had significant impacts on culture.

SOLE & VALVERDE [15] introduced a classification of the structure of many different types of networks, from the Internet to metabolic maps to food webs to brain networks, according to three axes: randomness, modularity and heterogeneity. In this classification, food web structure has moderately high randomness, low modularity and moderate heterogeneity and lies outside the domain of ‘scale-free-like networks’, while ecological mutualistic networks have low randomness, moderately high modularity and moderate heterogeneity and lie within the domain of ‘scale-free-like networks’. PROULX *et al.* [16] reviewed the rising use of network analysis in various subfields of ecology and evolution and suggested that the time was ripe for advancing beyond pairwise interactions and building a ‘predictive science of biological networks’. More specifically to ecology, BASCOMPTE [17] advo-

cated a network approach to the vital task of understanding how ecological interactions affect the emergent properties of complex ecosystems under increasing anthropogenic threat, while BROSE [18] and LEWINSOHN & CAGNOLO [19] highlighted the value of ecological networks for understanding and predicting the consequences of species loss on ecosystems.

Real ecological networks are highly complex, containing much omnivory and trophic looping [20]. Many studies of ‘networks’ and ‘food webs’, however, categorize the nodes into distinct trophic levels, and the inter-level links only connect adjacent levels. Moreover, such studies usually deal with a small number (2–3) of trophic levels [21]. It is important to account for vertical (trophic) diversity, as has been shown in the diversity-functioning debate [22]; the network approach is powerful in accommodating both horizontal and vertical (trophic) diversity [23].

Across the multidisciplinary network research landscape, ecological networks are becoming recognized for their contribution towards the understanding of general laws governing the properties of complex networks. CHIU & WESTVELD [24] demonstrated the application of social network analysis to food webs, while BRUMMITT *et al.* [25] drew parallels between power grids and ecological networks. Even more significantly, analogies between ecological and economic networks are getting increasing attention. Simple models of networks of bank loans have been built to demonstrate shock propagation through network structure, with conceptual comparisons to species extinctions in ecosystems [26, 27], and the power-law (scale-free) degree[†] distribution tendency of both economic and ecological networks has been found to make them more susceptible to catastrophic collapse [28]. Stability measures for financial networks are also being developed that have potential applications to ecology [29].

Ecological network dynamics. Change over time is what really defines the interesting and important characteristics of ecological communities and complex systems in general, and is integral to any attempt to understand the impact of perturbation on ecological networks or make predictions for practical management [16, 30–32]. The study of networks with temporal changes

[†]The number of nodes (species) to which a given node in the network is connected.

in information or energy flow between nodes is, however, still an emerging field in many areas of network science [33–37]. Ecology is no exception; much research on ecological networks has dealt with static networks, and there tends to be a disconnect between reductionistic dynamical studies of trophic modules versus static whole-network studies [38]. The importance of incorporating dynamics in whole-network studies has been underscored by the work of EVELEIGH *et al.* [39], who found different outcomes in diversity cascades caused by outbreak species when realistic non-equilibrium dynamics were accounted for.

Furthermore, most network-level dynamical ecological studies to date have dealt exclusively with food webs. Community-level conclusions from such studies may not hold true in real communities, where multiple non-predator-prey interaction types co-occur and interact with one another and with trophic interactions [40]. Forays into dynamical representations of multiple interaction types are still in their infancy [41]. For example, MELIÁN *et al.* [42] incorporated dynamics for plant species in a community with multiple interaction types but assumed that animal population densities were constant. BLONDER *et al.* [43] review the methodology for incorporating temporal dynamics into network analysis, and its application to networks in ecology and evolution.

1.3 RESEARCH DIRECTION

1.3.1 MODELING STRATEGY

The broad aims of this work are to investigate, using theoretical models, how various interesting ecological phenomena at the mesoscale (species) level affect community-level behaviour and response to perturbation. I try to determine the presence or absence of general patterns that apply across different contexts, which addresses concerns about the predominance of specific case studies in community ecology with very little general understanding [44].

Given the long-standing dichotomy between ‘simple mathematical models’ and ‘large simulation models’ [45], it is essential to justify the simulation approach this research adopts. Ecological dynamics have traditionally been

understood via stability analysis of simple deterministic equations of a few interacting species [46–49], although community matrices of relatively large networks are increasingly being analyzed to elucidate the influence of network structure on interaction strengths [50] and the influence of both of these on stability [51]. Mathematical analysis continues to make valuable contributions to ecological network science, not least when allied with techniques such as model selection [52]. The so-called generalized modeling has also been promulgated [53,54], which examines the dynamical stabilities of a large number of ecological network replicates with different model structures and parameter values and therefore avoids making simplifying assumptions. Like the other analytical approaches, however, it is largely focused on quantifying deterministic equilibrium stability.

Simulation models, used in my study, are another powerful tool for understanding ecological network behaviour [55], and complement mathematical analysis [56], especially in nonequilibrium situations and where model complexity precludes analytical solutions. I depart from the emphasis on equilibrium stability, whether of traditional local equilibrium points in population dynamics or of the latest ‘structural stability’ of ecological networks [57], and focus on tackling the confusion of a reality where nonequilibrium dynamics prevail [58,59]. Indeed, in the latest overview of the continuing debate on model simplicity versus complexity, EVANS *et al.* [60] reiterate that complex, mechanistic models can be better than simple models when seeking ecological generality, as well as when attempting specific prediction outside the boundary of current conditions [61,62], and that the current preponderance of ecology on simple models may even be stifling ecological progress [63]. This is not to say that all models should be complex. We need to harness the complementary powers of both simple and complex models to give us the best overall understanding [60]. For example, efforts to isolate small trophic modules from theoretical or empirical food webs for the prediction of equilibrium responses to perturbations [64–66] should be matched by efforts that scale back up from modules to the larger ecological networks in which they are embedded [67], in order to capture all the feedback loops.

How does the oft-invoked complexity-stability relationship colour the dichotomy between simple and complex models? The relationship has been of central interest in ecology since the pioneering work of MAY [68, 69]. Despite significant advancements [58, 70–72], the issue of when and how ecological complexity stabilizes or destabilizes an ecosystem remains a hot topic of research and debate [73–75]. At the same time, deeper understanding of this relationship has become ever more relevant to scientists and policy makers hoping to mitigate potentially debilitating effects of anthropogenic pressures on ecosystems [74, 76]. My prognosis is that more complex ecological networks may be more resilient in overall function due to redundancy and degeneracy [77], but may also be more prone to unexpected endogenous behaviour caused by internal feedback loops and thresholds, making the complexity-stability relationship ill-defined. The purpose of my thesis, however, is not to leap into the fray of the complexity-stability debate which continues to receive ample attention. Instead, the complexity-stability issue serves here to highlight that simple and complex systems can behave differently. Although simple models may capture some of the essential features of the complex system that exists in reality, they may not capture the rare but potentially important or catastrophic behaviour, or the unprestatable future states [7, 78] discussed earlier (§I.I). Conversely, and rarely considered in ecological research, relationships that exist within simple models might well be nonexistent in more complex systems with large numbers of alternate pathways.

There are two main system-level simulation approaches to ecology that are of the level of complexity pertinent to this thesis: those of ecosystem ecology and community ecology. The ecosystem ecology approach [79–82] is an established system dynamics modeling methodology used mostly in marine ecology [83], where trophic flows of energy and nutrients between functional compartments in a particular system are specified and various indices of energy flow are calculated. More rarely, both trophic and nontrophic flows are included [84]. The ecosystem ecology approach has been used extensively for the analysis of aquatic ecosystems [85–88] and applied to the assessment

of environmental sustainability [89] and of the effectiveness of marine protected areas [90].

Aggregated biotic and abiotic compartments and flows, however, are perhaps not the most optimal design for studying the effects of species-species transactions. Moreover, the ‘positive effects’ sometimes referred to in ecosystem ecology mainly concern negative local interactions having net positive effects on network-level energetics [79,91,92], rather than facilitative interspecific interactions. This is where community ecology complements ecosystem ecology. Simulation modeling in community ecology is best represented by bioenergetic modeling of consumer-resource dynamics [41,93–95], which has recently acquired increased ecological realism via integration with models of ecological network structure [96] and with facilitative interactions. The bioenergetic approach, where species interactions are mechanistically parameterized in terms of energy and metabolism, is equally amenable to studying the response of complex ecosystems to environmental changes including those brought about by climate change (e.g. GILBERT *et al.* [97]). Current research in this area is moving towards a more applied flavour even if the actual modeling remains theoretical, such as a study of how food web diversity and modularity mediate the effects of hypothetical pollutants [98].

OLESEN *et al.* [99] (p. 37) suggest that networks of species interactions may be no more than arbitrary structures constructed by scientists that do not exist in reality, but the authors do not elaborate. Insights into what this might mean can be found in the paradigm of agent-based modeling (ABM). A strong case for ABM is that ecological interactions really take place between individual organisms rather than between the non-physical aggregations known as species. To be reasonably realistic, individual-level network models have to incorporate at least the two main classes of interactions: between conspecifics and between individuals of different species—perhaps this is the true ecological network that actually exists. Most existing ABM studies, however, have dealt with only either conspecific [100] or interspecific [101] interactions at the individual level. An additional challenge is that ABM can become very computationally intensive if many species are involved. Again, the kind of species-level model used in my study treads a reasonable

compromise between simplicity and complexity, while incorporating both interspecific and intraspecific interactions, the latter in a phenomenological yet realistically ‘individual’-inspired way via terms such as density dependence and cannibalism (§2.1).

1.3.2 THE DATA VOID

*But there are also unknown unknowns—the ones
we don't know we don't know.*

Donald Rumsfeld

A discourse on modeling cannot be complete without some discussion of empirical data for model validation. Ecology continues to stand apart from many other sciences as a particularly data-deficient discipline. It is often impossible to collect comprehensive data on entire communities. Where this is attempted, data may be insufficient or biased and the model is usually restricted to one part of a system at one specific locality. Data shortage is particularly severe in the case of ecological networks, where it is extremely difficult to detect the presence of all the interspecific interactions, let alone measure interaction strengths.

Many data sets of food web structure that are regarded as highly resolved are nevertheless incomplete [102], encompassing only a subset of taxonomic or ecological functional groups. For example, there is a ‘food web’ data set of over 1700 species that comprises only plants and herbivores [103], and a ‘predator-prey network’ data set of high temporal resolution over millennial time scales that comprises only mammals [104]. Most data sets also exclude parasites [105, 106], PRESTON *et al.* [107] being a rare exception. The system is often simply too diverse to sample comprehensively. For example, 156 ‘kinds of organisms’ (species, distinct life history stage of a species, or group of closely related species) are recorded in the data set from tropical forest at El Verde Field Station in Puerto Rico [108], but the actual number of species in tropical rainforests is widely estimated to be much higher. Large data sets from marine biomes are probably closer to the

actual number of species of the specific system [109–111], but there remains the aforementioned problem of imperfect observation of interactions. WIRTA *et al.* [112] recommended combining multiple data sources, including field observations, lab experiments and molecular data, to gain better resolution of ecological networks and reduce bias. This, however, may still be insufficient for diverse systems due to the sheer number of unobserved species and an even greater number of their interactions. Besides, the structural properties of any one or a few comprehensively sampled food webs may not be representative of food webs in general, especially with so much contingency of food web structure [113] and other ecosystem characteristics [114].

There is another way in which data are incomplete: all the above examples have only predator-prey interactions. Any given ecosystem is an intricate web of co-occurring trophic and nontrophic interactions (see Chapter 3 for further discussion about combining them in research), but data on these different types of interactions are rarely collected sympatrically. There are abundant trophic and nontrophic interaction data, such as the Interaction Web DataBase at the National Centre for Ecological Analysis and Synthesis, University of California at Santa Barbara (<http://www.nceas.ucsb.edu/interactionweb>), and calls continue for ecologists to pool their data into collective databases in order to harness the power of big data [115]. Such data, however, are from different localities and cannot be aggregated to represent a single system. Empirical datasets on the network structure of multiple interaction types in the same system are rare, notable examples being those from an agroecosystem in Britain [116] and from Chilean rocky shores [117].

When one considers superimposing community dynamics on top of network structure, there arises a further problem, that of interaction strengths. Reliable specific predictions of complex ecological communities require highly accurate estimates of the interaction strengths [118], but interaction strengths are very difficult to measure accurately in the field [119], especially in terms of rates of energy flux with standardized units of measurement across species. For example, mutualistic interactions are often quantified as the number of pollinator visits to flowers, but the relationship of visit fre-

quency to actual nectar consumption or flower fertilization rate is unclear. Admittedly, more work is needed to develop the empirical domain of a research topic that has been dominated by theoretical modeling [120].

Some advances have nevertheless been made in fitting mechanistic dynamic models to empirical data of medium-sized networks of 24–50 nodes. Two studies [121, 122] found that when fitted to data on food web structure, observed biomass and body sizes, such models reproduced seasonal dynamics and community patterns (such as size-abundance distribution) relatively well once dynamical parameters were allometrically scaled. This can be useful where taxonomically comprehensive time series data for dynamical parameterization are scarce [122]. These studies, however, involved only trophic interactions in specific systems; fitting a limited model to data from a specific locality may not be the most appropriate paradigm in my study searching for general patterns in communities with multiple interaction types.

There is a popular culture in science that regards models as useless or even misleading for the real world unless they are validated by sufficient quantity and quality of data [123]. More complex models are naturally more susceptible to this criticism. It is indeed the case that policy and action informed by predictions from such a model are considered risky [124]. But I do not think this is the whole story. Even with abundant and quality data, a model may not make specific real-world predictions to the required accuracy for practical use, even with sensitivity analysis. In contrast, whether data are sufficient or not, a suite of models based on sensible, documented assumptions and comprising a range of plausible model structures and parameter values [125, 126] can provide valuable general insights and anticipation about how real systems might behave under given circumstances—as is the premise of this work. Indeed, this so-called Monte Carlo approach has been advocated even for predictive purposes, as in the case of complex climate models which have so far not been subject to stochastic parameterization [127]. In any case, researchers have advocated general insights rather than specific prediction of ecosystem responses to disturbance [128], and suggested that the appreciation of and preparedness for the variability of the future is as important as, if not more important

than, prediction [129]. The virtues of the general approach should all the more be embraced given that the ecosystem-level ‘data vacuum’ [124] cannot be filled before conservation needs to happen [130, 131].

In summary, my model tries to capture the essential features of the system by incorporating all the main classes of interaction types and dynamics in a succinct way, producing a model that is ‘realistic yet simple’ [132]. Furthermore, it is grounded upon empirical data of network structure and knowledge of the dynamics of ecological processes, and subject to Monte Carlo methods. Any model should be based on the foundations of all available knowledge and data on the system of interest [133]—it is the synergy across multiple sources of quantitative data and qualitative knowledge that allows a model to transcend artificial boundaries and tell us something of which we would otherwise be ignorant. At the same time, however, the model does not blindly adhere to these data and knowledge, since they are not necessarily omnipotent representations of reality (recall the discussion above about incomplete data). Nevertheless, the model serves as a springboard to explore the endless possibilities of the state space. PATTEN [134] cautioned that too much of ecological research has been focused on empirical approaches for immediate local application, with too little effort in advancing the foundational science and theory that is important for deep understanding, especially at the systems level. My study aims to contribute to addressing this imbalance, in the hope of facilitating future synergy between empirical and theoretical efforts in the science of ecology [135] and beyond.

2 STOCHASTIC BIOENERGETIC NETWORK MODEL

This chapter is a documentation of the network simulation model used in this dissertation; see §1.3.1 for the philosophy and motivations behind the model. The architecture of the model involves the construction of a network of interacting species and the specification of allometrically scaled bioenergetic equations governing changes in species states over time [93–95]. The combination of structural models with bioenergetic dynamics has been suggested as a way towards greater ecological realism [96]. My model is among the first to extend the bioenergetic model to include nontrophic interaction types alongside trophic interactions (see KÉFI *et al.* [41]), and introduces various refinements for greater realism. Overall, it could be said to apply the principles of pattern-oriented modeling [136] by incorporating observed patterns in ecological networks that are important to the research question.

Simulations and analyses were programmed in R [137] and C++ with Boost libraries for random number generation. In addition, the simulations for Chapter 6 were executed in parallel using Message Passing Interface on the DARWIN supercomputer at the University of Cambridge. Numerical integration was performed using the fourth-order Runge-Kutta algorithm with $dt = 0.1$.

2.1 NETWORK CONSTRUCTION

A food web topology is generated using the niche model [138], which has been found to be one of the most robust so far in emulating the structure of real food webs using relatively simple rules [96, 139–142] and continues to be used in the latest research [41]. The model allows for the variety of complications observed in nature, such as trophic loops (rock-paper-scissors), omnivory, apparent competition and intraguild predation [143, 144], although no correction is made for the relative frequencies of occurrence of these topological ‘motifs’ (see BASCOMPTE & MELIÁN [144] and STOUFFER *et al.* [145]). There have been various generalizations of the niche

model [139, 142, 146–149]. Here a modified version of the generalization by STOUFFER *et al.* [146] is combined with that by WARREN *et al.* [148], as explained below.

Unlike the original niche model, real food webs are not fully interval [146]. The method of STOUFFER *et al.* [146] introduces an adjustable degree of diet discontinuity, with their parameter c fixed at 0.8, which closely matches empirical data [146]. One additional modification is made: if the upper bound of a predator's original diet range exceeds the predator's niche value, the so-called Δk (STOUFFER *et al.* p. 19017, last paragraph) number of species is selected from non-prey species of niche values smaller than or equal to the aforementioned upper bound rather than the predator's niche value. This improvement, particular to my study, avoids the logical problems associated with reducing the upper bound of the potential range.

More recent generalizations of the niche model [139, 142, 149] have achieved better fit to data than STOUFFER *et al.* These versions, however, are less suited to the current application. It is difficult to specify the connectance in the formulation of ALLESINA *et al.* [139]. The models of WILLIAMS *et al.* [142, 149] do not assign parameter values using statistical distributions that would keep the model sufficiently simple. As my purpose is to construct multiple plausible food webs rather than predict the links of specific empirical webs as accurately as possible, the method of STOUFFER *et al.* is adequate, even in the light of more biologically motivated models based on optimal foraging (see PETCHEY *et al.* [150] and skepticisms as to whether optimal foraging reflects reality [151, 152]). Contrary to WILLIAMS *et al.* [142], I am not overly concerned by the assumption that species near the centre of a predator's diet range are not more likely to be prey than those near the edges, since unmodeled multidimensional niche space [149, 153]) could account for that. The one-dimensional niche axis I use does not preclude the effects of multidimensional niche space.

The inverse niche model of WARREN *et al.* [148] is used to optionally add parasite species to the food web. This institutes one of the most fundamental differences between predators and parasites, by 'letting little things eat big things' [105]. The inverse niche model excludes parasite-

parasite and predator-eats-parasite links, the connectance being defined as the proportion of possible host-parasite links that are realized [154]. Although predation on parasites is not included as direct links in the inverse niche model, it is manifested via predators consuming the hosts that harbour the parasites [148], which has been found to be the most common form of parasite ingestion in aquatic food webs [155]. Hyperparasitism and competition among parasites are not incorporated; these are avenues for future empirical and theoretical work. It has also been suggested that parasitism may be incorporated into food webs as indirect rather than direct interactions [156] (see §5.1).

The connectances of the predator-prey and host-parasite subwebs are set at 0.15 [154, 157]. Connectance in real webs can vary by as much as an order of magnitude [158]; the value used here is a reasonable starting point close to the connectances of several large and highly resolved food webs [158]. The niche algorithms are run repeatedly until a web is produced that has subwebs of the desired connectances ± 0.01 and that satisfies the criteria that the web must not contain any totally unconnected species, and that no heterotrophic species should consume only itself, since this is energetically unsustainable.

In the qualifying web, all nonparasite species having no prey are designated as basal species [94] flexibly representing autotrophs and detritivores, which are not distinguished. Species that consume prey could also qualify as detritivores or autotrophs, such as carnivorous plants, but these are excluded for simplicity. Model realizations containing only one basal species are discarded, as direct competition among basal species (see below) cannot be implemented in these realizations.

Random networks. For comparison with the niche models (Chapter 4 onwards), models with random network topology and at least two basal species were also generated. The species niche values conformed to a uniform distribution as in the niche model. The consumer-resource links were assigned in random pairs and directions regardless of niche values, with the condition that basal species could not be consumers. This implementation also implicitly incorporates more trophic loops or parasitism, because a consumer can

be of smaller body size (niche value) than its resource with a probability equal to the converse.

Competition. Direct competition interactions, where implemented, were assigned randomly to 25% of the total number of potential interactions between all pairs of basal species, rounded up to the nearest whole number. This procedure changes the overall connectance, but this is permissible because the previously published connectance values pertain only to their respective interaction types. The random assignment of competitive interactions gives rise to varying degrees of intransitivity [159], reflecting natural variability.

Mutualism. For both niche and random networks, mutualistic interactions are assigned randomly to the predator-prey subweb, excluding species pairs already allocated to other interaction types, with a connectance of 0.15 of the total number of potential interactions between all pairs of nonparasite species, rounded up to the nearest whole number. This procedure allows for a wide variety of motifs including plant facilitation, predator facilitation [160], intraguild mutualism [5, 161, 162], plant-animal mutualism and three-way mutualism such as that among sea anemones, zooxanthellæ and anemonefish [163]. It also does not exclude less commonly studied mutualistic associations in ecological networks, such as herbivore-detritivore mutualisms e.g. gut microbes. Some of the even more esoteric mutualisms, however, are not yet implemented, such as vector-parasite mutualism [164]; these are again avenues for future inquiry.

The non-implementation of the nestedness and modularity observed in bipartite mutualistic networks [165–167] is not considered problematic. This is because the overall structure of mutualistic interactions in the whole community is unlikely to be as highly nested or modular as that of many pollination- or seed dispersal-based bipartite mutualistic subwebs that have been observed in isolation, when species from the different subwebs interact with one another in other kinds of mutualism not encompassed by any of those subwebs, such as habitat provision² in return for nutrients [163, 168].

²Where habitat provision enhances protection of the occupant from particular predators, tripartite interaction modification (Chapter 5) is a more appropriate representation.

Table 2.1. Parameters of ecosystem assembly.

Parameter	Value	Reference
fraction of species that are parasites	0.33	[154, 173]
c	0.8	[146]
connectance (trophic subweb)	0.15 ± 0.01	[157]
connectance (host-parasite subweb)	0.15 ± 0.01	[154]
connectance (competition subweb)	0.25	this paper
connectance (mutualistic subweb)	0.15	this paper

Furthermore, nestedness may not be a significant predictor of community persistence [169]. The mutualistic connectance used here is lower than the value of approximately 0.3 measured from bipartite mutualistic networks [170]. It makes sense to have a lower connectance for the full ecological network because its constituent species encompass a broader range of taxa than any one specialized bipartite network of taxa that rely heavily on mutualism.

The overall concept of different types of binary interactions used here was first put forward by BURKHOLDER [171] who listed nine ‘coactions between weak and strong organisms’ comprising different combinations of ‘+’, ‘-’ and ‘0’ denoting gain, loss, and neither gain nor loss by each of a pair of interacting species. This concept has been further developed by FATH & PATTEN [91] and FATH [92]. My model simplifies it by incorporating the three ‘elementary particles’ that are arguably the minimum set that represents the different types of interactions at the most basic level: $+-$, $--$, $++$.

Finally, the complete ecological network (Fig. 2.1) is tested to ensure that there are no isolated components by computing the number of times 0 appears as an eigenvalue of the Laplacian, which is the number of components of the graph [172]. If isolated components have been produced, the network is regenerated until there is none. Network assembly parameters are summarized in Table 2.1.

FONTAINE *et al.* [174] were among the first to propose combining structured subwebs of different interaction types; my network takes their concep-

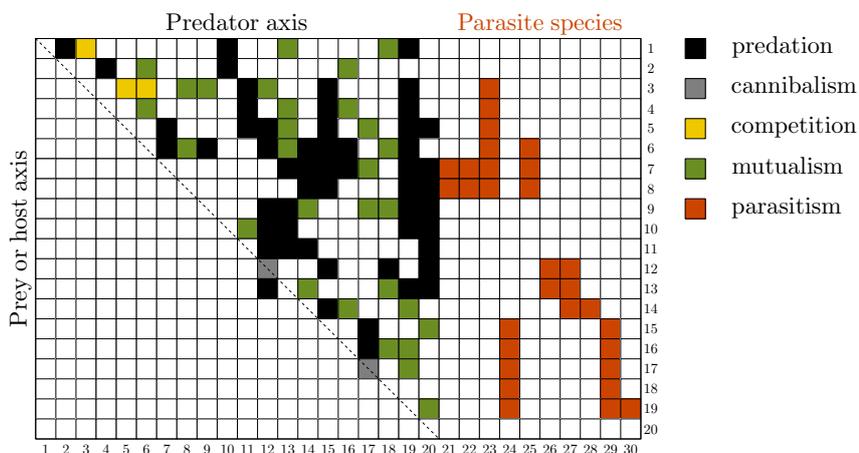


Figure 2.1. One stochastic realization of the network construction algorithm combining the niche model of predator-prey interactions (columns 1–20), inverse niche model of host-parasite interactions (columns 21–30), direct competition and mutualism. The first 20 columns represent the same set of species as the 20 rows. Black boxes below the diagonal dashed line represent trophic loops. Columns with no predation are defined as basal species. Direct competition interactions are assigned randomly among basal species. The number of parasite species is set at half that of nonparasite species. Connectances: 0.15 ± 0.01 for niche and inverse niche models and mutualism.

tual framework one step further in that the predator-prey and host-parasite subwebs are niche models rather than the more rudimentary nested or modular structures. For computational tractability, the number of species in the networks used in this dissertation (10–30 species) is only moderately large. The results nevertheless remain relevant to complex ecosystems—trophic ecological networks of less than 14 nodes and 40 links have been found to behave similarly to larger networks due to thermodynamic and other mechanisms constraining food chain length and trophic complexity [175].

2.2 MULTISPECIES DYNAMICS

Network dynamics are modeled using allometrically scaled bioenergetic equations [93,94] with various modifications. The dynamics of a given basal species i and a given non-basal species j with energy states E_i and E_j respectively in arbitrary units are described by the equations

$$\frac{dE_i}{dt} = r_i \left[1 - \frac{E_i}{K_i} \right] E_i - \gamma_i (1 - \epsilon_i) f_i E_i - \sum_{k \in \text{consumers}} \frac{\gamma_k \psi \Phi_{k,i} f_k E_k}{\xi} \quad (2.1a)$$

$$\frac{dE_j}{dt} = \gamma_j \left(-1 + \epsilon_j + \sum_{k \in \text{resources}} \psi \Phi_{j,k} \right) f_j E_j - \sum_{k \in \text{consumers}} \frac{\gamma_k \psi \Phi_{k,j} f_k E_k}{\xi} \quad (2.1b)$$

with time t , maximum consumption rate per unit metabolic rate ψ [94], assimilation efficiency ξ [93], predator-prey functional responses Φ (see below), nontrophic functional response f (see below) and ϵ , the species response to multiplicative environmental stochasticity (§2.3). ψ is assigned a value of 6 which is between 4 for ectotherm vertebrates and 8 for invertebrate predators [95]. ξ is assigned a value of 0.65 which is between 0.45 for herbivores and 0.85 for carnivores [95,125], since the model includes omnivory. It is assumed that parameter values for predator-prey and host-parasite relationships are similar.

The traditional intrinsic growth rate r and mortality rate γ are given versatile interpretations. In this case, r represents both somatic and reproductive growth arising from any net exogenous abiotic input such as detritus, insolation or inorganic compounds, subtracting egestion and excretion. This takes the cue from HALNES *et al.* [147] to embrace detritus in the niche model, but does it in a more species-oriented way suited to the focus of this study. The number of parameters for multiple basal species is minimized by drawing \vec{r} from lognormal distributions whose expected values and variances are equal to $\vec{\eta}^{-1/4}$, accounting for metabolic scaling where metabolism in plants is defined as photosynthesis instead of respiration [176,177]. The lognormal distribution is a sensible choice because it produces positive and

Table 2.2. Parameters of multispecies dynamics.

Parameter	Description	Unit	Constraints	Reference
η	species niche value	none	$(0, 1)$	[138]
ξ	assimilation efficiency	none	$[0.45, 0.85]$	[93, 95, 125]
r	net exogenous input rates to basal species	time ⁻¹	$(0, \infty)$	
K	carrying capacity	arbitrary biomass	$(0, \infty)$	
γ	net exogenous output rates	time ⁻¹	$(0, \infty)$	
θ	scaling coefficient for mutualism and competition	none		this paper
ψ	maximum consumption rate normalized to metabolic rate	none		[93, 94]
ω	resource preference	none	$(0, 1)$	[95]
h	Hill exponent	none	$[1, 2]$	[94, 125]

‘Exogenous’ refers to all abiotic energy and matter.

mostly moderate values, with allowance for some high values representing the occasional fast-growing species.

The parameters $\vec{\gamma}$ are coefficients of exogenous output in terms of both metabolism and mortality. Being related to body size [95, 178, 179], $\vec{\gamma}$ are assigned the values $0.01\vec{\eta}^{-1/4}$. There is no lognormal randomization here because doing so would give some species large mortality rates leading to rapid extinction; unlike for r , there is no (positive) density dependence implemented in the model to prevent this. The normalization constant [177] 0.01 is chosen to produce ecologically sensible outputs i.e. to minimize extinctions and prevent excessive segregation into high-energy basal species and low-energy non-basal species, while keeping species states mostly within $(0, 1)$ and producing a long-tailed species biomass distribution at steady state, as observed in preliminary simulations. Environmental stochasticity is formulated to act on γ , as γ is a basic population parameter common to both autotrophic and heterotrophic species.

Negative density dependence is enforced on each basal species, with its carrying capacity $K = \eta^{1/4}$ where $0 < \eta < 1$. This complies with the positive general relationship of total species biomass to body size [177]. The fact

that η is not perfectly correlated with trophic position, due to dependence on the species' behavioural and life-history traits, is already manifested in the randomized assignments of diet midpoints and diet ranges in the niche model.

The predator-prey functional responses are given by the fraction of consumer i 's maximum consumption rate allocated to resource j [94,95],

$$\Phi_{i,j} = \frac{\omega_{i,j} E_j^h}{0.5^h + \sum_{k \in \text{resources}} \omega_{i,k} E_k^h} \quad (2.2a)$$

$$h \sim \mathcal{U}[1, 2], \quad (2.2b)$$

where resource preference ω is kept uniform and constant as $1/(\mathbb{N}^{\circ}$ of resource species), the half-saturation density, i.e. resource density at which consumption rate is half the maximal rate [93], is fixed at 0.5 [125], and the Hill exponent h is drawn from a uniform distribution in the range [1, 2] giving a continuum between Holling types II and III functional responses [94, 125]. The half-saturation density is kept constant for simplicity; 0.5 is ecologically reasonable in this model because species energies are initialized on the scale of [0, 1]. Overall, this kind of formulation allows interaction strength to be modulated as a function of prey preference and half-saturation density.

Ratio dependence. Most research on community dynamics, particularly bioenergetic modeling of food webs, has assumed prey dependence. Ratio dependence, a form of predator-prey functional response that depends on the abundances of both predator and prey, was introduced by ARDITI & GINZBURG [180] in 1989. It has long been a matter of controversy [181] as to whether real communities are prey- or ratio-dependent; the ecological community now generally accepts that reality is somewhere in between [182]. ARDITI & GINZBURG [183] review the latest empirical evidence-based arguments for ratio dependence. Specific studies on ratio dependence have mostly been restricted to single prey and predator species or aggregated functional groups [184, 185]. In a theoretical discourse with multiple prey

and predator species, VAN DEN BERG [186] found that ratio dependence explained the attenuation of energy fluxes of trophic cascades in food webs. Ratio-dependent functional responses have been highlighted as an important mechanism to account for in models [185], and as a promising avenue for future theoretical work [187]. The present study draws comparisons between exclusively prey-dependent (with no predator interference term) versus exclusively ratio-dependent functional responses, representing the two ends of the continuum in order to clearly reveal any effects of predator influence. My ratio-dependent functional response is adapted from PIANA *et al.* [184],

$$\Phi_{i,j} = \frac{\omega_{i,j}(E_j/E_i)^h}{1^h + \sum_{k \in \text{resources}} \omega_{i,k}(E_k/E_i)^h} \quad (2.3a)$$

$$h \sim \mathcal{U}[1, 2], \quad (2.3b)$$

where the half-saturation of the prey:predator ratio is given a value of 1 as an ecologically sensible first approximation. If the state of a predator is zero, the ratio for that predator is assigned a value of 0 to avoid division by zero. This is also ecologically sensible since it would give $\Phi = 0$.

Nontrophic interactions. The bioenergetics of nontrophic interactions are very rarely implemented compared to trophic interactions. Here, mutualism and/or competition act on γ for a given species i , according to

$$f_i = \frac{1 + \theta_{\text{comp}} \sum_{g \in \text{competitors}} E_i E_g}{1 + \theta_{\text{mut}} \sum_{g \in \text{mutualizers}} E_i E_g} \quad (2.4)$$

where θ controls the overall strength of mutualism or competition and is assigned a value of 1 in this study. In my model, mutualism reduces γ while competition augments γ (Eqns. 2.1); when mutualism and competition are absent, γ is unchanged. The functional response is linear; this is not an unreasonable assumption as the real shape of the functional response of mutualism is not yet generally known [41]. Although the formulation is more rudimentary than that suggested by KÉFI *et al.* [41] and assumes that

a given species benefits or suffers to the same degree with every interactor, it is a reasonable starting point given that data are unavailable.

Parameter values for community dynamics are summarized in Table 2.2. My parameterization procedure is somewhat different from that of BROSE *et al.* [95], who use basal growth rate as a starting point for defining the time scale and metabolically scaling the other parameters. Nevertheless, my parameter values are metabolically scaled and ecologically sensible, while slightly relaxing the metabolic scaling constraints to allow for species with unusual or extreme natural histories that occasionally occur in real ecosystems. Like BROSE *et al.*, in my study the time scale is not defined in absolute terms; the emphasis is on producing ecologically plausible simulated trajectories and on the simulation duration being long enough to capture the patterns of density dependence, species interactions and stochasticity, such that any general results found would be applicable to a wide variety of ecosystems operating at different time scales.

At the start of the simulation, each species in both niche and random networks, including basal and parasite species, is assigned an initial state $E_0 = \eta^{1/4}$, with the same rationale as for carrying capacity K . Basal species are therefore at carrying capacity at the start of a simulation; their interactions may nevertheless bring them to equilibrium states different from their carrying capacities. In plausible extreme cases, we may have $r(1 - E/E_0) < 0$ or $\gamma(-1 + \sum \psi\Phi) > 0$ when the population exceeds the carrying capacity or when resources are abundant, causing mortality to exceed growth or vice versa. No distinction is made between parasite and nonparasite species when assigning initial states; contrary to intuition, parasites in an ecosystem can sometimes have a total biomass equal to or greater than that of nonparasites [188].

The model has two other simplifications. Firstly, there are real-world cases where an interaction between two species is both trophic and mutualistic, for example in pollination; considering merely the net effect may obfuscate some aspects of the dynamics [161]. There is scope for more research in this area [41]. Secondly, the model does not implement adaptive rewiring of network links [189] in a mechanistic way based on optimal

foraging theory [190–192]. The model, however, does have intrinsic adaptive rewiring in both trophic and nontrophic interactions, via the dependence of interaction strength on species energy, although the values of the resource preference ω are kept fixed over time. It also accounts for the formation of new links if one interprets the links assigned to a given species at the beginning as including all the species it could potentially interact with under all scenarios. This has the merit of not assuming optimal foraging behaviour. The overall model specification strikes a compromise between simplicity and complexity, and avoids setting arbitrary and discrete thresholds at which to change links.

2.3 ENVIRONMENTAL NOISE

This section documents the implementation of environmental noise in the models; see §3.1 for background. Code written by the author can be downloaded at <https://github.com/linyanchen/noise>. The noise term ϵ is based on a time series N generated using the equations of Cohen *et al.* [193] given by

$$N_t = \sum_{i=1}^{\frac{T}{2}} \sqrt{\left(\frac{T}{2\pi i}\right)^\varrho} \sin\left(\frac{2\pi i}{T} t + \Omega_i\right) \quad (2.5a)$$

$$\Omega \sim \mathcal{U}[0, 2\pi] \quad (2.5b)$$

where i is the number of cycles (frequency) within the total duration of N , T is the length of N , ϱ is the spectral exponent i.e. noise colour, and Ω is the phase shift. T is set to the length of the network model simulation, in which case the period of the shortest noise cycle is $2dt$ and the period of the longest cycle is equal to the simulation duration. Each sine curve can be interpreted as representing one environmental variable; summing multiple sine curves of different phases and periods creates the overall environment experienced by the species.

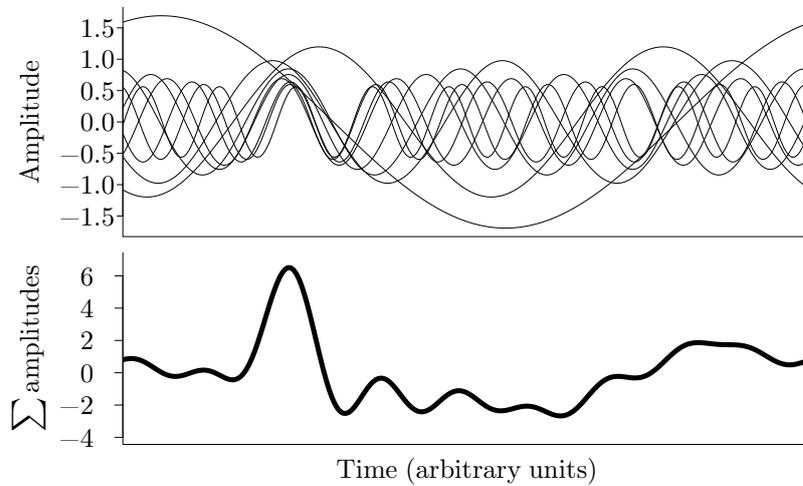


Figure 2.2. Generation of coloured environmental noise of spectral exponent $\varrho = 1$ using the spectral synthesis method [193] of sine wave summation (Eqn. 2.5a).

The time series of noise terms ϵ is finally produced using spectral mimicry [194], permutating a Gaussian-distributed random sequence of mean 0 and specified variance such that it matches the spectral density of N . This gives a Gaussian-distributed colour noise series for a fair comparison with white noise cases [195], although it does not necessarily have to be Gaussian in reality [196]. This mechanistic noise implementation has advantages over the commonly used phenomenological autoregressive models [193], and does not underestimate extinction risk in red environments like both $1/f$ and autoregressive models [195]. There remains a limitation in the method; as $\varrho \geq 3$, the noise increasingly looks like a smooth sine curve, which is not realistic (L. RUOKOLAINEN pers. comm.).

The total variance of the noise experienced by each species is fixed at 0.1 (see SÆTHER *et al.* [197]), with ϵ constituting all, half or none of this variance. In the second of these three different treatments, the remaining variance experienced by each species comprises values independently drawn from Gaussian distributions with means equal to $\bar{\epsilon}$ and variance 0.05. In the third treatment, the variance experienced by each species over time comprises values independently drawn from Gaussian distributions with mean 0 and variance 0.1. These procedures produce different degrees of interspecific

Stochastic bioenergetic network model

synchrony; partial synchrony represents the environment being either good or bad for most species in a given time step, but to different extents for each species.

a multispecies Pythagorean time series

A handwritten musical score consisting of five staves, labeled I, II, III, C, and B on the left. The notation is dense and includes various musical symbols such as notes, rests, and dynamic markings. The first staff (I) has the instruction 'molto gradissimo' written above it. The second staff (II) has 'poco' written above it. The third staff (III) has 'poco' written above it. The fourth staff (C) has 'poco' written above it. The fifth staff (B) has 'poco' written above it. The score is divided into four measures by vertical bar lines. Dynamic markings include 'cresc.' (crescendo) and 'dim' (diminuendo) in several places. The notation is highly detailed, with many notes and rests, and some markings like '4' and 'b' are visible.

Anton Bruckner: Symphony N^o 8

3 COLOUR AND SYNCHRONY OF ENVIRONMENTAL NOISE AFFECT NETWORK VARIABILITY

Abstract. I use stochastic bioenergetic ecological network models to explore the effects of non-predator-prey interactions, colour of environmental noise, and the degree of synchronization of environmental noise across species on the coefficients of variation over time of total ecosystem energy content and Shannon entropy. In regression trees derived by binary recursive partitioning, the presence or absence of synchrony gave the greatest difference in the means of data points for both system energy and Shannon entropy, followed in turn by white versus coloured noise and pink versus red and black noise. The effects are present despite the large variation in the Monte Carlo simulations reflecting the variability of real ecosystems. Non-predator-prey interactions explained relatively small proportions of the total deviance, and each had different directionalities of effects depending on the presence of the other interaction types and on whether energy or entropy was measured. These results underscore the importance of modeling more realistic colours of environmental noise in understanding and predicting the dynamics of ecological communities.

3.1 INTRODUCTION

God is noisy. Real ecosystems are ‘buffeted by a more or less continual series of perturbations, and transient behavior may be the norm rather than the exception in nature’ [198]. In the face of increasing environmental change, it is important to understand the impact of different types of environmental variation on populations and communities [199]. SUTHERLAND *et al.* [200] identified the question of how environmental stochasticity interacts with density dependence to influence population dynamics as one of the most important contemporary questions in ecology. Stochasticity cannot be understood adequately by linear analysis, because the stochastic system is never in equilibrium [201]. Indeed, RUOKOLAINEN & FOWLER [202] reported that

analytical solutions did not capture many of the features of the simulation outputs of stochastic Lotka-Volterra models.

The biggest problem is the real world.

MD at Goldman Sachs

The influence of stochasticity on population dynamics was first investigated in the 1960s and 1970s [196, 203, 204] and have attracted increasing attention in recent years. Stochasticity has been found to magnify extinction risk and reduce invasion risk [205, 206], and has been highlighted as an area for further research in community viability analysis [207]. With respect to species interactions, RIPA *et al.* [208] first presented a theory of the population-level effects of environmental noise in two-species ‘food webs’. A theoretical study [209] of the effects of noise on the transient dynamics of two, three and n interacting species with Lotka-Volterra dynamics found that noise can enhance stability, but that analysis used random interaction parameters. Subsequently, RIPA & IVES [210] took an analytical approach to understanding the effects of environmental synchrony on the dynamics of populations in a two-species Lotka-Volterra competition model, and showed that the effects can be large and unexpected as synchrony can either amplify or dampen cyclic behaviour. GRAVEL *et al.* [211] investigated population-dynamical criteria for species coexistence in a stochastic environment, while GJATA *et al.* [212] used stochastic simulations to study the effects of indirect interactions resulting from trophic interactions. VASSEUR & FOX [213], using a theoretical four-species ‘diamond’ food web, reported that noise can stabilize food webs by synchronizing population dynamics. WELLS *et al.* [32] found that environmental stochasticity, on top of population dynamics, affected the structural indices of ecological networks. Most recently, NOVAK [187] highlighted nonequilibrium dynamics as one of the promising avenues for future theoretical work.

Reddened noise is experienced by most natural populations [214–219] and is exhibited by many other complex systems ranging from stock markets to protein-DNA binding to rhythmic synchronization in music-making [220],

yet most stochastic studies have assumed white noise. The colour of noise has been shown to have significant impacts on the dynamics and stability of single populations [221–228] or simple systems with a few interacting species [202, 206, 210, 229]; also see review by RUOKOLAINEN *et al.* [199]. Multispecies studies include that of GREENMAN & BENTON [206], who reported that autoregressive noise caused resonance and threshold effects in a simple system of three species on three trophic levels. Using a two-species bioenergetic trophic model, VASSEUR [229] showed that the temporal variability of each species can respond differently to changes in environmental noise colour. RUOKOLAINEN *et al.* [230] and RUOKOLAINEN & FOWLER [202] constructed theoretical models showing how various factors affected the extinction risk of populations in competitive Lotka-Volterra communities exposed to different environmental noise colours. The question remains, however, as to whether findings from studies of noise in single-species populations or a few interacting species would hold for networks of many interacting species.

With multiple interacting species, the question also arises as to the extent to which individual species' responses to stochasticity are correlated, or synchronized, with one another. Total interspecific asynchrony has often been used in studies of competition and niche differentiation [231], but this setup is unsuitable for predictive models because environmental forcing itself is one of the synchronizers of population dynamics for many taxa [232–236], especially among species with similar traits [233, 237]. Niche differentiation nevertheless gives rise to asynchrony, which can make diverse communities less variable and more stable in the face of environmental disturbances [238, 239]; partial synchrony would therefore seem consistent with most real communities. Very little is known about how the degree of synchrony affects the dynamics and stability of ecological networks, existing studies being limited to white noise and either triangular tritrophic food webs [240] or Lotka-Volterra competitive communities [241].

Nontrophic interactions. Recent studies have investigated the properties of networks of various non-predator-prey interaction types, one of which is competition. For example, species coexistence has been reported to depend on the mean and variance of interaction strengths in competitive networks

[242]. Competitive networks constructed on game theory principles have been found to promote diversity [243], which implies that this enables more species to coexist in equilibrium. In networks of competing species that cannot be ranked in a strict hierarchy of competitive ability, negative frequency dependence can arise that promotes diversity [159]. In contrast, LOREAU & DE MAZANCOURT [241] found in a stochastic competition model that competition was generally destabilizing, but this may have been partly due to the inherent instabilities of the discrete-time modelling that was used.

Ecological theory has traditionally been dominated by research into antagonistic interactions with, until recently, a relative neglect of facilitative or mutualistic interactions [244]. Although the co-occurrence of negative and positive interactions was already recognized by BURKHOLDER [171], only in recent years have researchers begun to more widely acknowledge the importance of accounting for the mutualistic interactions that pervade real ecological communities [161]. Mutualism is not only of theoretical interest but has also been shown to enhance sustainability in systems exploited by man [245] and has become more prevalent under increasing environmental stress [246].

Various studies have taken the network approach towards mutualistic interactions. For example, SUWEIS *et al.* [167] analytically and numerically demonstrated the positive correlation between species abundances and the nestedness of animal-plant mutualistic networks. OKUYAMA & HOLLAND [247] found that the structural attributes of dynamic mutualistic networks give rise to positive complexity-resilience relationships, while RAMOS-JILIBERTO *et al.* [192] reported that incorporating adaptivity of interactions increased robustness in dynamic mutualistic networks. Discoveries about mutualistic networks have also inspired further inquiry into food webs. For example, KONDOH *et al.* [248] found that food webs had nested substructures like in bipartite mutualistic networks, and proposed that nestedness in food webs hinders coexistence because it increases consumer niche overlap, an effect opposite to nestedness in mutualistic networks. A comparative study by

THÉBAULT & FONTAINE [249] revealed how dynamic food webs and mutualistic networks achieve stability via different structural mechanisms.

The aforementioned studies have greatly advanced our understanding of complexity-stability relationships in ecosystems, but one of their limitations is that interaction types were considered in isolation [132, 249, 250]; little is known about the combined effect of all these interaction types. The relative neglect of non-predator-prey interactions can have profound ramifications for our understanding of ecosystem function [251]. For example, non-predator-prey interactions may exacerbate human impact on ecosystems [252]; not accounting for such interactions in fisheries models has reduced the capacity of these models to predict stock collapse [82]. Food webs implicitly include some non-predator-prey interaction in the form of indirect competition, but competition among basal species and, more strikingly, facilitation are absent. Conversely, studying non-predator-prey interactions in isolation can also compromise our ability to make useful predictions. For example, the dynamics of host-parasite interactions depend not only on those interactions per se but also on predators and alternative hosts, with implications for infectious disease control [253].

Several researchers have thus advanced the design of models containing multiple interaction types. The analytical models of GROSS [161], involving multiple consumer species feeding on a single resource, revealed that intraguild mutualism could be an important ingredient for species coexistence in otherwise competitive environments. FILOTAS *et al.* [254] simulated how spatial processes affect the structure and stability of multiple-interaction-type networks created with random topology and link strengths. Most recently, the so-called multiplex network approach [255] has increasingly been adopted, where different interaction types are partitioned into different networks that are interlinked with one another [174, 256, 257].

Some of the most general results so far emerging from networks of multiple interaction types come from ALLESINA & TANG [51], whose analytical models suggested that the addition of mutualistic and competitive interactions reduce the probability of stability of predator-prey networks. Stability of equilibrium points, however, is just one part of the story, as

first highlighted in §1.3.1; the response in nature of a system to perturbations constitute another important line of inquiry. Indeed, some researchers have advocated that the maintenance of resilience, rather than avoidance of disturbance, should be the focus for conservation efforts [258, 259].

Host-parasite interactions. The importance of incorporating parasites into mainstream food webs [260] and potential effects of parasitism on food web stability [154, 261] have also been highlighted recently, as most studies have investigated host-parasite networks in isolation [262, 263]. There have even been calls for including parasites in food webs by ‘default’ [264]. The impacts of parasites on food webs have been found to be diverse, various interspecific and intraspecific mechanisms having been reported for both stabilizing and destabilizing effects [105, 156, 265, 266] and for effects on network structure mainly via changes in diversity and complexity [267]. Parasitism has also been paired with mutualism in a study that explored the dynamics and equilibria of a theoretical ‘food web module’ comprising a plant, pollinator and nectar robber [268].

To date, no study has investigated the effects of the colour and synchrony of noise on networks of many species and multiple interaction types. Most of this kind of work has been on the dynamics of single populations; even when interspecific interactions are considered, often using Lotka-Volterra models of predation or competition, the focus is on population-level rather than ecosystem-level dynamics. In this study, I use the simulation model documented in Chapter 2 to ask how environmental stochasticity and synchrony, and non-predator-prey interactions, affect the variability of ecological networks. The foundations of the model include empirical data from which network structures have been derived, and well-established consumer-resource equations with known assumptions. Preliminary simulations using this class of model by KÉFI *et al.* [41], comprising food webs with added plant facilitation and predator interference, indicated that nontrophic interactions result in higher diversity at equilibrium, but their study did not look at environmental stochasticity. I show that the colour and degree of synchrony of noise have striking effects on the temporal variability of ecological networks.

3.2 METHODS

The models are based on Chapter 2, using the prey-dependent functional responses. WILLIAMS & PURVES [149] found no consistent trend across empirical food webs in the distribution of niche values within a given web and reported that the distributions were often nonuniform. In this chapter, I therefore modify the original niche model for greater realism by using beta-distributed ($\alpha = 1.5, \beta = 5$) niche values $\vec{\eta}$. Given that η in the niche model is roughly proportional to body size [269, 270], my values of α and β produce a distribution that approximates two relationships³: the proportionality of species diversity to (body size)^{-1/4} [177], and the lognormal distribution of body sizes as shown in studies of terrestrial and stream ecosystems [271]. As in the food web, I set $\eta \sim \mathcal{B}(1.5, 5)$ in the parasite web, since species having parasitic or parasite-like lifestyles can have macroscopic (e.g. hyenas and avian brood parasites) as well as microscopic body sizes, and there is higher diversity at small body sizes as for nonparasitic species.

Independent replicate 15-species models with different combinations of interaction types were generated. I used eight configurations: F, FC, FM, FCM, FP, FCP, FMP and FCMP, where F denotes food web (predator-prey), C competition among basal species, M mutualism and P parasitism. In the parasitic model configurations, five of the species were parasites; the proportion of parasites takes guidance from LAFFERTY *et al.* [154] and SUKHDEO [173]. Environmental noise was implemented as detailed in §2.3. ρ was varied from 0 to 2 in increments of 1, 0 being white noise, and 1 and 2 being widely regarded as pink and red respectively. For each degree of synchrony (none, half, full—see §2.3) in each noise colour treatment in each model configuration, 100 independent network models were generated.

The networks were simulated using the ranges of dynamical parameter values listed in Table 3.1. Temporal variability of the ecosystem was quantified in terms of the coefficients of variation (cv) over time [58, 272] of two metrics: the total system energy and the exponent of the Shannon entropy [273].

³ In later chapters, species niche values are uniform rather than beta distributed, to facilitate comparison with random-topology models where body size hierarchy no longer applies, and to avoid making species of lower niche values that go extinct more similar to surviving species.

Table 3.1. Parameter values of multispecies dynamics.

Parameter	Value	Reference
η	$\mathcal{B}(1.5, 5)$	this study
ξ	0.25	[276]
r	$\mathbb{E}(r) = \eta^{-1/4}$	[177]
K	E_0	this study
γ	$0.01\eta^{-1/4}$	[177]
θ	1	this study
ψ	6	[93]
ω	$1/(\mathbb{N}^{\circ} \text{ of resource spp.})$	[95]
h	$\mathcal{U}[1, 2]$	[125]

The cv combines the amplitude and frequency of temporal variation in one convenient index. The total system energy or biomass at each time step was obtained by summing the species states. The exponent of the Shannon entropy measures the directly comparable effective number of species [273], given by $\exp\left(-\sum_{i=1}^S p_i \ln p_i\right)$ where p_i is the proportion of system energy constituted by species i at a given time step and S is the total number of species. The metrics were measured from time step 10001 (to exclude initial transients)⁴ for a duration of 25000 divisions. Preliminary simulations indicated that this time scale of measurement encompassed all the main features and periodicities of the stochastic behaviour.

The effects of noise colour and synchrony on ecosystem temporal variability were analyzed using regression trees grown using binary recursive partitioning using the `tree` package [275] in R. Regression trees were also used to examine the effects of dummy variables representing the presence or absence of each non-predator-prey interaction. The advantages of regression trees over regression models are that the former is nonparametric and does not assume unimodality and linearity of the response variable.

⁴A possible question for future work is how transient dynamics modulate stochasticity and vice versa, as has been done for single-species plant populations [274].

3.3 RESULTS

The results reported here are from a rerun of the entire simulation study using a different pseudorandom number generator seed state from LIN & SUTHERLAND [1] and with noise for basal species implemented in mortality rate rather than growth rate, which represents a minor advancement in model design since publication. While the results for non-predator-prey interactions are slightly different (as would be expected and, as emphasized by LIN & SUTHERLAND [1], to be interpreted with caution given the very small effect sizes), those for the effects of noise are qualitatively unchanged, reaffirming them.

In a small number of simulations, numerical integration produced negative species states when $dE/dt < 0$ and $|dE/dt| > E$. These were due to the noise terms and the small errors inherent in numerical integration; the affected simulations were omitted from the analysis. The total sample sizes for the various model configurations are 894 (F), 894 (FC), 893 (FCM), 897 (FCMP), 896 (FCP), 893 (FM), 895 (FMP) and 895 (FP), of 900 simulations each.

The stopping criterion for growing the regression trees was set as the point where the within-node deviance became less than 1% of the root node deviance. The resulting trees are shown in Fig. 3.1 and numerically summarized in Table 3.2. The split between unsynchronized and synchronized (half and full) species environmental responses explains most of the deviance, with considerable differences in the mean values of the cv of system energy (0.0381 and 0.307 respectively) and exponent of Shannon entropy (0.0319 and 0.145 respectively). The next most important factor is noise colour, with white noise giving lower cv than coloured noise for system energy (0.0463 and 0.437 respectively), and white or pink giving lower cv than red noise for entropy (0.0884 and 0.258 respectively). The effects of synchrony were much more pronounced when the noise was coloured (Fig. 3.3). The non-predator-prey interaction types never explained more than 1% of the deviance when the dummy variables representing their presence or absence were analyzed together with the noise variables.

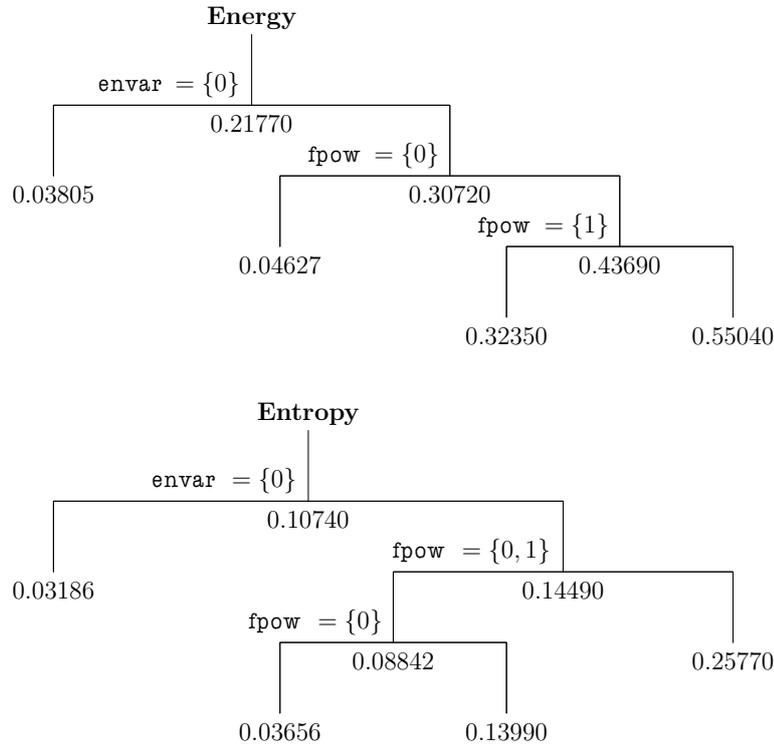


Figure 3.1. Regression trees of effects of noise colour and synchrony on cv of system energy (top) and of $\exp[\text{Shannon entropy}]$ (bottom). Explanatory variables: envar, noise synchrony; fpow, colour (denoted by spectral exponent). The categorical explanatory variable levels partitioned to the left-hand branches are indicated. Numbers under nodes are mean values of the response variables apportioned to the respective branches above.

Regression trees using only dummy variables of non-predator-prey interaction types, with data points pooled across different colours and degrees of synchrony of noise, are summarized in Fig. 3.2 and Table 3.3. Mutualism explains most of the deviance in the cv of system energy, while parasitism explains most of the deviance in the cv of the exponent of Shannon entropy. Both have stabilizing effects i.e. reduce system variability. Competition generally explains the smallest proportion of the deviances.

Table 3.2. Regression tree nodes and deviances of effects of noise colour and synchrony on the cv of total system energy or $\exp[\text{Shannon entropy}]$.

Tree	Node	n	Deviance	Mean cv
energy	envar	7157	482	0.218
	terminal	2379	17.3	0.0381
	fpow	4778	350	0.307
	terminal	1586	10.3	0.0463
	fpow	3192	178	0.437
	terminal	1597	34.7	0.323
	terminal	1595	102	0.55
entropy	envar	7157	136	0.107
	terminal	2379	5.99	0.0319
	fpow	4778	109	0.145
	fpow	3183	31.4	0.0884
	terminal	1586	4.34	0.0366
	terminal	1597	18.6	0.14
	terminal	1595	47.6	0.258

Tree and node names refer to Fig. 3.1; n , number of data points.

Regression trees were also grown separately for each noise colour-synchrony combination (Appendix 3.5.1). The results were similar to the aforementioned effects pooled across noise colours and degrees of synchrony. Mutualism explained most of the deviance most of the time for the cv of both energy and entropy, often causing considerable if not greatest increase in node purity. Where they account for most of the deviance, mutualism and parasitism both tend to have stabilizing effects, except in the case of unsynchronized species responses to noise, where mutualism tends to be destabilizing. The effects of direct basal competition are again inconsistent and relatively small. The effects of mutualism and parasitism, where they do not account for most of the deviance, are also relatively small and inconsistent.

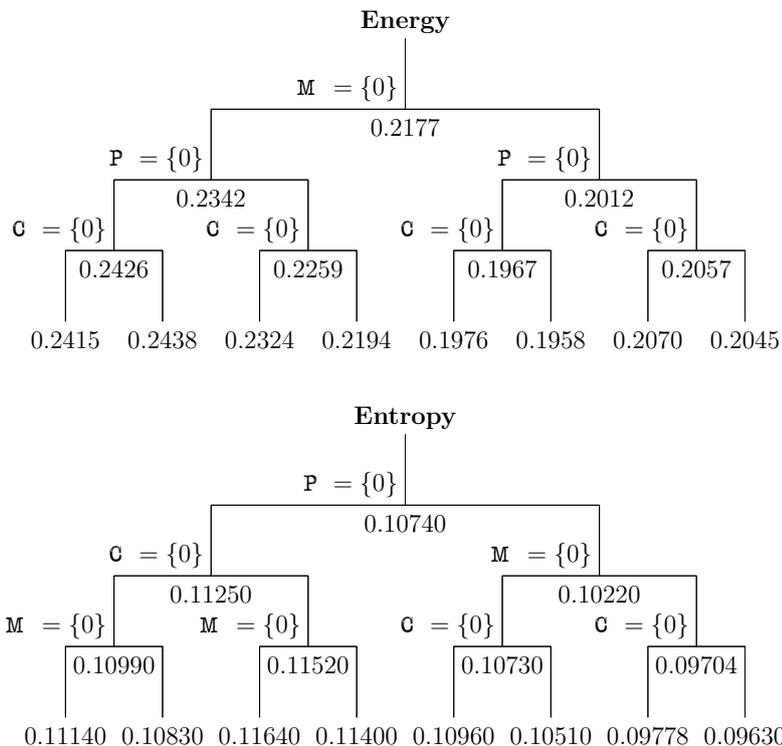


Figure 3.2. Regression trees of effects of non-predator-prey interactions on cv of system energy (top) and of $\exp[\text{Shannon entropy}]$ (bottom), pooled across noise colours and degrees of synchrony. Explanatory variables: C, direct basal competition; M, mutualism; P, parasitism. The categorical explanatory variable levels partitioned to the left-hand branches are indicated (0 and 1 respectively denote absence and presence of the interaction type). Numbers under nodes are mean values of the response variables apportioned to the respective branches above.

3.4 DISCUSSION

Models with coloured noise, but not white noise, exhibit considerably larger and longer-term fluctuations when species environments are partially or fully synchronized. This is most likely due to constructive interference with density-dependent dynamics within [224] and across populations, arising from temporal autocorrelation and synchrony of the environment. These large fluctuations may mimic periodic outbreaks and crashes of

Table 3.3. Regression tree nodes and deviances of effects of non-predator-prey interactions on the cv of total system energy or \exp [Shannon entropy].

Tree	Node	n	Deviance	Mean cv	
energy	M	7157	482	0.218	
	P	3579	281	0.234	
	C	1788	157	0.243	
	terminal	894	77	0.242	
	terminal	894	79.8	0.244	
	C	1791	124	0.226	
	terminal	895	65.2	0.232	
	terminal	896	58.7	0.219	
	P	3578	200	0.201	
	C	1786	88.1	0.197	
	terminal	893	44.3	0.198	
	terminal	893	43.8	0.196	
	C	1792	111	0.206	
	terminal	895	57	0.207	
	terminal	897	54.3	0.205	
	entropy	P	7157	136	0.107
		C	3574	77	0.113
M		1787	36.1	0.11	
terminal		894	20.9	0.111	
terminal		893	15.2	0.108	
M		1787	40.9	0.115	
terminal		894	24.3	0.116	
terminal		893	16.6	0.114	
M		3583	58.6	0.102	
C		1791	31.6	0.107	
terminal		895	16.6	0.11	
terminal		896	15	0.105	
C		1792	26.9	0.097	
terminal		895	14.7	0.0978	
terminal		897	12.2	0.0963	

Tree and node names refer to Fig. 3.2; n , number of data points.

species in real systems,⁵ something that my white-noise and/or unsynchronized models do not appear to represent adequately. These species

⁵ Or even bubbles and crashes in the economy.

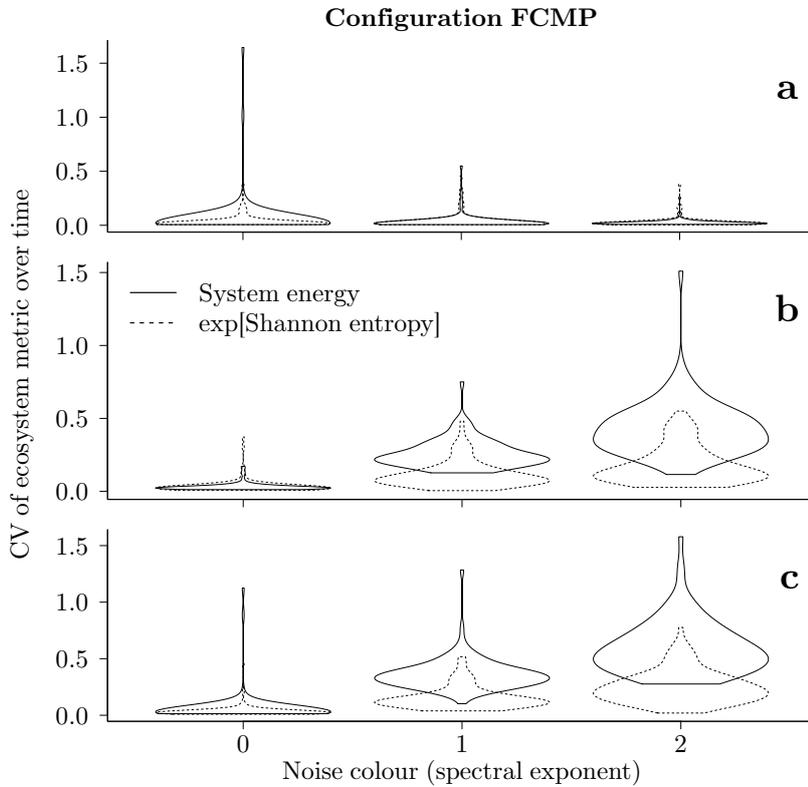


Figure 3.3. The influence of noise colour and degree of interspecific synchrony on variability of ecosystem energy and Shannon entropy, in terms of kernel density distributions of outputs from multiple simulations ($n \approx 900$), for model configuration `FCMP`. Plots for the other model configurations are qualitatively similar (Appendix 3.5.2). **a**, unsynchronized species environments; **b**, half synchronized; **c**, fully synchronized. Violins scaled to constant width.

may be native species, invasive pests or viruses, the latter two of which would be of direct concern to human welfare and development. It is also notable that with white noise, synchrony did not destabilize systems more than the unsynchronized case. This could be because of the weakness of reinforcing effects due to the absence of temporal autocorrelation in white noise, whether synchronized or not. Although LÖGDBERG & WENNERGREN [228] found that environmental reddening reduced rather than increased species extinction risk, the focus of their model on the spatial environment experienced by a single species was different from mine. My

results generally concur with the findings of GREENMAN & BENTON [224] for single populations subject to coloured versus white noise. Stochastic food web models that assume white noise may give the idea that ecosystems are less variable, less prone to large and sudden changes and more predictable than they really are, with implications for the reliability and efficiency of ecological and conservation projects that do not conduct research, monitoring, data collection or management over sufficiently long time scales.

There was more than a two-fold difference in both measures of ecosystem variability between simulations with synchronized compared to unsynchronized noise. These large differences highlight the importance of accounting for synchrony in ecological modeling and prediction. A multispecies model that implements stochasticity independently for each species may underestimate instability and extinction risk, especially if those models also assume white noise. That synchrony has relatively little influence on ecosystem variability in white-noise scenarios, but that even partial synchrony amplifies the effect of coloured noise (or vice versa) in increasing ecosystem variability, underscores the risks of making multiple simplifying assumptions in nonlinear ecological modeling in general and the need to minimize such risks by striking the best possible compromise between simplicity and realism of models. Modeling noise as realistically as possible is especially crucial in fields of research such as critical transitions in complex systems (see SCHEFFER *et al.* [277]), where stochasticity plays a key role in the dynamics before, during and after critical transitions. I recommend pink noise [216, 218] with partial synchrony as a starting point for a more realistic representation of environmental stochasticity in dynamic species interaction models.

In the literature, direct competition among basal species rarely appears outside exclusively plant-based research. Some studies [278–280] have taken the leap by combining direct basal-species competition and plant-herbivore interactions in bitrophic designs, but have not examined the effects of such competition on a web of many trophic levels and multiple interaction types, including facilitation. My full webs indicate that the

effects of direct basal competition depend on whether parasitism or mutualism, or both, are also present. Competition, being an antagonistic interaction, may stabilize systems containing facilitation (mutualism) by dampening the enhanced growth rates brought about by mutualism (see below), and amplify the variability of systems containing parasitism—another antagonistic interaction—by depressing species abundances further and thereby causing larger abundance fluctuations and knock-on effects through multispecies interactions. Continuing along this line of argument, the very small effects of competition on systems containing both mutualism and parasitism could be because the opposing effects of competition in the presence of either mutualism or parasitism alone balance out each other when both mutualism and parasitism are present. Although the ‘connectance’ of direct competition (0.25) seems higher than those of the other interaction types, the absolute number of competition links is relatively small because of the small number of basal species. We can expect any effects of direct competition to become clearer with increasing connectance. I did not, however, increase the connectance further because it is more important in the systems-oriented approach here to have a sensible balance between different interaction types. In any case, there is little basis for comparing the relative effect sizes between different interaction types.

The finding that mutualism tends to stabilize the system could be attributed to the tendency of mutualism to dampen predator-prey cycles. The occurrence of both negative and positive effects of mutualism in this study, however, indicates that the influence of mutualism could be highly context dependent. Nevertheless, the results complement the findings of MOUGI & KONDOH [281] who found that when increasing proportions of randomly selected antagonistic interactions in a model food web were converted⁶ to mutualistic interactions, intermediate amounts of

⁶A potential limitation with their methodology is that the conversion of antagonistic interactions to mutualistic interactions meant that food web structure could not be kept constant in their study.

such mutualistic interactions generally had stabilizing effects in terms of equilibrium stability based on the Jacobian community matrix.

In my model, the key difference between having and not having parasite species is the difference in the prevalence of species of smaller body size gaining energy at the expense of species of larger body size. This allowed me to examine the effect of this difference while keeping the other attributes of the parasite species, such as assimilation efficiency, distribution of niche values and metabolic scaling, statistically similar to those of the nonparasite species. Nevertheless, the model assumptions and parameterizations been made with nonparasite species in mind may not necessarily apply to parasites [105]. More investigation is needed on how parasites differ topologically and dynamically from nonparasites in the context of ecological networks [105, 106].

LAFFERTY *et al.* [105] reviewed various mechanisms by which parasites can destabilize or stabilize food webs, notably destabilization via the inversion of body size structure [282] and lengthening of trophic chains [154], and stabilization via shared pathogens. All these mechanisms are represented in my model. My finding that parasitism tends to reduce ecosystem variability appears to contradict part of the aforementioned literature, but there is in fact no contradiction because both stabilizing and destabilizing effects occur in my study depending on each of many model realizations with contingent network topologies and dynamics. In addition, the difference of the average result of parasitism from that of LIN & SUTHERLAND [1] could be partly due to the smaller number of species used there in nonparasitic configurations, implying that additional diversity may also have stabilizing effects on average, corroborating current consensus on the biodiversity-stability relationship.

Overall, the finding that environmental stochasticity has a far greater role in ecosystem variability than non-predator-prey interactions is not surprising insofar as stochasticity is the source of the variability. Nevertheless, the parameter values used for both environmental noise specification and network topology are reasonably realistic in ecological terms, and show that the effects of noise colour are qualitatively similar across different

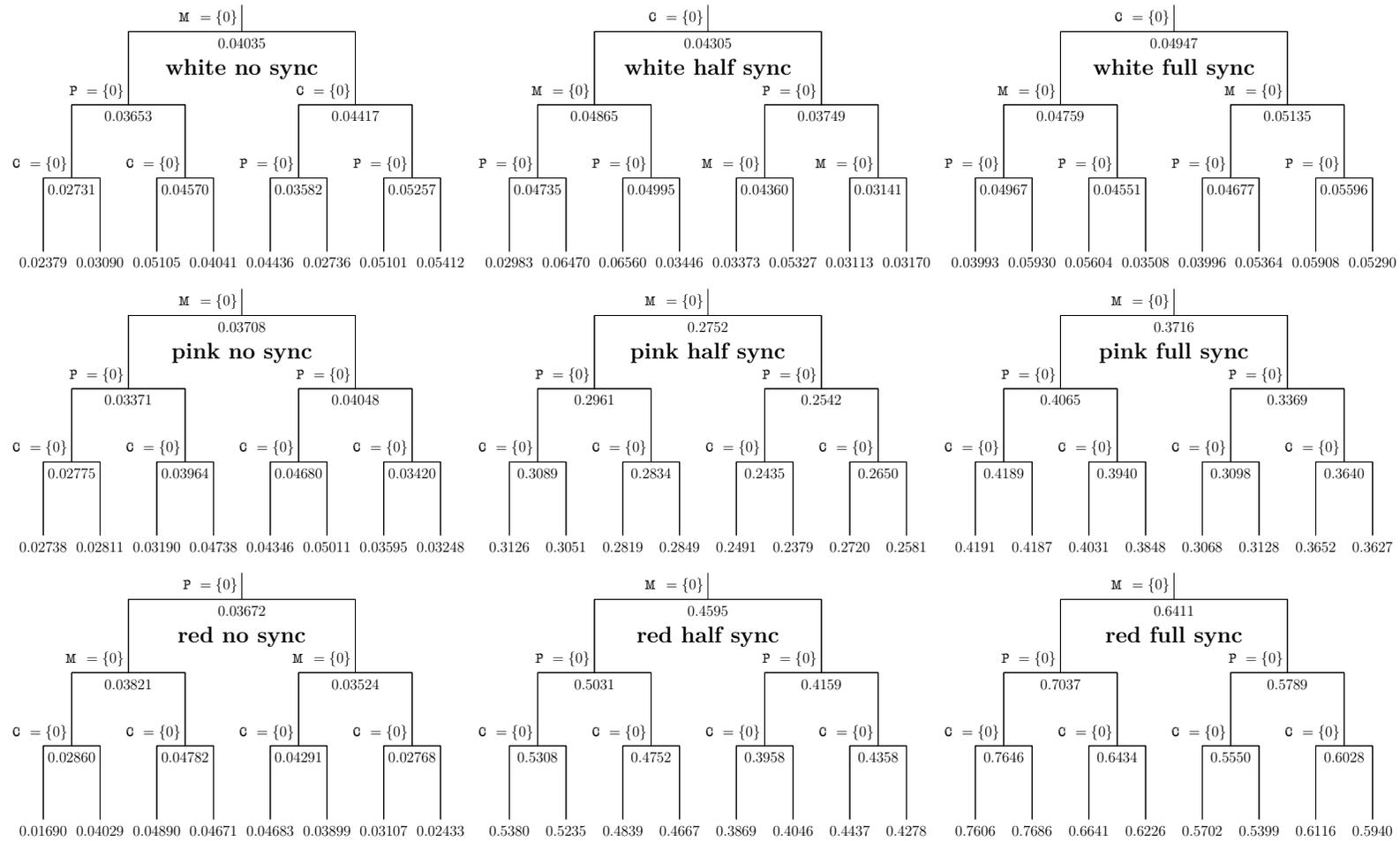
combinations of interaction types. Although one could possibly increase the effect sizes of non-predator-prey interactions relative to those of environmental noise by making the former interactions stronger and/or more abundant, and/or making the environmental noise weaker, doing so may compromise realism. These results illustrate the importance of incorporating stochasticity in ecosystem modeling and prediction, perhaps even more important but even less explored than incorporating non-predator-prey interactions in food webs. This study also shows that for either general understanding or prediction of the dynamics of a specific ecosystem, it is important to model the particular kind of stochasticity present in that ecosystem. For example, noise in terrestrial ecosystems tends to be whiter than that in marine ecosystems, and similarly for temperate versus non-temperate latitudes [219]. Overall, the patterns elucidated in this study emerged over and above the considerable variation in network model realizations emulating real-world contingencies across ecosystems.

The implications of this study extend to practical conservation. Focusing on single charismatic species without also paying attention to their ecological interactions, or forgetting about cryptic species with disproportionate influence, may be an obvious but not necessarily optimal approach [116]. A safer way might be to conserve ecosystem structure and function by protecting a suite of species that represent the widest possible range of ecological functional groups [283] and species that serve a given function but have the widest possible range of responses to different types of stress [284], including responses to environmental noise. Diversity and asynchrony in species responses to noise means less extreme overall fluctuations in ecosystem properties and function. Much research remains to be done to understand how the interactions of a species make it a better or worse candidate for these ends [285]. The results so far support the notion that more systems-oriented research strategies that accommodate stochasticity have an important role to play in cultivating such understanding and helping us make more judicious ecological decisions.

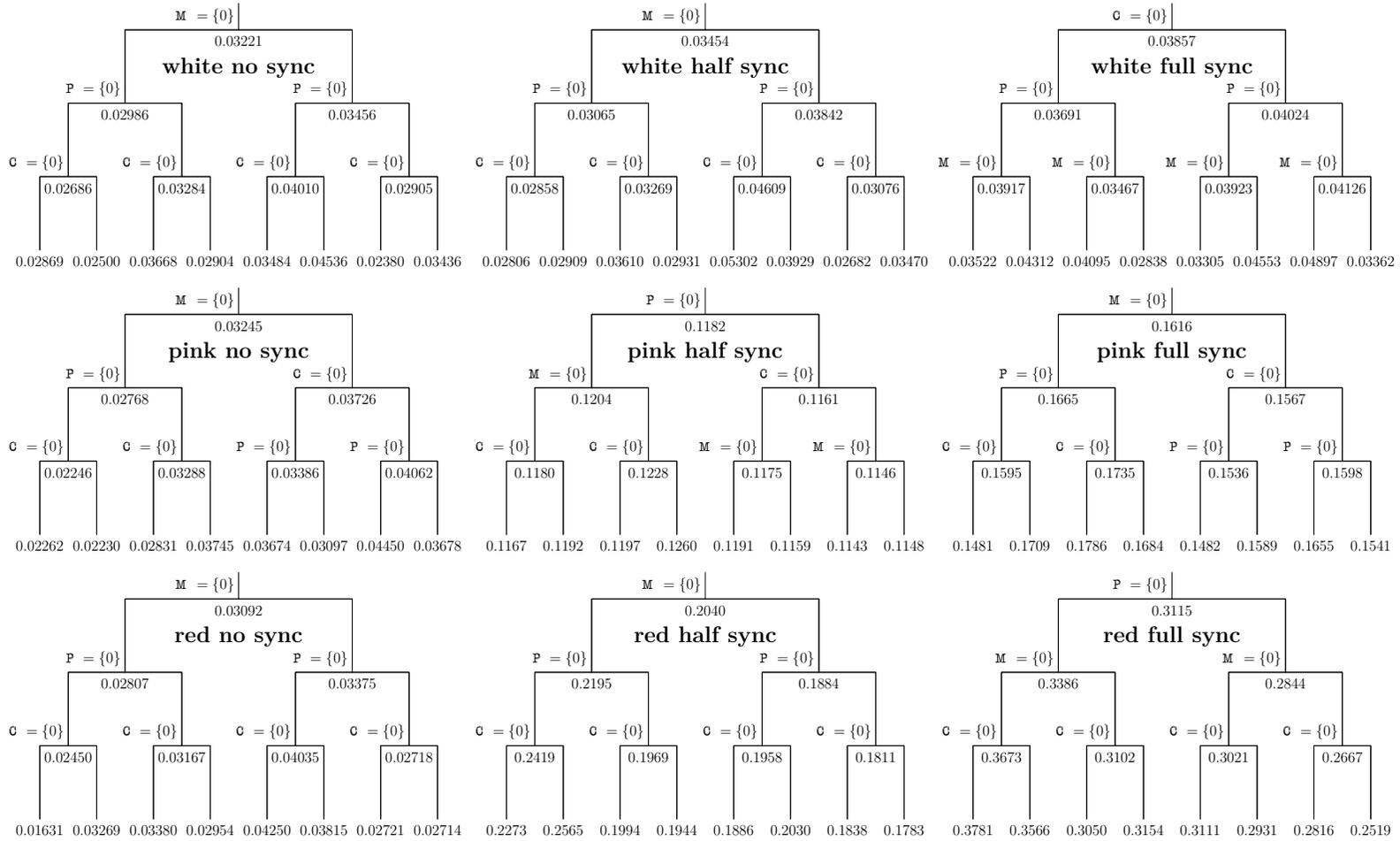
3.5 APPENDIX

3.5.1 EFFECTS OF NON-PREDATOR-PREY INTERACTIONS

Regression trees of effects of non-predator-prey interactions on cv of system energy and $\exp[\text{Shannon entropy}]$, by noise colours and degrees of synchrony. Explanatory variables: C, direct basal competition; M, mutualism; P, parasitism. The categorical explanatory variable levels partitioned to the left-hand branches are indicated (0 and 1 respectively denote absence and presence of the interaction type). Numbers under nodes are mean values of the response variables apportioned to the respective branches above.



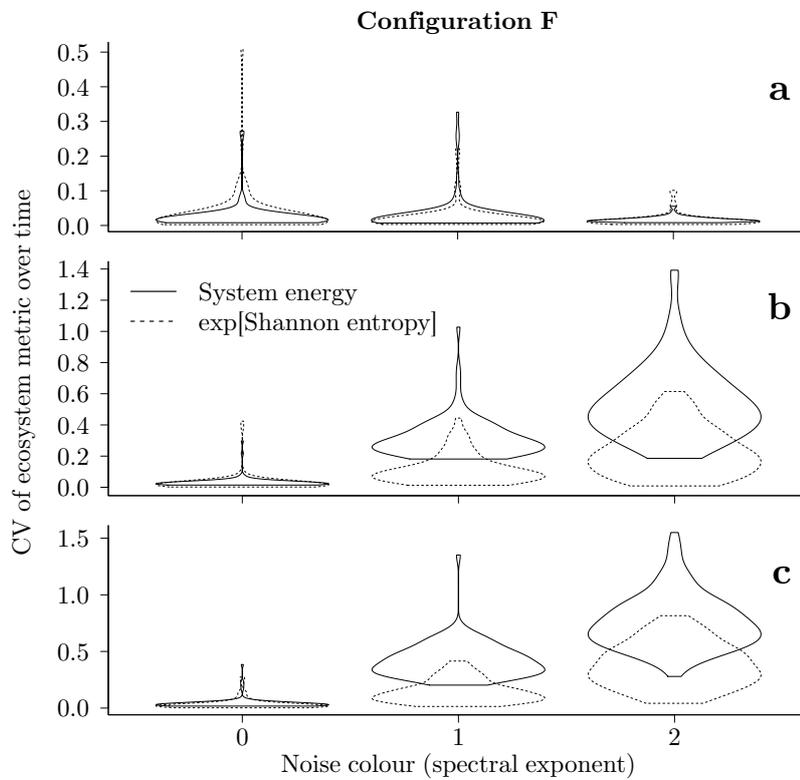
System energy.

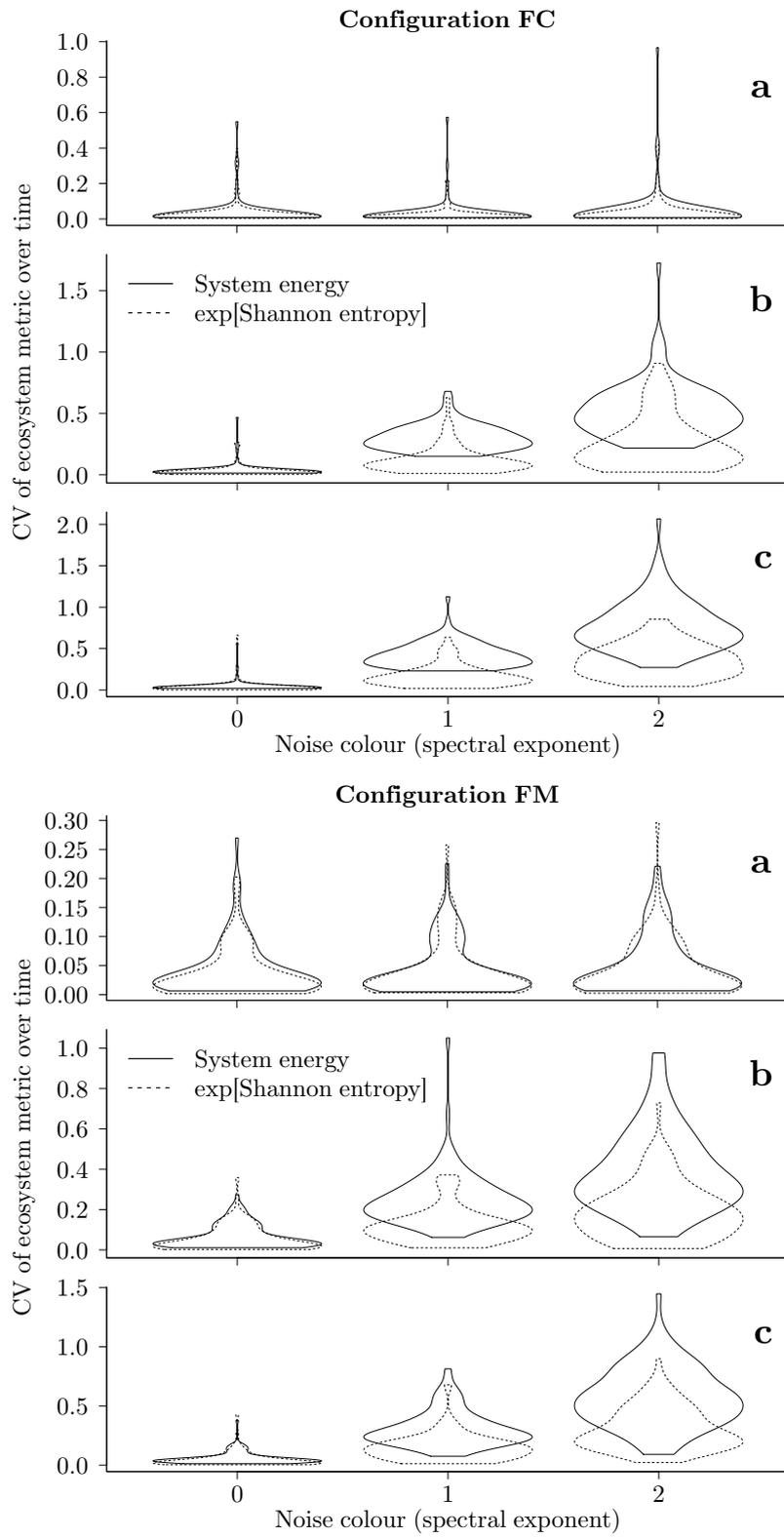


Exponent of Shannon entropy.

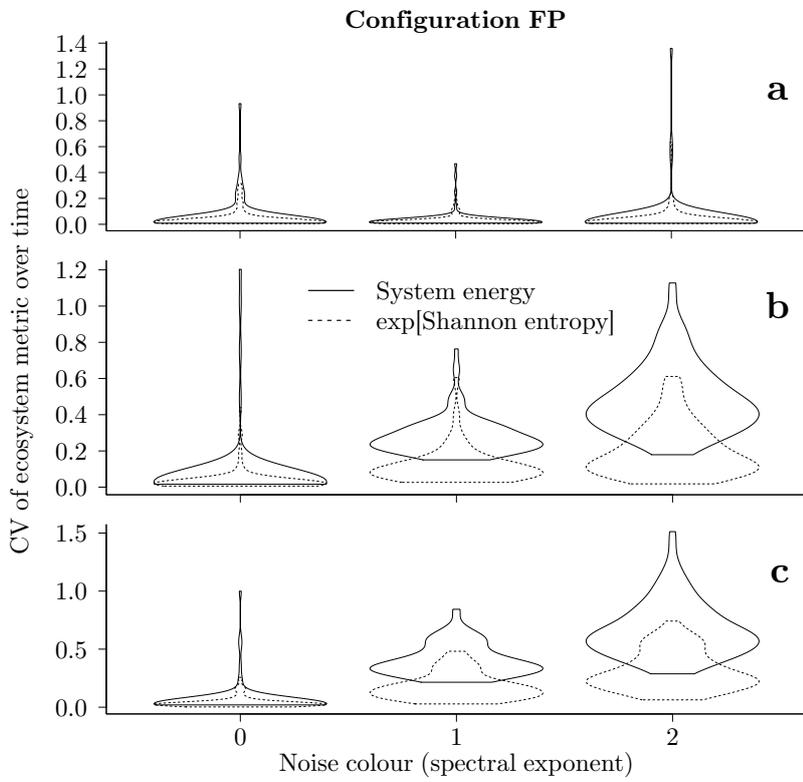
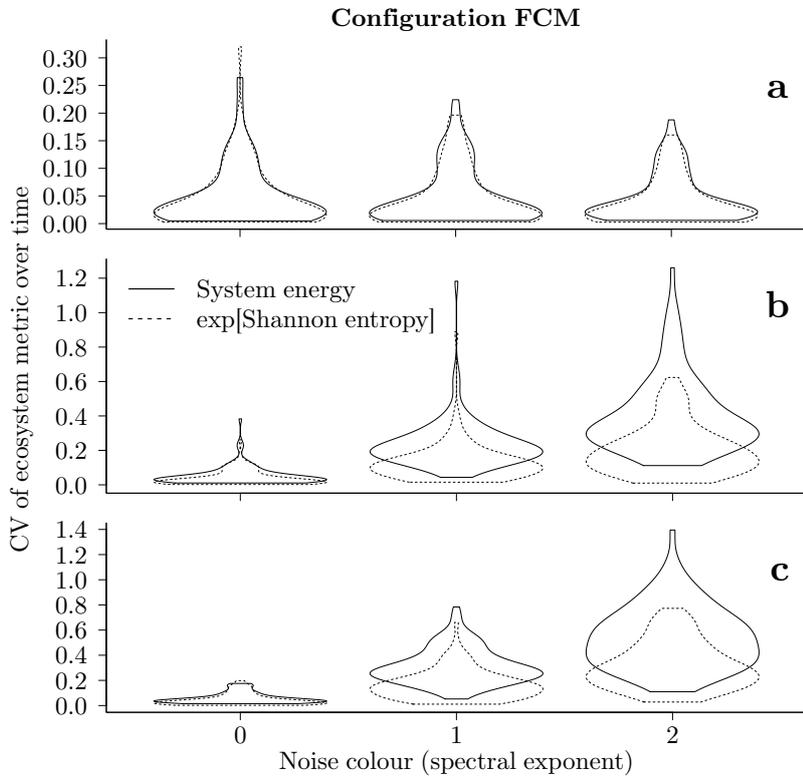
3.5.2 EFFECTS OF NOISE COLOUR AND SYNCHRONY

The influence of noise colour and degree of interspecific synchrony on variability of ecosystem energy and Shannon entropy, in terms of kernel density distributions of outputs from multiple simulations ($n \approx 900$), for model configurations other than FCMP (shown in Fig. 3.3 in the main text). a, unsynchronized species environments; b, half synchronized; c, fully synchronized. Violins scaled to constant width.





Colour & synchrony of environmental noise



4 EXTINCTION AND INVASION DO NOT ADD UP

Abstract. Species extinction and invasion concurrently affect the composition and properties of ecological communities, yet their effects have largely been studied separately, and with more focus on species and ecological functional groups than on the whole-community level. I adopted a dynamic ecological network approach to compare the effects of simultaneous single-species primary extinction and invasion to the effects of extinction and invasion in isolation, using a set of ecosystem metrics. I also investigated the relationship between the impact and reversibility of extinction or invasion through reintroduction or eradication respectively. I used Monte Carlo simulations of bioenergetic ecological network models that combined trophic and mutualistic interactions, contained either prey-dependent or ratio-dependent trophic functional responses, and incorporated either white or pink environmental stochasticity. As the separate extinction or invasion impact increased, the simultaneous extinction-invasion impact increased but was decreasingly additive of the two separate impacts, across all ecosystem metrics. Greater extinction or invasion impact was associated with lower reversibility for most model types and ecosystem metrics. There were also systematic differences between models with prey- and ratio-dependent functional responses. These results highlight the importance of considering the combined effects of extinction and invasion in ecological studies, management and restoration.

4.1 INTRODUCTION

Biodiversity loss is causing changes in ecosystem structure and functioning on a global scale [286], while biotic invasion has been listed as one of the most important global change drivers that influence biotic interactions [287]. Accordingly, there has been extensive research on the impacts of extinction and invasion on communities, with the ecological network approach being increasingly used for understanding and predicting impacts on complex ecosystems [18]. Furthermore, there is increased recognition of

the importance of incorporating community dynamics in network studies of extinction and invasion. For example, CURTSDOTTER *et al.* [288] found that the effects of sequential species extinctions differ between static and dynamic food webs.

Numerous studies have dealt with various aspects of food web structure and dynamics as causes [289–292] and consequences [125, 293, 294] of primary and secondary extinctions at different trophic levels. Because whole-network time-series data are scarce, most such studies are theoretical, although the models are usually constructed and parameterized using empirical network topologies and community dynamics. Nevertheless, they provide community- and ecosystem-level insights that are impractical to obtain empirically. Such studies, however, have been restricted to trophic interactions. Some recent studies have used empirical data to investigate the consequences of extinction on networks of nontrophic interactions either including [116] or excluding [295] trophic interactions, but these studies did not incorporate community dynamics.

The effects of invasive species on ecological networks also constitute an area of increasing research (see OLESEN *et al.* [99] p. 44 for a review). Empirical research has progressed from early descriptive studies [296] to recent analyses of long-term data combined with dynamical simulations [297]. Recent theoretical modeling studies have identified predictors of invasion success [126, 298] and which measures best predict invasion impacts on large food webs [30]. In terms of the effects of invasion on nontrophic networks, most research has been on bipartite mutualistic networks of pollinators and seed dispersers [299–301] and, as with extinction studies, largely restricted to network topology without community dynamics [302–304]. A few studies have examined other kinds of mutualistic [305] or parasitic networks [306] restricted to particular pairs of taxonomic groups.

Existing network research on the effects of extinction or invasion has one or more of the following limitations: they do not incorporate community dynamics, the models contain only one interaction type, the models are deterministic, or the metrics of perturbation impact pertain to population- rather than community- or ecosystem-level properties.

Indeed, responses of ecosystems as a whole to invasions are much less known than responses of populations or communities [307]. Furthermore, the vast majority of studies of the impacts of extinction and invasion on ecological networks have so far examined extinction and invasion in isolation from each other, or at invasion as a cause of extinction [308]. There is a lack of studies examining the combined effects of simultaneous extinction and invasion driven by separate causes [309]. The importance of examining both processes concurrently is suggested by FORYS & ALLEN'S [310] empirical study of functional group change caused by extinctions and invasions, and JACKSON & SAX [311] who promulgate the notion of 'biodiversity dynamics' in a changing environment as being the shifting balance between species loss and gain. Indeed, non-native species introduced by humans may mitigate the global 'trophic downgrading' of food webs [312,313].

Reintroduction of extinct species and eradication of invasive species are increasingly being carried out in restoration ecology; an understanding of the reversibility of extinction and invasion is therefore crucial to restoration [314]. LUNDBERG *et al.* [315] found in dynamic models of competitive communities that cascading extinctions could sometimes cause community changes that preclude reinvasion, although they did not include trophic and other types of nontrophic interactions and treated reinvasion as a binary rather than continuous variable. The eradication of invasive species can also have unexpected ecosystem-level outcomes because of species interactions (review by ZAVALETA *et al.* [316]). For example, alien plant removal has been found to have negative impacts on rare native plants in pollinator networks [317]. The importance of adopting a network perspective on ecological restoration is increasingly being recognized [116,300]. Existing studies are mostly empirical investigations of specific taxa and habitats (see KARDOL & WARDLE [314] and references therein); more recent research has begun to demonstrate the role of network simulation models. For example, RAYMOND *et al.* [318] dynamically simulated the effects of invasive species eradication in a subantarctic island's species interaction network using and comparing different model

structures, although they used random interaction strengths and did not metabolically scale parameter values.

As WARDLE *et al.* [309] state about the effects of alien consumers, ‘we have yet to move from a collection of impressive examples to the development of general principles’. In my study, ‘general principles’ are sought for the impacts and reversibilities of extinction and invasion in ecological networks, where extinctions and invasions are driven by independent processes. I also attempt to address issues recently identified as high ecological research priorities [200,307]: the role of rare species in ecosystem functioning, what kinds of invasive species will affect ecosystem properties, and how changes in ecosystem properties are related to changes in community structure.

My strategy entails ensemble simulations to seek universal patterns in the impacts of extinction and invasion (if any) across multiple contexts. Empirical studies have limitations such as being snapshots in time, which do not capture the actual mechanisms of biodiversity loss, or short-term studies capturing mostly transient effects rather than long-term impacts [319]. There can also be biogeographical or taxonomical biases, as has been seen in field studies of the impacts of invasive alien plants [320]. This is where simulation modeling can provide valuable insights.

More specifically, I look at the effects of network connectance and various extirpator (species going extinct) and invader species traits on the impacts of primary extinction and invasion, the impact of simultaneous extinction and invasion, and the reversibility of extinction and invasion via reintroduction and eradication respectively. The impacts and reversibilities are quantified in terms of changes in several ecosystem metrics representing community structure, biomass, diversity and periodicity. This multidimensional approach to quantifying ecological stability gives a more comprehensive understanding, anticipation and management of effects of perturbation on ecosystems [321]. In addition, it may be important to account for real-world environmental fluctuations in models; for example, Joo *et al.* [322] found that deterministic models of bacteriophage-mediated bacterial invasion did not adequately capture dynamics that involved stochastic

processes. This is the first study to incorporate positive interactions and environmental stochasticity into bioenergetic food web modeling to investigate how extinction, invasion and combined impacts propagate through noisy dynamics of species interactions to influence properties at the ecosystem level of organization. This may ultimately help determine extinction and invasion management actions with the best chance of success [323].

4.2 METHODS

The stochastic model is based on that documented in Chapter 2. Models of 11-species communities were generated with all different combinations of niche and random trophic network topologies, prey- and ratio-dependent functional responses and white and pink noise. No parasitism or direct basal competition was implemented, for comparability across niche and random network topologies. Trophic and mutualistic connectances were varied within the range $[0.05, 0.3]$ (similar to ROMANUK *et al.* [126]) using a Sobol' low-discrepancy sequence [324] across replicates within each topology-dynamics-noise configuration. The degree of interspecific synchrony of response to noise was set at half-synchronized for all models (see Chapter 3). Dynamical parameter values are listed in Table 3.1.

The starting sample size for each topology-dynamics-noise configuration was 100. Within each of the 100 replicates, four 'parallel universe' simulations were set up with the same parameters, initial conditions and pseudorandom seed states, but with different combinations of extinction and invasion (Fig. 4.1). For each simulation within a replicate, one randomly selected species was removed prior to the start of the simulations, to subsequently invade the system in the relevant simulations. Similarly, another species was randomly selected for future extinction.

For each extirpator and invader, several species traits were quantified. These, and the trophic and mutualistic connectances, constitute the explanatory variables (Table 4.1) whose effects on the impacts and reversibilities of extinction and invasion were investigated using regression trees using the *tree* package in R [275]. The effects of individual explanatory variables on the absolute magnitudes of the response variables

(except extinction-invasion interaction) were also analyzed separately using Kendall correlations, or Mann-Whitney U -tests in the case of categorical variables (extinctors and invader basality). This procedure was then repeated with [extinction and/or invasion impacts on community structure] as an explanatory variable, against extinction and/or invasion impacts on the five other ecosystem metrics.

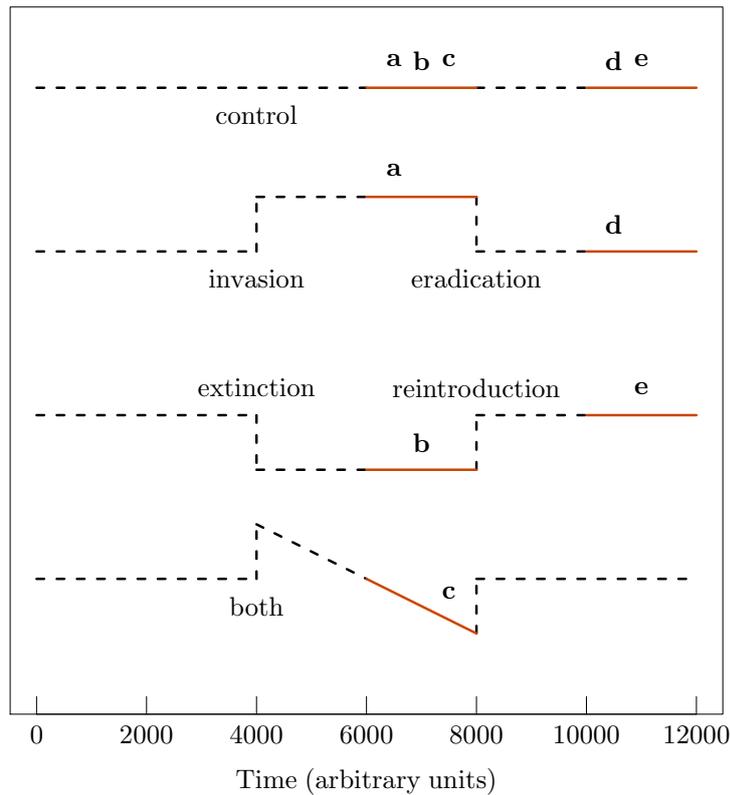


Figure 4.1. Simulation experiment design. Each of the four rows symbolizes a single stochastic simulation of multispecies dynamics. The four simulations had identical starting model structure, invader and/or extensor species, parameter values, initial conditions and noise time series. The diagram as a whole represents one of 100 replicates for each noise colour within each type of dynamics (prey-dependent and ratio-dependent) within each network topology (niche model and random). The red segments denote the parts of the time series over which various ecosystem metrics were calculated. The difference in each metric between pairs of time series was calculated as indicated by a (impact of invasion), b (impact of extinction), c (impact of simultaneous invasion and extinction), d (reversibility of invasion, by invader eradication) and e (reversibility of extinction, by extensor reintroduction).

Table 4.1. Abbreviations and description of explanatory variables.

Abbreviation	Description
trocon	trophic connectance
mutcon	mutualistic connectance
invbasalnon	is invader a basal species
extbasalnon	is extinator a basal species
invniche	invader niche value (trophic level)
extniche	extinator niche value (trophic level)
invsim	invader mean interaction similarity (modified from ROMANUK <i>et al.</i> [126] p. 1746 to combine trophic and nontrophic interactions)
extsim	extinator mean interaction similarity (modified from ROMANUK <i>et al.</i> [126])
iesim	mean interaction similarity of invader and extinator (modified from ROMANUK <i>et al.</i> [126])
ipred	N ^o of consumer species of invader
iprey	N ^o of resource species of invader
imut	N ^o of mutualiser species with invader
epred	N ^o of consumer species of extinator
eprey	N ^o of resource species of extinator
emut	N ^o of mutualiser species with extinator
dominance	relative extinator abundance prior to extinction, when not under extinction pressure (mean species energy over $20001 \leq \text{time } t \leq 40000$ divided by mean total system energy over same period)
ilink	total N ^o of network links of invader
elink	total N ^o of network links of extinator

Extinction, invasion or simultaneous extinction and invasion was enforced at time $t = 40\,001$, and reintroduction or eradication at $t = 80\,001$. A species was made extinct by instantaneously setting its state to zero. This implementation is the most straightforward in representing different causes of mortality. Isolated network clusters may occasionally be created by species removal, but this does not violate ecological laws and the separate clusters are still resource-limited. If a cluster ended up with no basal species, it would die out as expected in reality. The state of an invader at the time of invasion was set at 10% of what its initial state would be if it were present as a native species at the start of the simulation, as invasions usually begin with a few individuals; similarly, species previously made extinct were reintroduced at 10% of their initial states. Invader eradication was similar to extinction, with species state instantaneously set to zero. Six ecosystem metrics (Table 4.2) were calculated from time steps 20 001 to 40 000 (before extinction or invasion), 60 001 to 80 000 (after extinction or invasion) and 100 001 to 120 000 (after reintroduction or eradication) to allow for most transients to pass and to avoid capturing any spurious rate-dependent hysteresis caused by rapid extinction. Preliminary simulations indicated that this time scale of measurement encompassed all the main features and periodicities of the stochastic behaviour.

Table 4.2. Ecosystem metrics.

Metric	Description
cv energy	coefficient of variation over time of total biomass of all species
cv entropy	coefficient of variation over time of $\exp[\text{Shannon entropy}]$ of relative species biomasses [273]
average energy	average over time of total biomass of all species
average entropy	average over time of $\exp[\text{Shannon entropy}]$ of relative species biomasses [273]
community structure	set of all species states at each time step
power spectrum	amplitude distribution of frequencies of biomass fluctuation [225] of each species

Impacts of extinction, invasion and simultaneous extinction and invasion (hereafter referred to as ‘extinction-invasion impact’) were quantified by comparing the ecosystem metrics of the perturbed versus control simulations. Differences between parallel simulations make better measures of extinction and invasion impacts than measuring the same simulation before and after perturbation, because in the latter we would not know whether any changes in the system after extinction or invasion were actually caused by the perturbation or not.

Differences in the means and coefficients of variation of energy and entropy were calculated as proportionate change, with the control simulation as the baseline. The difference in community structure was quantified as the absolute root mean square deviation of the time series of a given species between the impacted system and the same time steps in the control simulation (i.e. as if nothing happened throughout), calculated species by species, and then summed across all species and divided by the number of time steps, given by

$$\sqrt{\frac{\sum_{s=1}^S \sum_t \{(E_{s,t_{\text{post},\text{start}}} - E_{s,t_{\text{pre},\text{start}}})^2, \dots, (E_{s,t_{\text{post},\text{end}}} - E_{s,t_{\text{pre},\text{end}}})^2\}}{t_{\text{pre},\text{end}} - t_{\text{pre},\text{start}} + 1}} \quad (4.1)$$

where the subscripts $_{\text{pre}}$ and $_{\text{post}}$ indicate pre- and post-decline periods, and $_{\text{start}}$ and $_{\text{end}}$ refer to the first and last time steps at which the ecosystem metrics were measured.

The difference in the log power spectrum was quantified as for community structure. The power spectrum, calculated as one of the ecosystem metrics using default settings in the spectrum function in R, is informative about the ‘internal dynamics’ of the system [214, 225, 325]. By revealing the detailed relationship between power and frequency, this measure paints a picture of stability and periodicity at different time scales—the system can be stable at one scale and unstable at another [326]. It can be indicative of changes in the interaction between stochasticity and deterministic density-dependent cycles. The power spectrum was calculated over 10000 uniform frequency intervals from 0.00005 to 0.5 (the Nyquist

frequency) cycles per time step. An alternative way to measure change in power spectra is by means of spectral entropy, or Shannon entropy of the power spectrum [327], but this method loses frequency information—a spectrum that is a mirror image of another will have identical entropy.

In addition to measuring the extinction-invasion impact per se, I also developed a measure of the interaction between extinction and invasion, hereafter referred to as the extinction-invasion interaction. For each ecosystem metric, the extinction-invasion interaction was calculated as

$$\begin{aligned} & (\text{extinction-invasion impact}) - \\ & [(\text{extinction impact}) + (\text{invasion impact})] \end{aligned} \tag{4.2}$$

from the parallel simulations. The expected impact of simultaneous extinction and invasion if they were purely additive is $[(\text{impact of extinction}) + (\text{impact of invasion})]$. If the interaction has a value of 0, extinction and invasion do not interact (i.e. have purely additive effects). In the case of changes in community structure and power spectra, which are always positive, a negative interaction value means that extinction and invasion mitigate each other's impact while a positive value means that they reinforce each other. In the case of changes in average or coefficient of variation of energy and entropy, which can take positive or negative values depending on whether the extinction and/or invasion causes them to increase or decrease, a negative interaction value simply means that the interaction between co-occurring extinction and invasion is less than purely additive, while a positive value indicates the opposite. In the case of coefficient of variation of energy or entropy, positive may be detrimental because it indicates that the variability has increased i.e. stability is lower; in the case of average energy or entropy, positive may be beneficial as it indicates that the overall biomass or diversity has increased.

Reversibility of extinction or invasion depends on two factors: the magnitude of the impact of extinction or invasion, and the extent to which the system can return to its pre-extinction or pre-invasion characteristics following reintroduction or eradication respectively. The impact was quan-

tified as above, while the difference of the post-reintroduction/eradication ecosystem from the control simulation where no disturbance ever happened (this difference henceforth referred to as ‘reintroduction or eradication effect’) was quantified by calculating the differences in the above metrics after reintroduction/eradication compared to the same time steps in the control simulation. The ‘relative reversibility’ of extinction or invasion—relative to the extinction or invasion impact—was then calculated as

$$\left| \frac{\text{extinction or invasion impact}}{(\text{reintroduction or eradication effect}) + 10^{-100}} \right|. \quad (4.3)$$

Thus the perturbation is relatively more reversible if after a larger perturbation the system reverts to its unaffected condition. The addition of 10^{-100} avoided division by 0; the value was chosen to be several orders of magnitude smaller than the smallest non-zero data point. As reversibility is a non-negative concept, what matters here is the magnitude but not the sign of the impacts, so the absolute value is taken. To see how the reintroduction or eradication effect itself is related to the impact of extinction or invasion, ‘absolute reversibility’ was calculated as 1 minus the sample-normalized absolute values of the reintroduction or eradication effect, where the smaller the effect, the greater the absolute reversibility:

$$1 - \frac{|\text{reintroduction or eradication effect}|}{\max|\text{reintroduction or eradication effect}|}. \quad (4.4)$$

Finally, the overall distributions of the response variables were compared across topology-dynamics-noise configurations, to probe the relative extents to which model type matters to model outputs. For the energy- and entropy-related response variables, which could take on either positive or negative values, the distributions would also indicate the relative directionality of the effects in addition to their magnitudes as described above.

4.3 RESULTS

Replicates were discarded in which noise terms and numerical integration errors resulted in negative species states. The final sample size of each topology-dynamics-noise configuration ranged from 72 to 98. Relatively extreme values of response variables occurred in a small proportion of replicates because some of the response variables, being proportionate changes in some quantity, are divided by the original value of the quantity which sometimes takes on very small fractional values, when populations are very small. This is ecologically plausible and not abnormal, especially as species states are in arbitrary units.

The regression trees showed no consistent interaction structure among the explanatory variables of web connectances and species traits. The explanatory variable explaining most of the deviance for each topology-dynamics-noise configuration is listed in Appendix 4.5.1. For extinction impact and extinction-invasion impact in most topology-dynamics-noise configurations, extirpator dominance often accounts for most of the deviance in changes in power spectra and average entropy. Invader niche value usually explains most of the deviance of invasion reversibility in ratio-dependent niche models, across noise colours and ecosystem metrics. An explanatory variable that explains most of the deviance in a regression tree is not necessarily highly correlated with the response variable.

Tables of effects of individual explanatory variables on magnitudes of response variables are found in §3.5 of the online supplement to LIN & SUTHERLAND [2] at <http://dx.doi.org/10.1016/j.baae.2014.07.008>. Extirpator dominance is moderately strongly correlated to extinction impact for many model types and ecosystem metrics across both white and pink noise, in addition to explaining most of the deviance in many of the regression trees. The correlations are mostly positive for all ecosystem metrics except power spectrum, where the correlations are all negative. The number of invader predators is usually moderately to moderately strongly negatively correlated to invasion reversibility for all model types except prey-dependent niche models, despite not often explaining most

of the deviance in regression trees. Relationships for other explanatory and response variables are mostly insignificant in comparison.

Relationships between impacts on community structure and impacts on the other five community metrics are shown in Fig. 4.2 (tabulated in Appendix 4.5.2). There are mostly moderately strong positive correlations between community structure and energy- and entropy-related response variables, across model types and noise colours (sample sizes: prey-dependent models, 387; ratio-dependent models, 319). Correlations of community structure with power spectra are generally not as strong, but there is a notable difference between the positive correlations for prey-dependent models and negative correlations for ratio-dependent models in terms of invasion impact.

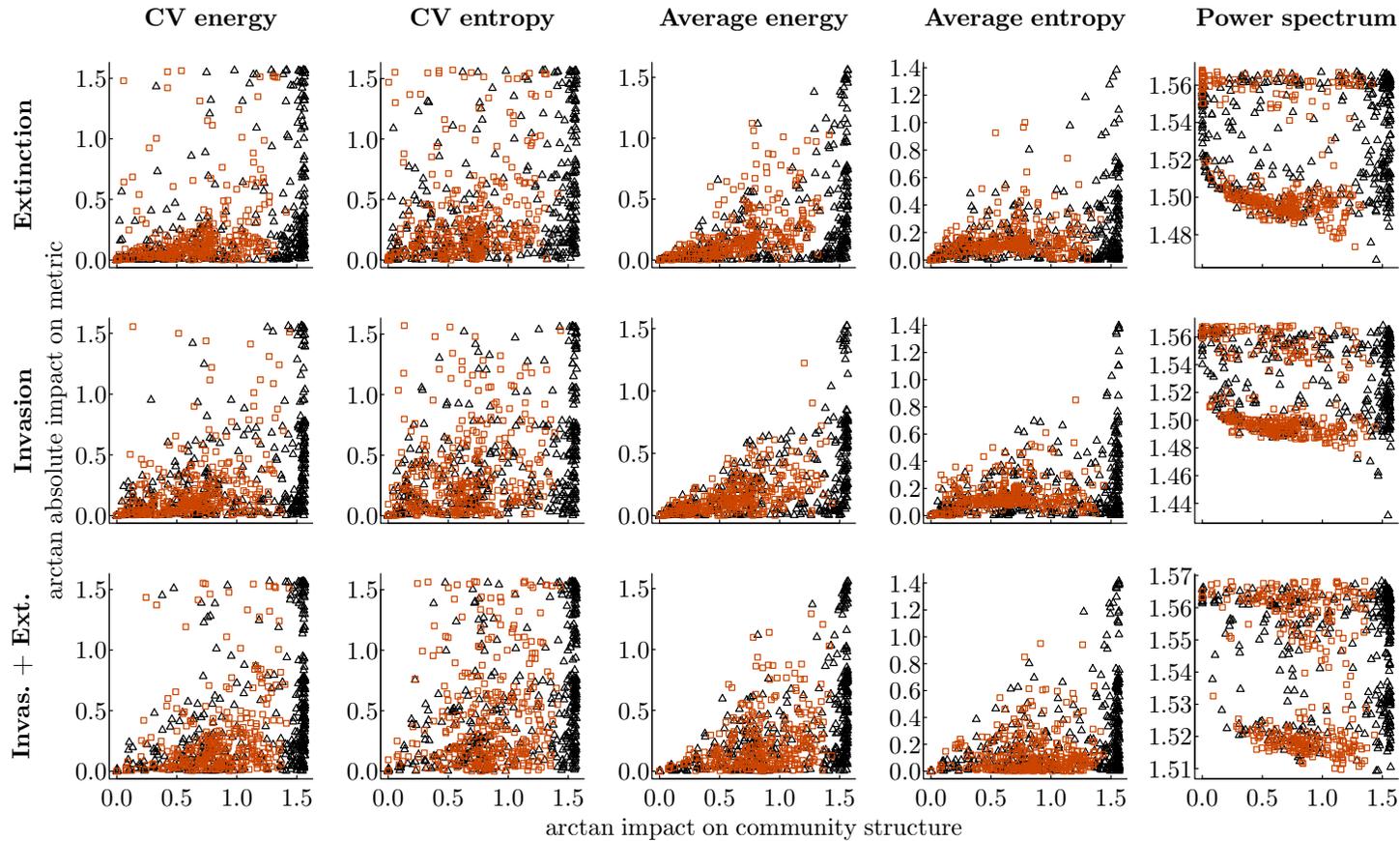
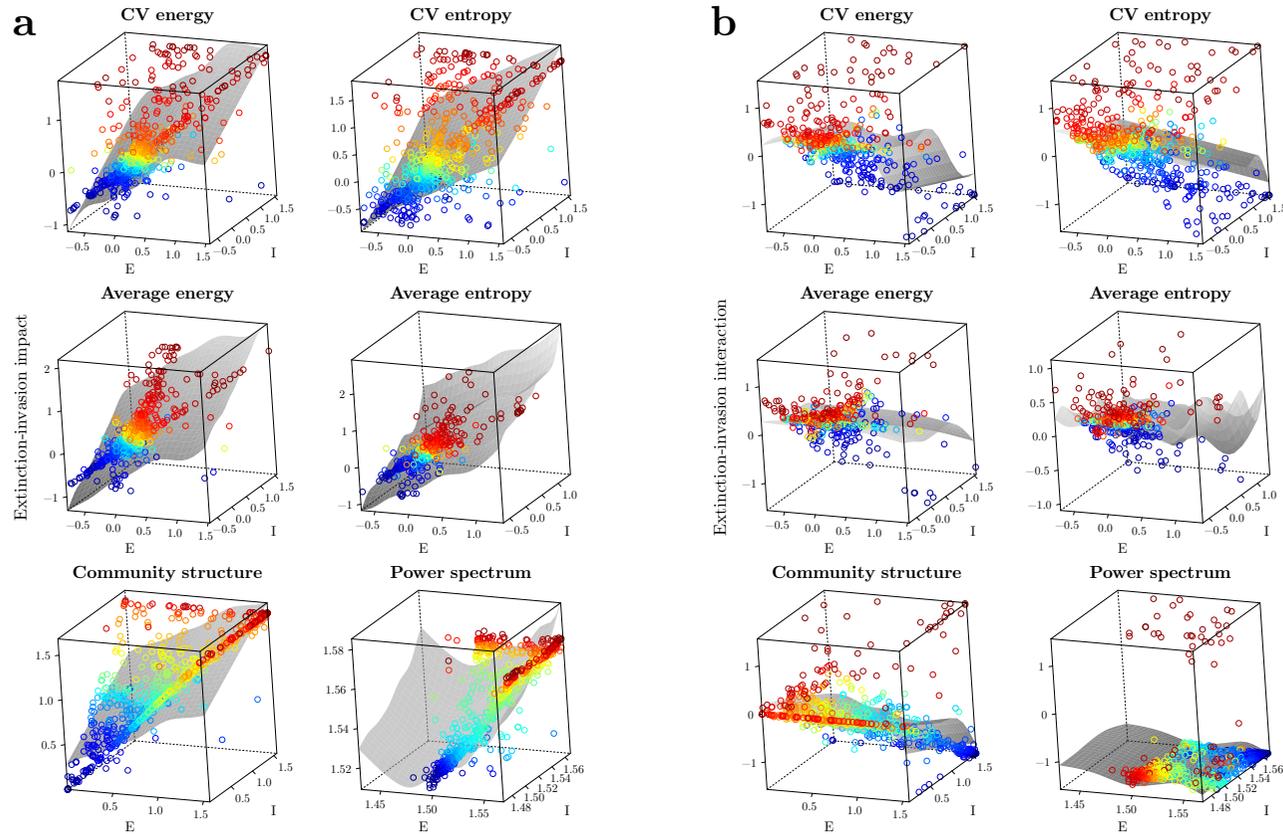


Figure 4.2. Relationships between impacts on community structure and absolute values of impacts on the other ecosystem metrics, pooled across network topologies and noise colours within each of prey-dependent (black triangles) and ratio-dependent (red squares) model types. Apparent bimodality of data points is an artifact of arctangent transformation which facilitates visual comparisons but compresses large values into a small range. Appendix 4.5.2 gives correlations of untransformed data.



Extinction & invasion do not add up

Figure 4.3. Relationships of separate extinction and invasion impacts to (a) extinction-invasion impact and (b) extinction-invasion interaction, pooled across model types and noise colours ($n = 706$), with fitted generalized additive model surface. Axes: E, extinction impact; I, invasion impact; all arctangent transformed for visual interpretability. Data points coloured according to relative extinction-invasion impact, for clarity. Occasional bimodality of data points is an artifact of arctangent transformation that does not affect the statistical analysis. In b, impacts of extinction and invasion are purely additive when extinction-invasion interaction = 0.

Table 4.3. Kendall correlations of separate impacts of extinction and invasion to extinction-invasion impact and to extinction-invasion interaction, pooled across model types and noise colours.

Extinction-invasion...	Ecosystem metric	τ_{ext}	p_{ext}	τ_{inv}	p_{inv}
impact	community structure	0.621	0	0.605	0
	cv energy	0.484	0	0.389	0
	cv entropy	0.42	0	0.388	0
	average energy	0.509	0	0.431	0
	average entropy	0.515	0	0.344	0
	power spectrum	0.547	0	0.558	0
interaction	community structure	-0.488	2.75×10^{-84}	-0.552	3.27×10^{-107}
	cv energy	-0.257	1.78×10^{-24}	-0.17	1.14×10^{-11}
	cv entropy	-0.235	8.51×10^{-21}	-0.282	2.42×10^{-29}
	average energy	-0.0705	0.00505	-0.123	9.66×10^{-7}
	average entropy	-0.0451	0.0726	-0.204	5.32×10^{-16}
	power spectrum	-0.47	3.93×10^{-78}	-0.471	1.89×10^{-78}

Subscripts: $_{\text{ext}}$, extinction; $_{\text{inv}}$, invasion. Sample size $n = 706$, significance level $\alpha = 0.00833$ after Bonferroni correction.

Kendall correlations were calculated for impact of extinction against extinction-invasion impact and against the extinction-invasion interaction, and for impact of invasion against those same two variables ($n = 706$). The analysis was done on data pooled across all model types and noise colours, since there was little qualitative difference between them. Increasing impact of extinction or invasion is strongly associated with increasing extinction-invasion impact (Fig. 4.3a, Table 4.3). The extinction-invasion interaction, however, becomes less additive and, as separate positive extinction and invasion impacts increase, smaller than what it would be if the impacts of extinction and invasion were purely additive (Fig. 4.3b, Table 4.3).

The relationship between extinction impact and absolute reversibility, and between invasion impact and absolute reversibility, are shown in Fig. 4.4. Niche and random network topologies and white and pink noise colours were pooled within each of prey-dependent and ratio-dependent model types (sample sizes: prey-dependent models, 387; ratio-dependent models, 319), since there were no qualitative differences in the data between the pooled categories. All correlations are negative and often weak to moderately strong. Impacts of extinction and invasion are usually more strongly correlated with their respective reversibilities for prey-dependent models than for ratio-dependent models.

Across all topology-dynamics-noise configurations, differences in the outputs of prey- and ratio-dependent models are generally greater than those between different network topologies and noise colours, except for power spectra where niche and random network topologies make the greatest difference (Fig. 4.5; sample sizes: prey-dependent niche, 194; prey-dependent random, 193; ratio-dependent niche, 172; ratio-dependent random, 147). Ratio-dependent models tend to produce less variable impacts, reversibilities and extinction-invasion interactions, except for power spectra. As expected, extinction tends to reduce average energy and entropy while invasion tends to increase them (Fig. 4.5a), and extinction and invasion tend to cancel out each other's effects (in a statistical-distribution context) when combined (comparing Figs. 4.5a and 4.5b). The directionality of energy- and entropy-related impacts, however,

is less symmetric, the upper tails of the distributions tending to be longer than the lower tails for both extinction and invasion (upper rows of Figs. 4.5a and 4.5b). Interestingly, the shapes of distributions are more similar between extinction impact and invasion impact for a given model type than they are across model types within either extinction or invasion (Fig. 4.5a). The extinction-invasion interaction is mostly near zero (i.e. almost purely additive impacts of extinction and invasion) for energy and entropy-related ecosystem metrics, but tends to negative and highly negative for community structure and power spectra respectively, but this is because of the abundance of high extinction-invasion impacts for those metrics.

Figure 4.4 (facing page). Relationship between (a) extinction impact and absolute reversibility and (b) invasion impact and absolute reversibility, pooled across network topologies and noise colours within each of prey-dependent (upper row) and ratio-dependent (lower row) model types. Kendall τ significance level $\alpha = 0.00833$ after Bonferroni correction. Legend: triangles/circles, niche/random network topologies; black/red data points, white/pink noise.

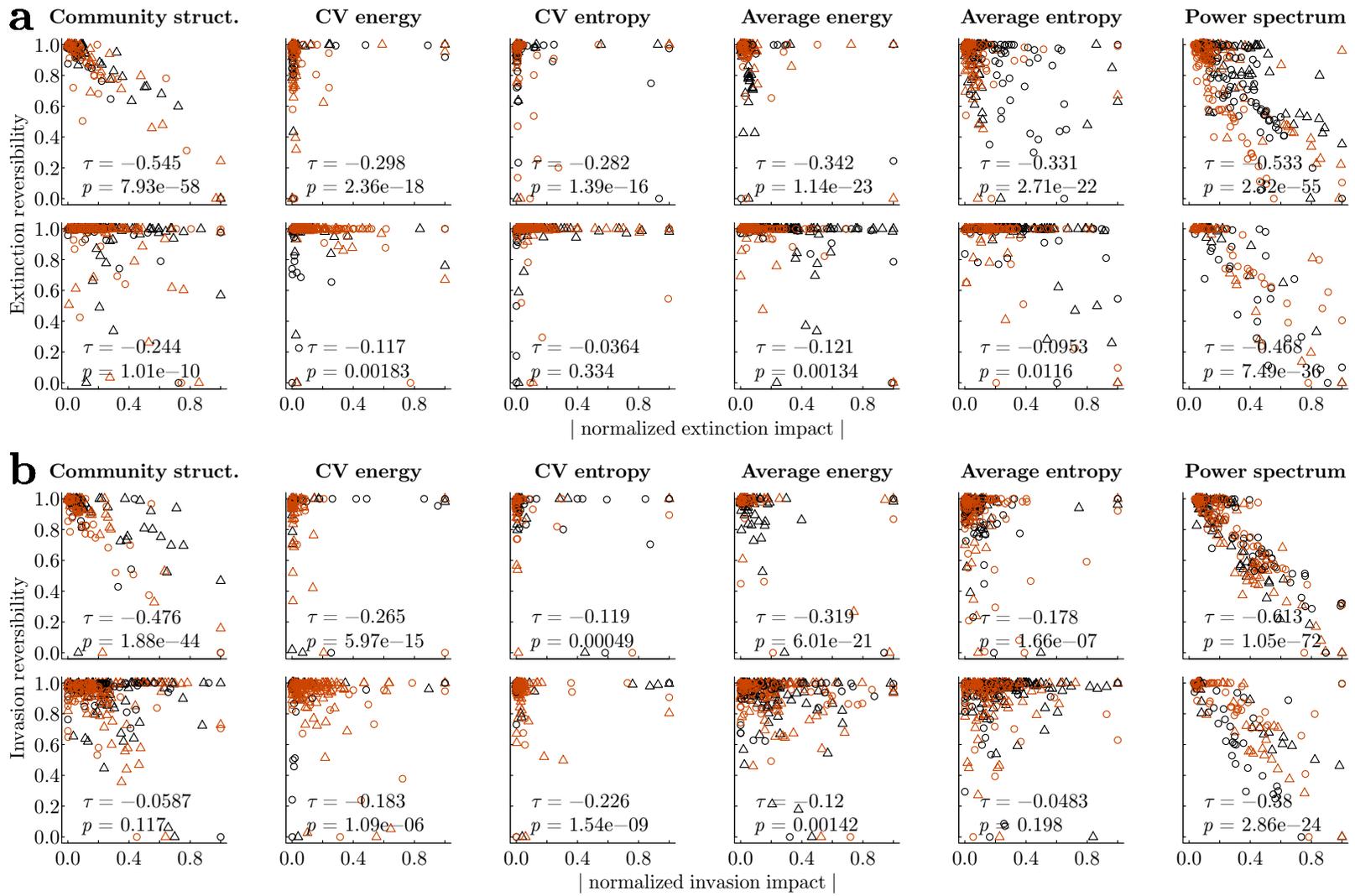
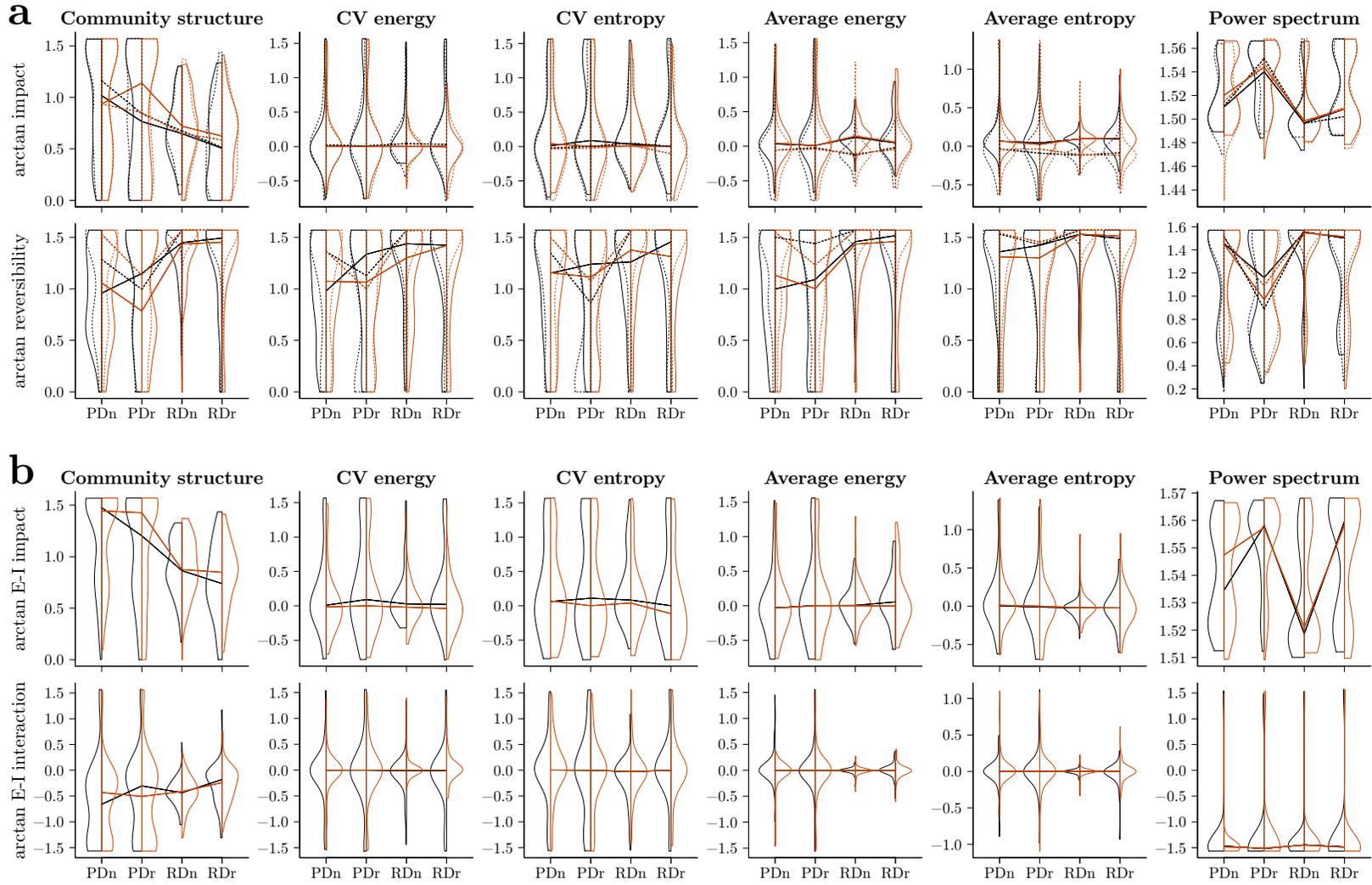


Figure 4.5 (facing page). Effects of model type on (a) the impacts (upper row of a) and relative reversibilities (lower row of a) of extinction (dashed lines) and invasion (solid lines) and (b) the extinction-invasion impact (upper row of b) and extinction-invasion interaction (lower row of b). Black half-violins, white noise; red half-violins, pink noise. Model types: PDn, Prey-Dependent niche model; RDr, Ratio-Dependent random-network model. Violins scaled to constant width and connected at medians. The arctangent transformation produces the artifact of bimodality in some violins, but facilitates visual comparisons. Statistical analyses used untransformed data.



4.4 DISCUSSION

That more dominant species tend to have greater impacts after extinction is not surprising, since one would expect the loss of a dominant species constituting a large proportion of the abundance or biomass to bring a greater change to community structure, system energy and entropy. For extinction-invasion impact, the effect of dominance may have been weakened by the impact of invasion. Interestingly, consistent negative rather than positive correlations of extirpator dominance with changes in power spectra were observed. This may be because dominant extirpators tend to have fewer predators (Appendix 4.5.3a); the extinction of a sparsely linked dominant species may cause less disruption to the overall profile of interacting population and noise cycles. The relationship between extirpator dominance and number of predators was not substantially due to niche model structure and metabolic scaling (Appendix 4.5.3b). Question 55 of SUTHERLAND *et al.* [200] asks, ‘How important are rare species in the functioning of ecological communities?’ These results suggest that rare species may not necessarily be more important than common (dominant) species in the functioning of ecological communities. Rare species may, however, be more prone to total extinction owing to their rarity, and there may be cumulative impacts if multiple rare species are lost concurrently. Where historical data are lacking, it may also be difficult to distinguish between species that are naturally rare and species that are normally common but are rare at sampling time because they are in the process of going extinct.

STRAYER [307] suggested that there does not seem to be a general answer to the question of which invasions will change ecosystem function; my results support this view that the impact of invasion is highly context-dependent. Similarly, insights into Question 50 of SUTHERLAND *et al.* [200]—‘How relevant are assembly rules in a world of biological invasion?’—can be gained from my results in that assembly rules, insofar as the rules relate to the degree of niche overlap of the invasive and native species, may have limited predictive power in invasion given the

multitude of counteracting factors. For example, for invasion success *per se*, it is widely recognized that greater niche overlap may make it harder to invade, but a smaller overlap may mean that the invader is less well-adapted to the ecosystem than the natives and therefore less successful in invasion [328]. This tradeoff may carry over to the invasion impact on the ecosystem as a whole, and be further tempered by other factors. My results support SIMBERLOFF'S [323] prognosis that invasive species management decisions should be considered on a case-by-case basis, and underscore the importance of multi-pronged strategies synthesizing other lines of inquiry as disparate as invasive species distribution modeling [329] and risk and decision analysis [330,331]. Community ecology and network dynamics are essential components of any such strategy, as might be illustrated by a case of unexpected community consequences of a species introduced for biological control [332].

For both extinction and invasion (and the two combined), larger changes in community structure can potentially be accompanied by larger changes in energy- and entropy-related ecosystem metrics, as expected, although large changes in community structure are more likely to accompany small than large changes in the energy- and entropy-related metrics given the distribution of points in Fig. 4.2. Nevertheless, the results imply that if large changes in the variability or magnitude of biomass or overall species evenness are observed in an ecosystem of interest, it may be generally expected that there has been a considerable change in community structure that could potentially translate to changes in various aspects of ecosystem function and ecosystem services.

The extinction, invasion and extinction-invasion impacts on energy- and entropy-related ecosystem metrics are similarly likely to be negative or positive in most cases (Fig. 4.5), suggesting that extinction and invasion can be both beneficial and detrimental in terms of ecosystem function, insofar as high carbon storage (system energy) and high diversity (Shannon entropy) are widely recognized to be of ecological benefit. This outcome supports shifting attitudes towards invasive species partly brought about by a more system-oriented world view, with increasing debate on both

positive and negative impacts at the ecosystem and socioeconomic levels [333–335]. The upper tails of the distributions of those impacts tend to be longer than the lower tails; this is attributed not to any ecological phenomenon but to the measurement of impacts as proportionate change, which sometimes generates large positive values as explained in §4.3.

In most of the models, the magnitude of the impacts on energy- and entropy-related metrics is relatively small, partly due to just a single extirpator or invader. The impacts on community structure and power spectra, however, take on a wider range of magnitudes, probably because these metrics deal with more mechanistic aspects of the ecosystem's behaviour, which can be affected in many qualitatively different ways, rather than the total energy and diversity. In cases where separate impacts of extinction and invasion are high, the extinction-invasion impact increases but the extinction-invasion interaction becomes increasingly less than purely additive. This might be attributable to a kind of system-level 'density dependence' arising from the intrinsic resistance of the system to perturbation, due to reproduction- and mortality-mediated negative feedback loops acting within and across interacting species. Such homeostasis, however, may break down with multiple invasions and extinctions including secondary extinctions, and should not therefore be taken for granted in the maintenance of ecosystem function.

The difficulty of reversing extinctions or invasions with large impacts may be discouraging, but is not unexpected news. In the case of extinction, this may be due to secondary extinction cascades that cannot be reversed by simply reintroducing one species. In the case of invasion, it may be due to invasive species having self-reinforcing effects on ecosystem processes over time [336]. The results suggest that reversal efforts may sometimes not be worth the difficulty, because of either small extinction or invasion impact or low reversibility. One, however, needs to consider reintroduction or eradication on a case-by-case basis, as the desired end result need not be identical to the original state, and there have been spectacular success stories in wolf reintroduction [337] and rat eradication [338]. Further research in simultaneous extinction and invasion and their

reversibilities will also help in reconciling the sometimes conflicting goals of endangered species management and invasive species eradication [339]. It has also been reported that complex interactions among multiple invading species can affect invasion impact and reversibility on native species [340]; this kind of approach could be extended to account for network structure and dynamics.

Differences in behaviour between prey- and ratio-dependent models tend to be more pronounced than differences in topology or even whether extinction or invasion is involved. If niche models are considered as much more appropriate than random networks, then perhaps more attention should correspondingly be paid to whether prey or ratio dependence is more ecologically appropriate. The proportionate fluctuations of predators and prey that characterize ratio dependence may be responsible for the differences from prey-dependent models observed in this study, such as smaller variability in model behaviour across models of the same type of dependence. This recalls the long-debated question as to whether prey- or ratio-dependent models better represent biomass distributions in the real world, and underscores the need to ‘get it right’ in predictive models of specific systems.

The median extinction, invasion and extinction-invasion impacts on power spectra are considerably higher for models with random topology than those with niche topology (Fig. 4.5). This is possibly because random networks are less hierarchical and less nested than niche-structured networks; when one perturbs a niche model, it is more likely that there are surviving species more similar to the extirpator and/or invader to maintain the periodicity structure than when one perturbs a random model. Random networks also translate to more trophic complementarity (sensu POISOT *et al.* [341]) in the network overall; this implies that trophic complementarity is potentially a predictor of the structure of community periodicity, in addition to the other ecosystem functions studied by POISOT *et al.* [341]. Nevertheless, looking at the rest of the ecosystem metrics other than power spectra, it appears that communities with interaction topologies that do not conform to the traditional niche model will not

behave in radically different ways from those that obey niche rules; indeed, SOLÉ & VALVERDE [15] regarded food webs in general as having relatively high randomness.

At the same time as general relationships were found across contingencies of model structure and parameter values,⁷ the considerable variation in model behaviour reflects real-world ecological variation and context dependence of extinction and invasion impacts [307, 342], potentially across both aquatic and terrestrial ecosystems. Future work along the lines of this study will provide further insights into how we might influence ecological network dynamics through selection of species (nodes) to eradicate or reintroduce for increased recovery and resilience sensu CORNELIUS *et al.* [343], perhaps using techniques inspired by control theory [344] and appreciating that overall network topology may be more important than individual node degree as a determinant of resilience [345]. Also worthy of further inquiry is the relatively little known phenomenon of degeneracy [77], in which species differing in traits can perform similar functions, potentially mediating the impacts of extinction or invasion in unexpected ways.

Finally, it may also be mutually beneficial for different disciplines to understand the similarities and differences between ecological and other kinds of networks in their responses to perturbations [346] and to control measures [347–350]. At the same time, it is important to bear in mind that the time-irreversibility of complex dynamical processes [8] precludes perfect reversal of disturbances. As ecology matures into a predictive discipline alongside the other sciences, the systems approach offers rich prospects for exciting new fundamental research and more effective environmental management.

⁷ The similar outcome across noise colours does not contradict Chapter 3, because the concern here is with the impacts of invasion and extinction and not with the ‘day-to-day’ behaviour of the system per se. Modeling noise correctly for any given system is still important if more specific predictions are desired.

4.5 APPENDIX

4.5.1 REGRESSION TREES

Root predictors that explain the largest proportions of deviances in extinction and invasion impacts, extinction-invasion interaction and relative reversibilities, for different model types, noise colours and ecosystem metrics. See Table 4.1 in main text for key to predictor abbreviations.

Extinction & invasion do not add up

Predictors of extinction impact.

Ecosystem metric	Model type	Noise	Root predictor
community structure	prey-dependent niche	white	dominance
		pink	extsim
	prey-dependent random	white	extbasalnon
		pink	dominance
	ratio-dependent niche	white	epred
		pink	extsim
	ratio-dependent random	white	dominance
		pink	dominance
cv energy	prey-dependent niche	white	eprey
		pink	dominance
	prey-dependent random	white	elink
		pink	extniche
	ratio-dependent niche	white	dominance
		pink	extbasalnon
	ratio-dependent random	white	elink
		pink	dominance
cv entropy	prey-dependent niche	white	eprey
		pink	eprey
	prey-dependent random	white	extniche
		pink	extniche
	ratio-dependent niche	white	extsim
		pink	emut
	ratio-dependent random	white	dominance
		pink	extniche
average energy	prey-dependent niche	white	eprey
		pink	extniche
	prey-dependent random	white	elink
		pink	extsim
	ratio-dependent niche	white	extbasalnon
		pink	dominance
	ratio-dependent random	white	dominance
		pink	extbasalnon
average entropy	prey-dependent niche	white	dominance
		pink	dominance
	prey-dependent random	white	dominance
		pink	dominance
	ratio-dependent niche	white	eprey
		pink	dominance
	ratio-dependent random	white	dominance
		pink	dominance
power spectrum	prey-dependent niche	white	dominance
		pink	dominance
	prey-dependent random	white	dominance
		pink	dominance
	ratio-dependent niche	white	extniche
		pink	dominance
	ratio-dependent random	white	dominance
		pink	dominance

Predictors of invasion impact.

Ecosystem metric	Model type	Noise	Root predictor
community structure	prey-dependent niche	white	invsim
		pink	ilink
	prey-dependent random	white	invbasalnon
		pink	imut
	ratio-dependent niche	white	ipred
		pink	ipred
	ratio-dependent random	white	ipred
		pink	invbasalnon
cv energy	prey-dependent niche	white	invniche
		pink	invsim
	prey-dependent random	white	invniche
		pink	ilink
	ratio-dependent niche	white	invsim
		pink	iprey
	ratio-dependent random	white	invsim
		pink	imut
cv entropy	prey-dependent niche	white	invniche
		pink	invsim
	prey-dependent random	white	invniche
		pink	invniche
	ratio-dependent niche	white	ipred
		pink	iprey
	ratio-dependent random	white	invniche
		pink	imut
average energy	prey-dependent niche	white	invniche
		pink	imut
	prey-dependent random	white	imut
		pink	ipred
	ratio-dependent niche	white	iprey
		pink	invbasalnon
	ratio-dependent random	white	invbasalnon
		pink	invbasalnon
average entropy	prey-dependent niche	white	invniche
		pink	invsim
	prey-dependent random	white	iprey
		pink	invniche
	ratio-dependent niche	white	invniche
		pink	iprey
	ratio-dependent random	white	invbasalnon
		pink	invbasalnon
power spectrum	prey-dependent niche	white	invniche
		pink	invbasalnon
	prey-dependent random	white	ipred
		pink	invsim
	ratio-dependent niche	white	ipred
		pink	invniche
	ratio-dependent random	white	ipred
		pink	ipred

Extinction & invasion do not add up

Predictors of extinction reversibility.

Ecosystem metric	Model type	Noise	Root predictor
community structure	prey-dependent niche	white	elink
		pink	eprey
	prey-dependent random	white	dominance
		pink	extsim
	ratio-dependent niche	white	dominance
		pink	dominance
	ratio-dependent random	white	dominance
		pink	extsim
cv energy	prey-dependent niche	white	elink
		pink	eprey
	prey-dependent random	white	dominance
		pink	extsim
	ratio-dependent niche	white	extsim
		pink	elink
	ratio-dependent random	white	dominance
		pink	extniche
cv entropy	prey-dependent niche	white	elink
		pink	eprey
	prey-dependent random	white	dominance
		pink	extsim
	ratio-dependent niche	white	extsim
		pink	elink
	ratio-dependent random	white	dominance
		pink	epred
average energy	prey-dependent niche	white	elink
		pink	eprey
	prey-dependent random	white	elink
		pink	extsim
	ratio-dependent niche	white	dominance
		pink	elink
	ratio-dependent random	white	dominance
		pink	dominance
average entropy	prey-dependent niche	white	elink
		pink	eprey
	prey-dependent random	white	dominance
		pink	extsim
	ratio-dependent niche	white	dominance
		pink	dominance
	ratio-dependent random	white	dominance
		pink	epred
power spectrum	prey-dependent niche	white	elink
		pink	eprey
	prey-dependent random	white	elink
		pink	extsim
	ratio-dependent niche	white	dominance
		pink	dominance
	ratio-dependent random	white	dominance
		pink	extsim

Predictors of invasion reversibility.

Ecosystem metric	Model type	Noise	Root predictor
community structure	prey-dependent niche	white	invsim
		pink	iprey
	prey-dependent random	white	ilink
		pink	invsim
	ratio-dependent niche	white	invniche
		pink	invsim
	ratio-dependent random	white	iprey
		pink	ipred
cv energy	prey-dependent niche	white	invsim
		pink	iprey
	prey-dependent random	white	ilink
		pink	invsim
	ratio-dependent niche	white	invniche
		pink	invniche
	ratio-dependent random	white	ipred
		pink	invniche
cv entropy	prey-dependent niche	white	invniche
		pink	iprey
	prey-dependent random	white	ilink
		pink	invsim
	ratio-dependent niche	white	invniche
		pink	invniche
	ratio-dependent random	white	imut
		pink	iprey
average energy	prey-dependent niche	white	invniche
		pink	iprey
	prey-dependent random	white	ilink
		pink	invniche
	ratio-dependent niche	white	invniche
		pink	invniche
	ratio-dependent random	white	ipred
		pink	invniche
average entropy	prey-dependent niche	white	invsim
		pink	iprey
	prey-dependent random	white	ilink
		pink	invniche
	ratio-dependent niche	white	invniche
		pink	invniche
	ratio-dependent random	white	ipred
		pink	invniche
power spectrum	prey-dependent niche	white	invniche
		pink	iprey
	prey-dependent random	white	ilink
		pink	imut
	ratio-dependent niche	white	invniche
		pink	invsim
	ratio-dependent random	white	ipred
		pink	ilink

Extinction & invasion do not add up

Predictors of extinction-invasion impact.

Ecosystem metric	Model type	Noise	Root predictor
community structure	prey-dependent niche	white	extsim
		pink	trocon
	prey-dependent random	white	iesim
		pink	dominance
	ratio-dependent niche	white	trocon
		pink	ipred
	ratio-dependent random	white	trocon
		pink	trocon
cv energy	prey-dependent niche	white	eprey
		pink	extsim
	prey-dependent random	white	trocon
		pink	extsim
	ratio-dependent niche	white	invsim
		pink	dominance
	ratio-dependent random	white	invsim
		pink	imut
cv entropy	prey-dependent niche	white	eprey
		pink	eprey
	prey-dependent random	white	invsim
		pink	extsim
	ratio-dependent niche	white	extniche
		pink	dominance
	ratio-dependent random	white	invsim
		pink	epred
average energy	prey-dependent niche	white	eprey
		pink	imut
	prey-dependent random	white	iesim
		pink	trocon
	ratio-dependent niche	white	extbasalnon
		pink	dominance
	ratio-dependent random	white	invbasalnon
		pink	dominance
average entropy	prey-dependent niche	white	dominance
		pink	dominance
	prey-dependent random	white	dominance
		pink	dominance
	ratio-dependent niche	white	dominance
		pink	dominance
	ratio-dependent random	white	dominance
		pink	dominance
power spectrum	prey-dependent niche	white	dominance
		pink	dominance
	prey-dependent random	white	dominance
		pink	dominance
	ratio-dependent niche	white	extniche
		pink	invniche
	ratio-dependent random	white	dominance
		pink	dominance

Predictors of extinction-invasion interaction.

Ecosystem metric	Model type	Noise	Root predictor
community structure	prey-dependent niche	white	ipred
		pink	extsim
	prey-dependent random	white	trocon
		pink	extniche
	ratio-dependent niche	white	trocon
		pink	ipred
	ratio-dependent random	white	dominance
		pink	epred
cv energy	prey-dependent niche	white	dominance
		pink	eprey
	prey-dependent random	white	invniche
		pink	extniche
	ratio-dependent niche	white	ipred
		pink	dominance
	ratio-dependent random	white	dominance
		pink	imut
cv entropy	prey-dependent niche	white	dominance
		pink	eprey
	prey-dependent random	white	invniche
		pink	extniche
	ratio-dependent niche	white	ipred
		pink	dominance
	ratio-dependent random	white	dominance
		pink	invsim
average energy	prey-dependent niche	white	emut
		pink	epred
	prey-dependent random	white	ilink
		pink	extsim
	ratio-dependent niche	white	invniche
		pink	extsim
	ratio-dependent random	white	mutecon
		pink	invniche
average entropy	prey-dependent niche	white	dominance
		pink	dominance
	prey-dependent random	white	imut
		pink	trocon
	ratio-dependent niche	white	imut
		pink	invniche
	ratio-dependent random	white	mutecon
		pink	dominance
power spectrum	prey-dependent niche	white	dominance
		pink	dominance
	prey-dependent random	white	dominance
		pink	dominance
	ratio-dependent niche	white	emut
		pink	invniche
	ratio-dependent random	white	dominance
		pink	dominance

4.5.2 EFFECTS OF COMMUNITY STRUCTURE

Kendall τ correlations between impacts on community structure and impacts on the other ecosystem metrics. Response variables were converted to absolute values before statistical testing. Asterisked parentheses $*(*)$ indicate $p < \alpha$ where $\alpha = 0.01$ after Bonferroni correction for five ecosystem metrics.

EXTINCTION IMPACT

Model type	Noise	cv.energy	cv.entropy	av.energy	av.entropy	powspec
prey-dep. niche	white	*(0.412)*	*(0.425)*	*(0.538)*	*(0.422)*	-0.0653
	pink	*(0.401)*	*(0.304)*	*(0.489)*	*(0.32)*	-0.0781
prey-dep. random	white	*(0.517)*	*(0.469)*	*(0.607)*	*(0.419)*	*(-0.191)*
	pink	*(0.439)*	*(0.378)*	*(0.564)*	*(0.359)*	-0.149
ratio-dep. niche	white	*(0.35)*	*(0.26)*	*(0.399)*	0.0812	-0.176
	pink	*(0.271)*	0.111	*(0.447)*	0.171	*(-0.206)*
ratio-dep. random	white	*(0.585)*	*(0.367)*	*(0.53)*	*(0.347)*	*(-0.355)*
	pink	*(0.247)*	0.159	*(0.5)*	0.182	*(-0.295)*

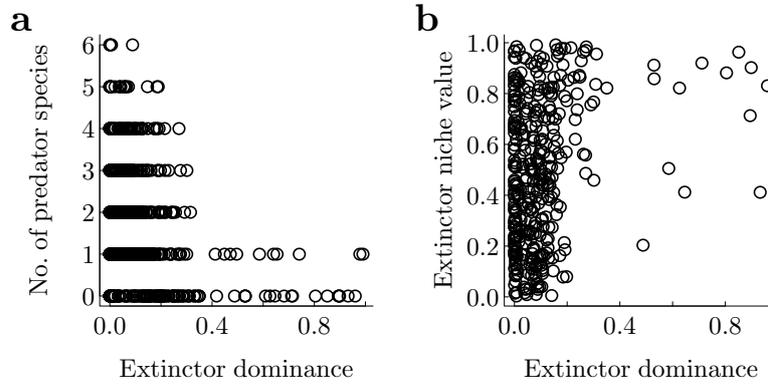
INVASION IMPACT

Model type	Noise	cv.energy	cv.entropy	av.energy	av.entropy	powspec
prey-dep. niche	white	*(0.437)*	*(0.379)*	*(0.424)*	*(0.234)*	0.0855
	pink	*(0.409)*	*(0.298)*	*(0.453)*	*(0.18)*	0.107
prey-dep. random	white	*(0.533)*	*(0.489)*	*(0.644)*	*(0.495)*	0.0421
	pink	*(0.461)*	*(0.454)*	*(0.54)*	*(0.408)*	0.0481
ratio-dep. niche	white	*(0.297)*	*(0.189)*	*(0.484)*	0.117	*(-0.309)*
	pink	*(0.211)*	0.127	*(0.367)*	0.028	*(-0.233)*
ratio-dep. random	white	*(0.569)*	*(0.498)*	*(0.659)*	*(0.423)*	*(-0.342)*
	pink	*(0.495)*	*(0.357)*	*(0.701)*	*(0.55)*	*(-0.225)*

EXTINCTION-INVASION IMPACT

Model type	Noise	cv.energy	cv.entropy	av.energy	av.entropy	powspec
prey-dep. niche	white	*(0.396)*	*(0.429)*	*(0.462)*	*(0.383)*	0.07
	pink	*(0.309)*	*(0.204)*	*(0.35)*	*(0.226)*	0.0667
prey-dep. random	white	*(0.389)*	*(0.291)*	*(0.474)*	*(0.272)*	0.00789
	pink	*(0.305)*	*(0.372)*	*(0.463)*	*(0.364)*	-0.105
ratio-dep. niche	white	*(0.279)*	*(0.257)*	*(0.22)*	0.145	-0.113
	pink	0.133	-0.00728	0.137	0.121	-0.188
ratio-dep. random	white	*(0.387)*	*(0.246)*	*(0.336)*	0.0931	-0.129
	pink	*(0.226)*	0.0544	*(0.341)*	0.0739	-0.0595

4.5.3 EFFECTS OF EXTINCTOR DOMINANCE



Relationships between extirpator dominance and (a) number of predators and (b) niche value. Pooled across all models (a); pooled across niche-topology models (b).

5 COLLECTIVE EFFECT OF INTERACTION MODIFICATIONS

Abstract. Interaction modification (IM), where one species modifies the strength of the density-mediated direct interaction between two other species, is an important ecological process, but little is known about the collective effect of multiple IM on overall community dynamics. I use stochastic bioenergetic modeling of ecological networks with different network topologies, functional responses and parameter values, to investigate the effects of IM connectance and IM strength on ecosystem properties including the evenness of species abundances and variability of system biomass. It was found that the maximum system biomass observed across the model systems increased with IM connectance and strength when the models had nonrandom topology and prey-dependent functional responses as opposed to random topology and ratio-dependent responses. The maximum observed species evenness increased with IM strength but decreased with increasing IM connectance, when all modifications were negative. These findings underscore the importance of accounting for multiple IM across the community for understanding complex community dynamics.

5.1 INTRODUCTION

Indirect effects are widely recognized as important drivers of the dynamics of ecological communities, and are a subject of active empirical and theoretical research [40,351,352]. There are two main types of indirect effects, acting via interaction chains and interaction modifications [353]. In an interaction chain, one species can indirectly affect the population density of a target species via density-mediated interactions with one or more intermediary species, such as in exploitative competition and trophic cascades [354], rather than direct interaction. On the other hand, an interaction modification [355], also known by the jargonologies of ‘trait-mediated indirect interaction’ [356], ‘non-consumptive effect’ [357] and ‘rheagogy’ [358], refers fundamentally to one species affecting the target

species by modulating the latter's interactions with other species. Both types of indirect effects have been found in both empirical and theoretical studies to vary widely in their impacts on the stability and relative species abundances of ecological communities, depending on the relative strengths of direct and indirect effects and the quantitative balance between positive and negative feedback loops in ecological networks [354, 359]. This chapter focuses on interaction modification (IM), which is also a useful implicit representation of behaviour [352].

The prevalence of IM in natural communities has been recognized in recent years. For example, predator modification of prey grazing has been shown to be a mechanism accounting for much of the observed variation in the strength of trophic cascades [360], and IM has been suggested as an alternative way to look at host-parasite interactions, where the parasite affects the feeding efficiency of the host [156]. Some mutualisms commonly formalized as pairwise interactions are actually part of tripartite IM, such as bipartite networks of ant-plant mutualisms where ants mediate plant susceptibility to herbivory, or fish protected from predation while living amidst and contributing nutrients to sessile marine organisms [163, 168]. WERNER & PEACOR [356] reviewed the mechanistic basis and empirical evidence for the presence of IM in both aquatic and terrestrial ecosystems and found that IM were widespread in ecosystems and often as strong as or stronger than density-mediated effects.

The importance of embracing IM in understanding the response of real-world communities to global change has recently been highlighted [342], especially since IM may play a role in engendering alternative stable states [355]. BOLKER *et al.* [361] found that most of the early theoretical work on the effects of IM on community dynamics pertained mostly to the mathematical stability of simple communities and that actual dynamics depended on details that were rarely measured empirically, such as functional responses. An ecosystem-level understanding also requires a grasp of the collective effects of the multiple IM present in a given community, but most research has involved analysis of one IM in a particular community (e.g. HSIEH & PERFECTO [351]). There is little knowledge on either

the overall topology and distribution of strengths of IM in the entire community, or how multiple IM collectively affect ecosystem properties. Multiple IM present in a community may interact antagonistically with one another to reduce the total IM effect on a given direct interaction, but little is known about the detailed relationships [40]. There is also evidence for cascading IM, where a species modifies the feeding activities of another species that, in turn, modifies the density-mediated direct interaction between yet another two species [362], but its implications at the ecosystem level are unknown.

Theoretical studies have begun to show that incorporating IM can have a range of ecosystem effects. In models with four trophic levels, the presence of positive IM gave rise to increased efficiency of abiotic nutrient use [358]. GOUDARD & LOREAU [251] showed that greater connectance or magnitude of IM in interaction web models with three distinct trophic levels tended to reduce species richness, biomass and production. More recently, KAMRAN-DISFANI & GOLUBSKI [352] found that different kinds of IM-related adaptive behaviour can either facilitate or inhibit the propagation of disturbances through food webs with three or four distinct trophic levels and that the effects also depended on food web structure. Although they examined each behaviour separately, they proposed that future models should incorporate multiple types of IM (representing both foraging and defence) simultaneously. The incorporation of IM in models of entire ecological communities is still in its infancy; most bioenergetic models of food webs, which represent the state of the art in dynamic community modeling, do not incorporate IM. Models that have incorporated IM are often simplified in terms of network topology, such as having a small number of trophic levels with no omnivory or looping [251, 352].

I investigate the collective effects of different degrees of IM on various ecosystem-level properties of bioenergetic ecological network models with realistic network structure and metabolically scaled community dynamics. I compare the responses of models with random and nonrandom network topologies and also with prey- and ratio-dependent functional responses,

while incorporating realistic partial synchrony of species responses to pink environmental noise. A wide range of ecologically plausible parameter values are explored. This approach aims to clarify how IM may influence the macroscopic properties of complex ecological communities in noisy real-world environments, with potential implications for their predictive modeling and management.

5.2 METHODS

Models were based on the specifications in Chapter 2 and categorized into four possible configurations of trophic network topology and functional response: (1) topology based on the niche model of food webs combined with prey-dependent consumer-resource functional responses, (2) random topology with prey dependence, (3) niche topology with ratio dependence and (4) random topology with ratio dependence. All networks comprised 25 species. Parasitism and direct basal competition were omitted for comparability with random-topology models. Pink environmental noise with partial synchrony of species responses (§2.3) was used, as this was considered the most realistic.

The prey-dependent consumer-resource functional response was modified from Eqn. 2.2a following the IM implementation of GOUDARD & LOREAU [251]) and is given by

$$\Phi_{i,j} = \frac{M_{i,j}\omega_{i,j}E_j^h}{0.5^h + \sum_{k \in \text{resources}} M_{i,k}\omega_{i,k}E_k^h} \quad (5.1)$$

with resource preference ω and Hill exponent h as before. The additional term M is defined as

$$M_{i,j} = \prod_{k=1}^S (1 + E_k)^{\delta_{i,j,k}}, \quad (5.2)$$

being the total effect on the interaction between species i and j caused by all species that modify that interaction, δ being the strength of interaction modification by a given species k [251]. This formulation of

IM satisfies basic ecological requirements [251], such as increasing with the modifier species' biomass, having no effect when the biomass is zero, and giving the same direction of energy flow regardless of the sign of the modification. The corresponding ratio-dependent functional response is given by

$$\Phi_{i,j} = \frac{M_{i,j}\omega_{i,j}(E_j/E_i)^h}{1^h + \sum_{k \in \text{resources}} M_{i,k}\omega_{i,k}(E_k/E_i)^h}. \quad (5.3)$$

Although IM, as implemented by GOUDARD & LOREAU [251], can be both antagonistic and facilitative, it is still important to retain in the model facilitative interactions that depend directly on the states of the interacting species, as this is fundamentally different from IM [353]. KÉFI *et al.* [41] recommended having both of them in dynamical models of ecological networks.

There is little empirical knowledge of real topologies of IM in ecological networks. The topology of IM across the network was therefore assigned randomly; any type of species could influence the interaction between one or more species pairs of any type, representing all possible types of adaptive behaviour—foraging, defence or otherwise (see DAMBACHER & RAMOS-JILIBERTO [355] p. 231). Furthermore, a modifier species can concurrently interact directly with one or both of the species whose mutual interaction it modifies (see DE ROODE *et al.* [363] for an empirical example). Cannibalistic links were excluded from IM.

IM connectance is defined in this study as GOUDARD & LOREAU's 'non-trophic connectance' [251]: the number of realized interaction modifications divided by the total number of possible interaction modifications, where number of possible modifications is the total number of species multiplied by the number of trophic links, minus two per link to account for the fact that the two species interacting via a given link cannot modify their own interaction. The IM connectance was varied from 0 to 1 [251] in increments of 0.1, and the calculated number of IM links was rounded to the nearest integer. I examined the effects of magnitude and spread

of IM strengths within each level of IM connectance. Two separate simulation experiments were conducted, one looking at different range sizes (hereafter ‘spread’) of IM strengths around mean 0, the other looking at different magnitudes of negative IM strengths. In the first experiment, δ was drawn from a uniform distribution of mean 0 and range size from $[-0.1, 0.1]$ to $[-0.5, 0.5]$ in increments of 0.1 on each side of the mean (GOUDARD & LOREAU [251] used $[-0.2, 0.2]$). In the second experiment, δ was drawn from a uniform distribution of range $[-0.5, -0.4]$ to $[-0.1, 0.0]$ in increments of 0.1. Positive magnitudes were not used because they were often found to give ecologically unrealistic behaviour, with species undergoing ‘runaway’ population growth to extreme values. For both experiments, a set of 100 control simulations was done with no IM.

For each combination of model configuration, IM connectance and IM strength, 100 independent model realizations and simulations were executed. The models were simulated for 20000 time steps, and time steps 10001 to 20000 were extracted for analysis, having allowed initial transients to pass and all species to either reach steady state or be close to steady state. Pilot simulations indicated that the extracted time window encompassed all the main features and periodicities of the stochastic behaviour.

Four ecosystem metrics were measured from the community time series as response variables: the means and standard deviations (SD) of system energy and entropy over time. Although a measure of the effective number of species [273], the entropy reduces here to a measure of species evenness, since the total number of species is constant in this study. Unlike previous chapters, the coefficients of variation were not extracted here, because I wished to distinguish between systems with high mean and variability and those with low mean and low variability, both of which would result in similar coefficients of variation. In addition to looking at the energy and entropy metrics individually, I also examined via the evenness-variability (mean entropy-SD energy) relationship, which is one way of looking at the diversity-stability relationship. Higher variability is interpreted as lower stability.

5.3 RESULTS

Simulations were discarded where extreme species behaviour resulted in computational infinity values caused by high positive IM strength (also responsible for a few very large data points discussed below), and occasionally where negative species states were produced due to the noise terms and intrinsic numerical integration errors. The sample size of each treatment ranged from 97 to 100. Overall, there was little difference between the control simulations with no IM and those with the lowest connectance and lowest spread and magnitude of IM , for all of the response variables; the control experiment is therefore omitted from the analysis.

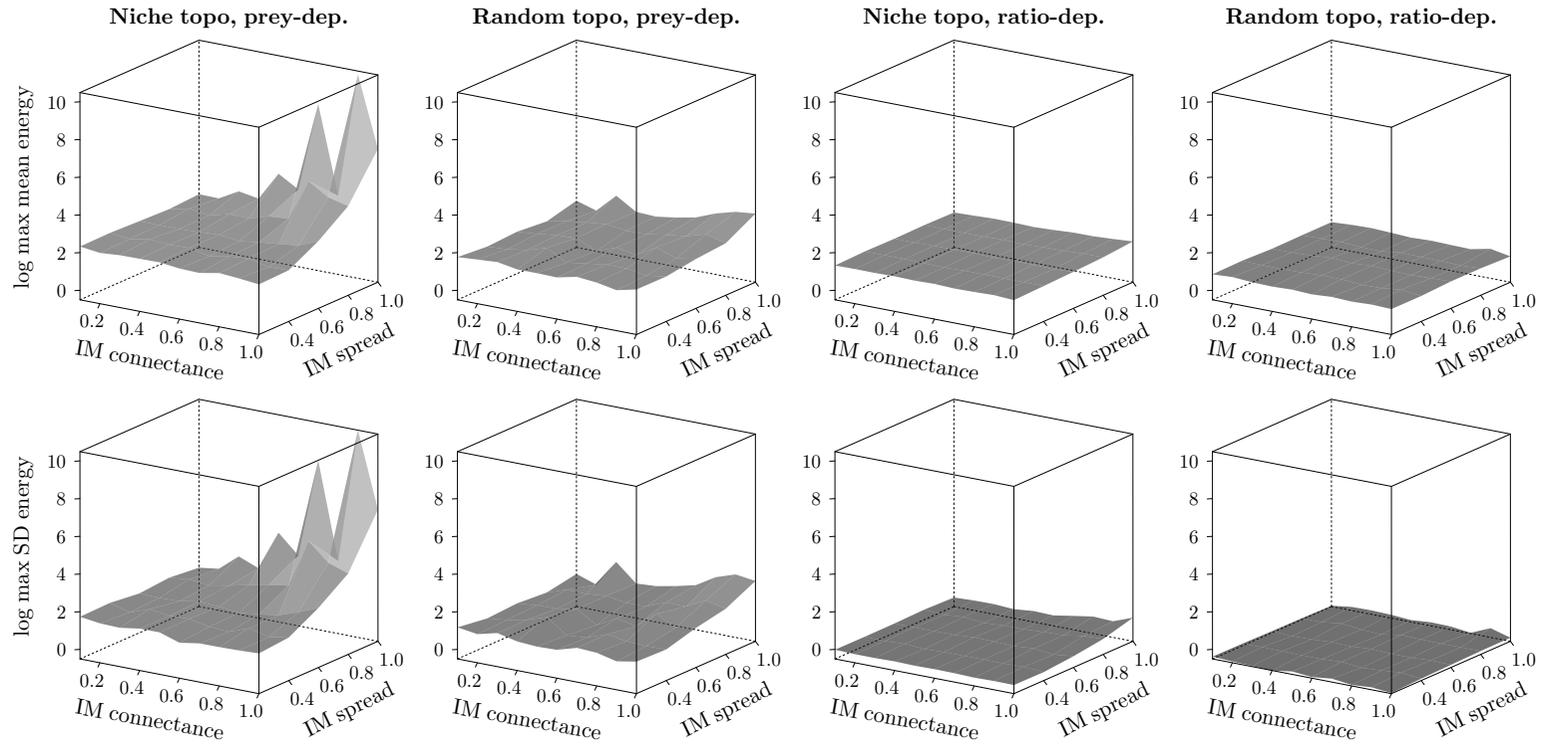


Figure 5.1. Effect of IM connectance and IM spread on maximum observed means (upper row) and SD (lower row) of system energy. The surface vertex at each connectance-spread setting denotes the mean response of the models with the highest 5% of response values among about 100 independent replicate models with the given connectance and spread. The four main model configurations are segregated by column.

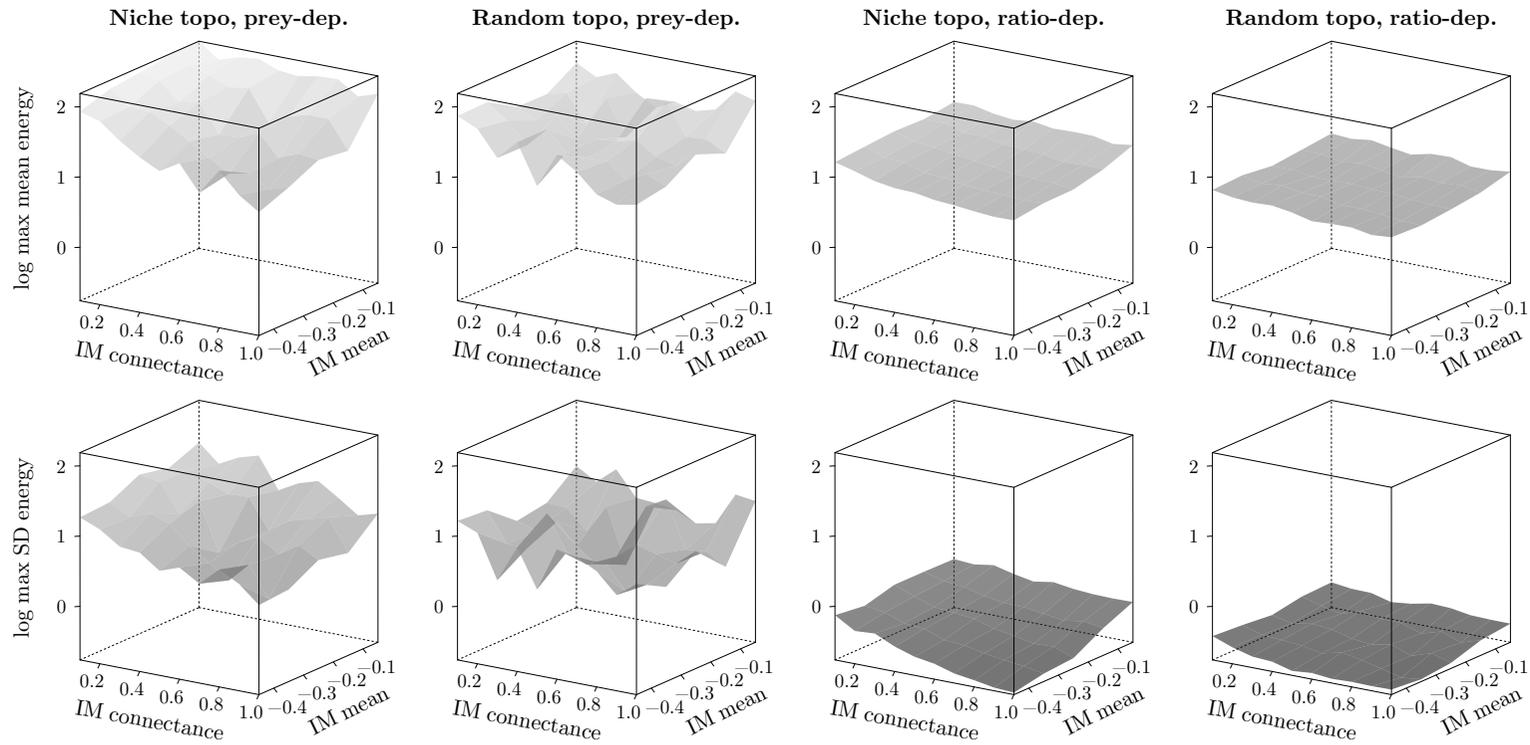


Figure 5.2. Effect of IM connectance and mean IM magnitude on maximum observed means (upper row) and SD (lower row) of system energy. The surface vertex at each IM connectance-mean setting denotes the mean response of the models with the highest 5% of response values among about 100 independent replicate models with the given IM connectance and IM mean. The four main model configurations are segregated by column.

In the ‘spread’ experiment where both positive and negative IM are present, the maximum mean energy over time, as observed across all models, increases dramatically with both IM connectance and strength for niche-topology prey-dependent models (Fig. 5.1, note log-transformed data), while the other three model configurations exhibit much less change, if at all. All model configurations show limited influence by all-negative IM (Fig. 5.2). In both experiments, the minimum observed energy changes much more slowly, if at all (Figs. 5.5, 5.6 in Appendix 5.5.1). The SD of system energy over time also increases with IM connectance and strength for niche-topology prey-dependent models (Figs. 5.1, 5.2). Ratio-dependent models also have lower maximum observed mean and SD energy, and are appreciably less variable in these maxima, across IM connectances and strengths compared to prey-dependent models (Figs. 5.1, 5.2). The mean and SD of system energy are strongly positively correlated across the board (Fig. 5.7 in Appendix 5.5.1) as both are caused by high production rates leading to greater tendencies of cycles of population overshoot and collapse.

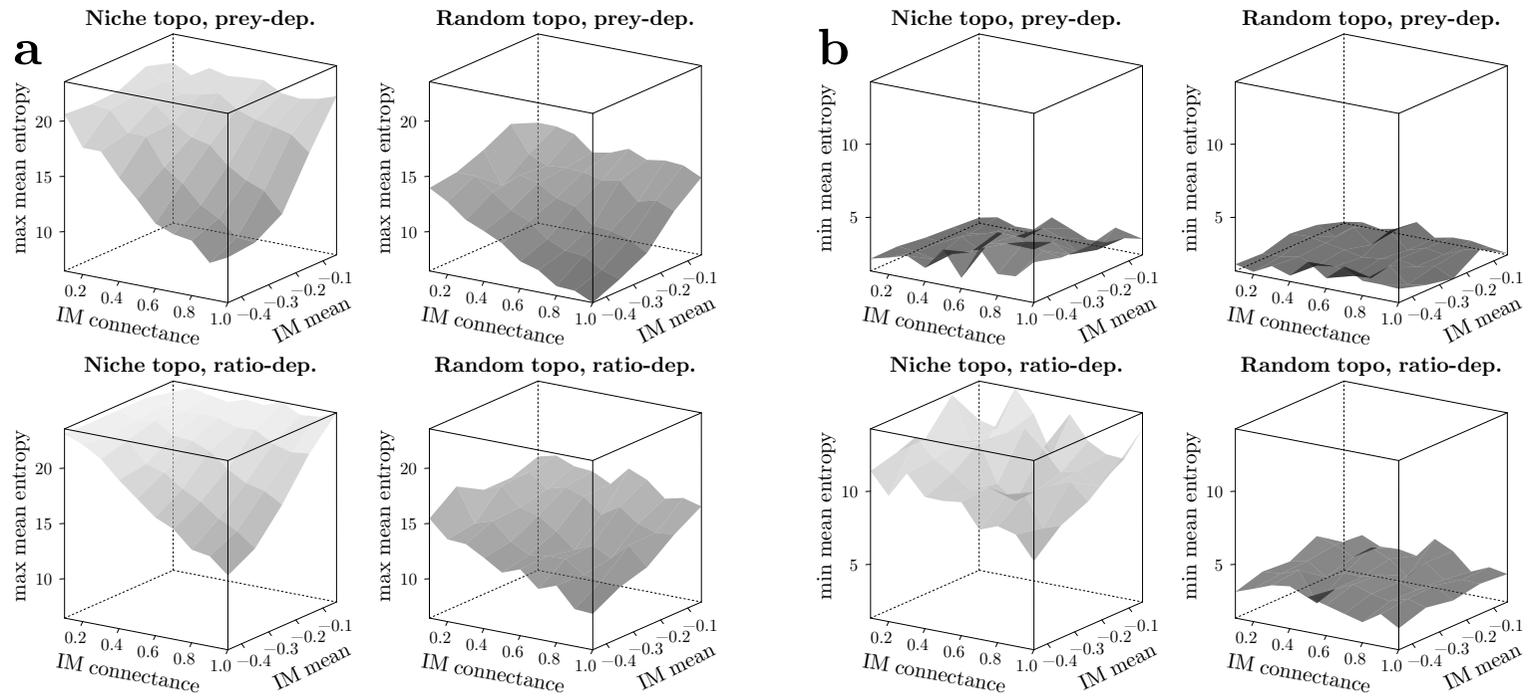


Figure 5.3. Effect of IM connectance and mean IM magnitude on maximum (a) and minimum (b) observed mean entropies, for different model configurations of topology and functional response. The surface vertex at each IM connectance-mean setting denotes the mean response of the models with the highest (a) or lowest (b) 5% of response values among about 100 independent replicate models with the given IM connectance and IM mean.

The maximum observed mean species evenness decreases when all IM in a given system are increasingly negative and of increasing connectance (Fig. 5.3a). Niche-topology ratio-dependent models have on average the highest maximum observed mean evenness for any given IM connectance and magnitude. The minimum observed mean evenness shows little or no systematic change, with niche-topology ratio-dependent models having on average considerably higher minimum evenness than the other model configurations (Fig. 5.3b). Models with random topology tend to have lower evenness than models with niche topology, for the same IM connectance and strength (Fig. 5.3a). The SD of evenness shows little or no change with increasing IM negativity and connectance; this is also the case when both negative and positive IMs are present (all Pearson $|\rho|$ and Kendall $|\tau| < 0.1$).

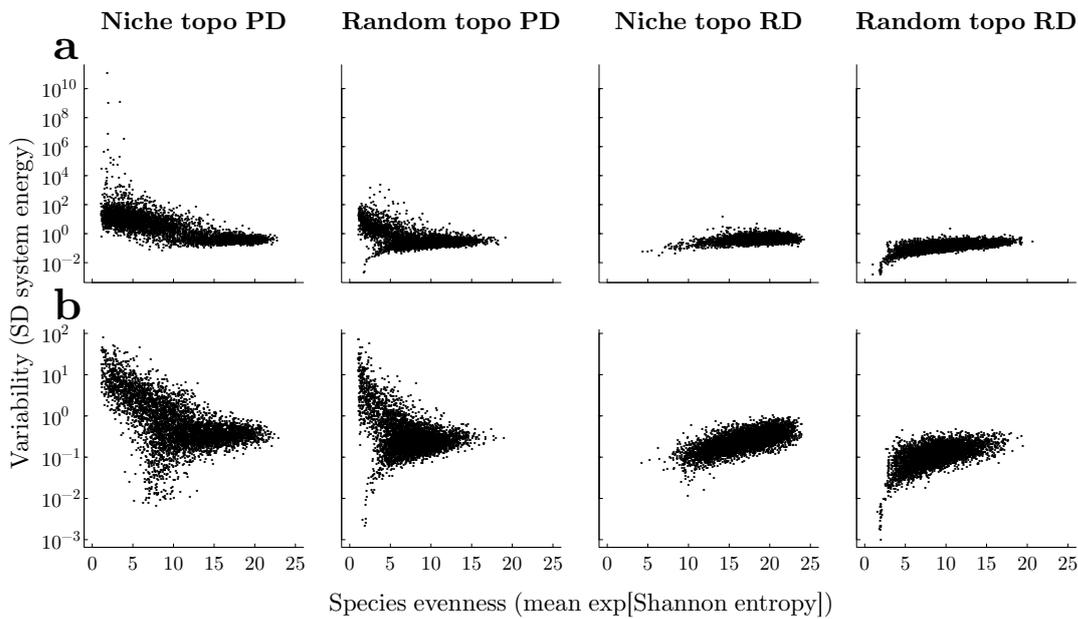


Figure 5.4. Relationships between species evenness and system variability, by model configuration (columns). Row a, both positive and negative IM co-occurring; row b, only negative IM present. Data pooled across IM connectances and strength levels. PD, Prey-Dependent; RD, Ratio-Dependent.

Evenness-variability relationship. Prey-dependent models exhibit two clusters of data points with opposite relationships, while ratio-dependent models have single clusters (weak to moderately strong positive Kendall τ , most $p < 0.05$) resembling the lower variability-higher evenness clusters of the prey-dependent models with the respective niche or random network topologies (Fig. 5.4). Inspection of simulated species trajectories of prey-dependent models showed that systems with both very low evenness and very high variability tended to be characterized by one or two species having considerably higher energy states than the other species and continuing to increase monotonically in energy within the measurement window for the response variables while the other species had reached steady state. These simulations constituted the minority of the sample and were not omitted because their behaviour merges gradually with those in which all species reached steady state, with no thresholds of evenness or variability. The data clusters with opposite relationships occur regardless of IM settings and therefore appear to be unrelated to IM (see Appendix 5.5.2 for plots of unpooled data).

5.4 DISCUSSION

The implementation of IM by GOUDARD & LOREAU [251] used in this study, with randomization of interaction modification strengths, is considered by GOLUBSKI & ABRAMS [40] as an ‘extreme simplification’. The overall formulation, however, is sufficient for studying the fundamental effects of IM compared with no modification, across contingencies represented by the randomization of the magnitudes and directions of IM strengths. OLFF *et al.* [82] suggest further types of indirect interactions that could be examined in future work.

When negative and positive IM are equally abundant, they tend to cancel out one another’s effects on maximum observed entropy and maximum observed system energy as expected, dampening the effects of IM connectance and strength except for the energy of prey-dependent models with niche topology (Fig. 5.1). The exceptional behaviour of the prey-dependent models may be partly because predators at higher trophic

levels can have many prey species in a system with niche topology, and can increase to particularly high abundances by collectively depressing their numerous diet species to low-energy steady states when their functional responses are only prey-dependent and enhanced by strong positive IM. In this case the negative IM do not cancel out the positive IM because the potential population growth due to positive IM has no upper bound while population reduction due to negative IM has a lower bound of zero. In contrast to niche topology and prey dependence, random topology averages out the number of prey species per predator, and ratio dependence regulates predator population growth more tightly with or without IM by making the predator and prey populations fluctuate proportionately (see ARDITI & GINZBURG [180]). Nevertheless, caution must be exercised in comparing prey and ratio dependence in terms of quantitative absolute values, because the half-saturation parameter value used in the functional response is different and because of the fundamental structural differences in the models.

In addition, strong and abundant negative modifications are associated with lower maximum observed evenness (Fig. 5.3a). This could be due to negative IM weakening the direct interaction strengths between species, causing their abundances to be less dependent on one another, everything else being equal. Interestingly, models with random topology have lower maximum observed evenness (Fig. 5.3a). This may be related to the random links between the metabolically scaled species rate equations giving rise to a higher proportion of consumers with smaller niche values (body sizes) than their resources, giving rise to a higher incidence of deviations from the smooth energy pyramid. Such a scenario may apply to real systems in which parasite diversity is on par with host diversity. In contrast, niche-topology ratio-dependent models have higher maximum observed evenness on average, and considerably higher minimum observed evenness on average, than all the other model configurations (Fig. 5.3b). This could be due to ratio dependence mandating a more even distribution of energy among predator and prey because of their proportionate population change, combined with the aforementioned energy-pyramid

effect. Along with the results for system energy, the results for evenness lean towards niche topology-ratio dependence as a high evenness-low variability configuration that may be beneficial in terms of ecosystem function and robustness.

For all IM settings examined, the evenness-variability relationship is generally higher evenness-higher variability for ratio-dependent models while prey-dependent models are split into two clusters with opposite relationships, the high evenness-low variability cluster representing those systems that have reached steady state and resembling the relationship for ratio-dependent models (Fig. 5.4). For ratio dependence especially, the results appear to be in conflict with the current consensus on biodiversity generally having stabilizing effects on various kinds of stability, including stability in terms of ecosystem variability [241]. The solution to this paradox may be that my measure of ‘diversity’ is restricted to the species evenness component: when species abundances are more evenly distributed, species are on average at greater liberty to ‘explore’ their dynamical state spaces, as contrasted with a highly uneven system heavily dominated by one species that monopolizes most of the resources leaving very little leeway for the others. Indeed, the latter kind of system simulated in this study may represent real systems under siege by invasive species or threatened by increasing activity by the human species. This study therefore provides fresh insights on the diversity-stability relationship, given that most studies have considered the number of species but not their relative abundances.

Notably, my results seem to depart qualitatively from those of GOUDARD & LOREAU [251] in terms of the maximum observed mean system energy being positively associated or not associated with IM connectance and spread, depending on functional response (Fig. 5.1), opposing the relationship found by GOUDARD & LOREAU for equilibrium biomass. Possible factors include the use of more realistic network topology, functional responses and stochasticity, and the lack of explicit nutrient limitation, in my model; further work may shed light on how important these factors are for building realistic ecological models.

In reality, IM are most likely to be antagonistic to each other [40] such that multiple positive IM are collectively less positive, and negative IM less negative, than their sum, but little is known empirically. My study assumes, as in GOUDARD & LOREAU [251], that the strengths of multiple IM are independent of one another, such that increasing the IM connectance causes the total IM strength to increase additively. This may lead to overestimation of the effect sizes, but I argue that the findings will be qualitatively similar. This is because it is likely that the total IM strength would still accumulate in nature with increasing IM connectance, only that it would be less than purely additive. In addition to such ‘density dependence’ of combined IM strength, the variation of IM strength over time i.e. adaptive trait dynamics [364] also needs better understanding.

In conclusion, although individual IM have been reported to have limited impact on food webs [352], I found for a wide range of parameter values that the multiple IM that would be present in a real ecosystem can have ecosystem-level effects depending on the strengths and connectance of those modifications, but the effects pertain mostly to the potential maximum boundary conditions rather than those in which most of the model ecosystems reside. This suggests that multiple IM in a community tend to cancel out one another’s effects under average conditions, supporting the view of GOLUBSKI & ABRAMS [40] that models that lack IM may still give ‘adequate predictions’ for more speciose systems, in which IM tend to have smaller net effects. In addition to elucidating the effects of IM, the model behaviours observed in my study also underscore the importance of modulating the balance between prey- and ratio-dependent functional responses appropriately. Prey-dependent models are much more frequently used and, if used in food webs, most commonly combined with niche topology. In such cases, model behaviour may exhibit higher productivity and variability and lower evenness than reality, if the community were actually more ratio-dependent. Finally, the study of IM can also provide insights into the role of ecosystem engineers, or species that physically modify their environment. One of the effects of ecosystem engineers is to ‘modulate’ the links between

other species via the environment [365]; this process is essentially im. Ecosystem engineering has been investigated only in simple food webs, and much remains to be discovered about its influence on larger and more complex ecological networks [365].

5.5 APPENDIX

5.5.1 SUPPLEMENTARY FIGURES

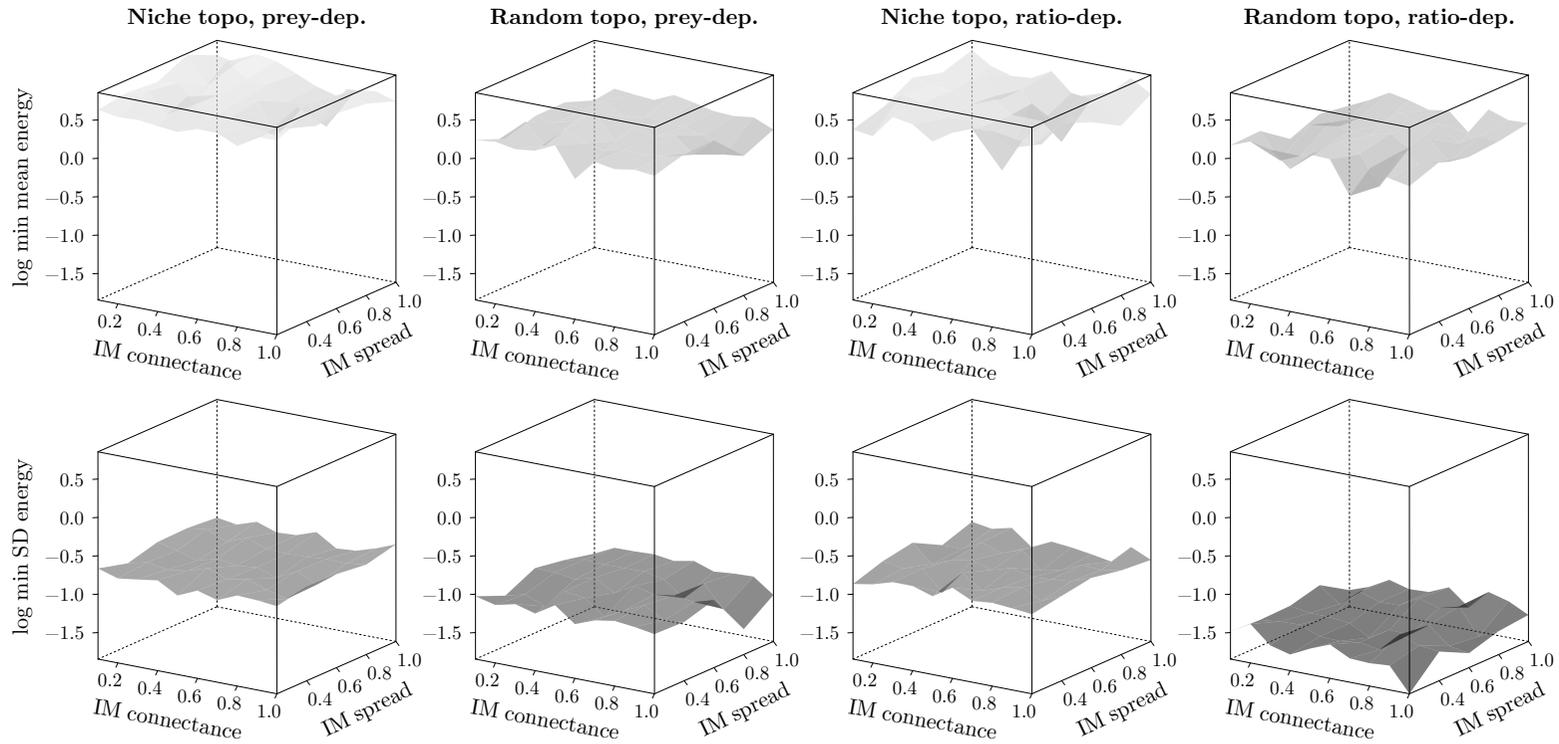


Figure 5.5. Effect of IM connectance and IM spread on minimum observed means (upper row) and SD (lower row) of system energy. The surface vertex at each connectance-spread setting denotes the mean response of the models with the lowest 5% of response values among about 100 independent replicate models with the given connectance and spread.

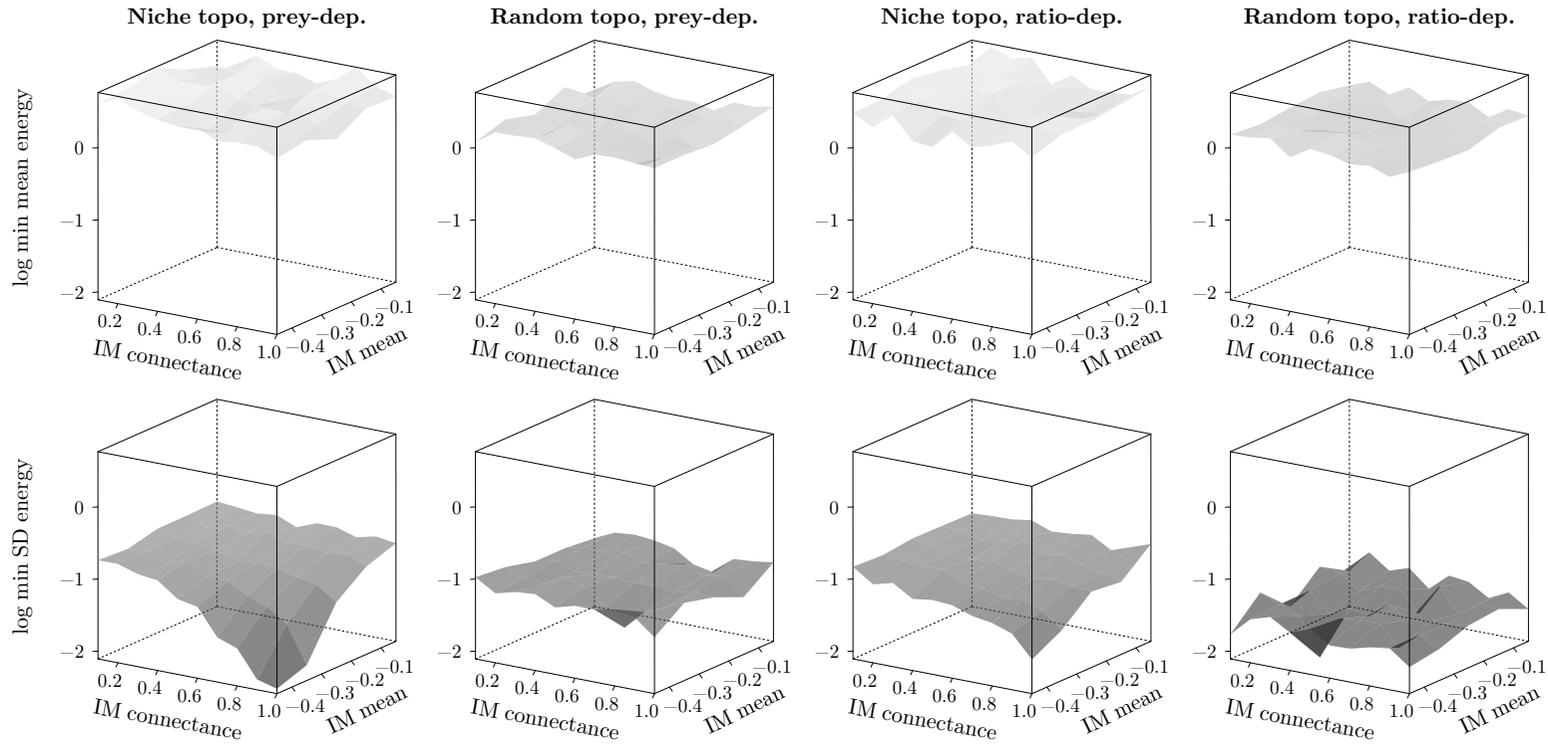


Figure 5.6. Effect of IM connectance and mean IM magnitude on minimum observed means (upper row) and SD (lower row) of system energy. The surface vertex at each IM connectance-mean setting denotes the mean response of the models with the lowest 5% of response values among about 100 independent replicate models with the given IM connectance and IM mean.

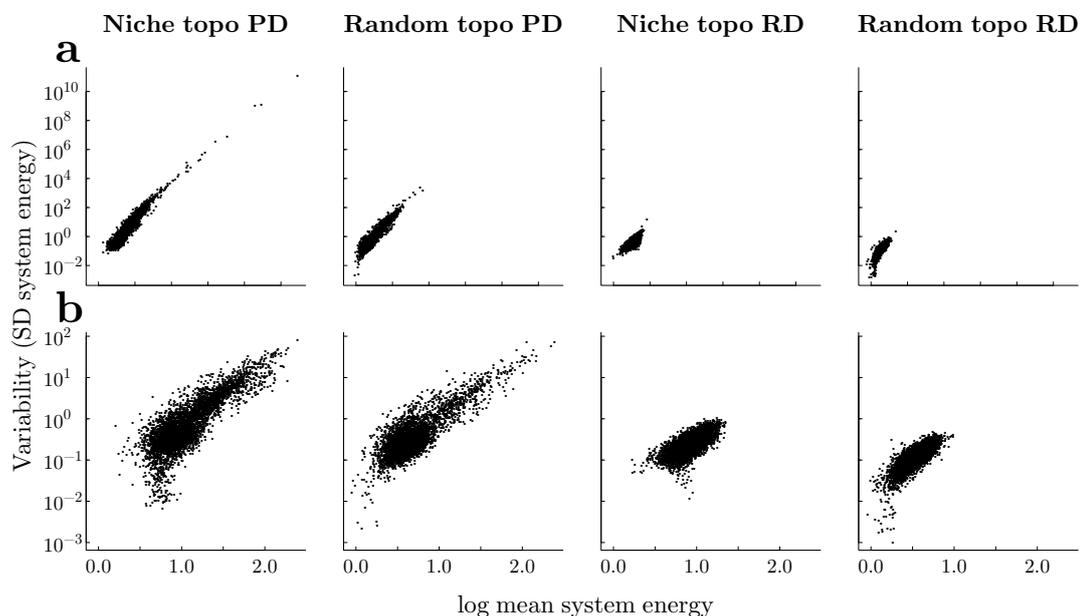
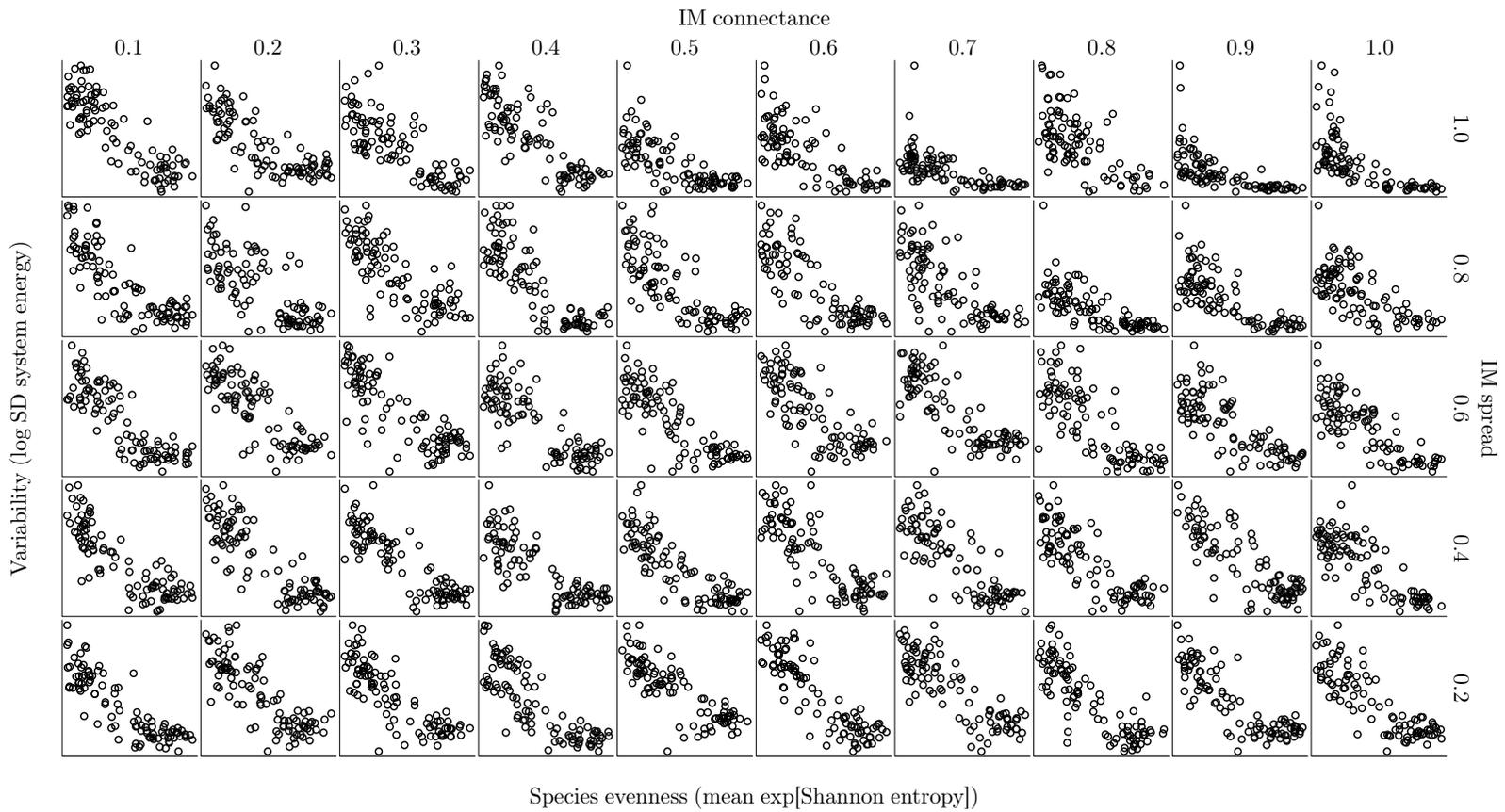


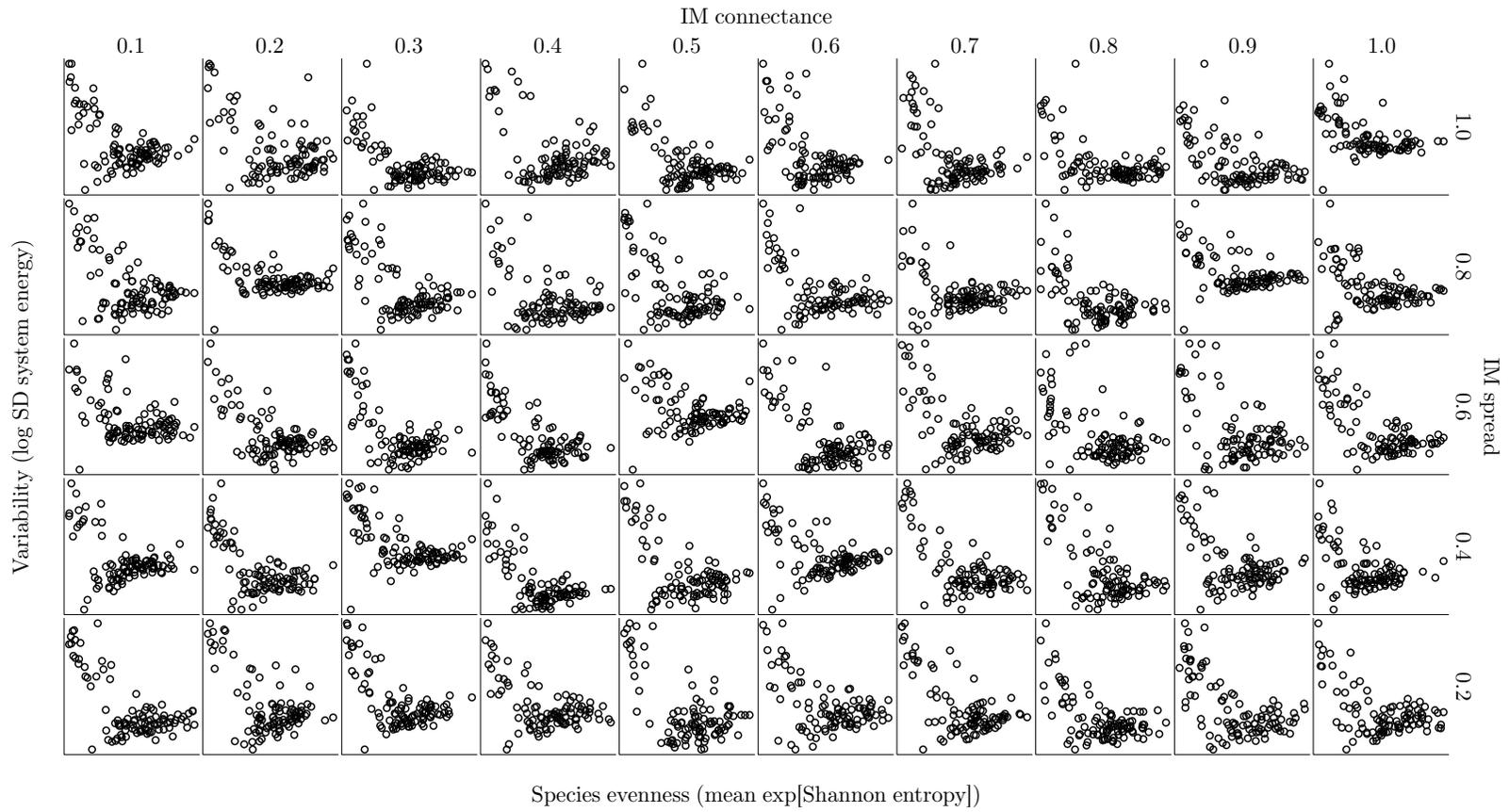
Figure 5.7. Relationships between mean and SD of system energy, by model configuration (columns). Row a, both positive and negative IM co-occurring; row b, only negative IM present. Data pooled across IM connectances and strength levels. PD, Prey-Dependent; RD, Ratio-Dependent.

5.5.2 PLOTS OF UNPOOLED DATA

Relationships between species evenness and system variability, plotted separately for each IM connectance and strength level within each model configuration within each simulation experiment (see §5.2 for methodological details). Axes same as Fig. 5.4 in main text. Axis limits are different (maximized) in each subplot.

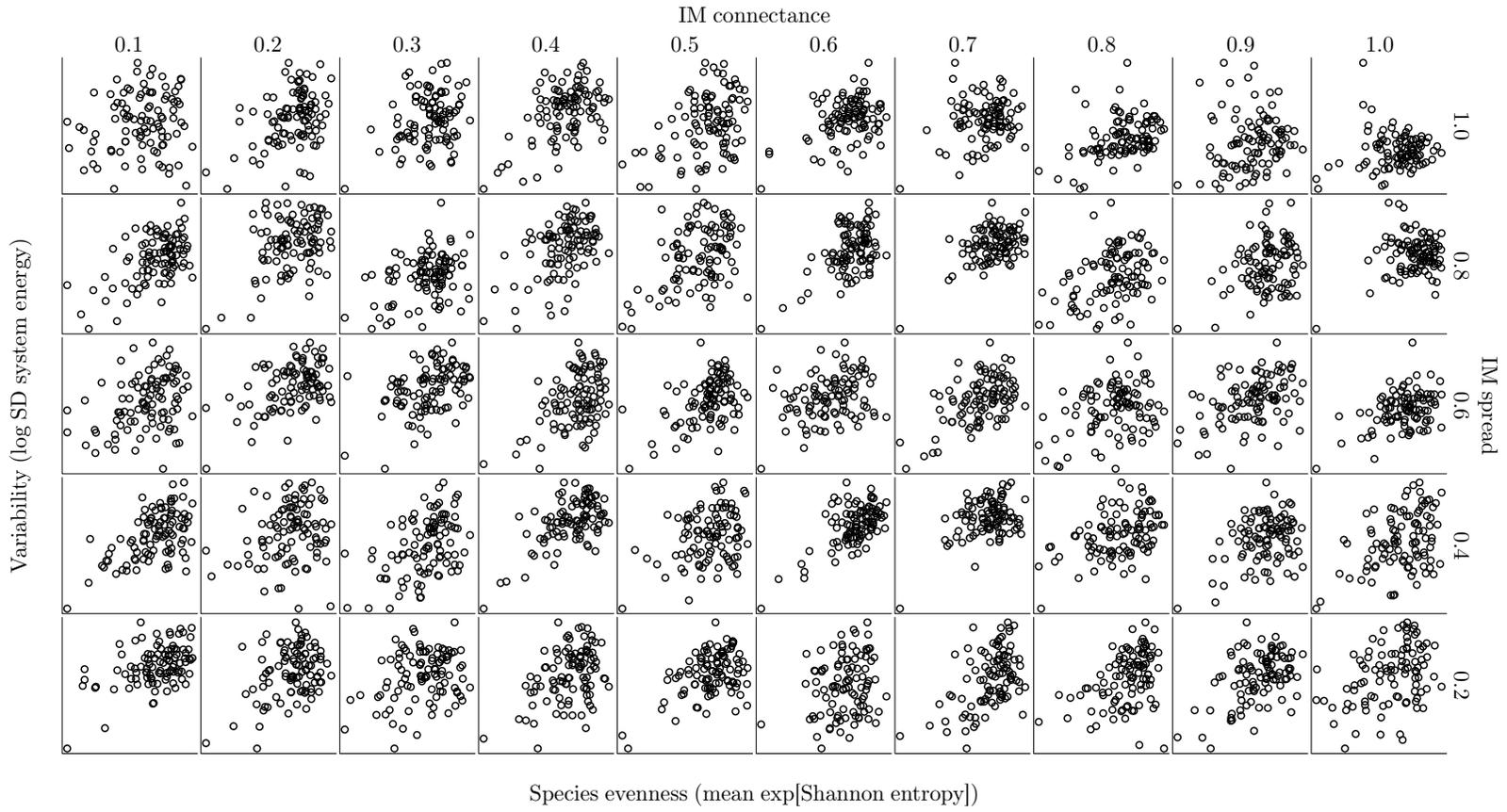


im spread experiment: niche-topology prey-dependent models



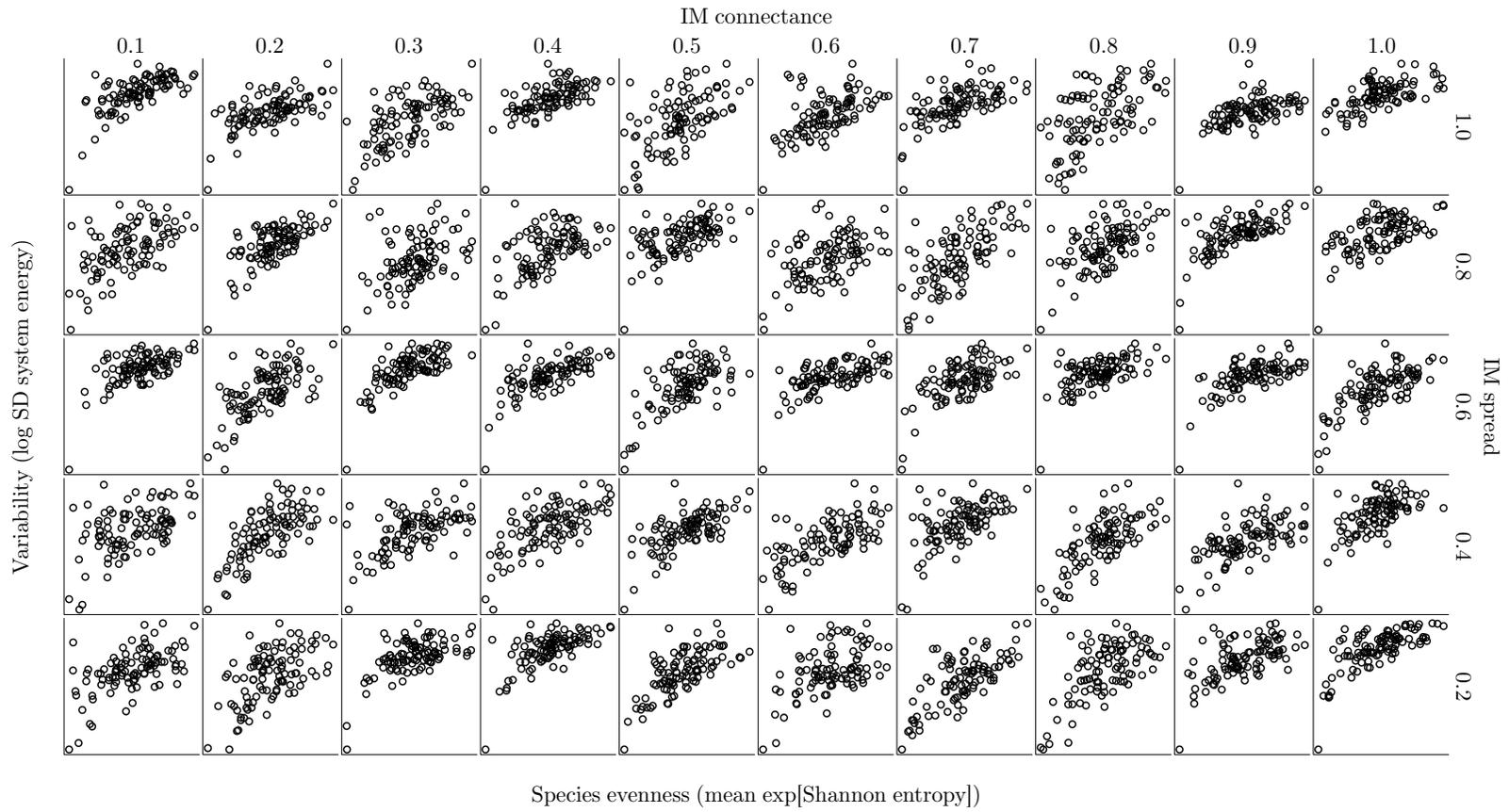
Yanqin Lin

im spread experiment: random-topology prey-dependent models



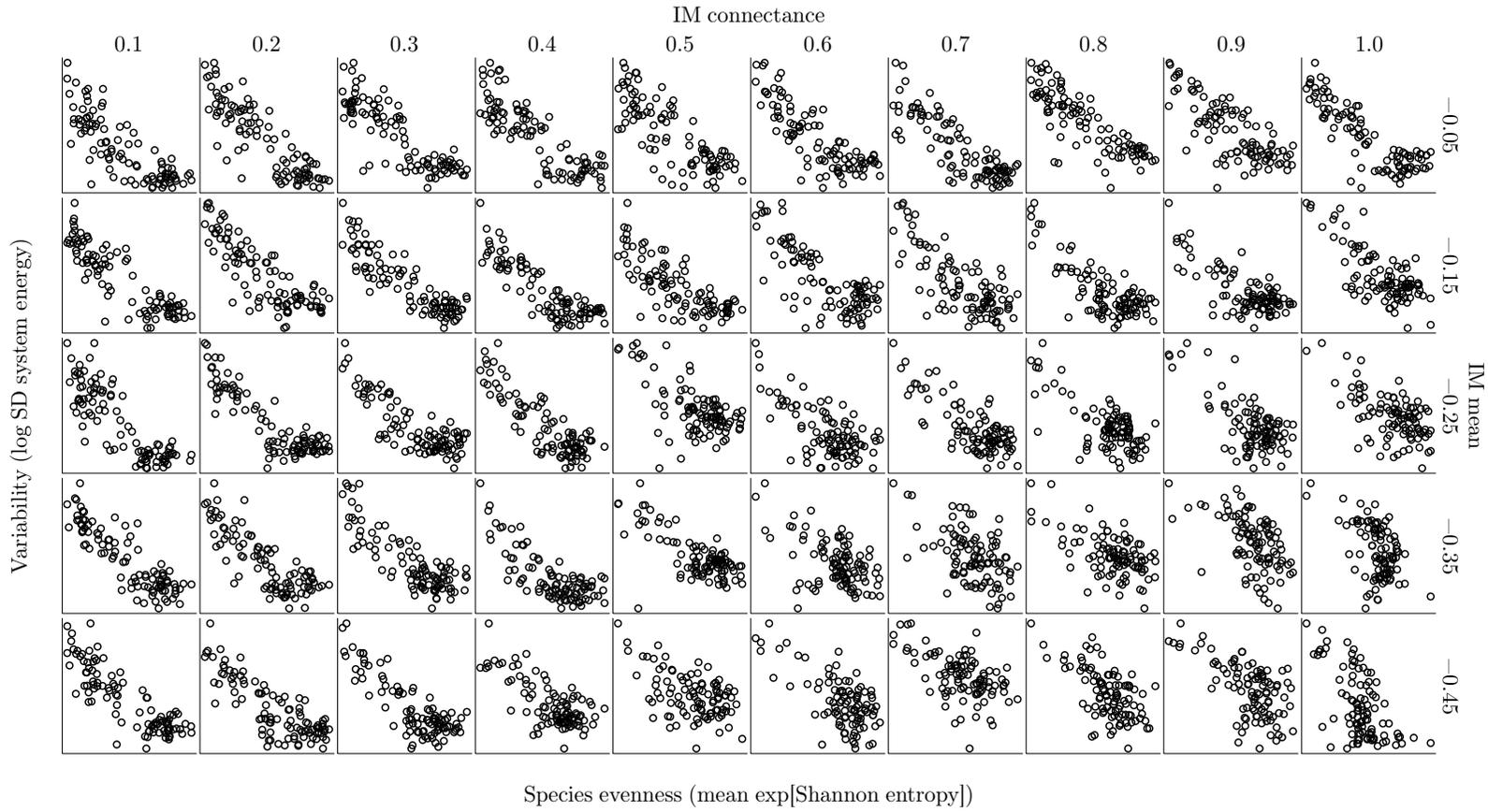
Collective effect of interaction modifications

im spread experiment: niche-topology ratio-dependent models



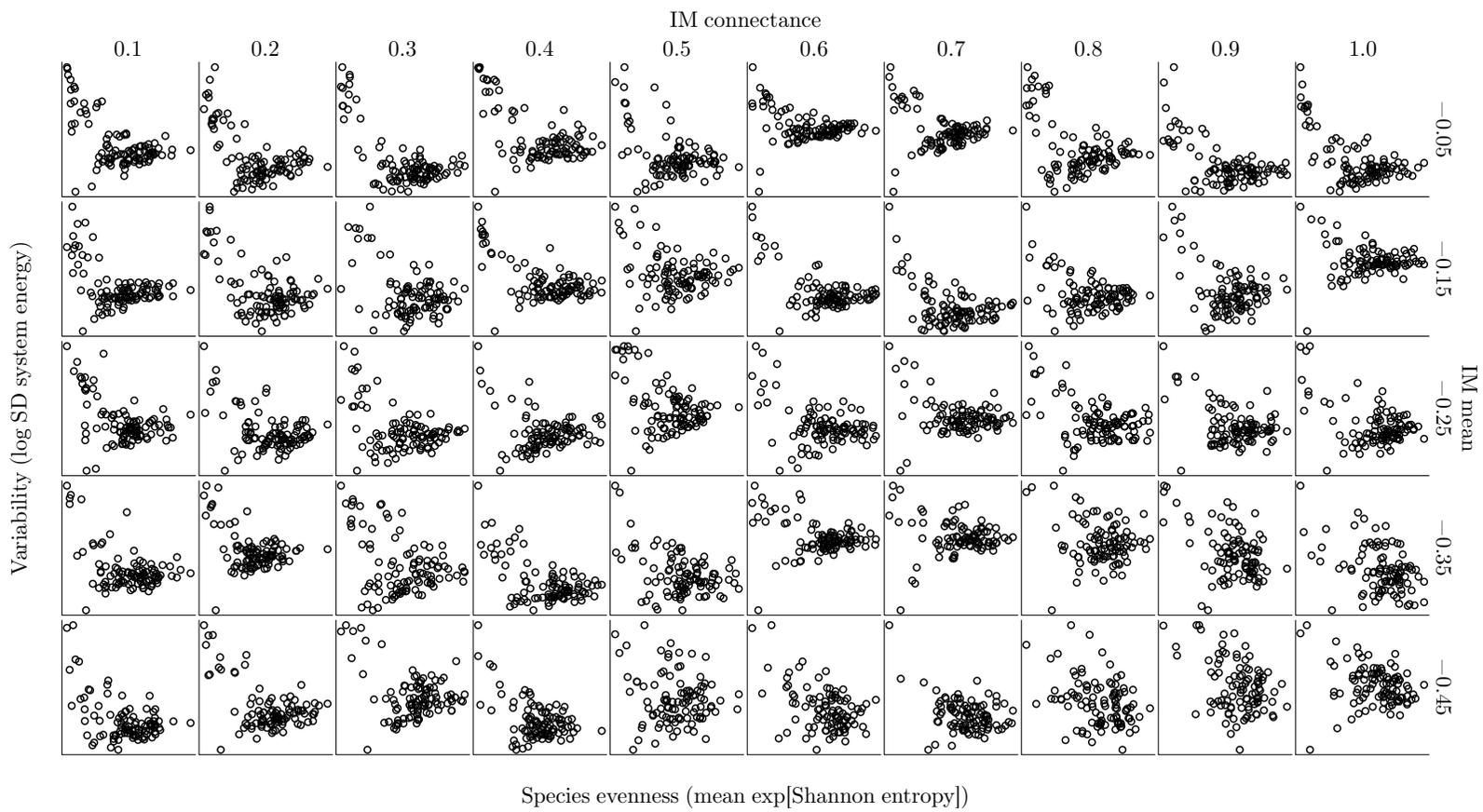
Yangchen Lin

im spread experiment: random-topology ratio-dependent models



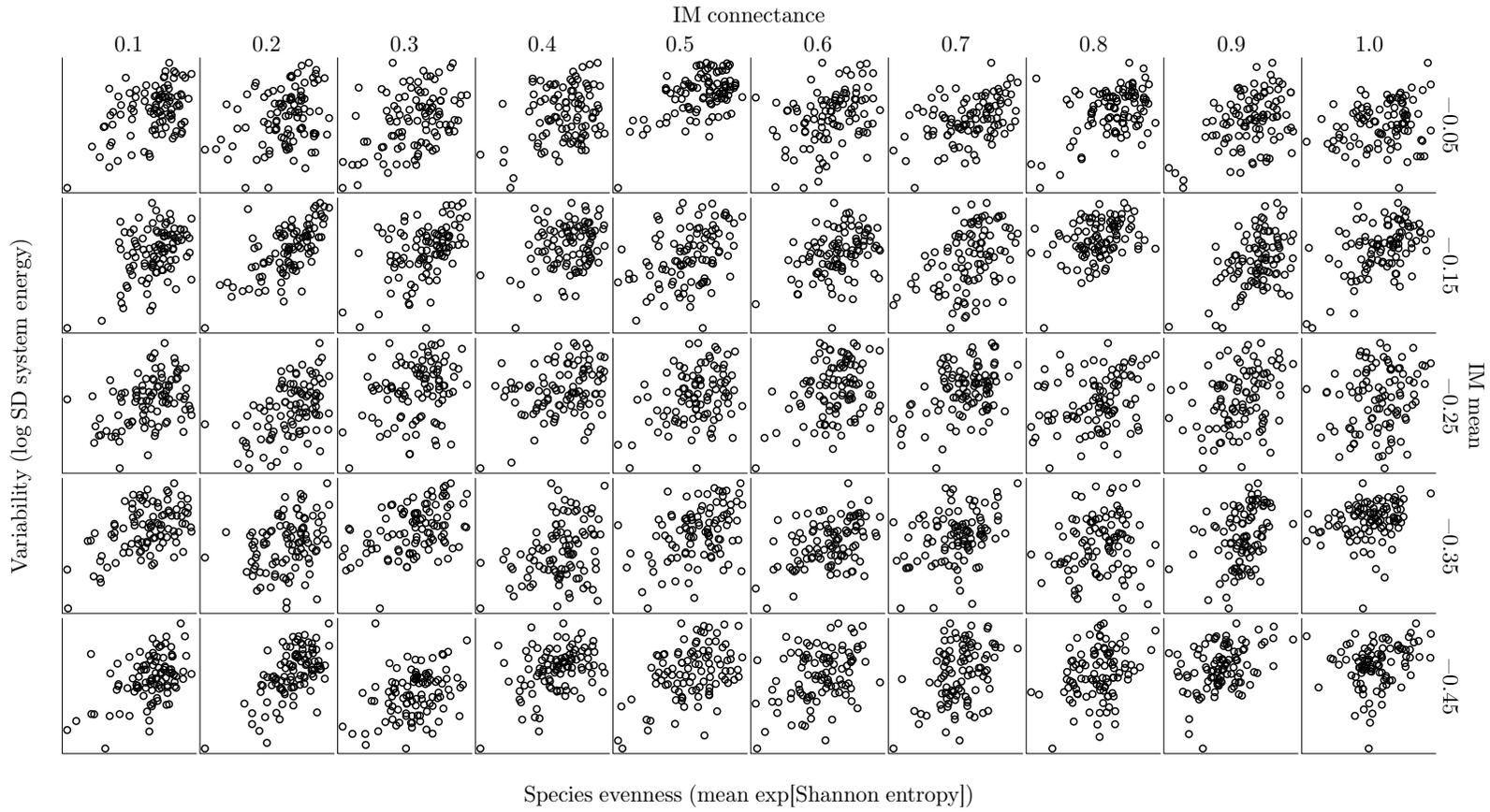
Collective effect of interaction modifications

im magnitude experiment: niche-topology prey-dependent models



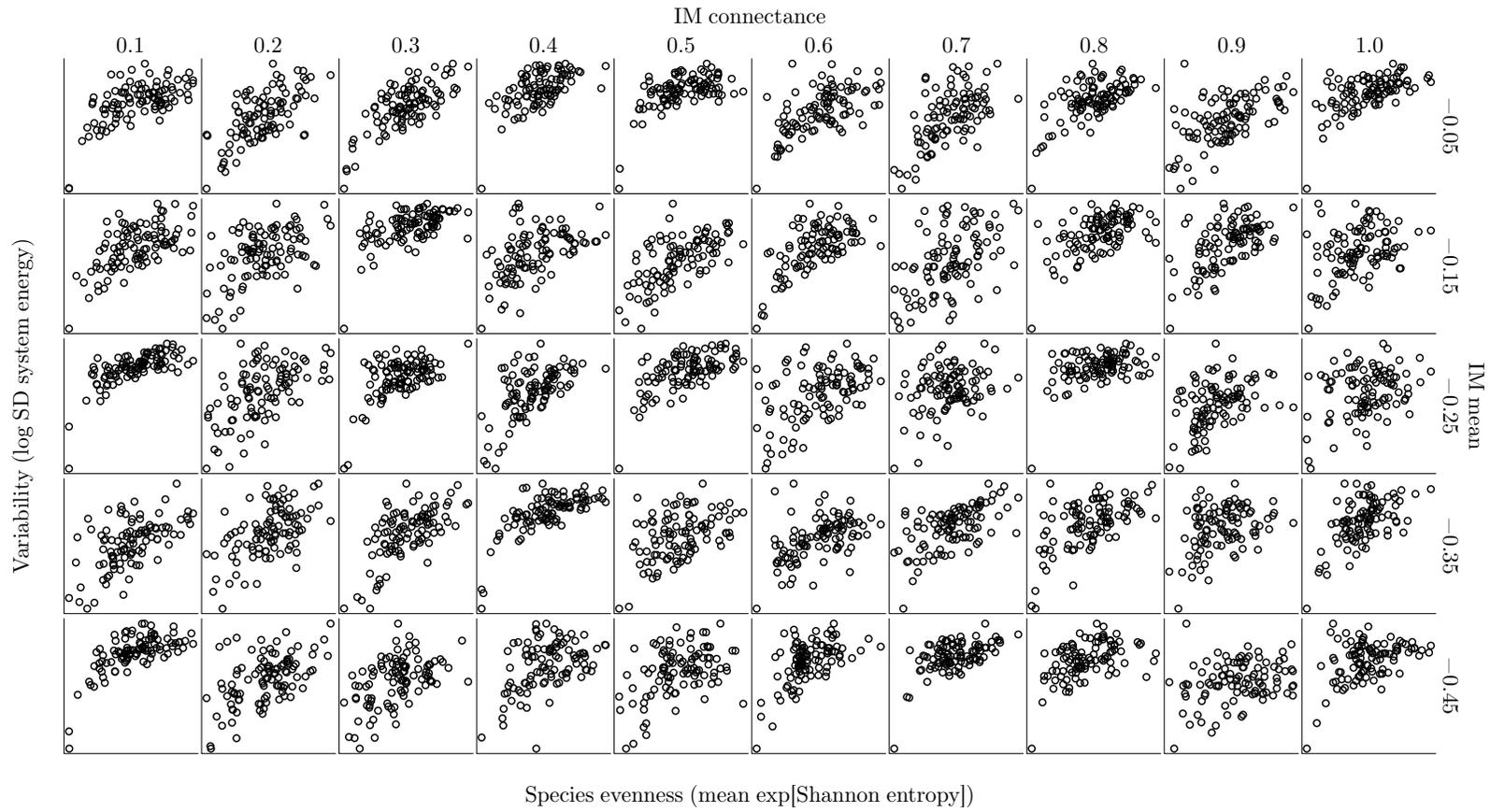
Yanqin Lin

IM magnitude experiment: random-topology prey-dependent models



Collective effect of interaction modifications

im magnitude experiment: niche-topology ratio-dependent models



Yangchen Lin

im magnitude experiment: random-topology ratio-dependent models

6 SPECIES DECLINE IN COMPARTMENTALIZED NETWORKS

Abstract. The complex network approach is increasingly used to further our understanding and management of complex systems in a wide range of disciplines, including ecology. It has recently been recognized that networks are often compartmentalized, and that this can have important implications for their resilience to perturbations. I constructed stochastic bioenergetic models comprising two compartments each containing trophic and mutualistic interactions, with varying levels of intercompartment connectivity. After steady state was reached, I simulated species declines in one compartment and quantified their impacts on the biomass, diversity, community composition and time series power spectra of both compartments. Intercompartment trophic connectivity (density of feeding links between the compartments) was positively correlated with the impacts of species decline on the Shannon diversity of the compartments, but negatively correlated with the impacts on power spectra of species time series. Impacts on community composition were positively correlated with connectivity when the network topology was based on the niche model of food webs, but negatively correlated when the topology was random. In contrast with trophic connectivity, the effects of intercompartment mutualistic connectivity (density of mutualistic links) were much smaller. The results show that differing intercompartment connectivity in networks can cause the impacts of species decline to have different magnitudes and directions depending on network topology and the ecosystem property being measured. The variability found across replicate simulations also highlights the context dependence of ecosystem behaviour and suggests that caution should be exercised when applying conclusions from one specific system to other systems.

6.1 INTRODUCTION

In our increasingly interconnected world there is a growing interest in, and relevance of, the network approach to understanding the complex

systems that pervade our environment, many of which have hitherto been studied in a reductionistic way, in disciplines as disparate as neuroscience and ecology. The scientific community is now appreciating the vulnerability of human-designed or human-impacted natural networks to catastrophic tipping points and need for multidisciplinary integrated global systems science to address such problems [366]. To this end of capturing the totality of interdependencies that govern the characteristics of real-world complexity, the study of ‘networks of networks’ has been hailed as the next frontier of complexity science [367,368].

Real networks are usually highly compartmentalized [369,370], ranging from the World Wide Web [371] to the brain connectome [372], to metabolic and signalling networks in cells [373,374] and to ecological networks of interacting species [375]. Compartmentalization can have consequences for the behaviour or resilience of networks to perturbation [376,377], such as by limiting the extent of cascades [26,378]. There has been a corresponding development of network structural complexity metrics that account for compartments and their nonplanarity [379].

In ecological networks of interacting species, a compartment can be defined as some group of highly interconnected species that are highly interconnected with one another but connected relatively sparsely to other such groups. PIMM & LAWTON [380] found little empirical evidence for compartmentalization in food webs within relatively homogeneous habitats. Since then, however, with more recent and more highly resolved data sets, it has been found that many kinds of ecological networks do exhibit compartmentalized topology, such as food webs [381,382] and insect-plant interaction networks [383,384]. Furthermore, compartmentalization is generally recognized to enhance stability and persistence in food webs [48,290].

In this study, I consider two-compartment networks, each compartment being a spatially distinct ecological network that contains a different set of species. Examples include canopy, understorey and soil compartments in forest, and aquatic-terrestrial systems. Little research has been done on compartmentalization at this scale, most studies having looked at either

green or brown webs in isolation [385] or compartmentalization within what is actually a functional group within a larger ecological network, for example host-parasitoid communities in forest [262,386]. Some recent empirical studies have demonstrated that intercompartment interactions at the habitat level play important roles in community dynamics. For example, GIERY *et al.* [387] demonstrated the existence of trophic interactions and corresponding resource flux between canopy and understorey food webs in woods. Trophic links between above-ground and below-ground webs cause dynamic feedbacks [385], while those between elements of a spatial mosaic of food webs in a floodplain affect the carrying capacity and recovery of predator populations [388]. Facilitative interactions can also occur between spatial compartments. For example, waterbodies created by beavers support insects that, in turn, benefit terrestrial bats [389].

Very few studies have considered the explicit interaction topology of compartmentalized networks at the ecosystem level. POOCK *et al.* [116] found varying effects of species decline on the various subnetworks, VALIENTE-BANUET & VERDÚ [295] reported that anthropogenic impacts can act synergistically to cause network collapse, while EVANS *et al.* [390] found that the loss of certain habitats has disproportionate effects on network integrity. These studies, however, did not investigate the effect of compartmentalization per se. Furthermore, each compartment in these studies collated a particular type of interaction of interest, rather than the actual co-occurrence of interactions of multiple types between all the closely interacting species in a given subhabitat, and considered only network topology without dynamics.

The aforementioned studies provide important insights for specific systems that are likely to be highly context-dependent; there thus remains scope for more general theoretical understanding of the role of compartmentalization in the dynamics of complex ecological networks, as most models of ecological networks are not compartmentalized [391]. An exception is KRAUSE *et al.* [375], who examined the effects of removing nodes from compartmentalized food webs constructed from empirical data, and found that compartmentalization limited the extent of cascades, re-

sulting in greater stability. They, however, did not incorporate community dynamics, which can be an important factor in mediating the stability of the system [32]. STOUFFER & BASCOMPTE [290] came to similar conclusions with compartmentalized food web models that incorporated community dynamics, but did not incorporate nontrophic interactions or interaction modifications.

Here, I use holistic models of ecological networks to investigate the simplest case of compartmentalization, in which two such networks are connected to each other by varying numbers of trophic and mutualistic links, or connectivity. I ask how differing levels of intercompartment trophic and mutualistic connectivity affect the impact and propagation of species declines in one compartment both on itself and on the other compartment. I assess the impact using an array of ecosystem metrics that are indicative of ecosystem health, as well as of broad interest, such as biomass, diversity and community composition.

6.2 METHODS

The network models comprised two independently generated (Chapter 2) 15-species compartments linked to each other, making a total of 30 species in the system. In a given model realization, the two compartments had the same trophic topology, which was either random or based on the generalized niche model (see Chapter 2), and the niche range was kept constant at $(0, 1)$ for both compartments. These are not ecologically unreasonable simplifying assumptions, even though differences between compartments have sometimes been observed, such as between forest soil and above-ground food webs [392]. Ratio-dependent consumer-resource functional responses were used. Interaction modification (Chapter 5) was confined to within compartments, with connectance 0.1 and modification strengths drawn from a uniform distribution in $[-0.1, 0.1]$. Environmental stochasticity was implemented as pink noise with partial interspecific synchrony (§2.3).

As there is little empirical information on the actual topology of inter-compartment links, trophic and mutualistic links were randomly assigned

between the compartments. The intercompartment trophic and mutualistic connectivities were both varied from 0.05 to 0.3 in increments of 0.05 in a full factorial design, while the within-compartment trophic and mutualistic connectances were kept constant at 0.3, near the upper limit of the empirically observed range [158]. Assigning intercompartment links at random means that species most highly interconnected with one another (i.e. modules) may not correspond exactly to compartments in a given model realization. The two main modules in each model were therefore identified using the community detection algorithm in the `igraph` package [393] in R, and models in which the modules did not correspond exactly to the compartments were discarded.

The directedness of the intercompartment trophic links was decided as follows: for niche-topology models, the species of higher niche value in a species pair would be the consumer if both were non-basal species; for random-topology models, one of the species was randomly assigned as consumer. If one of the pair was a basal species, it was fed on by the non-basal species regardless of niche value or network topology. Basal species pairs were excluded from trophic interactions. Finally, the Laplacian matrix of the entire network was computed, as in §2.1, to ensure that there were no isolated components.

The models were simulated to 20000 time steps to allow initial transients to pass, and a set of four ecosystem metrics was calculated using the simulation output from time steps 20001 to 40000 after steady state had been reached. The ecosystem metrics (§4.2) were the average total system energy over time, average exponent of Shannon entropy over time, community composition⁸ and power spectrum. From time step 40001 onwards, five randomly selected species (hereafter ‘declinees’) in one compartment (hereafter ‘proximal compartment’, the other compartment referred to as ‘distal’) were subjected to chronic decline of 0.01 of the species states at each time step until the end of the simulation at

⁸This is the ‘community structure’ of previous chapters; the terminology is altered here to avoid confusion with the term of the same name in network science.

time step 80000.⁹ The decline rate was chosen such that its effect was considerably greater than that of the environmental noise.

The same ecosystem metrics were recalculated post-decline using time steps 60001 to 80000. The impact of decline on each ecosystem metric was then calculated as detailed in §4.2, separately for each compartment. A sample of 128 independent model realizations was generated for each intercompartment trophic-mutualistic connectivity treatment. Another set of simulations and analyses was also run as already described, but with the declines being non-basal species with the five highest niche values in the proximal compartment, representing the decline of large animals or top predators.

Simulations were discarded where negative species states were produced due to the noise terms and intrinsic numerical integration errors. In addition, extreme values occasionally occurred in impacts measured as proportional change, as explained in §4.3, resulting in infinity values via computer rounding error; these replicates were also taken out of the analysis. As stated earlier, models in which modules did not correspond to compartments were discarded. The final sample size for each intercompartment trophic-mutualistic connectivity combination ranged from 63 to 128.

Regression trees were constructed to identify the most important determinants of decline impact among the following: compartment topology (niche or random), niche range of the declines in a given simulation (either the full niche range of the community or the top five predators only), intercompartment trophic and mutualistic connectivities, numbers of intercompartment trophic and mutualistic links associated with declines, the number of declines that are basal species, and what I term the average trophic centrality and average mutualistic centrality of declines. The last two variables are defined as the average number of trophic and mutualistic links, respectively, that each declinee has in a given network realization; they are similar to degree centrality. The trophic centrality

⁹This implementation is more dynamically realistic than the instantaneous extinctions of previous chapters, although it is not absolute extinction.

combines both predator and prey links to capture the essence of energy flow through the declinees.

The main analysis then focuses on the relationships between inter-compartment connectivity and decline impacts on the various ecosystem metrics in the proximal and distal compartments.

6.3 RESULTS

The regression trees (Appendix 6.6.1) show that network topology explains the greatest proportion of the deviance for all ecosystem metrics in both compartments. There are small correlations (all Kendall $|\tau| < 0.2$, most $p < 0.0125$ after Bonferroni correction for four ecosystem metrics) between intercompartment trophic connectivity and impacts on proximal or distal compartments (Table 6.1); see below for details for each ecosystem metric. Correlations for intercompartment mutualistic connectivity are generally weaker (most $|\tau| < 0.1$; Table 6.1).

Table 6.1 (facing page). Kendall correlations between inter-compartment connectivity and decline impacts on ecosystem metrics.

Compartment	Ecosystem metric	Declinee niche range	Network topology	τ_{troph}	p_{troph}	τ_{mut}	p_{mut}
proximal	average energy	full	niche	-0.031	0.00457	-0.0786	6.06×10^{-13}
			random	0.0389	0.000426	-0.0424	0.000121
		high	niche	-0.106	1.57×10^{-22}	-0.121	1.04×10^{-28}
			random	0.0379	0.000561	-0.0366	0.000852
	average entropy	full	niche	0.1	0	-0.0786	5.95×10^{-13}
			random	0.118	0	-0.0394	0.000356
		high	niche	0.198	0	-0.0869	1.31×10^{-15}
			random	0.122	0	-0.0495	6.64×10^{-6}
	community composition	full	niche	0.0926	0	0.0367	0.000785
			random	-0.0386	0.000464	0.0045	0.683
		high	niche	0.135	0	0.0543	5.89×10^{-7}
			random	-0.0467	2.11×10^{-5}	0.0281	0.0105
power spectrum	full	niche	-0.119	1.52×10^{-27}	-0.0587	7.52×10^{-8}	
		random	-0.162	1.04×10^{-48}	-0.0182	0.099	
	high	niche	-0.105	4.18×10^{-22}	-0.114	9.99×10^{-26}	
		random	-0.165	9.31×10^{-51}	-0.0332	0.00249	
distal	average energy	full	niche	-0.0705	1.06×10^{-10}	-0.0368	0.000737
			random	-0.032	0.00374	-0.00228	0.836
		high	niche	-0.114	1.6×10^{-25}	-0.0456	2.74×10^{-5}
			random	-0.0157	0.153	0.0112	0.307
	average entropy	full	niche	0.046	2.48×10^{-5}	-0.0312	0.00427
			random	-0.0274	0.0129	-0.00451	0.683
		high	niche	0.0882	4.44×10^{-16}	-0.00776	0.476
			random	-0.0124	0.258	-0.000492	0.964
	community composition	full	niche	0.12	0	0.0284	0.00919
			random	-0.03	0.00644	-0.0212	0.0547
		high	niche	0.131	0	0.0393	0.000302
			random	-0.032	0.00353	-0.027	0.0139
power spectrum	full	niche	-0.0674	6.76×10^{-10}	0.0767	2.12×10^{-12}	
		random	-0.0996	1.66×10^{-19}	-0.00258	0.815	
	high	niche	0.00908	0.404	0.176	0	
		random	-0.107	2.95×10^{-22}	-0.00177	0.872	

Compartments—proximal: where declines happen; distal: the other compartment. Declinee niche ranges—full: random sample of all species in proximal compartment; high: species with five highest niche values. Subscripts: $_{\text{troph}}$, intercompartment trophic connectivity; $_{\text{mut}}$, intercompartment mutualistic connectivity. Significance level $\alpha = 0.0125$ after Bonferroni correction for four ecosystem metrics.

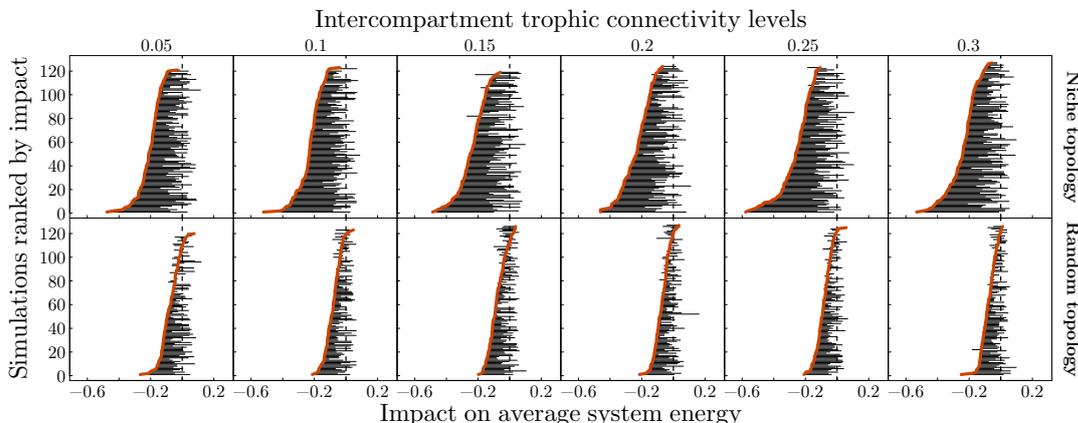


Figure 6.1. Decline impacts on average system energy for increasing intercompartment trophic connectivity with intercompartment mutualistic connectivity 0.05. Results for other mutualistic connectivities are not illustrated as they show a similar pattern. In each panel, the x -axis is the impact on system energy and the y -axis is the rank of simulations sorted in increasing order of the impact on system energy in the proximal compartment, demarcated by the red curve. Impacts on the distal compartments of the respective simulations are marked by the free ends of the black horizontal lines away from the red curve. A horizontal line thus measures the difference between impacts on the proximal and distal compartments of a given simulated network, and whether the distal impact is smaller (horizontal line extends leftwards from curve) or greater (opposite direction) than the proximal impact. Vertical dashed lines mark the value 0 on the x -axis (no impact). Upper row, niche-topology models; lower row, random-topology models; declines in each simulation were species with the five highest niche values. Axis ranges fixed across all model configurations and intercompartment connectivities.

Niche-topology models undergo greater changes in average system energy in the proximal compartment than random-topology models, especially in the niche-topology models where declinees are restricted to species with the highest niche values (Fig. 6.1). The impact on average entropy in the proximal compartment is relatively highly positively correlated with intercompartment trophic connectivity for all model configurations and declinee niche ranges (Table 6.1). Niche-topology models tend to experience less negative and greater positive impacts in the proximal compartment as intercompartment trophic connectivity increases, especially when declinees are restricted to species with the highest niche values

(Fig. 6.2). Unlike niche-topology models, random-topology models have mostly negative changes in average entropy in the proximal compartment, becoming decreasingly negative with increasing intercompartment trophic connectivity (Fig. 6.2).

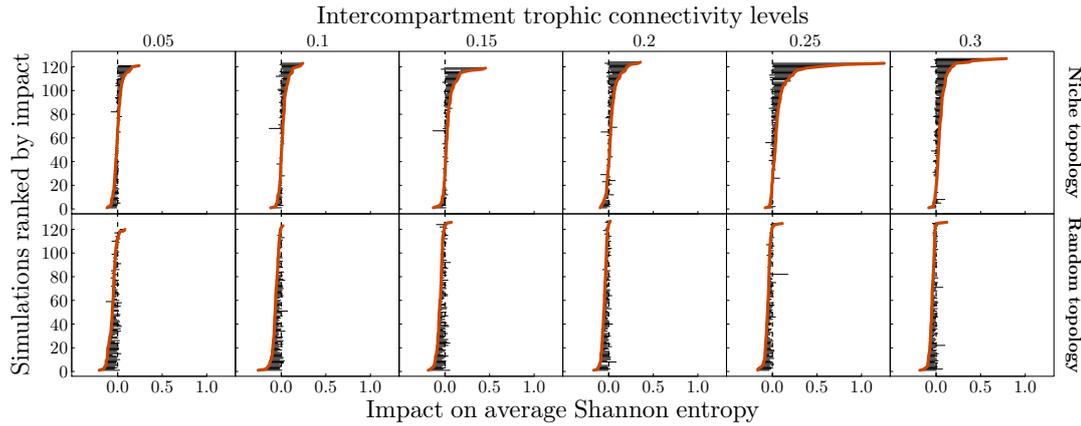


Figure 6.2. Pairwise comparisons between decline impacts on average entropy in proximal versus distal compartments. Detailed explanation as for Fig. 6.1.

Niche-topology models undergo greater changes in community composition in the proximal compartment than random-topology models, especially niche-topology models where the declines are restricted to species with the highest niche values (Fig. 6.3). Impacts on the community composition of both proximal and distal compartments of niche-topology models are positively correlated with intercompartment trophic connectivity, while the corresponding impacts for random-topology models are negatively correlated with intercompartment trophic connectivity (Table 6.1).

For all model configurations and declinee niche ranges, impacts on the power spectrum of the proximal compartment are relatively highly negatively correlated with intercompartment trophic connectivity (Table 6.1). For any given model, a large impact in the proximal compartment is usually combined with a small impact in the distal compartment, while a model experiencing a small impact in the proximal compartment may

Species decline in compartmentalized networks

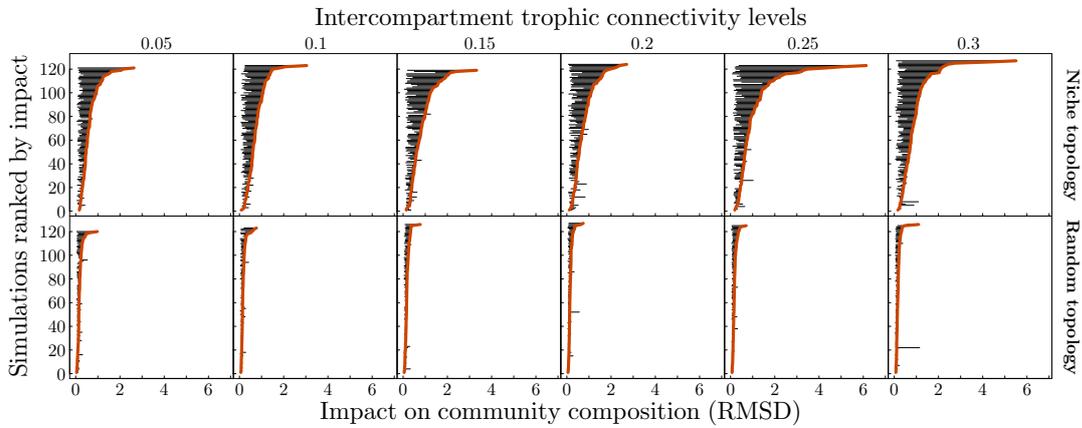


Figure 6.3. Pairwise comparisons between decline impacts on community composition in proximal versus distal compartments. Detailed explanation as for Fig. 6.1.

sometimes experience a large impact in the distal compartment (Fig. 6.4). Compared to niche-topology models, random-topology models have a higher frequency of larger impacts on the power spectra of both proximal and distal compartments overall (Fig. 6.4). These differences between niche and random models are similar to those found in Chapter 4 (p. 76, Fig. 4.5a, extreme upper right panel).

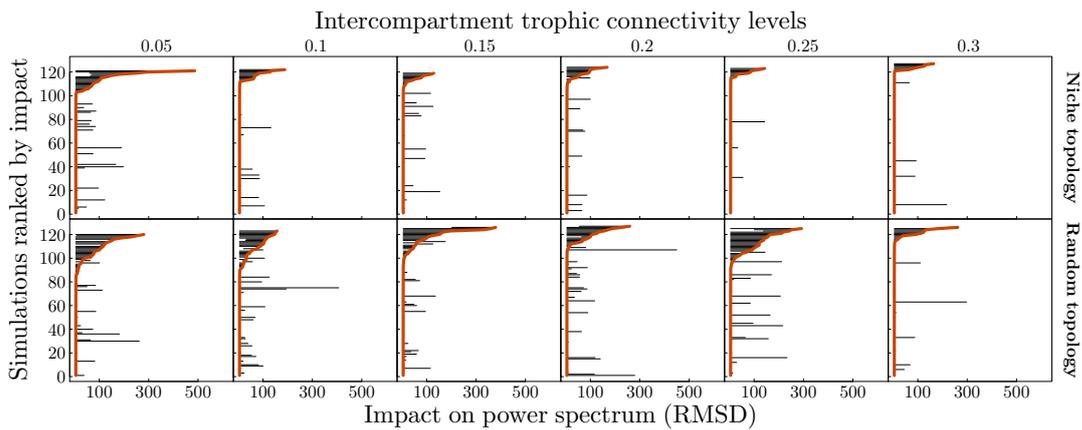


Figure 6.4. Pairwise comparisons between decline impacts on power spectra in proximal versus distal compartments. Detailed explanation as for Fig. 6.1.

Finally, there do not generally appear to be meaningful correlations between impacts in the proximal versus distal compartments, within each model configuration and intercompartment connectivity setting (most $|\tau| < 0.1$)—the impact in the distal compartment does not seem to depend on the impact in the proximal compartment (Figs. 6.1–6.4).

6.4 DISCUSSION

For all ecosystem metrics, compartmentalization has weak but systematic effects on the response of the compartments to species decline, even with the extensive parameter space of my simulations, although network topology is a more important driver. Another interesting finding is that, on average, the impact on the distal compartment usually changes little with the impact on the proximal compartment for any given model configuration and intercompartment connectivity, implying that cascading effects do not propagate far. This may seem to downplay the danger of cascading effects that have long been of concern for ecological prediction and conservation, but complacency should not be allowed to set in—the results of individual simulations (see also Appendix 6.6.2) clearly show that, depending on the specific suite of parameter values (i.e. context), the impact on the distal compartment may sometimes be relatively large even when the impact on the proximal compartment is small, suggesting a large cascade effect.

Negative impacts on the average system energy of proximal compartments of niche-topology models are greater when declinees are all top predators than when they are randomly distributed in the trophic spectrum (Appendix 6.6.2). This may be attributed to species of larger body size having higher population biomass [177], and has implications for the impact of biodiversity loss in real ecosystems, where top predators often decline first. More explicitly, lower trophic levels do not appear to increase appreciably in biomass compensating for top predator loss, meaning that a ‘topless’ ecosystem may have a diminished quantity as well as variety of ecological production, functions and socio-economically valuable services.

As entropy is a measure of the effective number of species, one would expect the average entropy of the compartment in which the declines took place to change more than the other compartment. The results confirm this. Interestingly, when top predators decline in models with niche topology, the impact on entropy in the proximal compartment becomes less negative and more positive on average as intercompartment trophic connectivity increases (Fig. 6.2). This may be attributable to the randomly assigned intercompartment links ‘diluting’ the hierarchical niche topology of the compartment, evening out the energy (biomass) flows across the community.

In terms of community composition, greater changes occur in niche-topology models where the declines are top predators (Appendix 6.6.2), suggesting that top-down effects and mechanisms such as mesopredator release [394] are relatively important, at least in communities where top predators have broader-than-random diets. This again has implications for real-world scenarios where top predators are more vulnerable. The opposing behaviours of models with niche and random topologies are striking. This result underscores the importance of using appropriate network topology when modeling a given system of interest for ecological prediction and management.

The slightly lower occurrence of large impacts on power spectra in either the proximal or distal compartment in models with higher intercompartment connectivity could be partly because the relatively large changes in periodicity regime caused by the perturbation in the proximal compartment are dampened or diluted more by the species in the distal compartment when the intercompartment connectivity is higher. There is considerable variation in the magnitude of impacts on power spectra across simulations, and the impacts in the proximal and distal compartments in a given simulation can be very different from each other. The higher frequency of larger impacts in random-topology models suggests that random topology tends to have lower resilience to perturbations in terms of the manner in which the community oscillates, as characterized by the power spectrum. The variability of impacts, also observed in the other

ecosystem metrics to a lesser extent, is a symptom of context dependency, and again underscores the difficulty of predicting how perturbations will propagate from one compartment to another. The details of species traits and interaction structure mediate the exact pattern of amplitude and frequency of oscillations. It also reminds us that caution should be exercised when extrapolating ecological conclusions and management recommendations for a specific system to other systems that, even if superficially similar, may differ in important details.

There is considerable scope for future research into network compartmentalization in ecology and beyond. Firstly, it remains to be seen whether the results would change with the number of compartments. A particularly interesting aspect of this question is that the answer may depend on how multiple compartments are connected to one another. The two-compartment case is nevertheless useful for understanding how perturbation propagates from one compartment to another, especially when two-compartment systems can occur at some spatial scale in reality, for example aquatic-terrestrial. Secondly, it is possible to combine compartmentalizations at different scales for more realistic representations that mimic the nested or fractal structure of nature, somewhat akin to the ‘super networks’ proposed by OLESEN *et al.* [99]. For example, SCOTTI *et al.* [100] modeled conspecific individual-individual networks within species interacting in food webs that are in turn linked to one another at the landscape level. Their model, however, lacked key interactions such as individual-based interspecific interactions and nontrophic interactions. Thirdly, the compartmentalized network approach could offer new insights into the emerging concept of keystone communities [395] whose removals have disproportionate dynamical impacts on metacommunities. The network approach can accomplish this by enabling important dynamic species interactions to be captured in ecosystem-level indicators of metacommunity resilience.

The findings of this study contrast with some other findings about other kinds of networks. For example, intermediate rather than minimum or maximum connectivity between power grid networks has been found

to minimize the risk and size of cascades [378]. This may be due either to real differences in the processes governing different kinds of networks, or possibly to my model assumptions such as equal average strengths of intra- and intercompartment interactions. More mechanistic studies like these will progressively give us a better idea of the degree of context dependence of the relationship between compartmentalization and network robustness to node failure. Furthermore, even deeper insights may be gained by examining compartmentalization as an effect as well as a cause, an ecological example being the effect of invasions on the way plant-pollinator networks are compartmentalized [396]. Finally, pervading the various proposed avenues for further inquiry is the challenge of acquiring data on compartmentalization in ecological networks at the large scale that has recently been efficiently accomplished [397] for compartments in other kinds of large real-world networks, such as social networks and the Internet.

6.5 CONCLUSION

My results show that ecological network compartmentalization can mediate the impacts of species decline in different ways depending on the ecosystem property of interest, implying that there are no straightforward rules governing how compartmentalization affects ecosystem stability or resilience. In addition, the impact in the proximal compartment not only exists as a direct effect of the decline, but also changes with the intercompartment connectivity. These phenomena underscore an important characteristic of the system, that of two-way feedback: perturbations in one compartment are not only propagated to the other compartment but also ‘bounced’ back to the originating compartment, sometimes as a buffering effect. The results also suggest that both network topology and declinee body size may be important in predicting the impacts of declines on compartmentalized networks. My simulation configuration of top predators declining from the niche-topology network is probably the most frequent real-world scenario among those tested, based on empirical observations of species loss [398] and food web structure (§2.1). It should

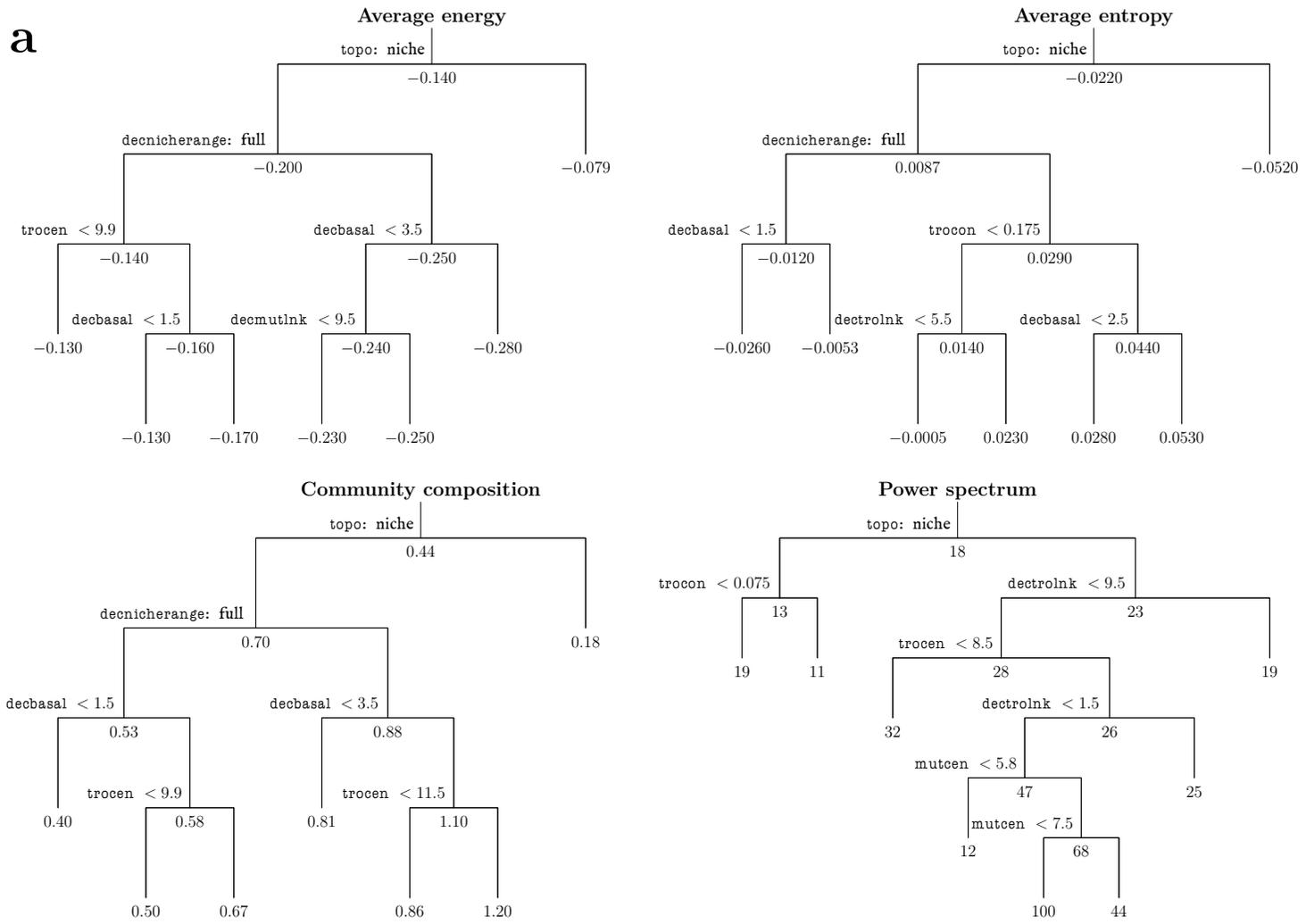
also be appreciated that overarching all of the above observations is the context dependence clearly manifested in my results as variation across individual model simulations—an emergent observation not apparent in isolated ecological studies of individual systems, of which only those with ‘positive’ results tend to get published. I recommend that efforts should continue to face up to the challenge of context dependence in ecology, because it has implications not only for the understanding of the complexity of ecological systems, but also for practical management. There have been calls for combining food web theory and landscape ecology to understand food webs at the landscape level [399,400]; my work takes a step in that direction, incorporating community dynamics and different types of species interactions.

6.6 APPENDIX

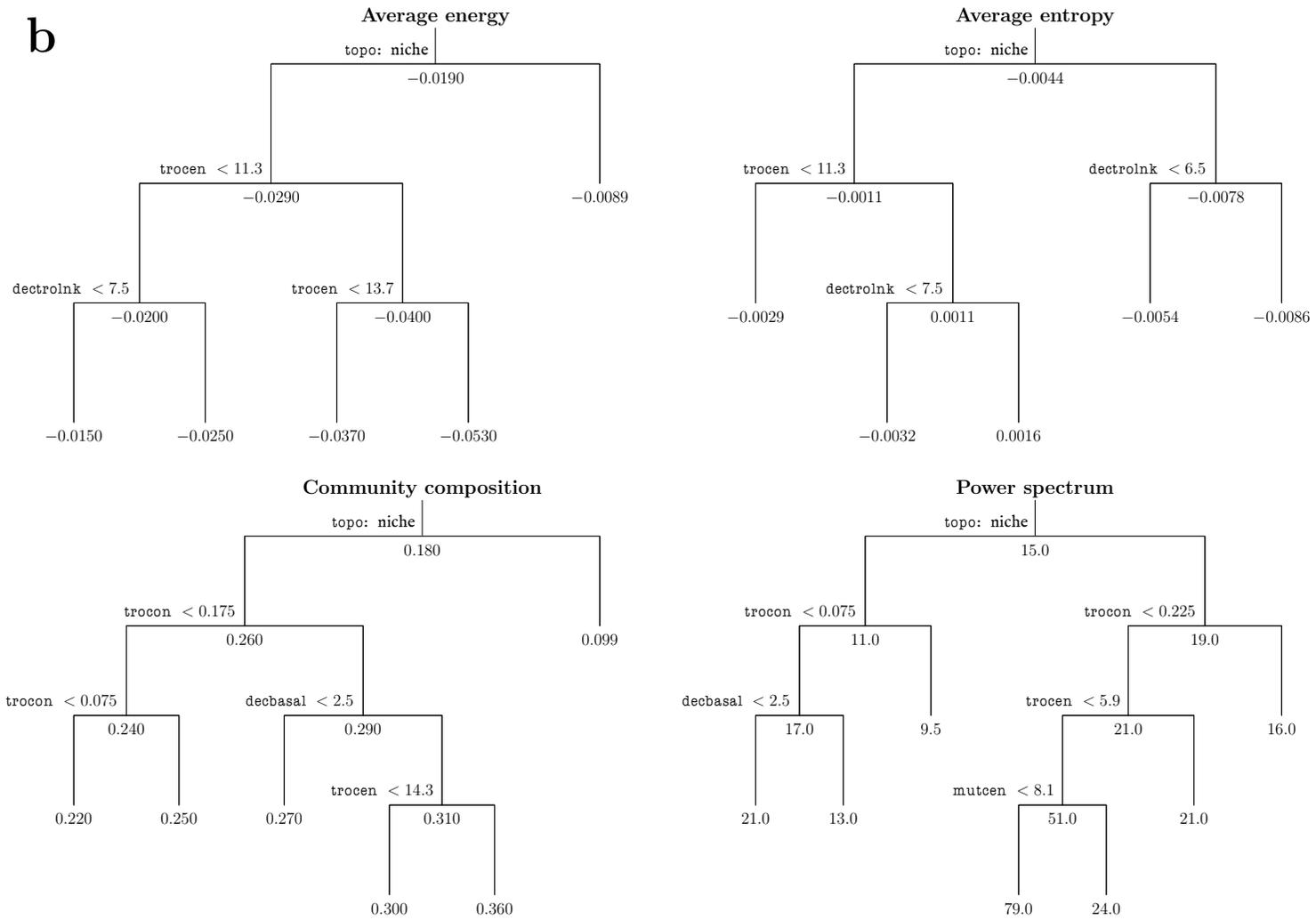
6.6.1 REGRESSION TREES

Regression tree for each of four ecosystem metrics, showing how various explanatory variables mediate the impact of species decline in the proximal (a) and distal (b) compartments of simulated ecological networks. Explanatory variables: *topo*, network topology; *trocon*, intercompartment trophic connectivity; *mutcon*, intercompartment mutualistic connectivity; *decnicherange*, declinee niche range; *decbasal*, number of basal declinee species; *dectrolnk*, number of declinee species with intercompartment trophic links; *decmutlnk*, number of declinee species with intercompartment mutualistic links; *trocen*, average trophic centrality of declinees; *mutcen*, average mutualistic centrality of declinees. Only the nodes with the greatest deviances are split, to show the most important explanatory variables.

a



b



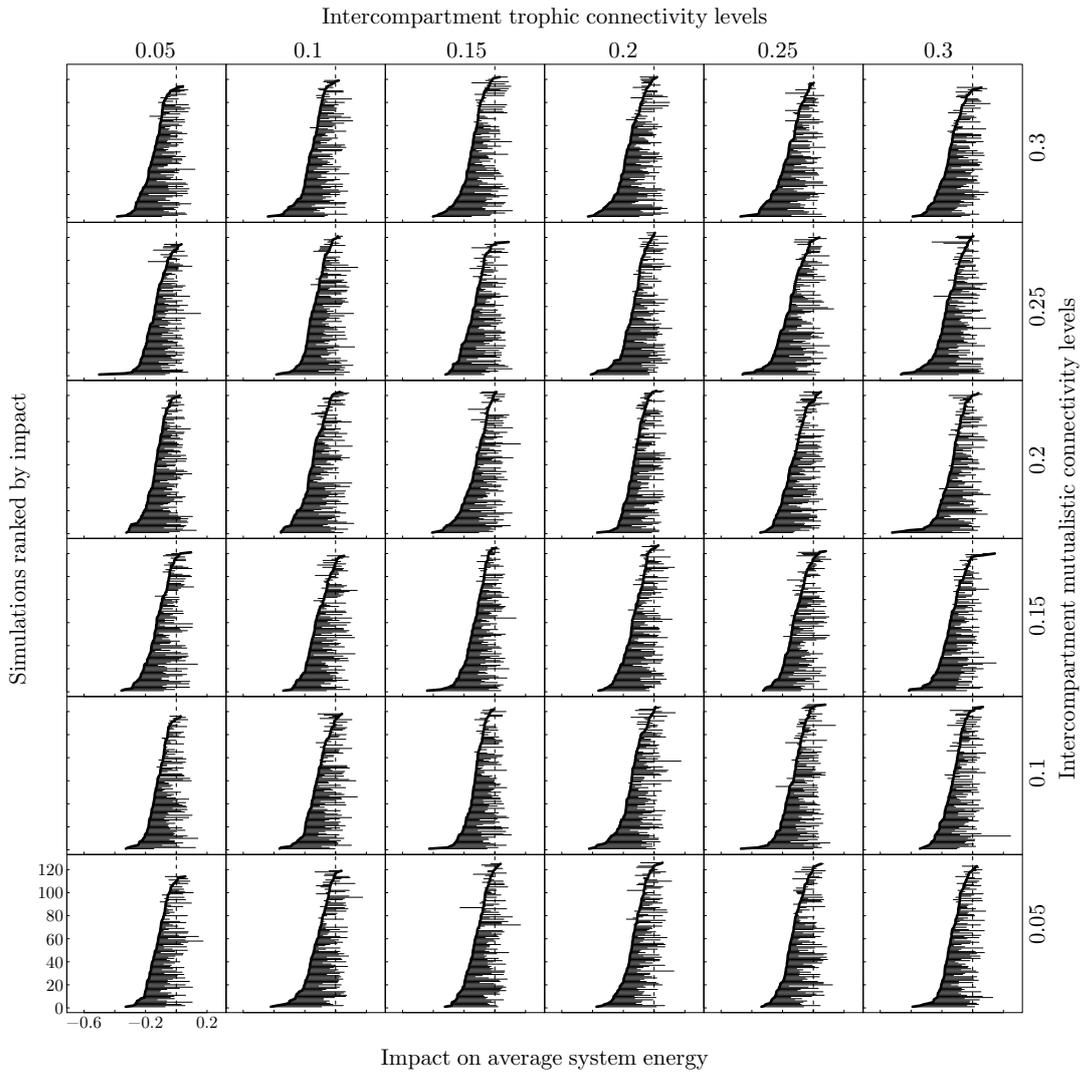
142

Species decline in compartmentalized networks

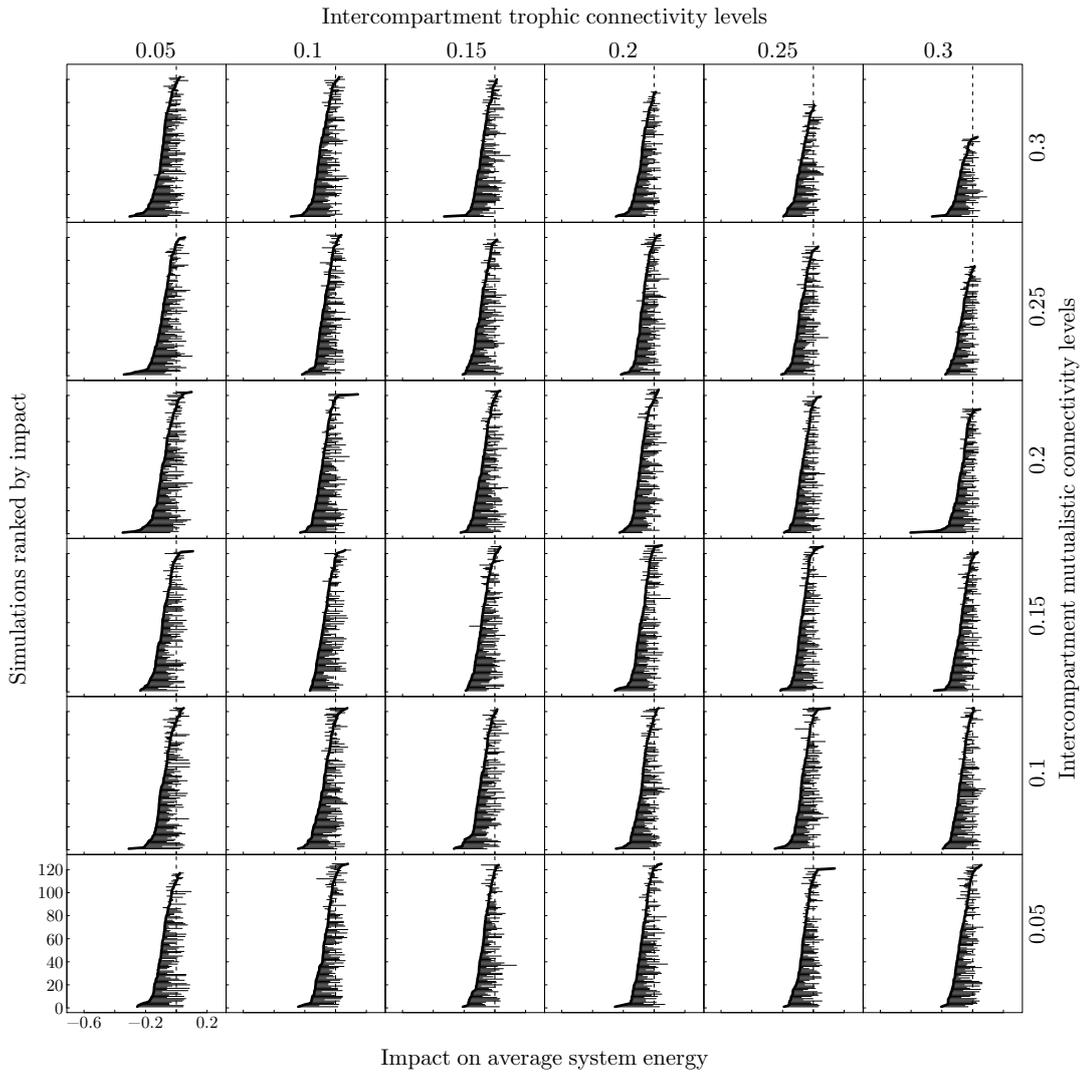
6.6.2 PLOTS FROM ALL TREATMENTS

In each subpanel, the x -axis is the impact on the ecosystem metric and the y -axis is the rank of simulations sorted in increasing order of the impact on the ecosystem metric in the proximal compartment, demarcated by the thick curve. Impacts on the distal compartments of the respective simulations are marked by the free ends of the grey horizontal lines away from the curve. A horizontal line thus measures the difference between impacts on the proximal and distal compartments of a given simulated network, and whether the distal impact is smaller (horizontal line extends leftwards from curve) or greater (opposite direction) than the proximal impact. Vertical dashed lines mark the value 0 on the x -axis (no impact). Axis ranges fixed across all model configurations and intercompartment connectivities within each ecosystem metric.

Species decline in compartmentalized networks

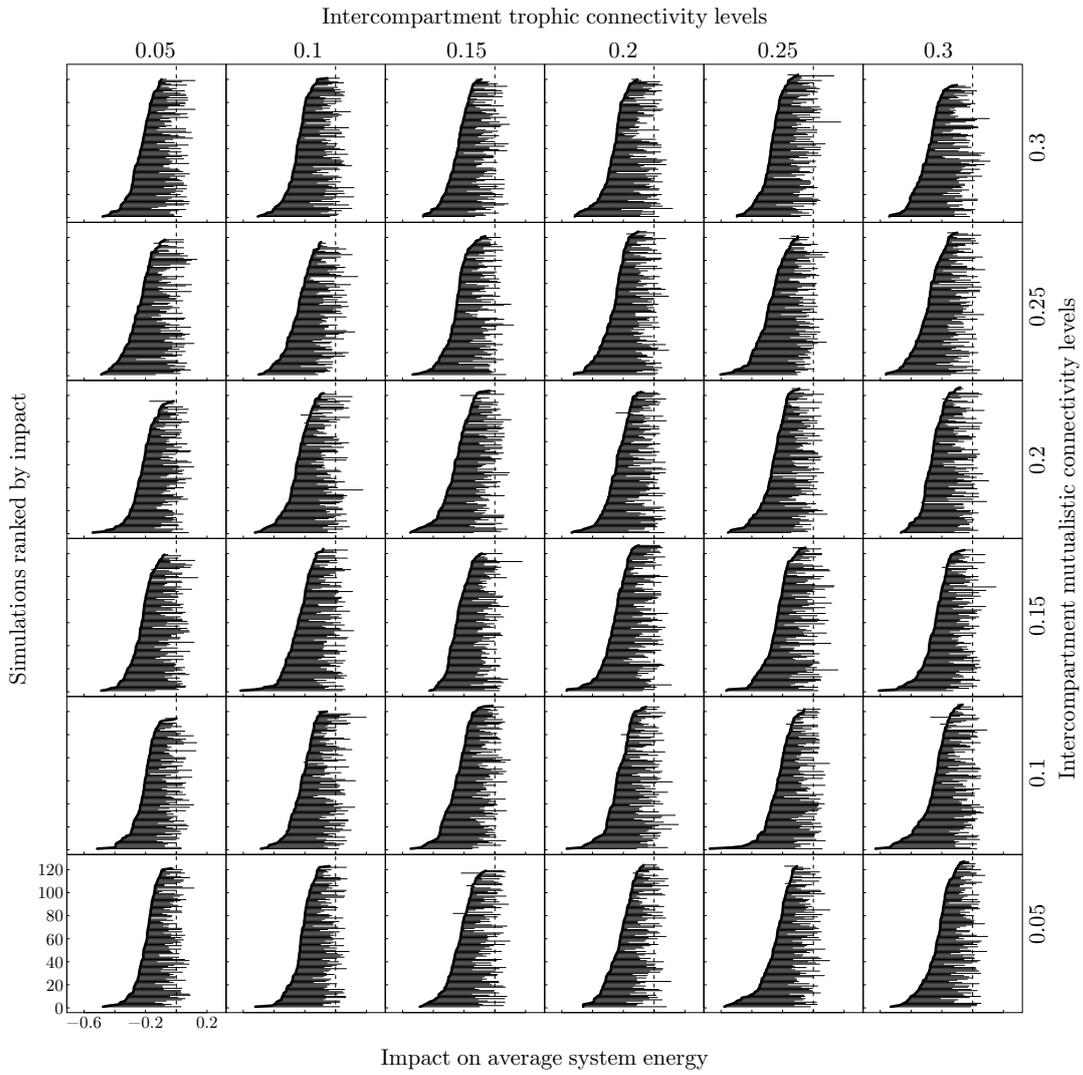


Average system energy: declines from full niche range, niche topology.

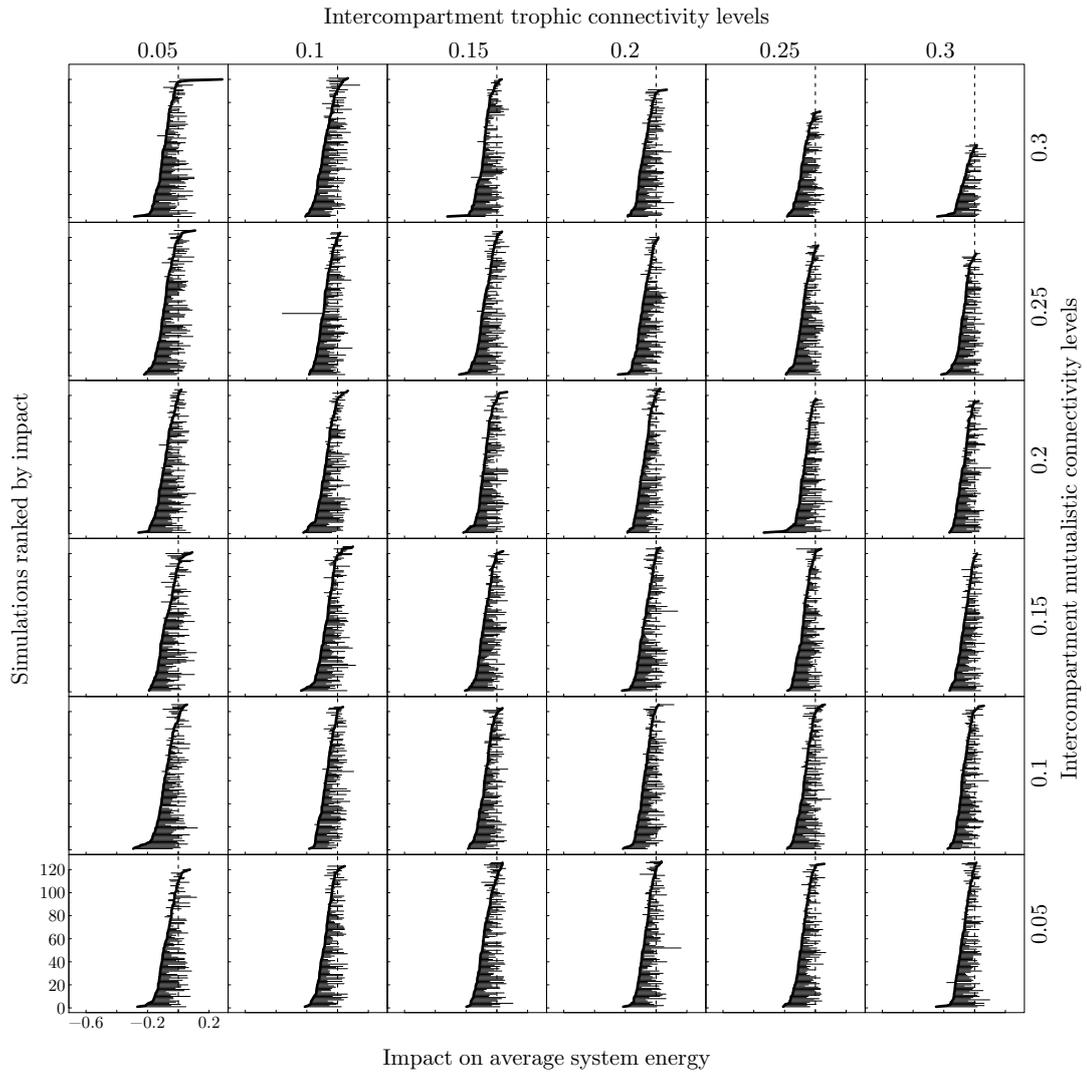


Average system energy: declines from full niche range, random topology.

Species decline in compartmentalized networks

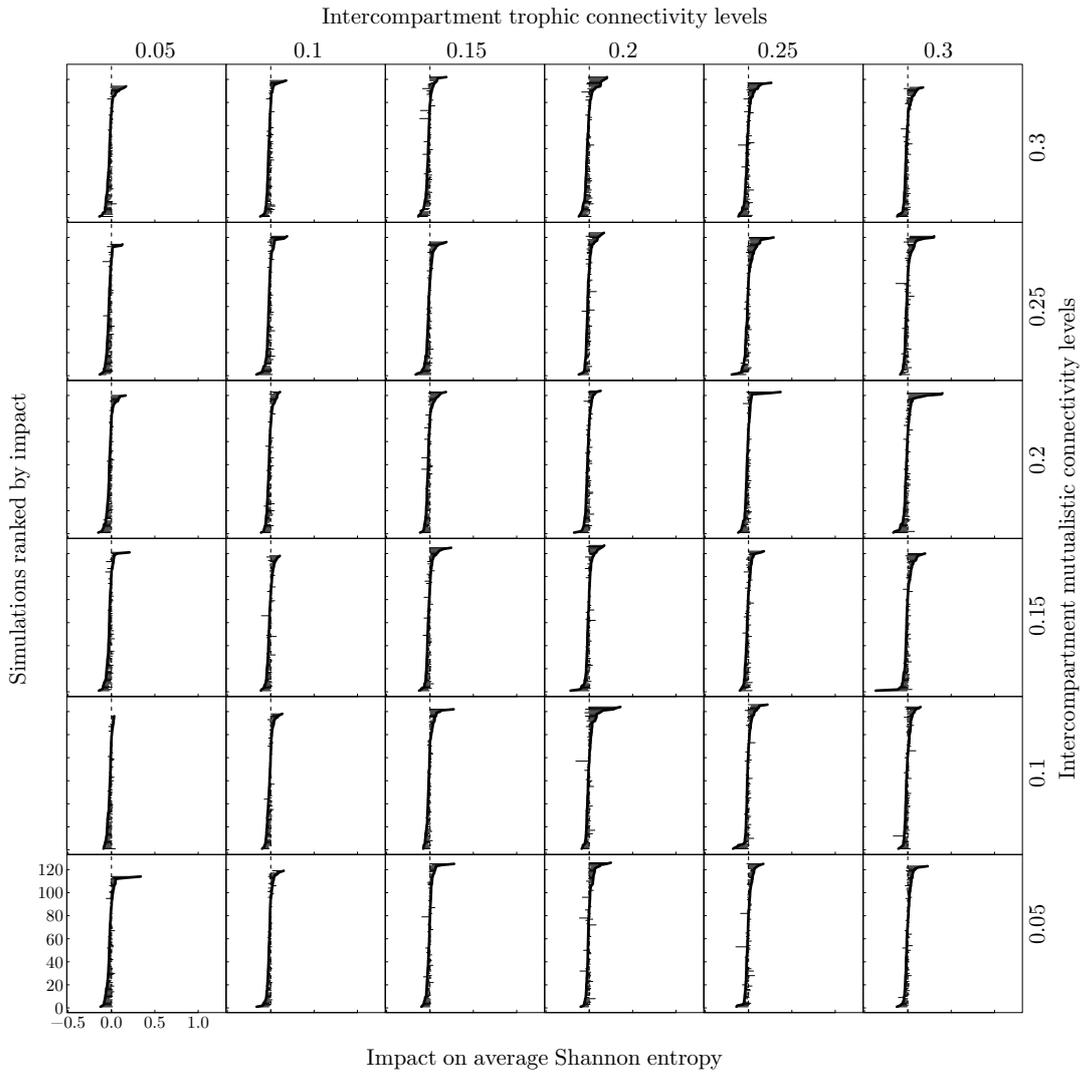


Average system energy: declines from high niche range, niche topology.

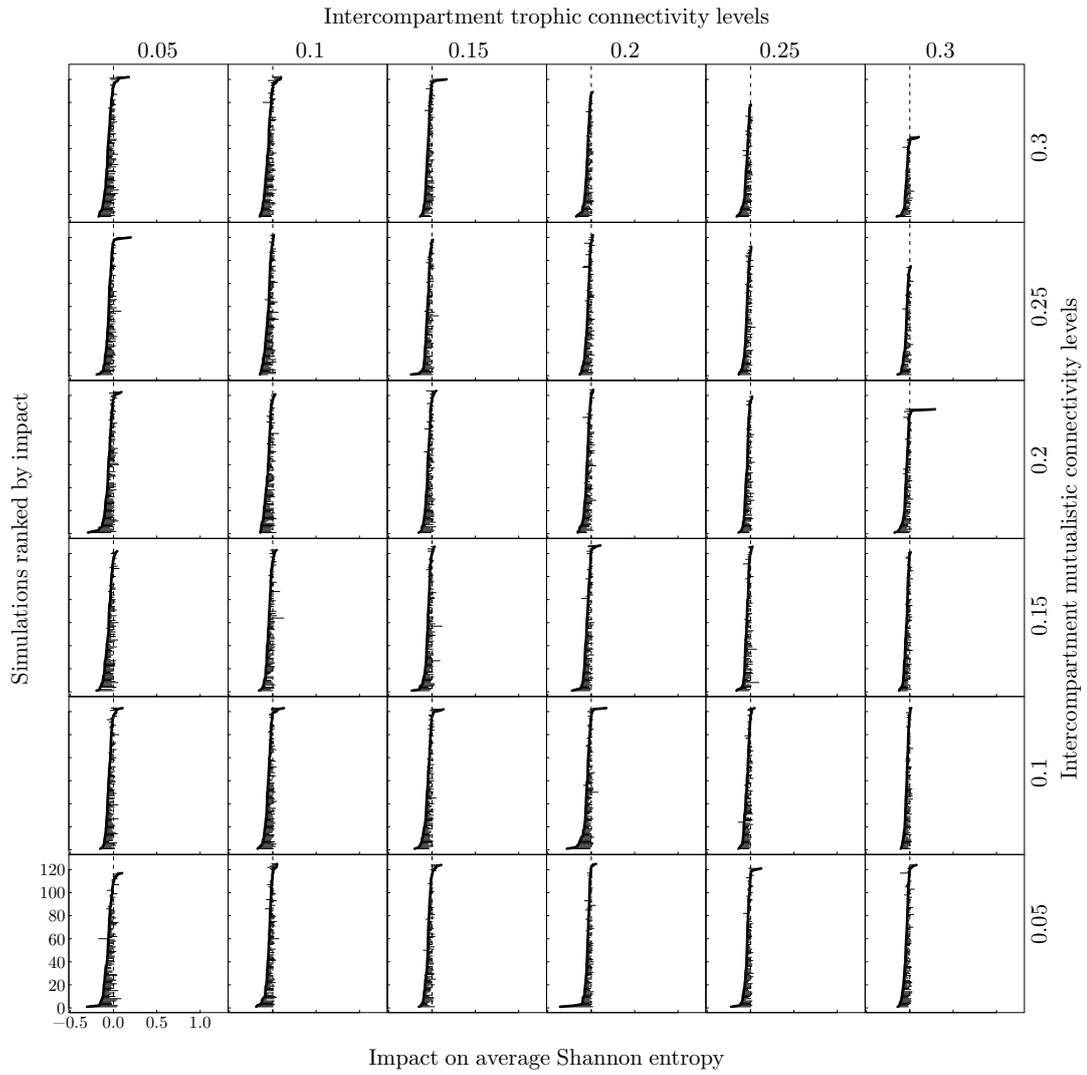


Average system energy: declines from high niche range, random topology.

Species decline in compartmentalized networks

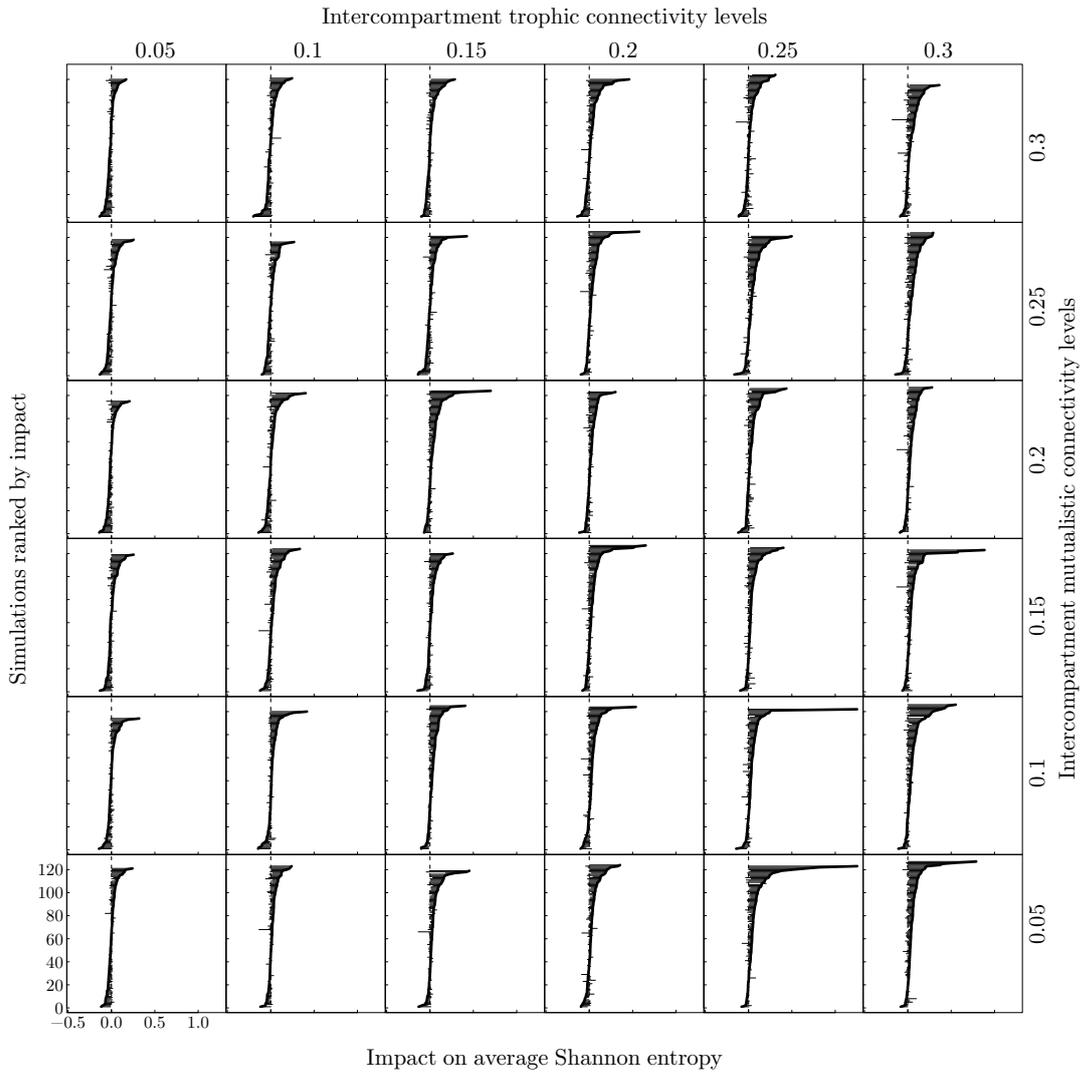


Average entropy: declines from full niche range, niche topology.

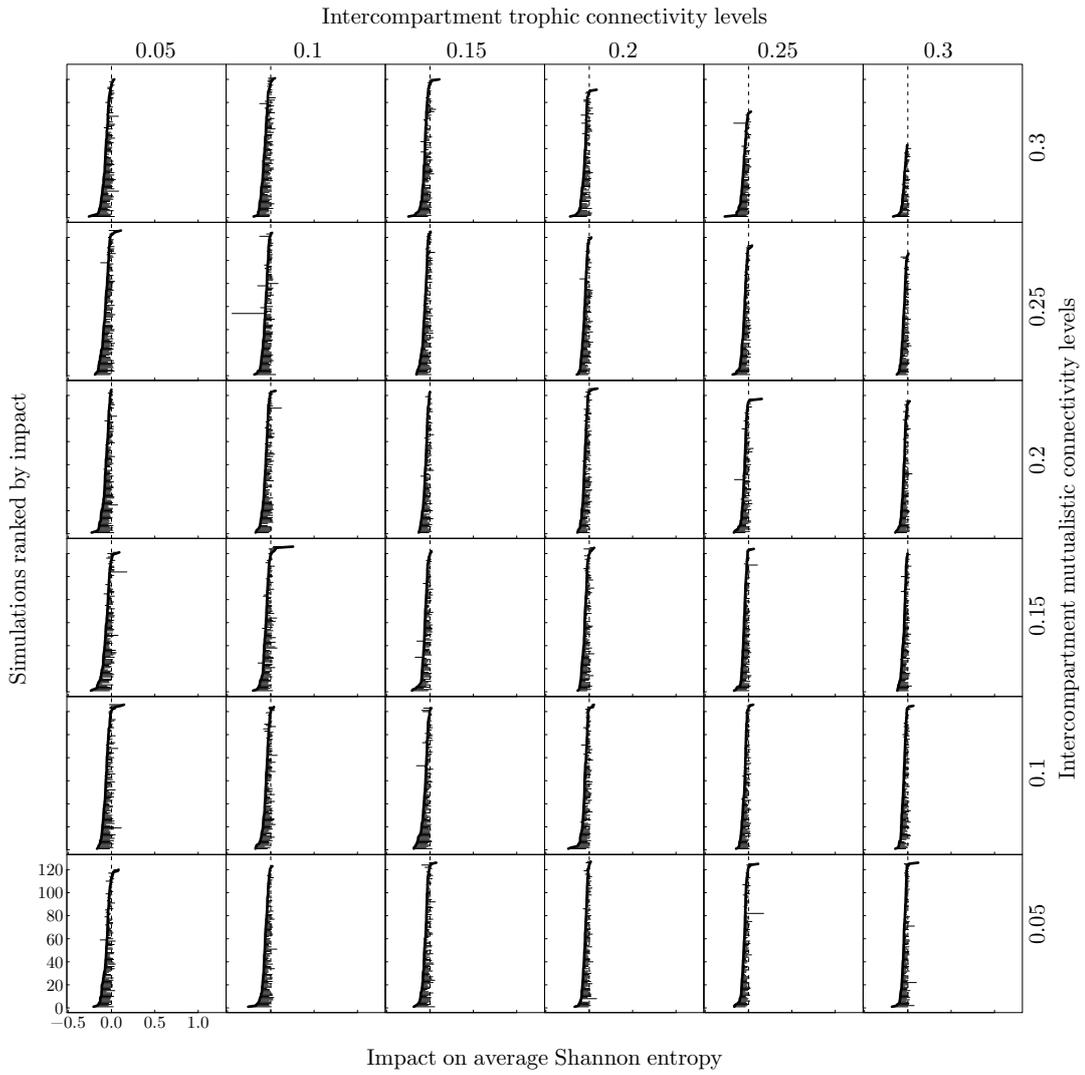


Average entropy: declines from full niche range, random topology.

Species decline in compartmentalized networks

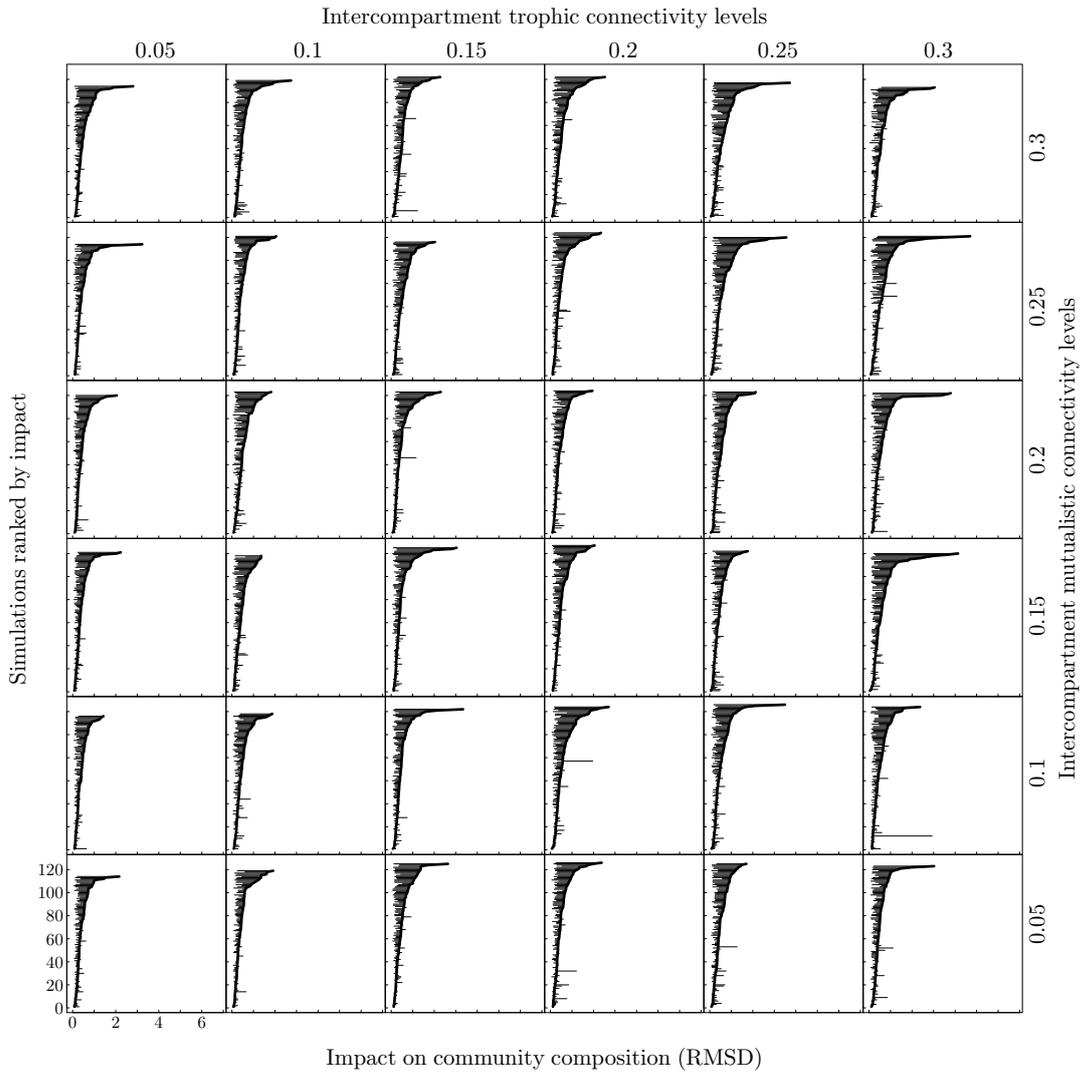


Average entropy: declines from high niche range, niche topology.

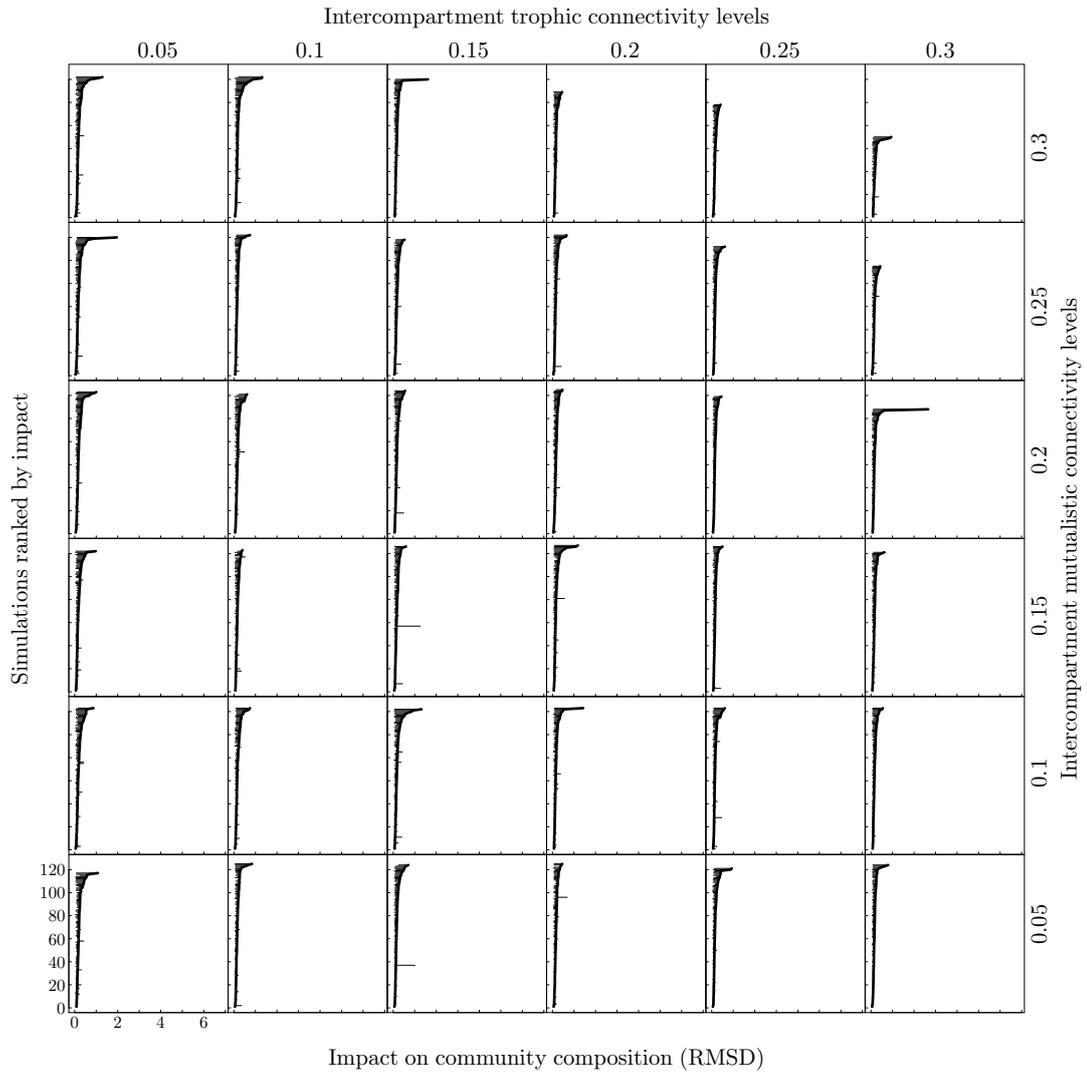


Average entropy: declines from high niche range, random topology.

Species decline in compartmentalized networks

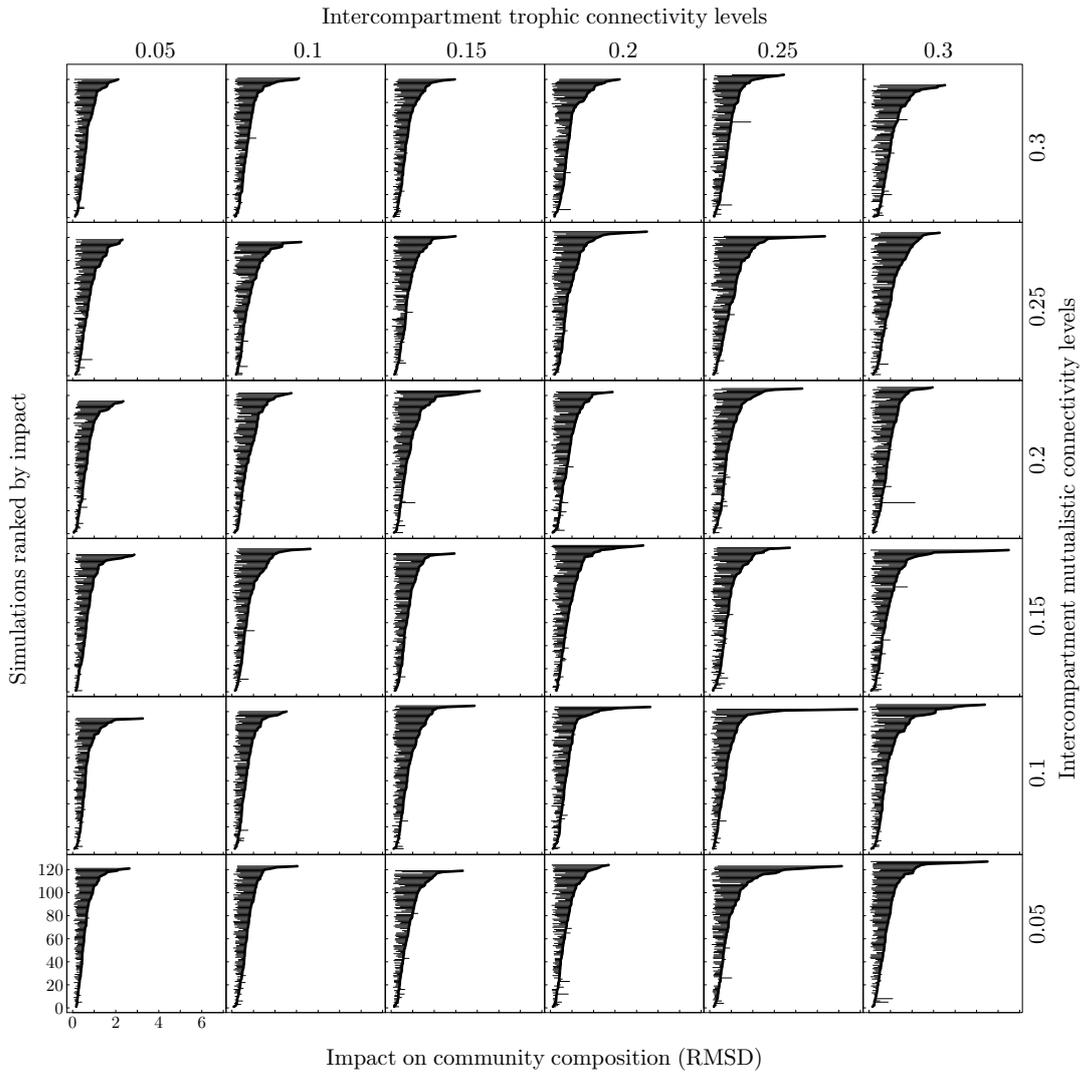


Community composition: declines from full niche range, niche topology.

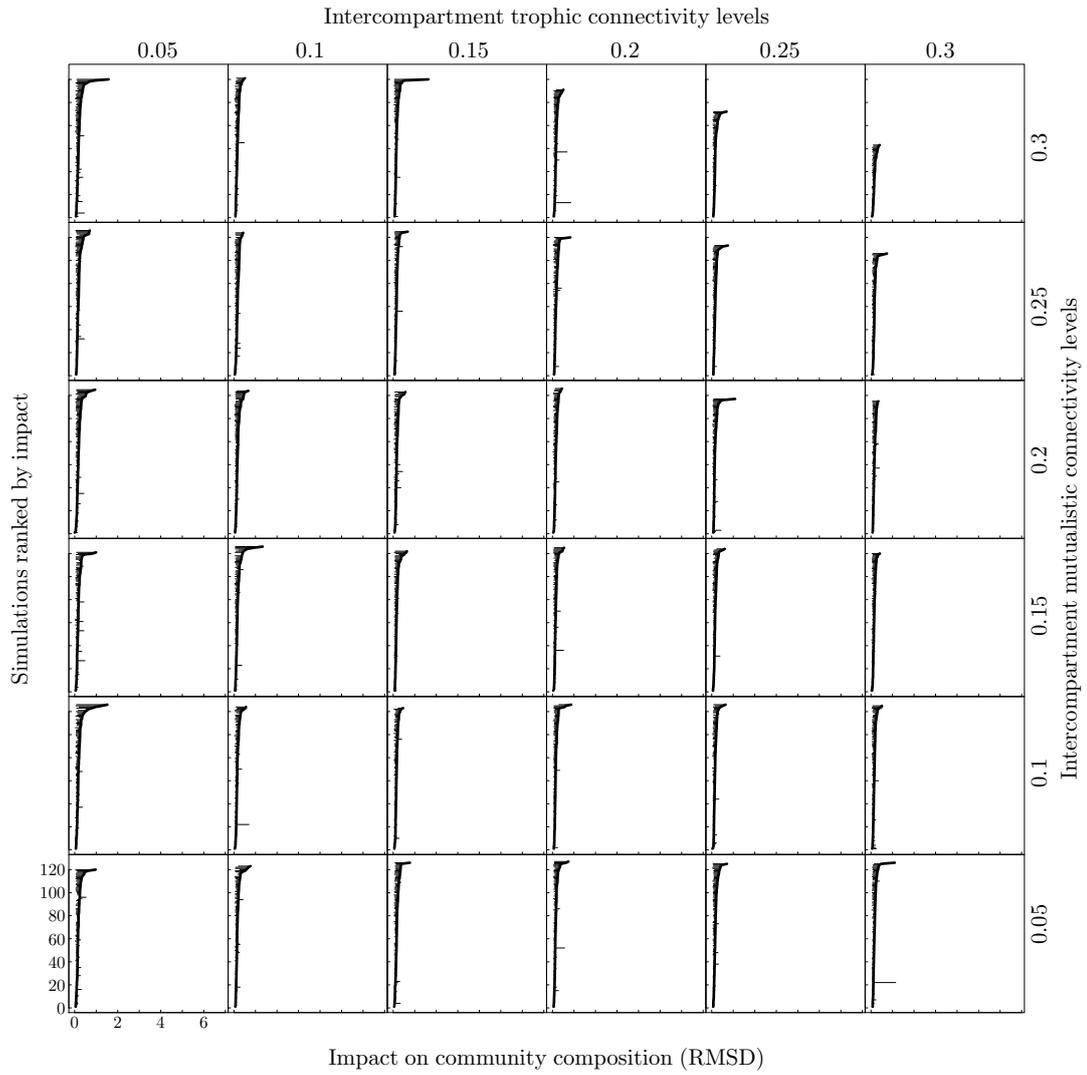


Community composition: declines from full niche range, random topology.

Species decline in compartmentalized networks

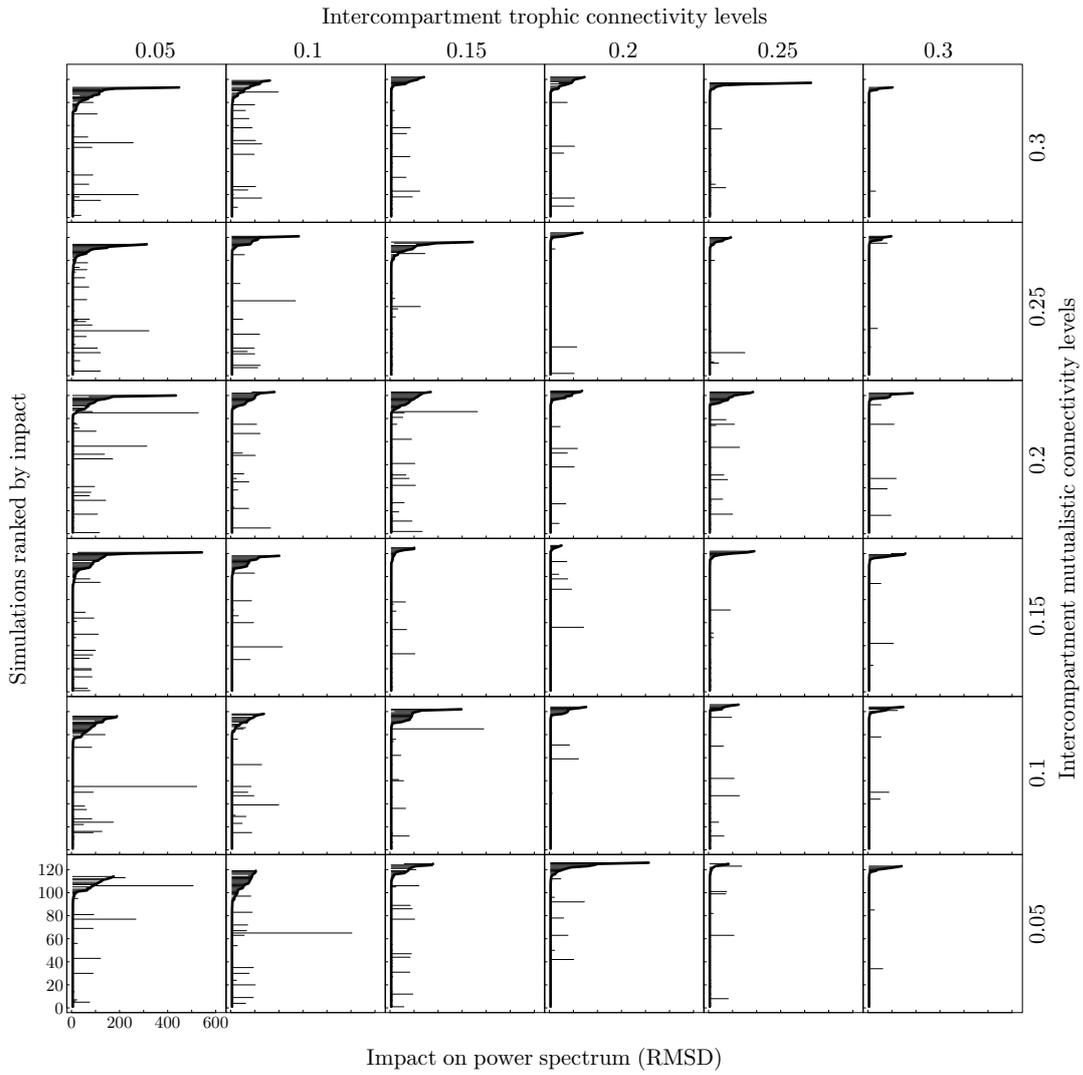


Community composition: declines from high niche range, niche topology.

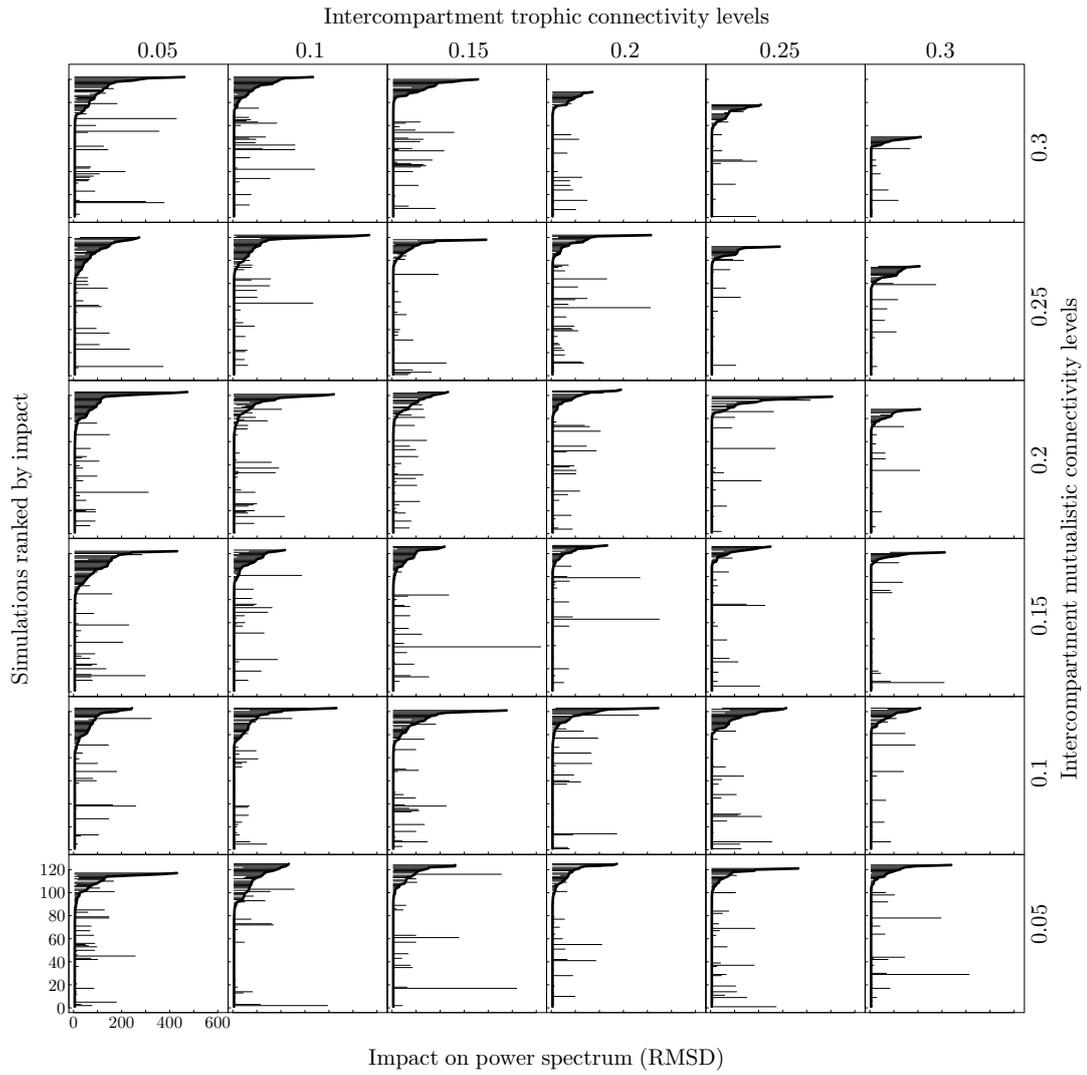


Community composition: declines from high niche range, random topology.

Species decline in compartmentalized networks

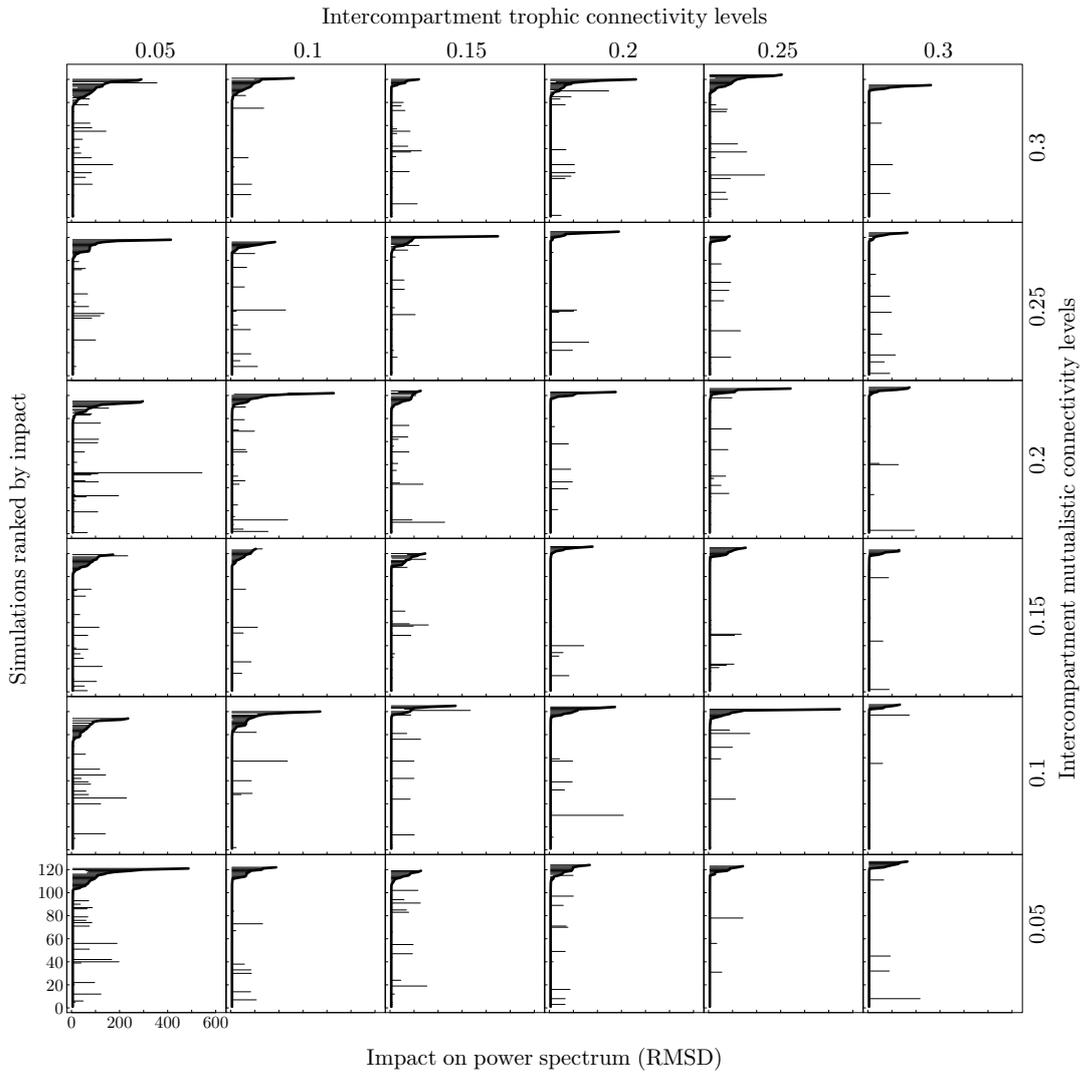


Power spectrum: declines from full niche range, niche topology.

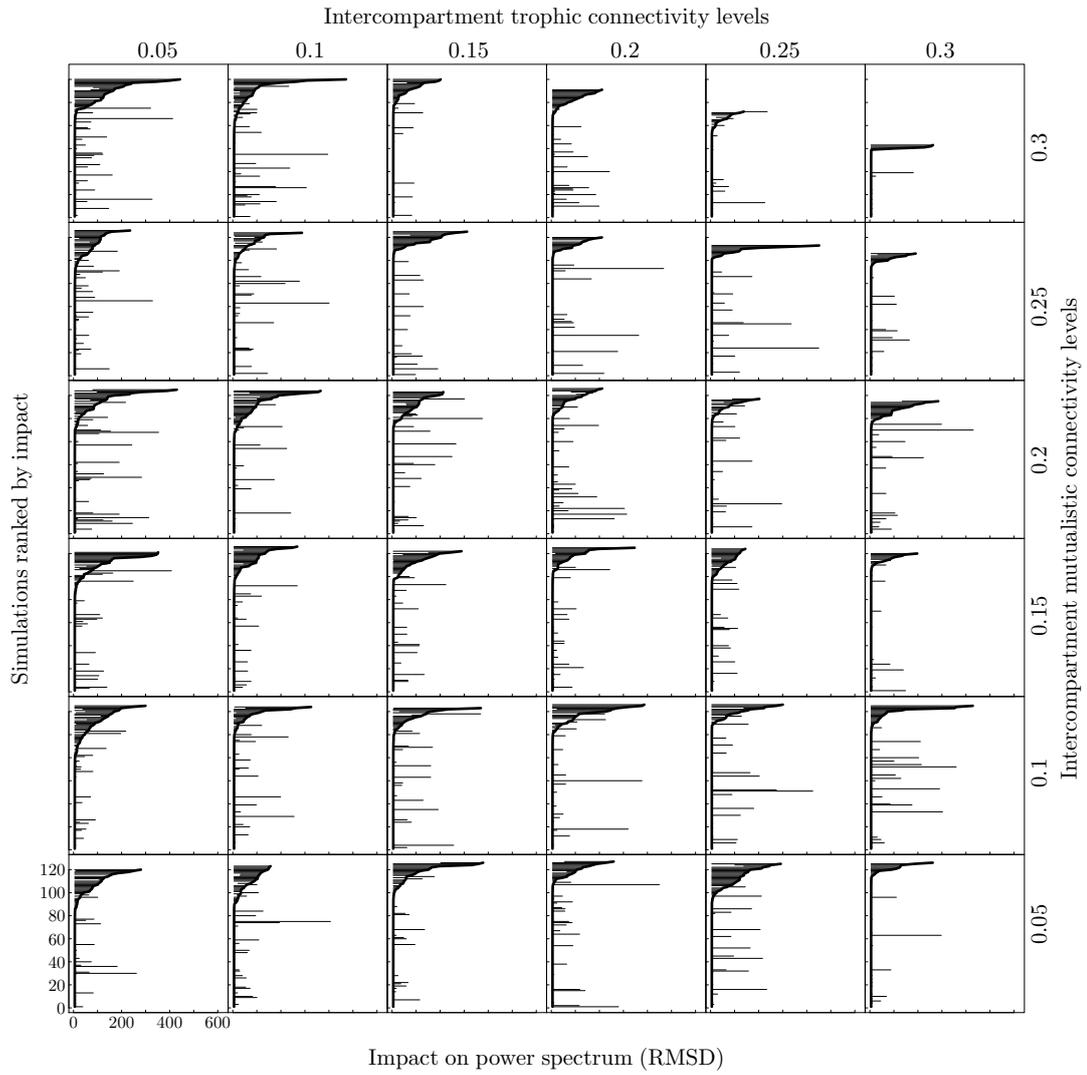


Power spectrum: declines from full niche range, random topology.

Species decline in compartmentalized networks



Power spectrum: declines from high niche range, niche topology.



Power spectrum: declines from high niche range, random topology.



The author's sanctum for inner contemplation. Mediæval brick arch (1490) and timber columns (1912) beneath the oriel window of the Long Gallery, Queens' College, Cambridge. Photograph by the author exhibited at the Arts Festival (2014) in the Old Hall (1449, visible at upper left), Queens' College.

7 CODA

As ecologists, we are very good at finding linear relationships while probing one component of a specific system under a specific set of conditions, but when it comes to the totality of interdependent components under diverse conditions, we hitherto have only a very blurry image. This thesis, synthesizing a broad range of fundamental mechanisms of species interaction in ecological network dynamics, has tried taking some tentative steps towards beginning to clarify that image. There are two overall revelations: that the structure, dynamics and perturbation of complex ecological networks have effects that are highly context-dependent, and that various interesting systematic patterns nevertheless emerge above this context dependence. Where do we go next?

One obvious path is towards application to real-world conservation. A systems approach can facilitate preventive proactive conservation, because one is less likely to let problems develop unnoticed in one part of the system while preoccupied with conserving another part. The public may be reluctant to implement system-level conservation measures, however, if such measures do not have direct and obvious benefits to their immediate component (e.g. charismatic species) of interest [19, 116]. There is also the challenge of identifying metrics can be easily measured in the field that are indicative of ecosystem health [401]. Nevertheless, we are increasingly conscious of the need for ‘system-level conservation ecology’ [38] and ‘conservation of networks’ [402], although some calls for exploiting the power of systems approaches in conservation still focus on particular species as the final deliverable [403]. The pioneering steps have been taken, such as in a field study of the consequences of urbanization on the structure of bird-plant networks [404], helping to understand demographic impacts of environmental change. In time, scientific advancements and changes in public perception will hopefully enable the full potential of systems strategies to be realized. Meanwhile, given that theoretical studies constitute a sizeable proportion of systems ecology research owing to data scarcity, it might be worthwhile considering whether and how

theoretical modeling outputs could serve as evidence for the evidence-based conservation paradigm championed by SUTHERLAND *et al.* [405].

More specific to modeling methodology, some overarching issues remain to be addressed in future work. It would be interesting to investigate network topologies that are influenced more by phylogeny, or other drivers, than by body size; research in this direction has so far considered different interaction types in isolation [24, 406–409]. YAN & ZHANG [410] also looked at how interactions that do not increase monotonically with population density affect community persistence, although they did it separately for predator-prey and bipartite mutualistic dynamic networks under a deterministic framework and did not subject their model communities to exogenous perturbation; there is scope here for more realistic, yet not drastically more complex, models of the type described in my work. There is also a recent rise of an eco-evolutionary perspective on ecological networks, ranging from the relationships between species' taxonomies and their topological positions and functions in food webs [285], to eco-evolutionary dynamics and their implications for climate change [411], and to using networks of interacting computer programmes to mimic and understand species evolution in ecological networks [412]. Such research has exciting prospects for not only ecology but also complexity science at large, as it may extend to more general cases of broad scientific, cultural and policy interest, such as the evolution of technology. Overall, a strategy of using a hierarchy of models of varying levels of complexity to more comprehensively understand the various aspects of the system [413] may be employed to explore all these avenues.

Zooming out again to see both the details and the bigger picture at the same time, one might envision a synthesis of general laws allying ecological networks with complex networks in other disciplines (see §1.2). Knowledge gleaned from the analysis of big data in other kinds of networks could provide insights into properties of ecological networks for which data are scarce. Conversely, ecological networks could potentially provide valuable insights into combinatorial optimization problems in manmade networks, analogous to the way that the adaptive spatial network evolution of

slime molds has been found to help simultaneously optimize transport networks for minimal cost, maximal efficiency and maximal fault tolerance [414]. Such insights could even apply to the arts and entertainment. For example, I would say that motion pictures with complex feedbacks between multiple players resulting in unexpected nonlinear evolution of the story line may be more exciting.

Going back to ecology, an interesting and useful research and management strategy is to look at ecological systems actually interacting with other systems. In modeling terms, this could take the form of an ecological network ‘plug-in’ to system dynamics models of the wider environment. Indeed, linking ecological models with economic, social and other kinds of models has been suggested as a way to make ecology more useful to policy makers and practitioners [415]. Various researchers have pioneered the so-called social-ecological or bio-economic models, with conceptual models (see MILNER-GULLAND [416] for an overview) and simulation models [417, 418] synthesizing ecological system dynamics, human behaviour and management policies. Complex systems science has also been applied to the management of actual social-ecological systems [419, 420]. These efforts, however, have not yet embraced the interaction complexities of ecological networks.

In the policy arena, this multidisciplinary system dynamics approach could prove useful for further boosting the effectiveness of horizon scanning, with the aim of identifying issues of potentially far-reaching future consequences for the global environment [421, 422]. The value of horizon scanning lies not only in identifying a specific issue but also in being able to infer its possible interactions with other components of the system that could engender unexpected and disproportionate consequences for seemingly unrelated components and for the system as a whole. System dynamics and complexity science at large are poised to tackle this challenge at a point in history that many have hailed as the ‘Information Revolution’ (drawing inspiration from the Industrial Revolution). Related fields such as risk analysis [330, 331], and info-gap decision theory [423] where the lack of data and complexity of processes

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make probability calculations impossible, also stand to gain from the insights of complexity science.

Such advancements in networks and complex systems are setting the stage for us to be more proactive with having an oversight and control of everything to secure the well-being of mankind [366,424]; recall the discussion on network control (§4.4). But caution is needed here, for in trying to suppress unfavourable but relatively small ‘earthquakes’ in complex networks, we may inadvertently force a buildup of pressure that triggers big catastrophes, although conversely we might judiciously encourage small cascades in order to avoid a big one. Rigorous control measures may also have the side effect of making the world more tedious, more regimented and less exciting to live in, as well as possibly reducing its adaptability to unexpected exogenous drivers. We should use our understanding of complexity to exist harmoniously within nature, acknowledging the fact that things cannot always be in our favour if overall resilience is to be sustained. An ecosystem does not try to maximize one overall goal, because its constituent agents engage in conflicting selective processes [425]; this, I argue, is what gives rise to diversity and resilience in the face of change. We are seeing something unprecedented in the history of life on earth—an especially intelligent species actually having global oversight rather than solely abiding by local rules giving rise to self-organisation. Who knows where this will lead us?



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