

The Effects of Foraging Behaviour on Food-web Structure and Dynamics



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Declaration of Originality

I hereby certify that the content of the present thesis is my own work, which was developed under proper supervision by my supervisors. No part of this thesis has been previously submitted for a degree or diploma. All material in this thesis that is not my own work has been properly acknowledged in the following sections. As a sign of respect and gratitude to coauthors with whom I cooperated on the published (submitted) chapters, and also for the consistency throughout the present thesis, all chapters are written in the first-person plural.

Hsi-Cheng Ho

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Abstract

A food web summarises the foraging relationships among creatures within a community. Therefore, to understand how food-web structural and dynamical properties emerge, it is essential to clarify how foraging behaviour (as the underpinning driver) shapes the properties at the level of the whole food web. In this thesis, we examine the influence of several behavioural aspects of foraging on food webs, as well as the mechanisms that cause these influences. In Chapter 2, by conducting food-web dynamical modelling that is constrained by species' metabolism (following Metabolic Theory of Ecology, MTE), we bring to light how the foraging strategy and dimensionality interact with food-web structures to determine species coexistence in food webs. In Chapter 3, by further introducing Optimal Foraging Theory (OFT) as a diet choice mechanism, we explore the food-web structural and dynamical consequences when species are able to adjust their diet depending on resource abundances. We show that incorporating OFT indeed significantly affect both the structure and the dynamics of food webs, while the impacts can be varied and dependent on parameters that control the properties of both the community and its species' behaviour. We then proceed in Chapter 4, by modelling using the same MTE-OFT framework, to investigate the emergent food-web structure under conditions where species cannot fully comply with OFT but rather are constrained by the predation risk they undertake. We develop a new model that describes consumers' diet choice under this predation-risk effect, and find that we can capture better the empirical food-web structure than can the classical OFT model without predation-risk considerations. By showing how foraging strategy and dimensionality, adaptive diet choice, and predation risk-driven response scale up their effect to determine food-web properties, overall, the findings of this thesis shed light on how food-web properties emerge from organismal foraging behaviour. Also, the present thesis lays a firm quantitative foundation for future work in food-web ecology.

“

*He who fights with monsters might take care lest he thereby become a monster.
And if you gaze for long into an abyss, the abyss gazes also into you.*

”

– Friedrich Nietzsche, *Beyond Good and Evil*

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Chapter 1

Background

A food web is a network that depicts the foraging relationships among species¹. It is necessary for ecologists to understand the properties of food webs to resolve ecosystem-level questions that are directly relevant to trophic interactions, such as those regarding energy, nutrient, or biomass flows (e.g., Gravel *et al.* 2016; Harvey *et al.* 2017) and the sustainability of biodiversity (e.g., Dunne *et al.* 2002b; Tylianakis *et al.* 2010). Trophic interactions, as the links in food webs, are in fact summarising accumulations of foraging events between individual organisms. All food-web structural and dynamical properties are hence “emergent properties” that arise from individual foraging behaviour (Beckerman *et al.* 2006; Petchey *et al.* 2008; Stouffer 2010). In this sense, to better understand food webs, it is vitally important to explore the effects of underpinning behavioural mechanisms, and how they may scale up to determine the whole-web properties.

In the sections below, we first introduce the key properties of food webs. Then, we give an overview of the behavioural aspects of foraging that are likely to be critically influential to the emergence of these food-web properties. Lastly, we summarise the knowledge gaps that we aim at filling with this PhD study.

¹Henceforth we focus on species-to-species trophic interactions but not those with non-living participants, e.g., detritivores consuming organic particles

1.1 Structural and dynamical properties of food webs

In a food web, species² are depicted as nodes, whereas the trophic interactions among them as links. The links are directional, indicating the resource and consumer roles of the interacting pair. For a species, its diet and its consumer(s) together define which other species it connects to. Meanwhile, some node-level features can be derived from its resource-consumer relationships with others. For example, the trophic role (e.g., trophic guild, trophic level) of the focal species, and its in-degree (generality) and out-degree (vulnerability). A summary of these commonly measured node-level features and their definitions can be found in Table 1.1.

Viewing the whole picture of all species and their interactions, the way that nodes and links are distributed within the web (i.e., the pattern of how nodes are connected) gives the topology of the food web. Topology, by definition, does not contain quantitative information of either the nodes or links. Thus, when quantifying topology, all nodes and links can be considered identical without distinguishing the exact species identities among them. Many whole-web topological features have been used in the study of ecological networks. For instance, connectance measures the proportion of all potential links that are realised; modularity quantifies the tendency that a web comprises several relatively independent sub-webs. A summary of these commonly measured topological features, along with their definitions, are given in Table 1.2.

While the topology considers purely the arrangements of the nodes and links of food webs, these food-web components in fact each have biologically quantifiable numerical sizes, e.g., species' abundances and body sizes for the nodes and interaction strengths for the links. This quantitative information, together with the trophic relationships among species that are reflected in the topology, yield the quantitative structures of food webs (Woodward & Hildrew 2002; Banašek-Richter *et al.* 2004; van Veen *et al.* 2006). Because species abundance and interaction strength have been shown to exhibit clear scaling relationships with species body size (which will be elucidated further below in the following chapters), the body-size structure

²Throughout this thesis, we focus on the resolution where species serve as nodes. This includes our theory development, modelling, simulation, and the usage of empirical data. Indeed, nodes in a food web can be defined as trophic groups assembled at other scales, e.g., life stage, depending on the focal resolution. The resolution-relevant issues, e.g., the effect of ontogenetic growth of species, are discussed in the following chapters where appropriate.

can be seen as the most fundamental quantitative structure of food webs (Woodward *et al.* 2005). Quantitative structural features are usually measured as statistical summaries of some node or link quantities across the whole web with a given topology. For example, the mean resource-consumer body-size ratio of the whole web, and the correlation between species' body sizes and their trophic levels. Again, we summarise the commonly measured quantitative features of nodes, links, and the web as a whole in Table 1.2.

The food-web topological and quantitative structures introduced above are properties that reflect the instant state of the food web at a given time point, just like taking a snapshot. However, through their trophic interactions, species consume, and therefore lead to changes in the abundances of, each other. Food webs are thus essentially dynamical, with the quantitative sizes of their components (i.e., nodes and links) and also the structural properties of the whole web being able to vary over time. It is, therefore, necessary to consider the dynamical nature of food webs, along with their structure, to understand how they actually function. Understanding food-web dynamics is especially important when facing questions regarding the sustainability of biodiversity in complex ecosystems, where one would need to know the dynamical fate of species.

A major concern for ecologists, and therefore much of the focus of work on food-web dynamical properties, is the ability of a food web to maintain or recover its integrity over time. Largely, these properties are based on the quantification of the occurrence and severity of species extinctions during the course of food-web dynamics. Because long-term empirical food-web data with explicit population sizes are rare (see Ushio *et al.* 2018, as an example), our understanding of food-web dynamical properties has been built largely on the theoretical modelling of food-web dynamics. Such modelling approaches are diverse, focusing on different biological processes at different time scales. For example, the dynamics of species abundances has commonly been modelled using the Lotka-Volterra type of models (Volterra 1926), which describe (comparatively) instantaneous population size fluctuations. Meanwhile, there are also models that operate at the time scale of food-web assembly (i.e., focusing on species invasions and losses in the focal community) (e.g., Pawar 2009; Maynard *et al.* 2018) or evolution (i.e., focusing on trait evolution and trait-matching trophic relationship establishment) (e.g., Cal-

darelli *et al.* 1998; Rossberg *et al.* 2006). The miscellaneous approaches have thus given rise to a variety of dynamical properties—such as feasibility, local asymptotic stability, or robustness—that are each more or less built upon unique dynamical contexts. These properties, though, have often been generally called “stability” and carelessly used interchangeably, which has led to confusion and inconsistent interpretations regarding food-web dynamics (Ives & Carpenter 2007). We here summarise a thorough list of food-web dynamical properties with their definitions in Table 1.3, which will be followed throughout this thesis. Also, the detailed explanation and the biological meaning of some measurements regarding these dynamical properties will be provided in the following chapters where they are studied.

The structural and dynamical properties of food webs are not mutually independent. After all, the dynamics of a certain species within a food web is driven, collectively, by all the trophic interactions in which it is involved. Different topologies and body-size structures yield different interaction patterns among species, which therefore lead to different dynamical outcomes of the species and the food web as a whole. Indeed, plenty of studies have reported that both the topological (e.g., Dunne *et al.* 2002b; Krause *et al.* 2003) and body-size (e.g., Otto *et al.* 2007; Brose 2010) structures can be influential to food-web dynamics. Given this knowledge, however, the connection between underpinning behavioural mechanisms and the formation of some non-random food-web structures remains weakly explored. Also, how mechanistically these non-random structural properties interact, alongside foraging behaviour, to affect the dynamics of food webs remains unclear. Further exploration in these directions could greatly facilitate our understanding of a long-lasting fundamental question in ecology, that is, what maintains the grand complexity and diversity we observe in nature?

Table 1.1: Definition of measurements about node and link properties within a food web.

Measurement	Definition
Regarding the nodes	
Node size	Can either be the body size (mass) or the population size (numerical abundance, biomass, or density) of the focal species.
Trophic guild	A species can roughly be categorised into trophic guilds as basal resource (primary producer), intermediate consumer, or top consumer (apex predator) depending on if it is consuming/being consumed by other species. More detailed guild categorisation can further distinguish a consumer as primary consumer, secondary consumer and so on, based on the guild of its resources.
Trophic level	Ideally, the trophic level reflects the position of a species in the food web, such that the basal resources (e.g., plants) occupy the 1 st level, the primary consumers (e.g., herbivores) occupy the 2 nd , and so on. Practically, as a species' diet is likely a mixture of resources across guilds, there exist several ways to calculate trophic level. For details of these ways, see Williams & Martinez 2004. In this study, we use "prey averaged levels" whenever trophic levels are measured.
In-degree (Generality)	Number of links to resources from a species.
Out-degree (Vulnerability)	Number of links to consumers from a species.
Level of omnivory	- As a binary variable, where a consumer species is omnivorous if its diet includes both basal resources and consumer species. - As a continuous variable, where a consumer species is considered omnivorous if its diet covers more than one trophic level (not necessarily includes basal resources). A quantifying index is defined as the variance of trophic levels in the focal species' diet (Williams & Martinez 2004).
Regarding the links, or a subset of nodes with links, of the food web	
Interaction strength	Reflects the frequency or the size of effect of a trophic interaction between two species. One way to quantify the interaction strength is as the direct effect on growth rate that a species imposes on another, that is, the interaction coefficient in a Lotka-Volterra model (see Berlow <i>et al.</i> 2004 for more details).
Link functionality	Links can be classified as functional or redundant based on whether or not they have positive contribution to food-web robustness (which is defined further below). For details, see Allesina <i>et al.</i> 2009.
Trophic similarity between a pair of species	The degree to which two species shared the same interacting species in the food web. Can be quantified as the number of sharing consumers and resources of a pair of species divided by their total number of consumers and resources in combination (Williams & Martinez 2000). Species that share an identical set of resources and consumers sometimes are considered as a single "trophic species" in the web.
Food-chain length	The shortest path (i.e., number of links that goes through the least number of nodes) from a focal species to a basal one (Post 2002).
Loop length	A loop is a path that, following the resource-to-consumer direction of trophic interaction, starts from and ends with the same species without going through other species more than once. Loop length is the number of distinct species within the loop (Neutel <i>et al.</i> 2002).
Loop weights	The geometric mean of interaction strengths of all links in the loop (Neutel <i>et al.</i> 2002).

Table 1.2: Definition of measurements about food-web structural properties.

Measurement	Definition
Regarding the structure of the whole food web	
Food-web size (Richness)	Number of species within the food web.
Connectance	The proportion of realised out of all possible (potential) links of the food web.
Complexity	Either refers to richness, connectance, the product of the previous two, or other indices which positively reflect these measurements (e.g., May 1972). The rule of thumb is that the more nodes and links a web has, the more complex it is.
Food-web height	The longest food-chain length among all (see Cohen & Newman 1991).
Max trophic level	The highest trophic level of all species; the number of trophic levels in the web.
Fraction (proportion) of...	...measurements regarding nodes/links/subset of web that are mentioned above. For example, the proportion of basal/intermediate/top species. In this study, we use the proportion of links where the consumer is larger than the resource as the index of large-eat-small body-size structure of food webs.
Number, mean, or other distribution feature of...	...measurements regarding nodes/links/subset of web that are mentioned above. For example, the number of links, loops, or food chains (i.e., all possible paths from each basal species to each top species, with no loop involved), or the mean resource-consumer body-size ratio. In this study, we use the slope of the consumer-resource body-mass regression (in $\log_{10}$ scale) as the index of a large-eat-large body-size structure (i.e., larger consumers eat larger resources).
Modularity (Compartmentalisation)	The degree of having compartments, which are subgroups of species where many links take place within but few take place between. For details of quantifying methods, see Krause <i>et al.</i> 2003; Thébault 2013.
Nestedness	Viewing food webs as consumer-resource bipartite networks, nestedness reflects the degree that the diet of certain consumers being a subset of other's. For quantifying methods, see Ulrich & Gotelli 2007; Johnson <i>et al.</i> 2013.
Cluster coefficient (Transitivity)	The degree to which nodes form close-knitted subgroups with high density of links. For details, see Opsahl & Panzarasa 2009.
Trophic coherence	The degree of homogeneity of the difference between trophic levels of every consumer-resource pair within the web. For details, see Johnson <i>et al.</i> 2014.
Overall pairwise correlation between interaction strengths	The overall degree of correlation between consumer-on-resource and resource-on-consumer effects. For details, see Tang <i>et al.</i> 2014.
Lack of niches	The level to which species share the same niche, i.e., a particular set of interactions with resources and consumers, within the food web. For details of its quantification, see Haerter <i>et al.</i> 2016.

Table 1.3: Definitions and measurements of food-web dynamical properties.

Term	Definition and Measurements
Feasibility	Whether the system has a dynamical equilibrium at which all species have positive abundances. As a negative abundance is invalid in the real world, having a feasible equilibrium is the prerequisite of evaluating linear stability (see below) around it in biological systems (see Dougoud <i>et al.</i> 2018).
Linear stability (Lyapunov stability, Asymptotic stability)	Whether the system returns to an equilibrium (in terms of species abundances) after being perturbed from it. The equilibrium is considered <i>locally stable</i> if the system can recover from small perturbations or <i>globally stable</i> if can recover from all possible, large perturbations. Local linear stability can be judged by checking the eigenvalues of the Jacobian matrix evaluated at the equilibrium. The perturbation diminishes with time if, and only if, all eigenvalues have negative real parts. (May 1972, 1973). The values of such real parts can therefore be used to judge whether the system is locally stable at a given equilibrium (i.e., whether the real part of leading eigenvalue is negative) or how far is the system away from being stable (i.e., how small is the positive real part of leading eigenvalue).
Robustness (Persistence)	The ability of a community to maintain its biodiversity (species richness). It can be quantified in several ways, e.g., the number of species removed before all secondary extinctions lead to a cumulative 50% species loss (Dunne <i>et al.</i> 2002b), the proportion of species that survive the dynamics (Stouffer & Bascompte 2010), or the probability that all species survive after a perturbation in a given time (Kondoh 2003).
Resistance	The ability of a community to stay unchanged by perturbation to population sizes. Can be quantified by the degree of change, or the time needed for reaching a non-equilibrium perturbed state where longer time indicates higher resistance (Pimm 1984; Vallinaa & Le Quéréa 2010).
Resilience	The ability of a community to recover. It can be quantified by the rate of the system going back to a steady state after a perturbation (Pimm 1984; Vallinaa & Le Quéréa 2010).
Permanence	Without presupposing a steady state or equilibrium, permanence states whether a community has all components' population size positive and finite, and whether this is still true when population sizes are very small (Jansen & Sigmund 1988; Kristensen 2008).
Structural stability	Whether the system is able to keep its structure and behaviour (e.g., the dynamical trajectories of species) unaffected by perturbations to the system itself (i.e., not to the population sizes, but to the key parameters such as species growth rates).
Variability	The variance of population sizes over time (Pimm 1984). A lower variability indicates a higher stability.
Extinction rate	The rate that species go extinct. The system is considered internally stable if the extinction rate is low.

1.2 Foraging behaviour

As already mentioned, food-web properties emerge from foraging behaviour. The diets of every consumer species conjointly determine how species are linked to each other in the community,

and therefore the topological and body-size structures of the food web. The behavioural mechanisms of consumer species to make their diet choice should thus be the underpinning force that shapes the structures we observe in natural food webs (Petchey *et al.* 2008; Bestion *et al.* 2019; Portalier *et al.* 2019). Furthermore, food-web dynamics are essentially determined by the size of influences that species give to, and receive from, each other (i.e., interaction strengths), which are also driven by behavioural mechanisms. Indeed, the consumer's foraging strategy and dimensionality (both are defined below) largely influence the encounter rate between itself and its resource, and thus the frequency of realised foraging events (Pawar *et al.* 2012; Pawar 2015). Also, the consumer's consumption rate may have certain kinds of resource abundance-dependence, which regulates the strength of trophic interactions and makes it variable during the dynamics.

Below we elucidate further the fundamental concepts that underpin these behavioural aspects, and review what has been studied about their influences on the food-web structural and dynamical properties.

1.2.1 Strategy and dimensionality of foraging

In general, the strategy with which a consumer forages can be categorised into three types, namely grazing, active-capture, and sit-and-wait, based on the relative mobility of itself and its resources (Schoener 1971; Huey & Pianka 1981). Grazing refers to the condition where the consumer is mobile when searching for resources, while the resource individuals are immobile (or have negligible moving ability in comparison with the consumer's speed). The consumer thus searches through a space and harvests the encountered resource. For example, a deer grazes for grass on the ground. In active-capture, both the consumer and resource are mobile within the space where the foraging takes place. For example, an otter hunts fish in rivers. Sit-and-wait, lastly, refers to the condition where the consumer is not moving (or has negligible moving speed in comparison with the resource's) during foraging, but passively waiting for the visit of the mobile resource individuals (that are either actively moving, or passively drifted by the environmental substrate). For example, a rattlesnake ambushes small mammals that pass

by. Meanwhile, the spatial dimension in which these foraging acts are conducted can be either 2D or 3D. The former means that species are interacting on a 2D plane, e.g., on the ground, while the latter means that they are interacting in a 3D volume, e.g., within the pelagic zone of a water body (Pawar *et al.* 2012; Barrios-O'Neill *et al.* 2016).

The foraging strategy and dimensionality mechanistically determine the encounter rate between the consumer and the resource, and therefore the interaction strength between them. In this respect, the study by Pawar *et al.* (2012) has given detailed explanation of the mechanisms and provided well-founded parameters that were supported by empirical data. As their parameters will be used throughout this thesis, to provide a general mechanistic idea, we here briefly restate the main concepts of their work.

The searching and encountering between individuals can be conceptualised as particles' moving and collision within a space. The more individuals in a given habitat and the faster they move, the more frequent they may meet each other. Therefore, the encounter rate at species-level between a resource-consumer pair is in proportion to the abundance of either side, as well as the per-capita search rate of the consumer. The per-capita search rate is how fast an individual consumer could cognitively discover resource individuals within the habitat. It is the product of population-averaged relative velocity (i.e., how fast a consumer and a resource move toward each other across the physical landscape of the habitat) and detection region (i.e., the area/volume within which the consumer and resource can sense and react to each other) of the two species. Both the relative velocity and detection region are positively correlated to the body sizes of the interacting species, because larger individuals in general move faster and can sense (or be sensed) from further away than the smaller ones (Peters 1983; Pawar *et al.* 2012). Apart from body sizes, the relative velocity depends, obviously, on the mobility of both species and therefore the foraging strategy. Meanwhile, the shape of the detection region depends on the foraging dimensionality, as generally it would be a circle on a 2D plane while a sphere in a 3D volume. This is how both of these behavioral features—foraging strategy and dimensionality—play important roles in determining the encounter rates and thus the interaction strengths within a food web.

Given such mechanisms, these features have been proposed to be the determinants of key food-web properties (Pawar *et al.* 2012; Dell *et al.* 2014). Their effects, however, have mostly been explored focusing on resource-consumer pairs *per se* (e.g., Barrios-O'Neill *et al.* 2016, 2019), rather than the whole food web. Only recently have studies took the later perspective and revealed that foraging dimensionality can shape the resource-consumer body-size relationship in empirical food webs (Brose *et al.* 2019; Pawar *et al.* 2019). Following these early evidence, further explorations are therefore needed to fully clarify how key food-web structural and dynamical properties are influenced by foraging strategy and dimensionality.

1.2.2 Diet choice and abundance dependence: an optimal foraging perspective

What mechanisms drive an individual's diet choice has long been a central focus in behavioural ecology. By using theoretical methods from economics, the Optimal foraging Theory, OFT (Charnov & Orians 1973; Stephens & Krebs 1986), presents a theoretical body for modeling the mechanism of diet choice of species. In OFT, foraging is considered as a series of encounter-decision events of the consumer, who either decides to pursue or ignore the encountered resources of various types. There are three major constraining assumptions of OFT, that is, for a consumer: (i) Searching for and handling resource items (e.g., individuals) are mutually exclusive acts. (ii) Resource items are sequentially encountered. (iii) It has perfect knowledge of all necessary information to make the foraging decision (Danchin *et al.* 2008). The fundamental concept of OFT is that a consumer's diet should maximise fitness (i.e., achieve "optimality"), thereby be favoured by natural selection, and the mechanism of making such diet choice should thus be maintained in the population (Pyke *et al.* 1977; Danchin *et al.* 2008). The consumer's energy intake is taken as the proxy of its fitness. When the consumer searches for food in the field, it may encounter, and potentially engage into foraging with, different types (e.g., species) of resource. The consumer's encounter rate with each type of resource depends on their abundances, meanwhile the rate of consuming them is constrained by the time spent on handling (given the constraining assumption (i) above). Therefore, the energy

intake rate of the consumer is resource-abundance-dependent and adopts a (multi-species form of) Type-II functional response. Natural selection should make the consumer able to adjust its diet composition (i.e., the resource types that it pursues/eats) in response to the current state of resource abundances, so as to make the diet an optimal set of resources that generates the highest possible overall energy intake rate in this given context. Essentially, OFT embeds the effect of abundance dependence in the mechanism it describes, meanwhile making diet choice a dynamical and context-dependent process, rather than a fixed one.

The mathematical logic of OFT is straightforward. Consider that all types of potential resource of the consumer are ordered by a quantity called profitability, i.e., the energy content of a resource item divided by the handling time for the consumer to acquire the energy from that item. The most profitable type ("type-A" in the following for ease of explanation) should always be taken by the consumer if it is encountered, as consuming it gives more energy per unit time than consuming any other type of resource. However, for the second-most profitable type ("type-B") it depends: In the case that type-A is very abundant and frequently encountered, the more efficient way for the consumer to acquire energy will be to ignore any encountered type-B to save the time from handling a type-B item, but concentrate on catching type-A instead. Only when type-A is rare enough, including also type-B into the consumer's diet becomes the better choice. Notably, the rarity of type-A does not alter the fact that it is the most profitable resource of all, so even in the latter condition, type-A remains in the consumer's diet, which includes both types, not merely type-B. Extrapolating this logic to all potential resource types, the characteristics that OFT diet choice predicts are: (i) The most profitable resource type is always included in the consumer's diet. (ii) The inclusion of a certain resource type is abundance-dependent, not on its own abundance but on the rarity of those more-profitable ones. (iii) If a consumer's diet consists of n types of resource, they definitely are the top- n profitable ones for the consumer (i.e., the abundance-driven broadening/narrowing of diet follows the profitability order of the resources)³.

Despite the idea that food-web properties are driven by the underpinning diet choice behaviour of individuals being intuitive, food-web ecology and behavioural ecology have largely

³For more details, including a mathematical inference, please see Appendix B.1

been studied independently in the past. Some classic food-web models, such as the Cascade (Cohen & Newman 1985) and Niche (Williams & Martinez 2000) models, did embed and highlight this intuition by modelling the emergence of food-web structure based on certain arbitrary diet choice rules. However, there had been limited development in this direction until recently, when ecologists have begun to comprehensively look into the connections between the two fields with more detailed and realistic perspectives on the behavioural components, mainly through theoretical approaches (for reviews, see Abrams 2010; Beckerman *et al.* 2010; Loeuille 2010; Stouffer 2010; Valdovinos *et al.* 2010). Regarding OFT in particular, its optimality-driven diet choice mechanism has been shown to be able to capture empirical food-web structure to a degree (Beckerman *et al.* 2006; Petchey *et al.* 2008, 2010). Meanwhile, allowing species to optimally “rewire” their trophic links after extinctions has been shown to affect species persistence within food webs (Thierry *et al.* 2011a). However, these findings were based on limited parameter combinations, and are not yet sufficient for capturing the whole picture of how OFT could mechanistically shape food-web structure. Also, rewiring after extinctions does not truly reflect adaptive foraging, i.e., abundance-dependent diet choice with population dynamics, which is described by OFT. Thus, our understanding of OFT-driven structural and dynamical consequences of food webs remains fragmented and a several questions remain to be explored.

It should also be recognised that OFT is, after all, a simplified model with several non-trivial assumptions. Empirically, these assumptions can be violated to different degrees, and this is presumably the reason why OFT diet predictions are usually qualitatively, but not perfectly, supported by case studies (e.g., Krebs *et al.* 1977; Elner & Hughes 1978; Estes *et al.* 2003; Carnicer *et al.* 2009). Also, OFT diet choice has largely been considered only from a consumer’s view. However, it is usual that species consume, while also being consumed by, some others in food webs—that is, they are consumers and resources at the same time. Behaviour from a resource’s view, such as those predation risk-driven responses, may thus also be influential in determining species’ diet choice. However, this possibility remains an absent piece to be incorporated to the OFT framework. Therefore, for a thorough exploration of how food-web properties emerge from OFT diet choice, these drivers that induce deviations from

optimal diet choice should be considered, alongside their implications at the food-web level.

1.3 Aim and outline of the PhD thesis

In this thesis, we aim at deepening our understanding of how foraging behaviour could shape the structure of food webs and influence their dynamics. To this end, we fill the knowledge gaps that are mentioned in the above subsections by investigating the food-web level effects of certain aspects of foraging behaviour in different chapters. In particular, in Chapter 2, we examine, in a species abundance-independent manner, how structural properties (i.e., topology and body-size structure) and behavioural properties (i.e., foraging strategy and dimensionality) interactively determine species coexistence in food webs. In Chapter 3, we then introduce the abundance-dependence of foraging, focusing on disentangling the effects of the Type-II functional response and optimal foraging diet choice on species extinction rates in food webs, meanwhile exploring the food-web structural and dynamical consequences when such diet choice operates to different extents. In Chapter 4, we develop a new diet-predicting model that includes predation risk-induced constraints as an extension to the classical optimal foraging model, then show how this new model could be applied to better capture empirical food-web topology. Each of these chapters is presented as a self-contained unit with sections of introduction, materials and methods, results, and discussion. Their supplementary materials are in appendices at the end of this thesis. Lastly, in Chapter 5 we draw the conclusion of the thesis and suggest possible directions for future work.

1.4 Publications

Chapter 2 has been reviewed in *Ecology Letters* and is under consideration following revision.

Chapter 4 has been published in *Ecology Letters* as: Ho, H.-C., Tylianakis, J. M., Zheng, J. X., & Pawar, S. (2019). Predation risk influences food-web structure by constraining species diet choice. *Ecology letters*, 22(11), 1734-1745.

Chapter 2

Behaviour moderates the impacts of food-web structure on species coexistence

Declaration

This chapter has been submitted to *Ecology Letters* with Dr Samraat Pawar and Prof Jason Tylianakis being my coauthors, and is under consideration following review and revision when the present thesis is submitted. When writing the content, I received valuable input from coauthors, as well as the editor and reviewers with whom I interacted during the peer review process.

2.1 Abstract

How species coexistence (i.e., mathematical “feasibility”) in food webs emerges from species’ trophic interactions remains an long-standing open question. Here we investigate how structural (network topology and body-size structure) and behavioural (foraging strategy and spa-

tial dimensionality of interactions) properties interactively affect feasibility in food webs. By performing metabolically-constrained modelling of food-web dynamics, we find that feasibility is promoted in systems dominated by large-eat-small foraging (consumers eating smaller resources) whenever (i) many top consumers are present, (ii) grazing or sit-and-wait foraging strategies are common, and (iii) species engage in two-dimensional interactions. Congruently, the first two conditions were associated with dominance of large-eat-small foraging in 74 well-resolved real-world food webs. Our findings provide a new, mechanistic understanding of how behavioural properties can modulate the effects of structural properties on species coexistence in food webs, and suggest that “being feasible” constrains the spectra of behavioural and structural properties seen in natural food webs.

2.2 Introduction

Identifying the conditions that allow many species to coexist in food webs remains a central aim in ecology. Known key determinants of food-web dynamics include their non-random topology (i.e., the pattern of interactions) (Gravel *et al.* 2016; Grilli *et al.* 2017; Dougoud *et al.* 2018) and body-size structure (i.e., the overall pattern of consumer-resource body-size relationships) (Brose *et al.* 2006a; Otto *et al.* 2007; Riede *et al.* 2011; Tang *et al.* 2014), largely because the strength of trophic interactions among species scales with their body masses (Yodzis & Innes 1992; Brose *et al.* 2006b; Pawar *et al.* 2012). However, interaction-strength scaling is modulated by foraging strategy (e.g., grazing, active-capture, or sit-and-wait) and the spatial dimension in which foraging happens (e.g., 2D vs. 3D, “dimensionality”) (Pawar *et al.* 2012, 2019). For instance, the encounter rate between a grazing consumer and its sessile resource is governed by only the consumer’s velocity (and thus its body mass), whereas when a consumer actively hunts mobile resources, encounter rate depends on the velocities of both. Thus, we might expect the impacts of topology and body-size structure on food-web dynamics to be moderated by these behavioural aspects (Pawar *et al.* 2012; Dell *et al.* 2014; Portalier *et al.* 2019).

Despite this evidence that topology, body-size structure, and foraging behaviour together

drive food-web dynamics, there has to date been no comprehensive exploration of how these aspects collectively influence species coexistence. Specifically, it remains unclear whether the behaviour of species enhances flexibility versus constrains the range of topology and body-size structure that enable species to coexist. We address this knowledge gap here, focusing on the emergence of mathematical equilibrium feasibility (henceforth, “feasibility”) in food webs. Feasibility signifies whether all species have positive abundances at the system’s dynamical equilibrium. It reflects the likelihood of species not going extinct (Grilli *et al.* 2017), and is thus the prerequisite for species coexistence. More generally, a range of concepts of community stability (Ives & Carpenter 2007) pertain to the avoidance of primary or secondary extinctions, so feasibility is an intuitive measure of dynamics, which links to measurable ecological phenomena. Yet, it has been often neglected by research on food-web dynamics (Grilli *et al.* 2017; Dougoud *et al.* 2018). Since the seminal study by May (1972), theoretical ecologists have largely focused on the conditions under which a community matrix (i.e., the Jacobian matrix evaluated at an equilibrium) exhibits local asymptotic stability. This work frequently assumes the existence of an abstract feasible equilibrium and focuses directly on the community matrix itself (e.g., Allesina & Tang 2012, 2015). However, equilibrium abundances and the community matrix are not mutually independent—by definition, the latter should be derived from the former (Dougoud *et al.* 2018). Therefore, approaches that directly assign random values to the community matrix without considering explicit equilibrium abundances, and that directly examine stability without guaranteeing the existence of underlying feasible systems, may be exploring parameter values that are biologically impossible to emerge (Dougoud *et al.* 2018; Gibbs *et al.* 2018).

Although feasibility may more closely match empirical concepts of stability, while averting the above issues with local asymptotic stability, disentangling the interactive effects of topology, body-size structure, and foraging behaviour on food-web feasibility is theoretically challenging. We ensure that feasibility emerges in a biologically sensible way by simulating synthetic food webs that are constrained by new and robust mass-scaling rules. We firstly show how these properties collectively influence feasibility. Particularly, we identify the topological and behavioural conditions that maximise body-size structure’s contribution to feasibility.

Meanwhile, large empirical food-web data in consistent format are becoming available, which suggest that there are systematic differences between food webs in the composition of species' body size and foraging behaviour (Brose *et al.* 2019). We therefore use our model to test whether dynamical constraints can explain these differences. Specifically, we expect “being feasible” to be a dynamical necessity of real-world food webs that constrains their properties to the above-identified conditions where feasibility is maximised.

2.3 Materials and methods

2.3.1 Overall procedure

We firstly simulated a pool of 100000 synthetic species, whose body masses (unit: kg) were randomly drawn from a log-normal distribution (Preston 1948; Engen & Lande 1996) with mean equals 0.01 and standard deviation equals 10 (output masses: $\sim 10^{-7}$ – 10^3). We then randomly drew a 50-species set from the pool each time, and established trophic relationships among species by using six topological models to generate a range of interaction topologies. We subsequently applied node-shuffling methods to yield three body-size arrangements for each topology. For these 18 simulated food webs of each species set, we derived all interaction strengths with behaviour-specific scaling rules (i.e., based on combinations of three foraging strategies and two foraging dimensions). We drew 30 sets of species as replicates for these 108 topology $\times$ body-size arrangement $\times$ foraging strategy $\times$ dimensionality schemes, thereby generating 3240 synthetic food webs in total. We then simulated and compared the feasibility among all schemes. Based on simulation results, we further proposed predictions regarding body-size structure in real-world food webs, and tested them with empirical data. Details are provided below.

2.3.2 Topological models

To understand the influence of food-web topology on feasibility, we applied six topological models—namely Random, Cascade, Niche, Nested, Modular-1, and Modular-2, each with a distinctive algorithm taking species’ body masses as the input—to establish the resource-consumer links in ways that generated a broad range of topologies for the given 50-species set. We thereby generated six sets of topologically different webs with roughly the same number of links (i.e., connectance ~ 0.1). For all models, as we were modelling food webs based on whole-organism consumption (see Section 2.3.4), we fixed the smallest one-tenth (i.e., five) of species of the input set to be basal resources (i.e., being consumed by, but not consuming, others), to capture empirically-observed proportions of basal species (Appendix Section A.4) with the remainder being consumers. Omnivory (i.e., consumers feed on both basal resources and other consumers) was allowed in the network topologies, while cannibalistic and bi-directional trophic interactions (i.e., two species feed on each other) were not (Section A.1.1).

The algorithms of these models are given in Section A.1.1. Briefly: the Random model establishes consumer diets stochastically; the Cascade and Niche models also establish stochastic diet, but each with a distinct body-size constraint that improves realism (see Cohen & Newman 1985; Williams & Martinez 2000); the Nested model generates highly nested webs, where the diet of smaller consumers comprises subsets of larger consumers’; the Modular-1 and Modular-2 models both generate (but under different body-size constraints) highly modular webs where species form subgroups with many links within but few/none between. We developed the latter three phenomenological models to generate specifically nested or modular webs, because these two holistic topological features are frequently observed in empirical food webs (Krause *et al.* 2003; Kondoh *et al.* 2010) and are considered to influence food-web dynamics (Thébault & Fontaine 2010; Stouffer & Bascompte 2011; Grilli *et al.* 2016). The resulting food webs visualised as diet matrices are illustrated in Fig. 2.1A.

We quantified the topology of the generated webs as the number of top consumers and the proportion of links between and within three guilds (i.e., top consumers, who consume but are not consumed by others; intermediate consumers, who consume and are consumed by

others; and basal resources). We also measured nestedness and modularity of the whole web (see Section A.1.3).

2.3.3 Body-size arrangements

We focused on two non-mutually-exclusive body-size structures that are often observed in empirical food webs: (i) “Large-Eat-Small” (LES) structure, whereby consumers eat resources that are smaller than themselves, and (ii) “Large-Eat-Large” (LEL) structure, whereby resources’ body size increases with that of their consumers (Brose *et al.* 2006a; Barnes *et al.* 2010; Brose *et al.* 2019). To investigate how these body-size structures affect feasibility, we kept the web’s topology fixed but shuffled the species identities (and thus the corresponding body masses) as nodes. This yielded three schemes of species body-size arrangement:

- “Original” arrangement is the non-shuffled output of our topological models, whereby webs are body-size structured to different degrees (see Section 2.4).
- “Within-Guild-Shuffled” arrangement is derived from the Original one, but consumer species are shuffled within each consumer guild (i.e., the top and the intermediate).
- “Across-Guild-Shuffled” arrangement is the same as the previous but the two consumer guilds are pooled when applying the shuffling.

The three arrangements can be seen as a sequential peeling-off of the body-size structure. Compared with the Original arrangement, the Within-Guild-Shuffled arrangement maintains the inter-guild species body-size variation, while the Across-Guild-Shuffled arrangement further destroys it. We kept the identities of basal resources non-shuffled throughout.

To quantify body-size structures of each web, we took the proportion of links where the consumer’s body mass is larger than the resource’s as the index of LES structure. We also regressed the resources’ body masses against the consumers’ (both in $\log_{10}$ scale), and took the slope as the index of LEL structure. Both indices positively reflect the prominence of the

corresponding body-size structure. We compared body-size structure across the combinations of topological models and body-size arrangements.

2.3.4 Interaction strength: considering behavioural features

We assigned the interaction strength of each trophic link by assuming that it is primarily governed by the consumer's search rate, rather than other foraging constraints such as handling time. That is, we applied a Type-I functional response throughout. According to literature on the body-mass scaling of search rate across different foraging strategies and dimensions (Pawar *et al.* 2012; Rizzuto *et al.* 2018), the per-capita interaction strength (a , units: m^2/sec in 2D and m^3/sec in 3D) of a consumer (subscript C) feeding on a resource (subscript R) can be mass-scaled as

$$a_{RC} = \begin{cases} -1.07 \times m_C^{0.42} m_R^{0.21} & \text{in 2D grazing} \\ -1.07 \times m_C^{0.21} m_R^{0.21} \sqrt{m_C^{0.42} + m_R^{0.42}} & \text{in 2D active-capture} \\ -1.07 \times m_C^{0.21} m_R^{0.42} & \text{in 2D sit-and-wait} \\ -2.72 \times m_C^{0.63} m_R^{0.42} & \text{in 3D grazing} \\ -2.72 \times m_C^{0.42} m_R^{0.42} \sqrt{m_C^{0.42} + m_R^{0.42}} & \text{in 3D active-capture} \\ -2.72 \times m_C^{0.42} m_R^{0.63} & \text{in 3D sit-and-wait} \end{cases}, \quad (2.1)$$

where m is the species' body mass (in kg). The negative sign represents the negative effect on the resource's abundance (here, numerical density) due to being consumed by the consumer. These mass-scaling relationships are based on whole-organism predator-prey consumption, and would not be as valid for estimating the strength of other types of trophic interaction, such as partial-organism consumption or parasitism. Our exploration thus focuses on food webs dominated by the former.

The positive effect on the consumer's abundance due to consuming the resource can be

derived from the above as

$$a_{CR} = \epsilon |a_{RC}| \frac{m_R}{m_C},$$

where ϵ is the biomass-to-biomass conversion efficiency (bounded between 0 and 1, unitless), which we assumed to be a constant of 0.5 throughout¹. a_{CR} calculates the contribution of ingested resource to the increase of the consumer (in per-capita unit) based on the size of a_{RC} . The values of a_{RC} and a_{CR} are thus coupled in a biologically sensible way (*sensu* Tang *et al.* 2014).

We thus derived interaction strength of all links for each of the simulated webs (i.e., those of topology $\times$ body-size arrangement combinations) under six behavioural schemes, i.e., the combination of foraging strategy (grazing/active-capture/sit-and-wait) and dimensionality (2D/3D). We recognise that in natural food webs, trophic interactions are usually a mixture of foraging strategies and dimensions. However, our aim here with synthetic food webs is to clarify how these behavioural features affect interaction strengths and, therefore, feasibility. Consequently, we generate webs with extremes of foraging strategy and dimensionality to provide the necessary range in explanatory variables, and presumably to capture the full range of possible feasibility response of webs situated between these extremes (*sensu* Grilli *et al.* 2017).

2.3.5 Food-web dynamics and feasibility

We modelled food-web dynamics using a generalised Lotka-Volterra model (Barabás *et al.* 2016; Dougoud *et al.* 2018). For a web with S species, the dynamics of species abundances can be described by differential equations

$$\frac{dn_i}{dt} = n_i \left(r_i + \sum_{j=1}^S a_{ij} n_j \right), \text{ for } 1 \leq i \leq S, \quad (2.2)$$

¹Empirically, ϵ tends to exhibit systematic difference between consumers with different diet types (e.g., herbivores vs. carnivores). As we were not specifying diet type of consumers in our synthetic food webs, we used a 0.5 constant for simplicity, which falls within the range of empirical values (Lang *et al.* 2017). Preliminary simulations showed that the choice of ϵ value did not qualitatively affect the results.

where n_i is the numerical density (unit: $1/\text{m}^2$ or $1/\text{m}^3$) of species i , r_i its per-capita intrinsic growth rate (unit: $1/\text{sec}$), and a_{ij} its per-capita trophic interaction strength with species j (when $i \neq j$) as derived above. When $i = j$, a_{ii} represents species i 's intraspecific interference strength, which is the per-capita loss due to interference independent of foraging.

For species per-capita growth rates, there are well-established mass-scaling rules based upon the Metabolic Theory of Ecology (Brown *et al.* 2004). We assigned the rates according to empirically verified values (Pawar *et al.* 2012) such that

$$r_i = \begin{cases} 1.71 \times 10^{-6} m_i^{-0.25} & , \text{ if species } i \text{ is a basal resource} \\ -4.15 \times 10^{-8} m_i^{-0.25} & , \text{ if species } i \text{ is a consumer} \end{cases}. \quad (2.3)$$

This follows the common assumption of the Lotka-Volterra type of models where producers have positive, while consumers have negative, intrinsic growth rates.

Although intuitively we may posit that species' intraspecific interference strength should scale in a certain way with body mass (Virgo *et al.* 2006; Pawar 2015), to our knowledge this is yet to be definitively established (van Altena *et al.* 2016; Barabás *et al.* 2017). We therefore deduced this scaling relationship from the concept of carrying capacity (K , in $1/\text{m}^2$ or $1/\text{m}^3$). The dynamics of a predation-free basal resource in both Lotka-Volterra (i.e., eqn (2.2)) and Rosenzweig-MacArthur model forms give

$$\frac{dn_i}{dt} = n_i(r_i + a_{ii}n_i) = r_i n_i \left(1 - \frac{n_i}{K_i}\right),$$

which gives

$$a_{ii} = -\frac{r_i}{K_i}. \quad (2.4)$$

According to Brown *et al.* (2004), a species' per-capita carrying capacity scales as

$$K_i \propto m_i^{-0.75}. \quad (2.5)$$

From eqn (2.3)–(2.5) we derive the scaling relationship of species i 's per-capita interference

strength as

$$a_{ii} = a_{0,i} m_i^{0.5},$$

where $a_{0,i}$ is a negative scaling constant (units: $\text{m}^2/(\text{sec} \cdot \text{kg}^{0.5})$ in 2D and $\text{m}^3/(\text{sec} \cdot \text{kg}^{0.5})$ in 3D). Without further knowledge, and for modelling simplicity, in the following we assumed that all species share the same a_0 , and the 0.5 scaling exponent applies also to consumers. Simulation results with other scaling exponents are given in Section A.3.

The equilibrium is where species abundances are not changing over time. Knowing species' growth rates and interaction (including interference) strengths, their equilibrium abundances can be found by solving eqn (2.2) (i.e., find n_i^* , for all i , that makes dn_i^*/dt zero). For each web, we solved the equilibrium abundances across a range of a_0 that spans orders of magnitude (10^{-8} – 10^8). We took the maximal number of feasible species (i.e., with positive equilibrium abundance) as the index of feasibility, as it represents the most feasible state a food web could achieve given an appropriate interference-strength magnitude. More on this index in Section A.2.

2.3.6 Empirical evaluation

After using simulations to reveal the conditions that promote feasibility, we explored whether empirical food webs showed patterns consistent with these conditions. If species are observed to exist in real-world food webs, this indicates that they are feasible at some scale. However, we recognise that within the spatial and temporal sampling range of a single empirical food web, it is plausible that non-equilibrium conditions or source-sink dynamics could allow species to occur (i.e. have positive abundance) without the web being feasible *per se*. We predicted that empirical food webs should show a more prominent body-size structure if they match better to the topological and behavioural conditions that our simulations found to maximise the positive contribution of body-size structure to feasibility (i.e., where “being body-size structured” is important).

We exploited a recently-published, large yet very detailed food-web dataset by Brose *et al.*

(2019) to test our predictions. Our analysis was based on a selected set of 74 empirical food webs across three ecosystem types, i.e., marine, lakes, and terrestrial-aboveground (for details of web selection, see Section A.4). The species’ body mass and foraging dimensionality information were directly accessible in the dataset, whereas the consumer’s foraging strategy of each link was deduced from species’ movement information: “grazing” if the resource is sessile; “sit-and-wait” if the consumer is sessile; “active-capture” if both the resource and the consumer are mobile during foraging.

To summarise the key features of topology that our simulations found to be influential (to the importance of being body-size structured; see Section 2.4), we defined a “T score” (T) that simultaneously quantifies the richness of top consumers as well as the rarity of top-eat-basal links in a food web as

$$T = T_{prop.} - 0.5 \times T_{prop.} \times \frac{TB_{real.}}{TB_{pot.}},$$

where $T_{prop.}$ is the proportion of top consumers among all species. $TB_{real.}$ and $TB_{pot.}$ are the number of realised and potential top-eat-basal links, respectively. $TB_{pot.}$ by definition is the product of the number of top consumer and basal resource. The 0.5 constant is for weighting the influence of top-eat-basal links relative to $T_{prop.}$. Its value is based upon our synthetic food-web simulations, as the among-model pattern of T scores derived with this value (Fig. A.1) well matched the pattern of the importance of being body-size structured (Fig. 2.3B). A high T score indicates the topological state where top consumers are common and they less feed on basal resources, while a low T score the converse.

We measured the T score, the proportion of interactions that belong to each foraging strategy/dimension, and the indices of LES and LEL body-size structures for each empirical food web. We then performed both linear regression and linear mixed-model regression (with ecosystem type as the random effect) analyses based on these measurements, using R version 3.4.4 (R Core Team 2013) with functions `lm` and `lmer` from the package `lme4` (Bates *et al.* 2014). We tested whether the topological features (i.e., summarised as the T score) and behavioural features that our simulations found to be influential (the proportions of active-capture and of 3D interactions; see Section 2.4) are indeed significant predictors of the prominence of the body-

size structure (i.e., the LES and LEL indices, separately) of food webs. The LEL analyses were weighted by the R-squared of the resource-consumer ($\log_{10}$) body-mass regression. Ecosystem-specific responses, if present, would be detected by the systematic difference between the linear and linear mixed-model regressions.

2.4 Results

Structure of synthetic food webs

As anticipated, the six topological models generated topologically distinct food webs. With respect to the guild-relevant properties, we can group the models into three pairs: the Random and Modular-2 webs seldom had any top consumers, and thus mostly had only intermediate-eat-intermediate (II) and intermediate-eat-basal (IB) links. The Cascade and Niche webs on average had a few top consumers, and a non-negligible proportion of links being top-eat-intermediate (TI) in addition to the II and IB links. The Nested and Modular-1 webs both had the majority of species being top consumers and a dominant proportion of TI links, but they differed largely in the proportion of top-eat-basal (TB) links (Fig. 2.1B–C; Table A.1). This grouping—as we described further below—reappeared in the comparisons of body-size structure and feasibility among topological models, indicating that these guild-relevant characteristics are the key topological drivers of feasibility. Conversely, as to food-web holistic properties, the models each generated distinct levels of nestedness and modularity (Fig. 2.1D), but no obvious pattern could be summarised and related to the body-size or feasibility patterns we found below.

Different food-web topologies led to different levels of Large-Eat-Small (LES) and Large-Eat-Large (LEL) body-size structures. The way that food webs lose these body-size structures during “node shuffling” (i.e., across the three body-size arrangements) was also topology-dependent. Regarding the LES structure, the Random and Modular-2 webs were not LES-structured throughout all body-size arrangements. The Cascade, Niche, Nested, and Modular-1 webs were strongly LES-structured with the Original arrangement. The former two largely

lost this structure with the Within-Guild-Shuffled arrangement, and lost it further with the Across-Guild-Shuffled arrangement. The latter two, in contrast, remained LES-structured with the Within-Guild-Shuffled and largely lost this structure with the Across-Guild-Shuffled arrangement. (Fig. 2.2; Fig. A.2). Regarding the LEL structure, all but the Random model were LEL-structured (to different degrees) with the Original arrangement. The Cascade, Niche, Nested, and Modular-2 webs lost almost entirely the LEL structure with the Within-Guild-Shuffled arrangement, while the Modular-1 webs retained half of the Original level but lost it with the Across-Guild-Shuffled arrangement (Fig. 2.2; Fig. A.2). As our node shuffling applies on guilds, the changing pattern of body-size structure (across arrangements) should largely be influenced by the webs' guild-relevant properties. Indeed, the LES patterns could be summarised with the same model grouping (i.e., Random with Modular-2, Cascade with Niche, and Nested with Modular-1) as above-mentioned regarding the guild-relevant topology. However, no such grouping could be observed with the LEL patterns.

How do behaviour and food-web structure influence feasibility?

The feasibility of synthetic food webs was influenced by their topological and body-size structures, but this influence was moderated by foraging behaviour (the strategy and dimensionality of foraging) (Fig. 2.3A). Despite the variety of exact feasibility values, the patterns of how feasibility of each topological model responds to the removal of body-size structures (through node shuffling) were qualitatively consistent across foraging strategy $\times$ dimensionality combinations: the feasibility of the Random and Modular-2 webs kept roughly a constant value across all arrangements. The Cascade and Niche webs had higher feasibility when body-size structure was intact (i.e., with the Original arrangement), but converged to the previous two models with the two node-shuffled arrangements. The Nested and Modular-1 webs had even higher feasibility with intact body-size structure, and showed a gradual decrease with the gradually removed body-size structure (Fig. 2.3A). Notably, these patterns echo the model grouping that emerged in the above-mentioned guild-relevant topology and LES body-size structure results, implying a close correlation between the feasibility and these measures. Indeed, among the two

types of body-size structure, LES appeared to be more influential in determining feasibility (Section A.1.2).

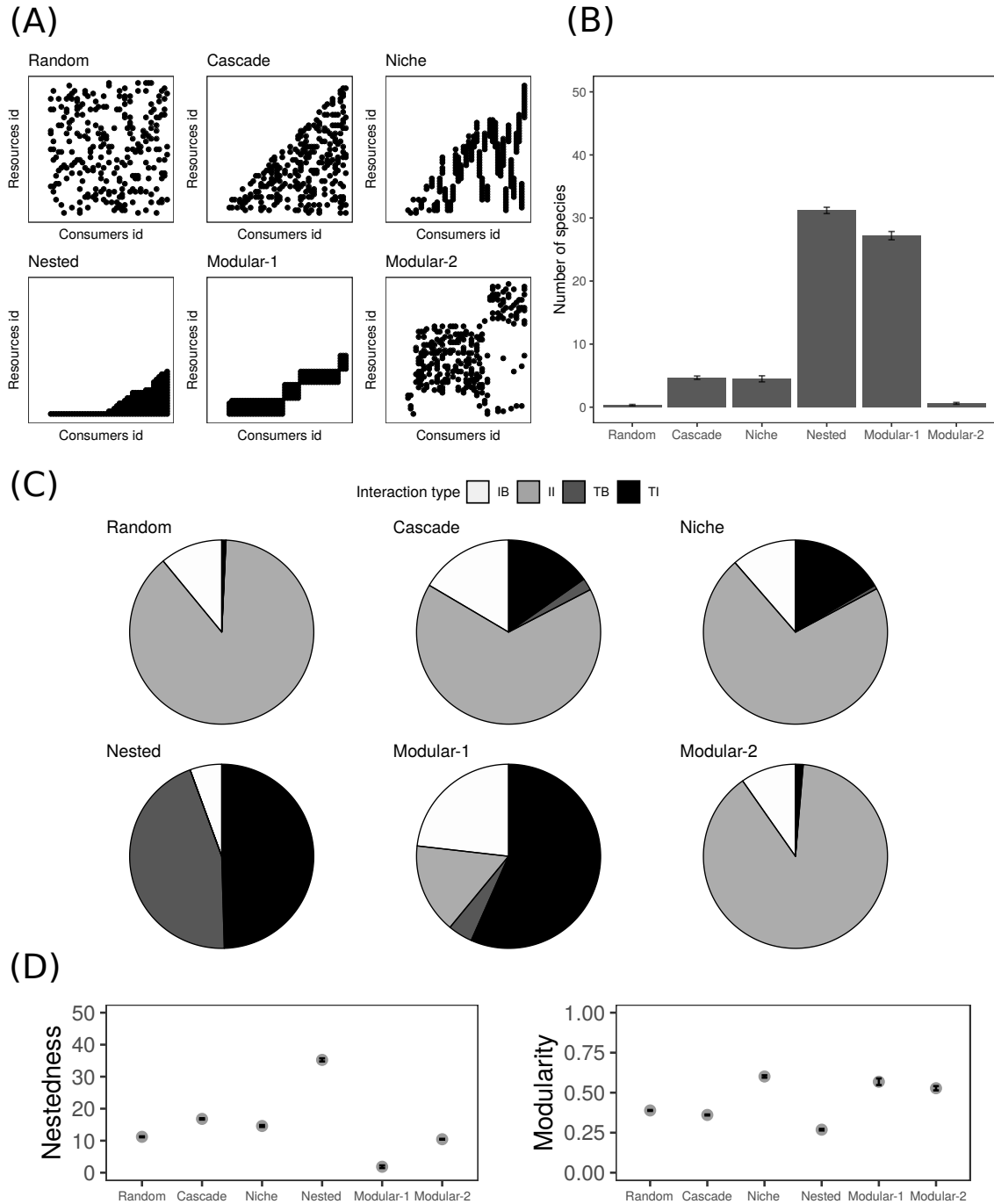


Figure 2.1: **Topology summary of model-generated food webs** ($N = 30$ for each **model**). (A) The diet matrices (illustrated with one replicate). The black entries indicate realised trophic interactions between consumer (columns) and resource (rows) species. The left-most five columns are empty as these are fixed to be the basal resource. (B) Mean number of top consumers (with standard error). (C) The proportion of each type of interaction. (D) Nestedness and modularity of the webs (with standard error). (Abbreviations B, I, and T in (C) stand for the basal resource, intermediate consumer, and top consumer, respectively. IB means Intermediate-eat-Basal links, and so on.)

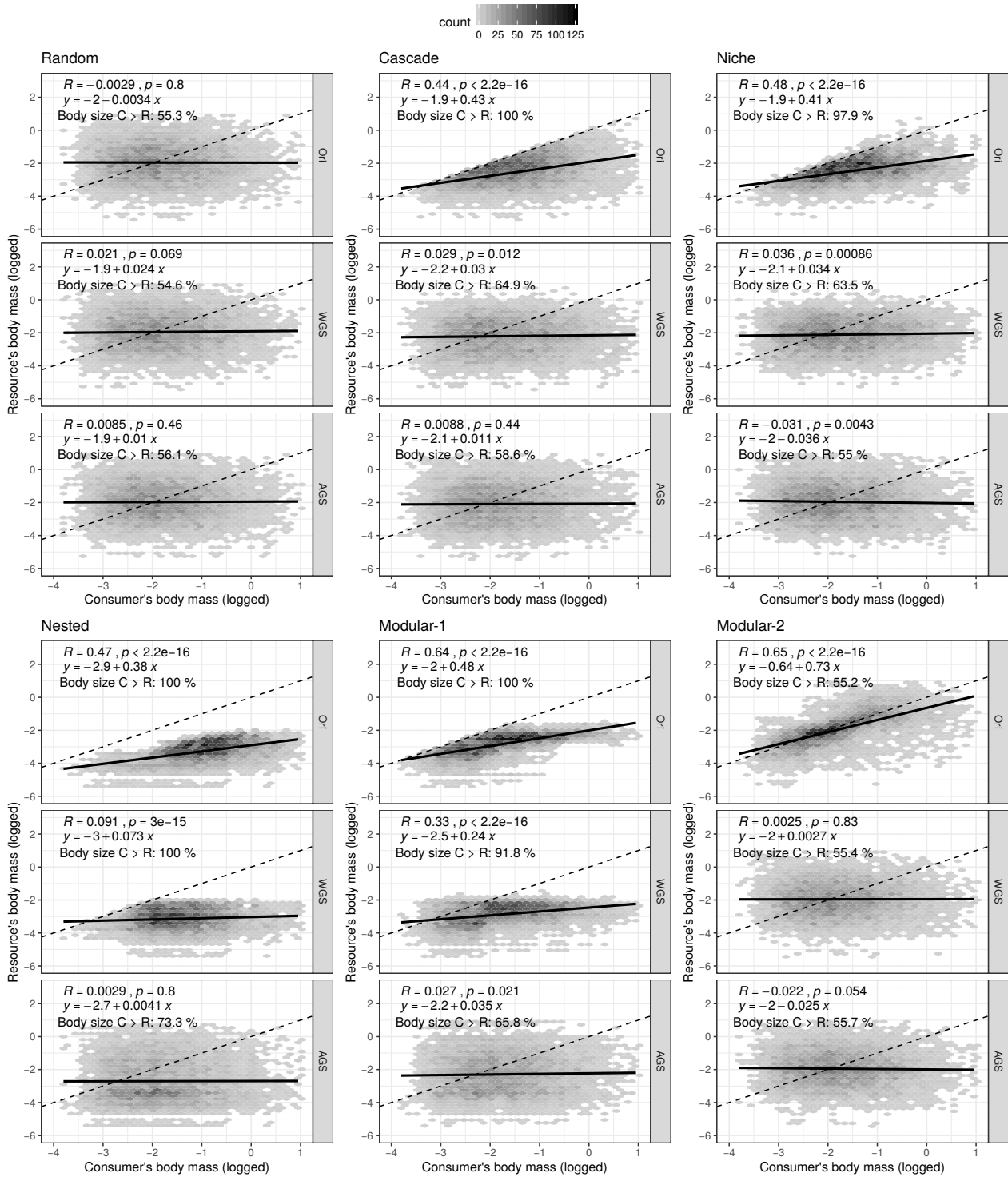


Figure 2.2: Body-size relationship between resource-consumer pairs in all topological model $\times$ body-size arrangement combinations. The solid line is the ordinary least squares regression fitted to the data, with the corresponding regression equation, and goodness of fit measures at the top-left. The dotted line represents the $x = y$ line. Interactions below this line have consumer larger than resource. The percentage of such large-eat-small links among all is also indicated at top-left. Here we collapse all 30 replicates, whereas an replicate-based comparison is in Section A.1.2. (Abbreviations Ori, WGS, and AGS stand for the Original, Within-Guild-Shuffled, and Across-Guild-Shuffled body-size arrangements, respectively.)

We further calculated, for each topological model in each foraging strategy $\times$ dimensionality scheme, the difference in feasibility between the Original and Across-Guild-Shuffled body-size arrangements. This value indicates how much feasibility is influenced by having/losing body-size structures, and we took this value as an index of the importance of being body-size structured in terms of maximising feasibility (Fig. 2.3B). Considering topology, being body-size structured was more important in webs with many top consumers (i.e., the Nested and Modular-1) than those with just a few (i.e., the Cascade and Niche), while non-influential in those with almost none (i.e., the Random and Modular-2). Comparing Nested with Modular-1 webs showed that this importance was lower in Nested webs, which had remarkably more TB links. Importantly, foraging behaviour moderated these effects of body-size structure on feasibility; being body-size structured was more important with grazing and sit-and-wait (i.e., non-active-capture) strategies (in the Nested and Modular-1 webs) and with 2D foraging (Fig. 2.3B).

Does feasibility explain empirical food-web patterns?

Based on our simulation results, we predicted that empirical food webs should show a stronger LES body-size structure when they exhibit more top consumers but fewer TB links (i.e., higher T score; see Section 2.3.6) and more 2D and non-active-capture interactions (Fig. 2.4). The empirical evaluation largely supported this prediction. Indeed, the prominence of LES structure in empirical food webs was related positively to the T score, and negatively to the proportion of active-capture interactions. The proportion of 3D interactions, though, showed a positive relation, which contradicted our prediction (Table 2.1). Also as expected, there was no obvious effect of these predictors observed for the LEL structure, except that the proportion of 3D interactions showed a positive relation when ecosystem type was set as a random effect (Table 2.1).

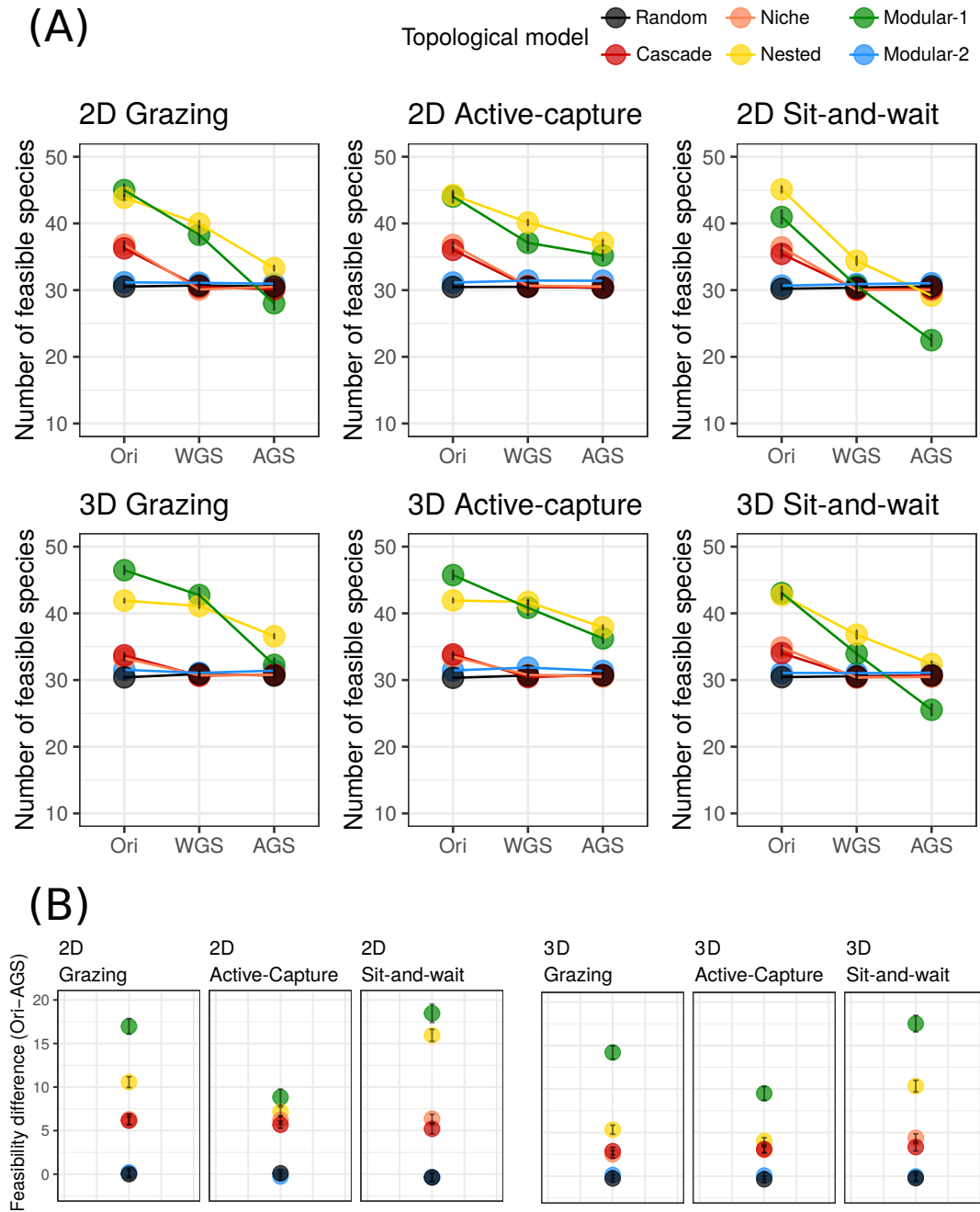
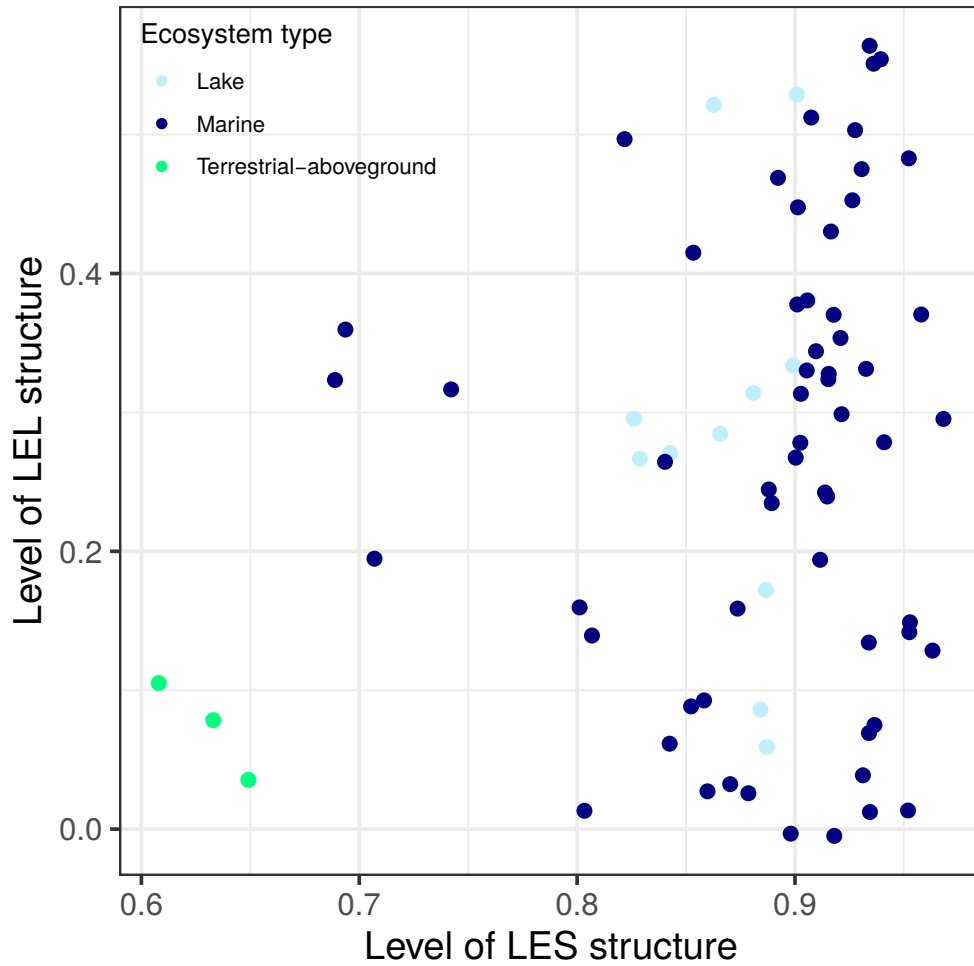


Figure 2.3: **Feasibility of synthetic food webs of all topology $\times$ body-size arrangement $\times$ foraging strategy $\times$ dimensionality combinations.** (A) The feasibility index (i.e., the peaking number of feasible species at equilibrium for each web, across magnitudes of interference strength). It appears that food webs with many top consumers (i.e., Nested and Modular-1 webs) and a strong body-size structure (i.e., with the Original arrangement) have high feasibility. (B) The difference in feasibility between the Original and Across-Guild-Shuffled arrangements (i.e., Ori – AGS), which reflects the importance of being body-size structured for maximising feasibility. Such importance is higher in webs with many top consumers but fewer Top-eat-Basal links (i.e., Modular-1), and with 2D, non-active-capture foraging. The error bars indicate the standard error. (Abbreviations Ori, WGS, and AGS stand for the Original, Within-Guild-Shuffled, and Across-Guild-Shuffled body-size arrangements, respectively.)



Ecosystem type	Number of webs	LES index	LEL index
Lakes	11	0.8695 ± 0.027	0.2848 ± 0.149
Marine	60	0.8917 ± 0.063	0.2627 ± 0.166
Terrestrial-aboveground	3	0.6301 ± 0.021	0.0730 ± 0.035

Figure 2.4: **The level of Large-Eat-Small (LES) and Large-Eat-Large (LEL) body-size structures of empirical food webs ($N = 74$).** Three ecosystem types (i.e., lake, marine, and terrestrial-aboveground) are indicated by colours in the plot, and the stats are supplied in the table below. We note that the level of LES structure is marine > lake > terrestrial-aboveground empirically.

Table 2.1: **The results of the linear (mixed-model) regression analyses (N = 74).** The sign of the estimated effect indicates whether the predictor has a positive/negative contribution to the level of the Large-Eat-Small (LES)/Large-Eat-Large (LEL) structure.

For LES body-size structure				
	Estimated effect	SE	t value	P value
<i>Model: Level.LES ~ T.score + Prop.Act + Prop.3D</i>				
Intercept	0.91	0.018	49.96	< 1e-10
T.score	0.22	0.099	2.20	0.03
Prop.Act	-0.34	0.037	-9.20	< 1e-10
Prop.3D	0.30	0.037	8.16	< 1e-10
<i>Model: Level.LES ~ T.score + Prop.Act + Prop.3D, ecosystem type as random intercept</i>				
Intercept	0.87	0.042	20.67	< 0.01
T.score	0.23	0.097	2.37	0.02
Prop.Act	-0.33	0.057	-5.82	< 0.01
Prop.3D	0.36	0.070	5.17	0.05
For LEL body-size structure				
	Estimated effect	SE	t value	P value
<i>Model: Level.LEL ~ T.score + Prop.Act + Prop.3D</i>				
Intercept	0.35	0.055	6.35	< 0.01
T.score	-0.11	0.334	-0.33	0.74
Prop.Act	0.07	0.163	0.44	0.66
Prop.3D	-0.01	0.155	-0.06	0.95
<i>Model: Level.LEL ~ T.score + Prop.Act + Prop.3D, ecosystem type as random intercept</i>				
Intercept	0.12	0.148	0.83	0.47
T.score	0.02	0.303	0.08	0.94
Prop.Act	-0.09	0.177	-0.50	0.62
Prop.3D	0.50	0.222	2.26	0.03

Level.LES/LEL: the level of this body-size structure, with corresponding index as described in main text.
Prop.Act/3D: the proportion of active-capture/3D interactions.

2.5 Discussion

We have revealed how topological and body-size structures determine food-web feasibility, but that these effects are moderated by foraging behaviour. We also found that real-world food-web patterns can be explained by constraints on the topology, body-size structure, and foraging behaviour that allow species to coexist (i.e., that maximise feasibility). Specifically, our results

indicated that food webs with many top consumers and a strong large-eat-small body-size structure have high feasibility, especially when non-active-capture foraging strategies are common. Food webs with many top trophic positions generally provide more-differentiated trophic niches that could allow more species' coexistence (Chase & Leibold 2003; Johnson *et al.* 2014). However, these top trophic positions are consequently deprived of energy supply by being at the top of a trophic pyramid (Trebilco *et al.* 2013). It may thus be difficult for small-sized species to secure enough intake to balance out their high metabolic loss (and thus intrinsic mortality) at these positions, especially with grazing or sit-and-wait strategies which yield comparatively lower intake rate than active-capture (eqn (2.1)). Notably, because we modelled whole-organism consumption interaction strengths and selected empirical web data accordingly (Section A.4), these findings may mainly be compatible with systems dominated by this type of interaction, e.g., aquatic predator-prey food webs, but not the other types, e.g., mutualistic or parasitic interaction networks. Nevertheless, our modelling framework is applicable for studying these other systems, given that measures of their respective interaction strengths become available.

We focused on feasibility as an outcome of food-web dynamics, as ecologists have started to acknowledge the precedence of feasibility over stability (Grilli *et al.* 2017; Dougoud *et al.* 2018; Song & Saavedra 2018), and found the criteria for establishing feasibility are often stricter than for establishing stability (Stone 2018). Indeed, dynamical systems may not necessarily ever reach a steady equilibrium, but adopt fluctuating or chaotic dynamics instead. In either case, though, a mathematically feasible equilibrium as the attractor is still essential for the system to avert species extinction (Serván *et al.* 2018). Moreover, as feasibility measures the likelihood of species extinctions in communities, it is also conceptually connected to other ecological stability measures, such as resistance to perturbation or variability in biodiversity, where a stable system requires species to persist. By identifying the forces that promote feasibility, we can understand how currently-feasible food webs were shaped and how they might change in the future.

We combined model-simulated topologies with body-size arrangements to generate some “extreme” food-web structures (e.g., perfectly Large-Eat-Small webs). These exaggerated structures facilitated detection of the effects of certain key topological/body-size features. Nevertheless, our dynamical modelling explored biologically sensible parameter spaces by adopting

several well-founded, metabolically constrained mass-scaling rules. In nature, both topological and body-size structures emerge from fundamental mechanisms that determine species' diets, such as trait matching (Gravel *et al.* 2016; Laigle *et al.* 2018) or foraging decisions (Charnov & Orians 1973; Beckerman *et al.* 2006). Also, theoretical studies have suggested that the two structures can constrain each other during food-web assembly (Loeuille & Loreau 2005; Thierry *et al.* 2011b; Heckmann *et al.* 2012; Pawar 2015). Such mechanisms potentially prevent food-web structures from being as extreme as our synthetic webs. Extending our simulation framework with incorporation of these mechanisms would be promising future work. Moreover, feasibility does not necessarily require the conditions we found to be associated with feasible webs. Rather, topological and body-size structures of empirical webs do not strictly converge (Fig. 2.4; Section A.4), and webs could deviate from these conditions yet accomplish feasibility by having a distinctive combination of parameters that violates our constraints. For example, there are likely to be species-wise deviations from body-mass scaling in nature (Brown *et al.* 2004; Pawar *et al.* 2012). Therefore, we do not claim any condition that guarantees feasibility, but instead reveal the influences of the focal factors, and show that, in nature, “being feasible” as a constraint (Kristensen 2008) likely imposes a stronger body-size structure on food webs with certain topological and behavioural features.

As is normal for Lotka-Volterra modelling studies (e.g., Barabás *et al.* 2016; Haerter *et al.* 2016; Dougoud *et al.* 2018), we used fixed and abundance-independent per-capita interaction strengths (i.e., Type-I functional response) that allowed the analytical derivation of equilibrium abundances. This is arguably a reasonable modelling simplification as the analytical solution is a reliable proxy of species' dynamical outcomes (see Section A.2). Also, empirical data suggest that species' abundances are usually low under natural conditions (i.e., without experimental manipulation), where Type-I functional response makes good approximation of true consumption rates (see Pawar *et al.* 2012 and Section A.6). This, however, also has limited the application of our modelling and findings to systems in the such conditions. It would be intriguing for future work to explore how incorporation of abundance-dependent effects—e.g., Type-II functional response and abundance-induced diet change (Thierry *et al.* 2011a; Heckmann *et al.* 2012)—may mediate the effects identified in this study. Such studies could further

expand our mechanistic understanding of food-web dynamics.

We deduced that per-capita intraspecific interference strength should scale positively with species' body masses, but we additionally simulated neutrally- and negatively-scaled cases for comparison. Intriguingly, for LES-structured food webs (i.e., the Cascade, Niche, Nested, and Modular-1 webs with Original body-size arrangement), positively-scaled interference strengths yielded higher feasibility than the neutrally- or negatively-scaled ones. The contribution of being body-size structured to feasibility was also the highest with positive scaling (Section A.3). Since empirical food webs are usually body-sized structured (Brose *et al.* 2006a), these results imply that empirical interference strength is likely to be positively mass-scaled, under which high feasibility allows species coexistence. Regardless of the scaling exponent, food-web feasibility generally peaks with an intermediate interference scaling constant (a_0) (Section A.3), indicating that an intermediate level of intraspecific interference maximises the feasibility (and stability, see Barabás *et al.* 2017). Species' interference seems intuitively likely to be intermediate, but has been mainly examined as a modifier to the consumers' foraging rate (Delong 2014), not as the per-capita loss that we modelled here. Therefore, we urge future empirical studies to quantify intraspecific interference, preferably in the same unit as interspecific interaction strength.

Our finding that guild-relevant topological properties determine feasibility illustrates that a species' dynamical fate is largely influenced by its trophic role. It also highlights that, when approximating the behaviour of complex systems by simpler ones—such as applying the Mean Field Theory to study food-web dynamics (e.g., Wilson *et al.* 2003)—the systems need to be complex and stochastic. Otherwise, the distinct roles of a highly structured network would mitigate the validity of summarising many-body effects into an one-body effect. Our results also showed that nestedness and modularity were not effective in determining feasibility. As this finding is built on our analytical approach and focus on feasibility only, it is not necessarily incompatible with some seemingly conflicting findings based on other subjects/approaches. For instance, nested structure has been shown to increase biodiversity in mutualistic networks (Bastolla *et al.* 2009). Also, being modular has been shown to promote food-web species coexistence by limiting the propagation of secondary extinctions (Teng & McCann 2004; Stouffer &

Bascompte 2011)—an effect that is not directly relevant to feasibility and can only be detected with numerical dynamics simulation. Thus, how these holistic topological features contribute to species coexistence depends on the type of interaction network, and the way coexistence is measured.

In our empirical food webs, the Large-Eat-Small (LES) body-size structure was most prominent in marine systems, followed by lakes and further by terrestrial-aboveground systems (Fig. 2.4). This order echoes findings by Potapov *et al.* (2019) regarding the positive correlation between species' body sizes and their trophic positions across ecosystems using a different dataset. They proposed that morphological constraints (e.g., gape size) and size-specific parallel food chains within food webs may explain the emergence/lack of LES structure in different ecosystems. We here provide a new explanation from the whole-web perspective: the topological and behavioural features of food webs—e.g., the high T score and dominant grazing/sit-and-wait interactions of the marine webs (Fig. A.21 & A.22)—may impose the necessity of being LES-structured on themselves to be feasible. Conversely, both our simulations and empirical evaluation showed that the Large-Eat-Large (LEL) body-size structure was not as influential to feasibility as the LES one. Therefore, the LEL structure observed in natural food webs may emerge from mechanisms other than the necessity of being feasible, e.g., preferred (optimal) resource-consumer body-size ratios (Barrios-O'Neill *et al.* 2016; Portalier *et al.* 2019). The potential shaping effect of a preferred body-size ratio on the topological/body-size structures is beyond the scope of this study. Nonetheless, as a comparison we additionally conducted simulations with an arbitrary universal preferred body-size ratio that determined interaction strengths. The feasibility responses of topological models to the node shuffling remained qualitatively robust (Section A.3).

Foraging strategy and dimensionality were key moderators of the importance of food webs being (LES) body-size structured for maximising their feasibility (Fig. 2.3B). The patterns of this importance, though, were relatively sensitive to the sign of the interference mass-scaling exponent (Fig. A.17–A.19). Thus, the importance is not solely determined by interspecific trophic interaction strengths, but collectively by intraspecific interference strengths as well. Our predictions were based upon, and therefore specific to, a positively mass-scaled inter-

ference. In this aspect, our prediction regarding foraging strategy was empirically supported, again implying that the positive mass-scaling of interference may occur in nature (Pawar 2015). Conversely, the empirical evaluation contradicted our dimensionality prediction that 3D interactions should negatively relate to food-web LES structure. This may be partly because the effect of dimensionality is smaller than the effect of foraging strategy (Fig. 2.3B), and partly due to the collinearity between these two factors. Indeed, we see a positive correlation between the proportion of 3D and of active-capture interactions in the empirical data we used (Fig. A.22). As we can easily imagine more real-world examples of 3D active-capture trophic interactions than of 3D grazing or 3D sit-and-wait ones, this could be a true correlation in nature. We performed additional regression analyses (see Section A.5) to evaluate the robustness of the predictors' effects. The effect of 3D foraging, on one hand, was not consistent across regression models (Table. 2.1 vs. Table. A.4), which indicated that its reported significance (Table. 2.1) may indeed be a by-product of the collinearity. On the other hand, our predictions regarding topology and foraging strategy remained well supported (Table. A.2, A.3 & A.5).

This study provides a framework for applying theory-based mass-scaling rules to give sensible estimations for the dynamical parameters, and also a practical example of how such a framework could generate empirically testable hypotheses. We call for future theoretical works to examine how feasibility can be achieved if allowing the properties we here manipulated, and the parameters we here fixed, to interact—i.e., a thorough structural stability analysis (Rohr *et al.* 2014; Grilli *et al.* 2017; Pascual-García & Bastolla 2017) from a dynamical perspective. We also call for empirical works to comprehensively quantify dynamical parameters in complex yet measurable food webs, e.g., with micro- or mesocosms, to generate high-quality data that can bridge theories with the real world. In light of our study, behaviour as a key factor influencing feasibility, and “being feasible” as a constraint for species to coexist, should both be considered more in discussions of the emergence of biodiversity in nature.

Chapter 3

The effects of optimal-foraging diet choice on food-web structure and dynamics

3.1 Abstract

Consumers can potentially choose their diets according to resource abundances to achieve optimal foraging. However, we still lack a comprehensive understanding of how influences of such an adaptive diet choice behaviour are scaled-up to determine properties of large complex food webs. Particularly, because the abundance of resources determines the optimal diet of consumers, species' optimal foraging with population dynamics would make food-web structure itself a dynamical property that varies with time. It remains largely unclear how food-web structure fluctuates, and how its interplay with population dynamics affects species persistence in the community. To investigate the structural and dynamical consequences of food webs driven by species optimal foraging, we performed metabolically-constrained food-web modelling with trophic interactions established by optimal foraging predictions. Food-web structure predicted by species' optimal diets are affected by attributes of the community (e.g., abundance magnitude) or consumers' behaviour (e.g., preferred body-size ratio), where commonly-observed

food-web structural features, e.g., being nested or modular, can emerge under certain conditions. Dynamically, optimal foraging makes fluctuate the food-web structure but can stabilise it in the long run. Species' optimal diet choice can affect community robustness in either direction, depending on how efficiently the consumers can adjust their diets to forage optimally—frequent diet adjustment prevents species extinction, while infrequent adjustment does the opposite. Our findings show that rapid changes in diet to achieve optimality can both prevent extinction and generate food-web architecture, and thereby link foraging behaviour to food web properties and dynamics.

3.2 Introduction

The structure of a food web, as well as its interaction-driven dynamical consequences, are collectively determined by the diet of all consumers within the community. Therefore, to better understand the formation of food-web properties, it is necessary to consider mechanisms that govern consumer species' diet choice (i.e., which subset of the potentially edible resources are consumed), and to establish how diet choice scales up its effect to determine phenomena at the community level (Beckerman *et al.* 2006; Berlow *et al.* 2008; Stouffer 2010).

Optimal foraging theory (OFT, Charnov & Orians 1973) presents a mainstream theoretical mechanism of consumer diet choice based on an energetic payoff consideration of foraging. That is, among all possible combinations of resources, the consumer should take the set that yields the highest energy intake rate (i.e., the “optimal diet”) in a given condition¹. Thus, the OFT diet choice mechanism is “adaptive”, as the consumer would adjust its diet for maximising its intake in a context-dependent manner. If it complies with OFT, the structure of a food web should also be context-dependent and dynamic over time, as each of the consumers adjusts its diet composition according to the varying abundances of its potential resources. Indeed, the OFT diet choice mechanism has been applied in static (i.e., non-dynamical) models that predict food-web structure (“DBM”, Beckerman *et al.* 2006; “ADBAM”, Petchey *et al.* 2008) from

¹See Section 1.2.2 and also Appendix Section B.1

diverse inputs (namely, different parameters of attack rate, handling time, and species body-size distributions) (Thierry *et al.* 2011b). However, these pioneering studies explored only a limited set of parameters and topological characteristics. We therefore still lack of a comprehensive understanding of what food-web structural features can be generated by OFT. It also remains unknown whether the emergence of some commonly observed structural characteristics in empirical food webs, such as being nested or modular, can be achieved with OFT.

Predicting the placement of interactions in a food web with static models is an important first step. However, it is well known that the structure of food webs can change through time and space (Blanchard 2015; Tylianakis & Morris 2017; Bartley *et al.* 2019), as species “rewire” their interactions in response to the resources available. The rewiring process provides another opportunity for optimisation of foraging by each consumer, yet the optimal diet will change continuously as the abundance of both consumers and resources change through time as a result of community dynamics. To fully understand the effects of diet choice on food-web structure, it is therefore important to consider the former as a continuous process and the latter a dynamical property (Beckerman *et al.* 2010; Loeuille 2010). As static models cannot capture such a dynamical aspect, the structural changing trajectories of food webs that emerge from the OFT diet adjustment and population dynamics of species remains to be explored.

Besides the structure, whether species could persist within is another key attribute of food webs which has important ecological implications (Tylianakis *et al.* 2010). Regarding species dynamics within a food web, OFT diet choice is adaptive for each of the consumers, but is not necessarily so for the food web as a whole. Indeed, ecologists have been exploring the dynamical effect of OFT diet choice on trophic interaction systems for decades, but mostly by taking a very simplified 3-species (i.e., one-consumer two-resources) food web as the study unit. It has been shown that complying with OFT can stabilise such a system (Fryxell & Lundberg 1994), while different kinds of violation or deviation from OFT, such as imperfect diet judgment (Fryxell & Lundberg 1994; Mougi & Nishimura 2009) and response time-lag (Ma *et al.* 2003) could have different influences on the system’s stability. These approaches with small systems, though, inherently cannot reveal properties that only emerge from larger food webs. Similarly, these dynamical findings from small systems cannot be directly extrapolated

to large, complex food webs (*sensu* Brose 2010). In this regard, the effects of adaptive foraging on dynamical consequences of large food webs have been explored in different forms, e.g., diet rewiring after extinction (Thierry *et al.* 2011a) or abundance-dependent reallocation of foraging effort (Kondoh 2003, 2006; Uchida *et al.* 2007; Guill & Drossel 2008), mostly suggesting that adaptive foraging stabilises the system (makes species more persist). However, none of previous work has included dynamical diet adjustment as formulated by OFT. Therefore, it remains unknown whether the OFT diet choice mechanism can make large food webs more robust (i.e., risking fewer species extinctions over time) as in small systems, or as with other forms of adaptive diet rewiring. Moreover, while optimal foraging assumes consumers have perfect knowledge about their foraging (Section 1.2.2), in reality, there are inherent (e.g., sensory and cognitive) limitations. Therefore, consumers may not be able to adjust their diets as much as predicted by (perfect) OFT. Whether different extents of OFT diet choice mediate its effects on food-web dynamics is still poorly understood.

In this chapter, we aim at filling the above-mentioned knowledge gaps regarding the food-web structural and dynamical consequences of the abundance-dependent selection of diet, such as that described by OFT. Specifically, we take both static and dynamical approaches to model food webs with OFT. The static simulation captures snapshot-like OFT prediction of food-web structure under various conditions, where key parameters determining attributes of the whole community, as well as the behaviour of consumers, are manipulated. The dynamical simulation, on the other hand, reveals how different extents of OFT diet choice (i.e., abilities of species to fast adjust their diets) shape food-web structure in a dynamical way (i.e., along with species' population dynamics), as well as their influences to the robustness (quantified by the number of species extinctions over time) of the community.

3.3 Materials and methods

3.3.1 The mathematical model

For a focal consumer, its energy intake rate of eating any given diet (i.e., set of resource species) can be described by a multi-species Type-II function (Holling 1959; Drossel & McKane 2002). Under the assumption that a unit biomass of any resource species provides the same amount of energy, and the efficiency with which the focal consumer converts its consumed biomass to energy is approximately constant, irrespective of consumer or resource identity (Kondoh 2007; Petchey *et al.* 2008) and independent of body size (Peters 1983; DeLong *et al.* 2010; Lang *et al.* 2017), the energy intake rate can be approximated by the biomass consumption rate. The total biomass consumption rate of the j^{th} consumer species is thus

$$C(D_j) = \sum_{i \in D_j} \left(\frac{\epsilon a_{ij} A_{ij} X_i m_i}{1 + \sum_{k \in D_j} a_{kj} (A_{kj} + (1 - A_{kj}) F_{kj}) h_{kj} X_k} \right), \quad (3.1)$$

where D_j is the set of species that constitutes its diet, ϵ its conversion efficiency (here assumed to be a constant 0.5, following Chapter 2), and, for the i^{th} resource species in its diet, a_{ij} is its per-capita search rate (m^2s^{-1} in 2D or m^3s^{-1} in 3D foraging), A_{ij} its attack success probability, h_{ij} its per-capita handling time (s) (the time from pursuing to subjugating the resource) of a successful foraging attack, while F_{ij} quantifies its time cost for engaging an unsuccessful attack attempt, expressed as a proportion (bounded between 0 and 1) of h_{ij} . X_i is the i^{th} resource species' numerical abundance (here, density, in m^{-2} or m^{-3}) and m_i its body mass (mean body mass, ignoring intraspecific variation).

According to optimal foraging theory (OFT), the consumer's optimal diet is constituted by the specific set D that maximises its resultant C . Moreover, the OFT-driven, resource-abundance-dependent diet breadth adjustment should always follow the profitability order of the potential resources (see Section 1.2.2 and B.1). Profitability is the expected energy (here, biomass) gain per time of an already-encountered resource item, which is independent from the resource's abundance. Dividing the expected biomass gain by the expected time spent on

attacking, the i^{th} resource species' profitability to the j^{th} consumer species is therefore

$$\frac{A_{ij}m_i}{(A_{ij} + (1 - A_{ij})F_{ij})h_{ij}} \quad , \quad (3.2)$$

with the same A_{ij} , m_i , F_{ij} , and h_{ij} as in eqn (3.1)². Therefore, to find the optimal diet of a focal consumer, instead of searching through all possible resource species combinations, one just needs to calculate with eqn (3.1) from the narrowest (i.e., eating only the most profitable species) to the broadest (i.e., eating all species) possibilities of optimal diet, and then identify the one that generates the highest C .

3.3.2 Static simulation: diet prediction with fixed contexts

The static simulation is for understanding what food-web structural characteristics the OFT diet choice mechanism can lead to. In particular, we explore how these emergent characteristics are influenced by the community's properties, as well as behavioural properties of the consumers. Under different combinations of factor schemes, we simulated synthetic 50-species communities, then applied eqn (3.1) to establish the trophic relationships (i.e., food-web topology) among species by letting all consumer species take their optimal diet, thereby deriving the optimal-foraging food webs (OF webs). We then quantified the structural features of the generated OF webs and compared them among the combinations of schemes. The simulation is a static prediction of food-web structures, as it makes a single-time trophic-link establishment with given fixed inputs (including species abundances) and thus no population dynamics are involved.

The community and behavioural properties on which we focused were determined as follows. As most of the foraging-relevant parameters in the OFT model (e.g., the search rate (a) and handling time (h)) have been shown to be determined by body masses of the interacting pair (Pawar *et al.* 2012), it can therefore be expected that food webs generated through optimal foraging will be influenced by the body masses of all species (and thus collectively, the

²Note that eqn (3.2) essentially is eqn (B.6) with explicit expression of A and F .

body-mass distribution) of the focal community (Woodward *et al.* 2005; Thierry *et al.* 2011b; Pawar 2015). Also, because the OFT diet choice mechanism depends on resource abundance, species abundances are likely to be another key driver of OF web structure. Moreover, from a consumer’s viewpoint, its preferred resource-consumer body-size ratio (i.e., at which the attack success probability is maximised) and time cost for failed attacks (i.e., F) both affect its evaluating of each resource’s profitability (see eqn (3.2)) and thus its diet choice. To explore the influence of these factors on OF web structure, we adopt a factorial design to set the combinations of different schemes of the species’ body-mass distribution and the magnitude (i.e., scaling constant) of their abundances, as well as the preferred body-size ratio and the time cost of unsuccessful attack of the consumers.

For the body-mass distribution of a food web, we first simulated four distinct synthetic species pools, with respectively small, intermediate, large, and broad (i.e., covering the range of the former three) body masses (details in Section B.3), then used the following four ways to draw the 50-species communities from the pools as four schemes:

- “Discrete”: 20 species from the small pool, 15 from the intermediate pool, and 15 from the large pool. This scheme is an analog to the condition where species can generally be grouped into discrete size categories and the community as a whole has a multi-peaked body-mass distribution.
- “Small”: all 50 species from the small pool.
- “Large”: all 50 species from the large pool.
- “Broad”: all 50 species from the broad pool.

Each scheme thus generates synthetic communities that exhibit distinctive body-size distribution features. Comparisons among them could reveal the influence of different mean (e.g., Small vs. Large), variation (e.g., Small vs. Broad), and continuity (e.g., Discrete vs. Broad) of species body masses on OFT-driven food-web structure.

For species abundances, we assigned the abundance values (here, densities) with the body-mass scaling rule of the Metabolic Theory of Ecology (“Damuth’s law” Damuth 1981; Brown *et al.* 2004). That is, the numerical density (X) of species i is

$$X_i = X_0 m_i^{-0.75}, \quad (3.3)$$

where m_i is its body mass and X_0 is a scaling constant. We then set three schemes of the overall magnitude of species abundances by using 0.1, 1, and 10 as the value for X_0 , respectively. Larger X_0 values make every species more abundant.

For preferred body-size ratio, we made the attack success probability (A) a dome-shaped function of the resource-consumer body-size ratio, whose value peaks at 1 when the resource’s size falls exactly on the consumer’s preferred ratio, and decreases when it deviates from this ratio in either direction. Following Chapter 2, we focused our modelling on food webs of whole-organism predator-prey interactions, where consumers tend to eat resources smaller than themselves (Brose *et al.* 2006a; Pawar *et al.* 2012). We thus set three schemes by using 0.001, 0.1, and 1 as the preferred ratio, to capture a range toward the smaller-than-one end. For the time cost for failed attacks, we set three schemes by assigning 0, 0.5, and 1 as the value for F . These capture the extreme cases where failed attacks cost no time at all ($F = 0$) or save no time even though the resource item is not captured ($F = 1$), while an intermediate value is likely more realistic. For details about the parameterisation of search rate (a), attack success probability A), and handling time (h), please see Section B.2.

In keeping with Chapter 2, we fixed the smallest five species to be the basal resources of the drawn community, and the rest to be the consumers. For each consumer species, all others but not itself were its potential resources (i.e., cannibalistic links were prohibited). We performed 30 replications of simulation as the replicates for each factor combination. We measured structural properties—both purely topological and body-size relevant ones, including: connectance, number of top consumers, nestedness, modularity, mean (realised) resource-consumer body-mass ratio (in $\log_{10}$ scale), and the level of large-eat-small (LES) and large-eat-large (LEL) structures. Definition of these measures can be found in Table 1.2 and also Chapter 2. All

simulations, structural quantification, and analyses were done in R version 3.4.4 (R Core Team 2013).

3.3.3 Dynamical simulation: diet adjustment with population dynamics

We used dynamical simulation to understand how OFT diet choice reshapes food web structure along with the population dynamics of the species within, and how these changes in turn affect the dynamical consequences (i.e., robustness) of the whole food web. In essence, we quantify these properties of the same community during the course of its dynamics, but with schemes where OFT diet choice is applied to different extents. The food-web dynamics were modelled by a generalised Lotka-Volterra model, where the dynamics of species' numerical abundances can be described by the differential equations in matrix notation as

$$\dot{\mathbf{n}} = \mathbf{N}(\mathbf{r} + \mathbf{A}\mathbf{n}) ,$$

where $\mathbf{r}$ and $\mathbf{n}$ are the vectors of species intrinsic growth rates and numerical abundances, respectively. $\mathbf{A}$ is the $S \times S$ (S : species richness) interaction matrix with trophic interaction strengths at off-diagonal entries (zero if no interaction) and intraspecific interference strengths at diagonal entries. $\mathbf{N}$ is the $S \times S$ matrix with values of $\mathbf{n}$ along its diagonal and zero elsewhere.

Synthetic 50-species communities for establishing food webs were simulated as in the static simulation for 30 replicates, with species drawn from the “Broad” body-mass distribution (the smallest five being the basal resources). Preferred body-size ratio was set to 0.1, and time cost for failed attacks was set to be half of the handling time of successful attacks (i.e., $F = 0.5$). All other parameters (e.g., search rate) were set as in the static simulation, except for the magnitudes (i.e., scaling constants) of species abundances (X_0) and handling time (h_0 , see Section B.2), which we manipulated to control the connectance of an “initial OF web” for starting the simulations. Based on OFT diet choice, a consumer's optimal diet breadth became narrower if the abundances of, and/or the handling time of dealing with, potential resources

generally increased (further demonstrated in Section C.3). As the same rule applies to all consumers in the food web, the connectance of an OF web can thus be controlled by assigning different values of X_0 and h_0 , while the body-mass scaling relationships remain the same (i.e., with fixed scaling exponents).

An initial OF web, and its corresponding initial states of parameters, are needed to serve as the starting condition for all dynamical simulation schemes from a given synthetic community. The initial OF web was constrained to have the following properties:

- It is itself the OF web at the given initial state of all parameters, including X_0 and h_0 .
- It has a 0.1 connectance, so that all dynamic simulation replicates (with different synthetic communities) are comparable.
- The species' abundances are as close as possible to the equilibrium of the food web, while still following the body-mass scaling rule (Damuth's law).
- The above equilibrium should be as feasible as possible, that is, it has the maximum number of species that exhibit positive equilibrium abundance (see Chapter 2).

These constraints, altogether, were for approaching an ideal condition that the food web is at a steady state, where the optimal diet of every consumer derived with these given steady-state abundances is exactly its current diet. That is, neither species' abundances nor their diets would change without perturbation at this condition. However, such an ideal condition cannot be solved *a priori* nor necessarily exist. We therefore chose to start with the best approximation we could derive, and observed the dynamics that began with this chosen non-steady initial state—which could be seen as the system having been slightly perturbed away from a presumptive steady state.

To find the OF web that fulfills the above constraints, the per-capita growth rate (r_i) and

interference strength (a_{ii}) of the species i were mass-scaled as

$$r_i = \begin{cases} 1.71 \times 10^{-6} m_i^{-0.25} & , \text{ if species } i \text{ is a basal resource} \\ -4.15 \times 10^{-8} m_i^{-0.25} & , \text{ if species } i \text{ is a consumer} \end{cases}$$

and

$$a_{ii} = a_0 m_i^{0.5} ,$$

respectively, as in Chapter 2. We then searched the parameter space of the value of X_0 from 10^{-6} to 10^2 (with a 0.2 increase in the exponent each time) and derived the corresponding h_0 that makes the generated OF web have 0.1 connectance. For each of these X_0 and h_0 combinations, the per-capita trophic interaction strengths (i.e., the off-diagonal entries of $\mathbf{A}$) can be derived from eqn (3.1) by resolving the fraction of biomass consumption rate of each consumer that is contributed by each of its resources, then converting to a per-capita unit. We then assigned species interference strengths with values of a_0 from 10^{-8} to 10^8 (with a 0.2 increase in the exponent each time). With the interference strengths, along with the already-assigned trophic interaction strengths and growth rates, the food web's equilibrium ($\mathbf{n}^*$) can be analytically calculated (as in Chapter 2) by solving

$$\mathbf{n}^* = -\mathbf{A}^{-1} \mathbf{r} .$$

We then focused on the a_0 that gives the most feasible equilibrium to each of the X_0 and h_0 combinations. Among these most-feasible equilibria across X_0 and h_0 combinations, the one with species abundances closest to Damuth's law's prediction of a -0.75 body-mass scaling exponent, judging by the smallest residual of a linear regression on species body masses to their abundances (both in $\log_{10}$ scale), was identified. The parameters (X_0 , h_0 , and a_0) that gave rise to this specific equilibrium and the equilibrium itself, as well as the OF web from which this equilibrium emerged, together presented the initial state of the system and the initial OF web, respectively.

With the initial OF web and state of a given synthetic community, we then numerically

simulated the dynamics of the system. This was done by using the **deSolve** R package (Soetaert *et al.* 2010) and its `ode` function. Simulation began with the initial OF web and state, and ran for 10^8 time units (10^3 as each integration time step). During simulation, once a species' abundance (density) falls below 10^{-9} , it is considered extinct and its abundance is instantly set to zero. Each synthetic community undertook five schemes of dynamical simulation:

- Type.I: the trophic interaction strengths are fixed (to the initial state) and non-resource-abundance-dependent. Also, species are not adjusting their diet along with species abundances change. Therefore, this scheme is essentially the food-web dynamics with a Type-I functional response-like trophic interaction strength (although the initial value of the strengths are derived with a multi-species Type-II function as above explained) and without dynamical OFT diet choice.
- Type.II: species are not adjusting their diet to changes in species abundances, but the trophic interaction strengths are now dynamically updated with real-time species abundances and follow the resource-abundance-dependent multi-species Type-II function.
- OF.fast: the trophic interaction strengths follow the multi-species Type-II function. The optimal diet of each consumer species is re-derived every 10^4 time units (10 time steps) based on species abundances at that moment. Species are meanwhile allowed to adjust their realised diet for one resource, following profitability order, toward each of their optimal diets. That is, a consumer may broaden or narrow its diet by one resource, or remain the same diet, depending on which act makes its diet closer to the re-derived optimal one. Numerical simulation is carried out after each diet adjustment, with the updated food web topology and interaction matrix. Species' diets and food-web topology are therefore changing throughout the dynamics in a resource-abundance-dependent manner.
- OF.mid: the same as the OF.fast scheme, but the re-derivation of optimal diets and diet adjustment happen every 10^5 time units (100 time steps), which is less frequent.
- OF.slow: the same as the OF.fast scheme, but the re-derivation of optimal diets and diet adjustment happen every 10^6 time units (1000 time steps), which is even less frequent.

Comparing Type.I with Type.II shows the influence on food-web dynamics of the Type-II functional response, i.e., the resource-abundance-dependent trophic interaction strengths. Comparing Type II with with any of the OF schemes shows the influence of OFT diet choice and adjustment, while a comparison among OF.fast, OF.mid, and OF.slow reveals the influence of how perfectly the consumers are able to carry out optimal foraging—the more frequently species are allowed to adjust their diet, the more perfectly they can approach the optimal diet given fluctuating abundances. Species’ population dynamics and food-web structural features (those as in the static simulation) were recorded throughout the simulation. We then compared among the schemes their patterns of food-web structure changing and species extinction through time.

3.4 Results

Food-web structural consequences of static optimal-foraging diet prediction

The static simulation revealed that species’ diet choice based on optimal foraging theory (OFT) can lead to various food-web structures, depending on the given community properties (i.e., mass distribution, abundance magnitude) and behavioural properties (i.e., preferred body-size ratio, time cost for failed attacks). Fig. 3.1 and Fig. 3.2 summarise the diet matrices and structural features, respectively, of food webs generated by OFT diet choice (i.e., OF webs) under combinations of parameters that control these properties. Particularly, among the examined properties, the influence of species’ mass distribution was rather small in comparison to the other three (that is, the patterns that food-web structure varies along with other properties were qualitatively consistent across the four schemes of mass distribution) (Fig. 3.2). Therefore, in the following, we focus mostly on elucidating the results regarding the remaining three factors, but mention the mass distribution only where it interacts with others.

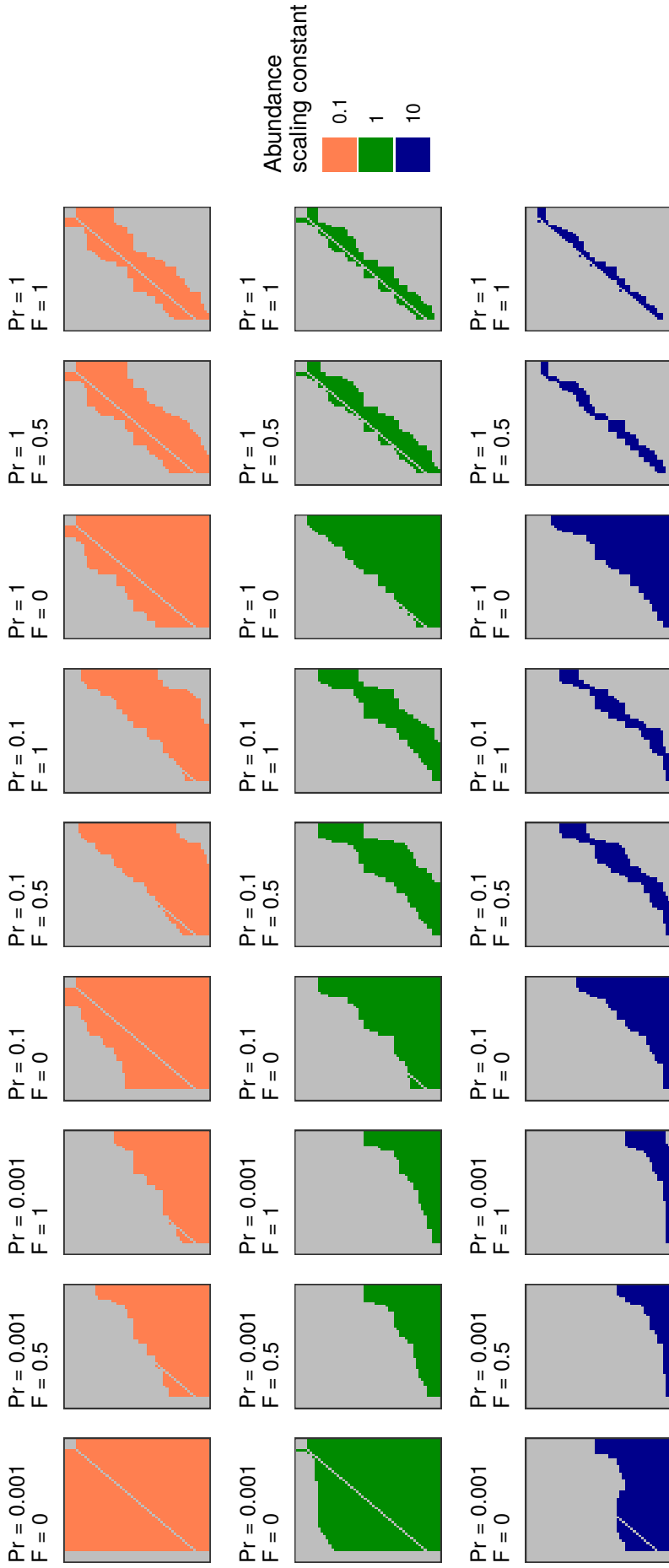


Figure 3.1: **Diet matrices of generated food webs in the static simulation (mass distribution Broad scheme only).** Here all matrices are derived from one replicate (i.e., the same community) but the patterns are representative. Optimal foraging can lead to various food-web structures under different combinations of preferred body-size ratio (Pr), abundance scaling constant (colours), and time cost for failed attacks (F). The non-grey entries indicate realised trophic interactions between consumer (columns, in body-mass order) and resource (rows, in body-mass order) species. The left-most five columns are empty as these are fixed to be the basal resource. For results of other mass distribution schemes, please see Section B.3

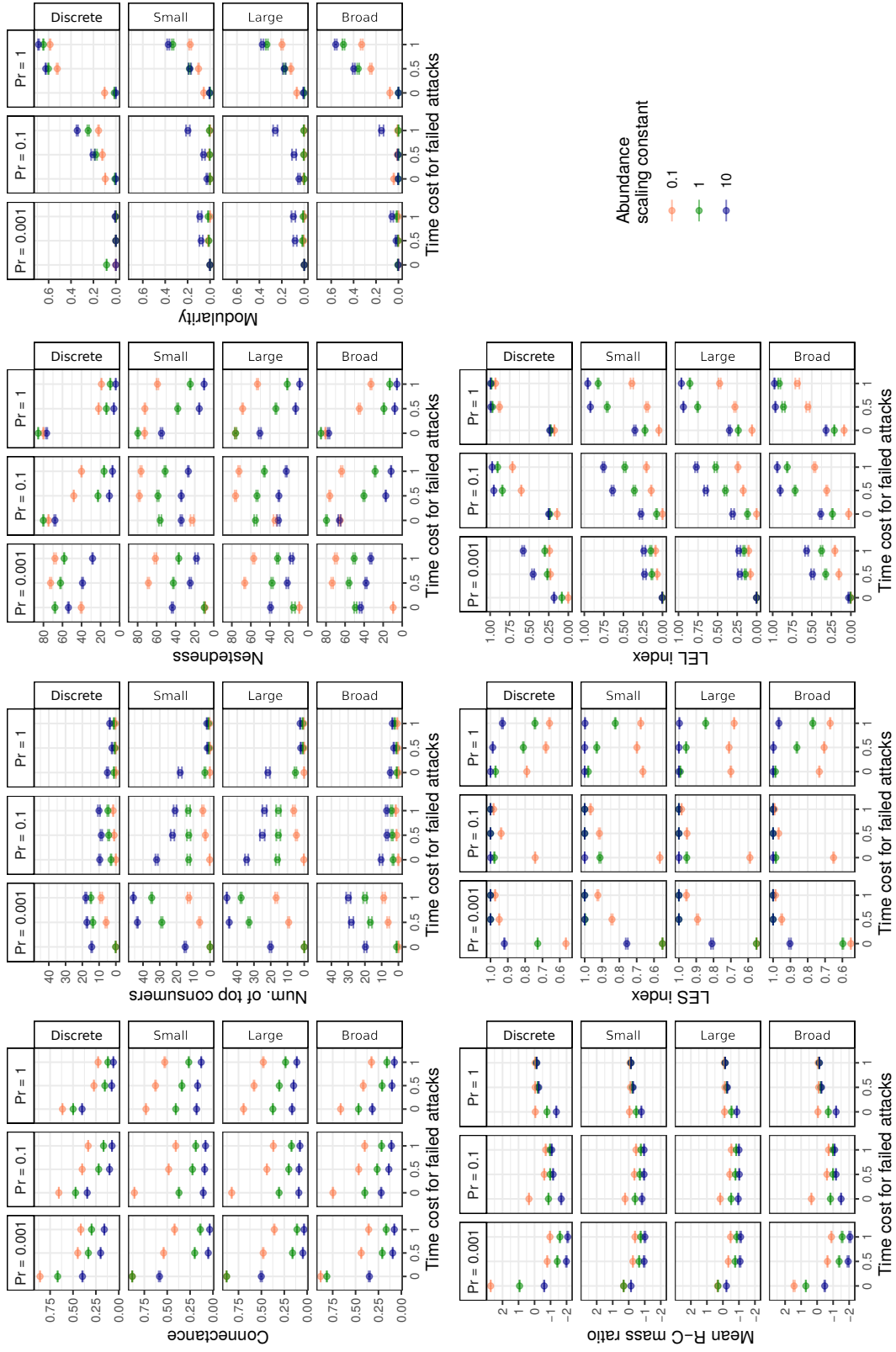


Figure 3.2: **Structural measures of the generated food webs ($N = 30$) in the static simulation.** In general, smaller species abundances were associated with webs that were highly connected, having fewer top consumers, more nested, less modular, and less body-sized (large-eat-small (LES) and large-eat-large (LEL)) structured. Higher time costs for failed attacks, conversely, were associated with the opposite food-web properties, while its effects partly depended on consumers' preferred body-size ratio (Pr). The error bars indicate the standard error. Mass distribution schemes are indicated at the right.

The connectance of OF webs decreased with increasing abundance magnitude (Fig. 3.2). This is well as anticipated, as a rule of thumb of OFT abundance-dependent diet choice is: only when the profitable resources are collectively rare enough, the consumer will start to include the less profitable ones into the diet (see Section 1.2.2 and B.1). Increasing the abundance magnitude essentially makes every species more abundant. This will inevitably make the consumers to narrow their diet to focus feeding on the more-profitable resources, thereby reducing the web's connectance. The connectance also decreased with increasing time cost for failed attacks (Fig. 3.2). When the time cost for failed attacks is very high (i.e., equals the handling time for success attacks, $F = 1$), the constraining effect of the dome-shaped (with resource-consumer body-size ratio) attack success probability is maximised—that is, attempting to attack a too large/small resource (where the attack is likely to fail) will cost much time and harm the total consumption rate (C) of the consumer. Therefore, consumers will avoid doing so in such a circumstance, but tend to feed only on resources whose mass is close to the preferred body-size ratio, and thus the web's connectance decreases. Conversely, low time cost for failed attacks leads to broad consumer diets and high food-web connectance.

The number of top consumers in general decreased with decreasing abundance magnitude and increasing preferred body-size ratio (Fig. 3.2). Because OFT diet choice model predicts a continuous diet (on the body-mass spectrum) for each consumer (Fig. 3.1), the number of top consumers in the food web is thus determined mostly by the size of the largest resource of the largest consumer. Consumer species beyond this size would have no predator and thus are top consumers, while rest are intermediate. Therefore, a larger preferred body-size ratio makes the largest consumer feed on larger resources, while a smaller abundance magnitude incurs a broader OFT-driven diet (as explained above), which further pushes the consumers' diet to include even larger resources. Both effects lead to fewer top consumers in the food web. On the other hand, the number of top consumers rose with increasing time cost for failed attacks with small preferred body-size ratio, but the reverse occurred with large preferred body-size ratios (Fig. 3.2). As mentioned above, a higher time cost causes the consumers to keep their diet closer to the preferred body-size ratio. Thus, a small preferred ratio with high time cost would generally lower the size of realised resources for every consumer, including the largest one, and

thereby free more species from being predated and lead them to act as the top consumers in the web. If the preferred ratio is large, the opposite occurs (Fig. 3.1).

The OF webs were, in general, more nested with smaller abundance magnitude and lower time cost for failed attacks (Fig. 3.2). Viewing food webs as diet matrices, the highest nestedness would emerge if the realised links perfectly occupy the lower triangle. Therefore, the small abundance magnitude, and the loose preferred body-size ratio constraining effect caused by the low time cost, both contribute to the broadening of consumers' diet, which in turn makes the realised links fill better the lower triangle of the diet matrix (Fig. 3.1). However, some OF webs with both low abundance magnitude and time cost deviated from this pattern, as they showed comparatively low nestedness (Fig. 3.2). This was due to the diet of consumers being rather broad under these parameter combinations, where the realised links occupied also the entries in the upper triangle of the diet matrices, thereby causing the web to become less nested (Fig. 3.1). On the other hand, the OF webs were more modular with larger abundance magnitude, larger preferred body-size ratio, and higher time cost for failed attacks (Fig. 3.2). In these conditions, the diet matrices tended to have the bottom-right corner vacant (Fig. 3.1), and thus the realised links distributed in ways that allowed them to be grouped into distinct modules.

The mean resource consumer body-mass ratio of the OF webs tended to converge to the preferred body-size ratio with large abundance magnitude and high time cost for failed attacks (Fig. 3.2). This was due to the stronger constraining effect of preferred body-size ratio caused by the higher time cost, as well as the narrower diet caused by the more abundant resources, as already explained above. Notably, these results also imply that even though all consumers in the community share a universal preferred resource-consumer body-size ratio, the realised diet may deviate from this ratio to different degrees depending on the conditions of other influencing factors.

The OF webs mostly had large-eat-small (LES) and large-eat-large (LEL) body-size structures (Fig. 3.2). Not surprisingly, the LES structure was not as prominent when the preferred body-size ratio equaled one and the abundance magnitude was small. In these conditions, the

attack success probability imposes no LES constraint on the consumers' diet choice, meanwhile the consumers have broader OFT-driven diets due to the low resource abundances. As a result, consumers partly fed on resources that were larger than themselves (i.e., small-eat-large), thereby weakening the LES structure. In some cases, OF webs with smaller preferred body-size ratios were still less LES structured. These were conditions where the diet of consumers were very broad and also caused small-eat-large links, as previously elucidated (Fig. 3.1). The LEL structure is largely driven by the effect of preferred body-size ratio through the attack success probability. Therefore, the LEL structure of OF webs was more prominent in conditions where the effect of preferred body-size ratio is stronger, that is, with large abundance magnitude and high time cost for failed attacks (Fig. 3.2).

Influence of consumer diet adjustment to resource abundance on food-web structural and population dynamics

Besides the structural outcomes caused by instantaneous diet prediction of OFT, the dynamical simulation further revealed how food-web structure could evolve through time when both OFT abundance-dependent diet adjustment and species' population dynamics are functioning. In the Type.I and Type.II schemes, species had no diet adjustment. Therefore, all structural changes with time were purely driven by the loss of nodes and links to species extinction during the dynamics. As species abundances at the initial state were chosen to be close to the analytical equilibrium of the initial OF web, the Type.I scheme indeed saw very few species extinctions (Fig. 3.3, 3.5), and food-web structure of this scheme largely remained unchanged through time (Fig. 3.4). The Type.II scheme, in contrast, accumulated a considerable number of species extinctions quickly in the early phase of dynamical integration (Fig. 3.3, 3.5). Accordingly, the food-web structure first changed rapidly then generally remained constant. Food webs in the Type.II scheme became less connected, less nested, less modular, and less LEL structured with time. Their number of top consumers also slightly decreased, while the mean resource-consumer body-size ratio slightly increased (Fig. 3.4).

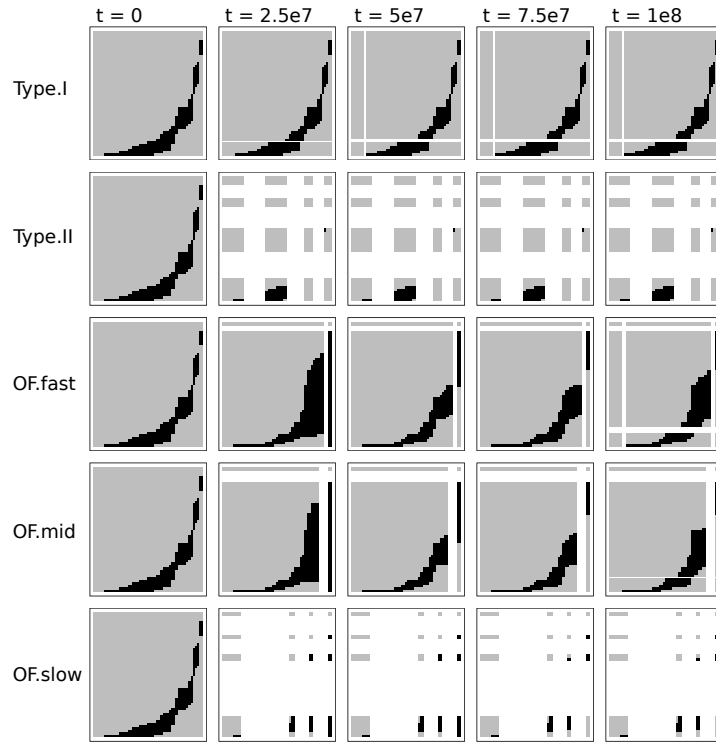


Figure 3.3: **Diet matrices of a generated food web over time for the five schemes that determined consumers' ability to frequently adjust their diet.** Here all matrices are derived from one replicate (i.e., the same community) but the patterns are representative. The black/grey entries respectively indicate realised/non-realised trophic links between consumers and resources (columns and rows, both in body-mass order). The white entries indicate that the corresponding species has gone extinct. The left-most five columns are empty as these are fixed to be basal resources. If trophic interaction strengths are abundance-dependent and saturate at high resource abundance (Type.II), species rapidly go extinct. Optimal foraging (the OF schemes) lead to changes in the realisation of interactions through time, and can offset the above quick extinction, but only when consumers can adjust fast enough their diet to changing resource abundance (OF.fast and OF.mid, but not OF.slow). As extinctions accumulate quickly in some schemes, a closer look into the first one-fifth of integration time is provided in Fig. B.2.

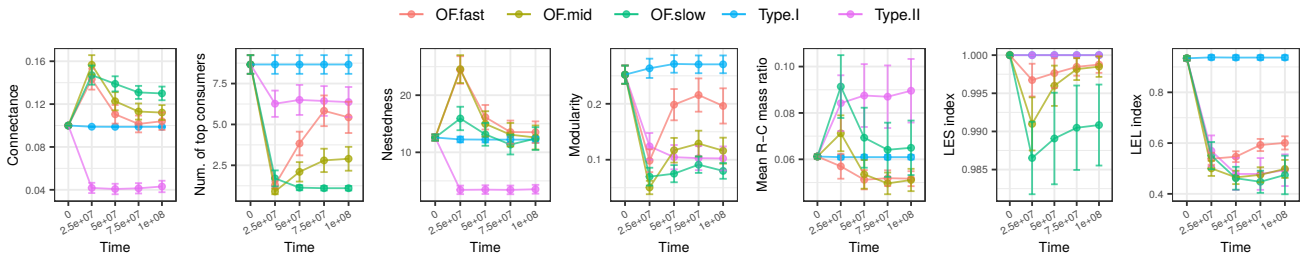


Figure 3.4: **Structural measures of the generated food webs ($N = 30$) in the dynamical simulation.** The error bars indicate the standard error. Each scheme developed distinctive sequence of OFT diet adjustment and species extinctions, and therefore the trajectory of food-web structural dynamics. As structures fluctuated quickly early in the integration, a closer look into the first one-fifth of integration time is provided in Fig. B.3.

In comparison with those of Type.I and Type.II schemes, food webs with OFT diet adjustment (i.e., the OF schemes) showed different trajectories of structural change. In general, these food webs became slightly more connected, equally nested, less modular, less LEL structured, had fewer top consumers (even fewer than the Type.II webs) and a slightly smaller mean resource-consumer body-size ratio by the end of dynamical integration (Fig. 3.4). Notably, unlike in the Type.II schemes, here the structural changes were driven by both species extinction and abundance-dependent diet adjustment (Fig. 3.3). As a result, food webs in these OF schemes did not reach their final state monotonically, but had fluctuation in structural features throughout the dynamics, and still had obvious structural change in the later phase of dynamical integration, when few extinctions were still occurring (Fig. 3.4). Among these OF schemes, the OF.fast ended up the closest to the final state of Type.I scheme (and therefore, the initial OF web) in most of the structural measures (Fig. 3.4). This finding suggested that, while optimal foraging enables food-web structure to change with consumers' diet adjustment, in the long run it actually stabilises the structure (i.e., being structurally closer to the initial state even though some species have gone extinct), especially when consumers are able to adjust their diet quickly.

Finally, regarding the robustness of the food webs, the Type.I scheme had very few species extinctions throughout, whereas the remaining four schemes showed a saturating accumulated extinction number (Fig. 3.5). Optimal diet adjustment made food webs more robust (OF.fast and OF.mid schemes had fewer extinctions than the Type.II), though this effect was reversed if consumers were unable to make this adjustment quickly (the OF.slow scheme had more extinctions than the Type.II) (Fig. 3.5).

A closer look at species identities within food webs (Fig. 3.6) further revealed the qualitative difference in extinctions (i.e. "who went extinct?") between the schemes, and provided the connection between species extinction, OFT diet adjustment, and food-web structural dynamics. In the Type.II scheme, the initial extinctions could affect consumer species of any size. Through time though, most large consumers went extinct, leaving some intermediate- and small-sized consumers in the food web. Though species were not adjusting their diet, due to the extinction of large consumers, some intermediate/small consumers were later freed

from predation and became the top consumers themselves (Fig. 3.6). Although many changes were seen in other structural properties, the decrease in number of top consumers was not severe (Fig. 3.4) because of this trophic role switching. The OF schemes, on the other hand, first had trophic role switching due to OF diet adjustment (Fig. 3.6). Early in the dynamics, the large consumers broadened their diet toward smaller species (Fig. 3.3), making the web more connected and nested while less modular. Also, the smallest few top consumers became the resources of larger ones, thus they were turned into intermediate consumers and caused a decrease in the number of top consumers of the web (Fig. 3.4, 3.6). Through time, species extinction was suppressed in the OF.fast schemes, where some larger intermediate consumers went extinct. Conversely, in the OF.mid and OF.slow schemes, as diet adjustment became less frequent, more of the smaller intermediate consumers went extinct (Fig. 3.6).

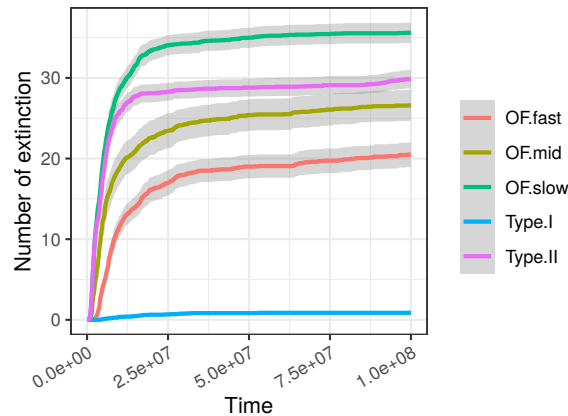


Figure 3.5: **The robustness (quantified as cumulative extinctions over time) of generated food webs ($N = 30$) in the dynamical stimulation.** The shaded areas indicate the standard error. Taking Type.II as the reference, the OF.fast and OF.mid scheme, with relatively frequent OFT diet adjustment, were more robust, whereas the OF.slow was less robust with its infrequent diet adjustment. As extinctions accumulate quickly in some schemes, a closer look into the first one-fifth of integration time is provided in Fig. B.4.

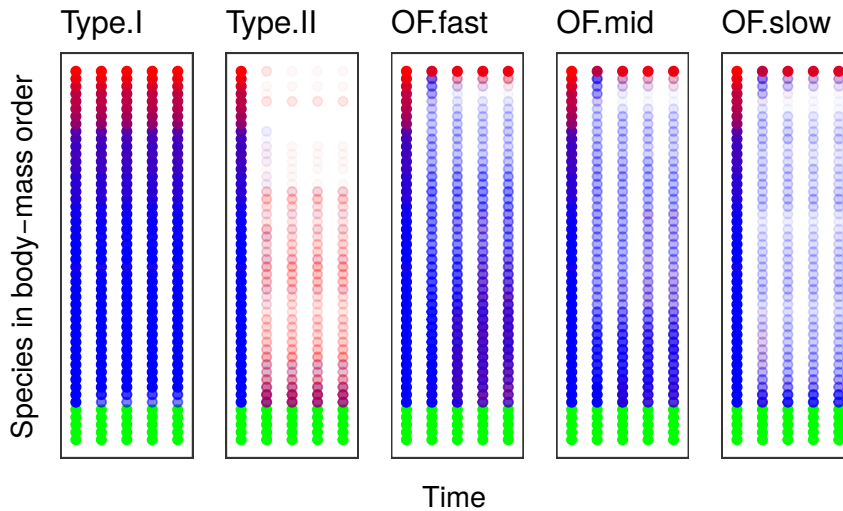


Figure 3.6: **Species body masses, trophic roles, and dynamical fate (extinct or not) within generated food webs ($N = 30$).** The five columns of each panel, from left to right, correspond to the time points that are tick-marked in Fig. 3.5. Red/blue/green colors indicate the trophic roles, i.e., top consumer/intermediate consumer/basal resource, respectively. White color indicates the species is either extinct or isolated from (not eating nor being eaten by) other species. As the nodes' status are averaged over 30 replications, greater colour fading indicates that a greater proportion of replicates at this body-mass rank went extinct. As extinctions accumulate quickly in some schemes, a closer look into the first one-fifth of integration time is provided in Fig. B.5.

3.5 Discussion

Understanding the mechanisms that shape the structure of food webs and lead to their dynamical properties is necessary for resolving the complexity of nature, and is the foundation for dealing with critical ecological issues regarding biodiversity and ecosystem functioning (Dunne *et al.* 2002b; Tylianakis *et al.* 2010). We have shown that a diet choice mechanism based on Optimal Foraging Theory (OFT), along with constrained parameters based on Metabolic Theory of Ecology (MTE), can give rise to a variety of food-web structural and dynamical consequences. The study of this chapter is in the spirit of the “ADBM” model by Petchey *et al.* (2008), whereas we developed further the mathematical modelling of diet choice, applied more detailed mass-scaling of parameters, tested unexplored parameters, and extended the investigation to the dynamical aspects of food-web properties.

In our model, the preferred resource body size for a consumer is set to be a certain ratio

to its own body size. Indeed, due to morphological trait-matching constraints of foraging, such as detection or gape-size limitation, the resource-consumer body-size relationships in the real world mostly follow such a pattern (Berlow *et al.* 2008; Pawar *et al.* 2012; Eklöf *et al.* 2013). Therefore, as intuitive as it is, the preferred body-size ratio effect (through determining attack success probabilities) that is embedded in OFT diet choice led to food webs where consumers mostly eat resources smaller than themselves (i.e., large-eat-small, as the preferred ratio was set no larger than one), while the resource's body size is positively associated with the consumer's (i.e., large-eat-large) (Fig. 3.1 & 3.2).

On the other hand, as we modelled handling time to increase superlinearly with the resource's body mass (see Section B.2), smaller resources are more profitable (see eqn (3.2)) to the consumer than larger resources with the same extent of deviation from the preferred body-size ratio³. As a result, when consumers are to broaden/narrow their diets (e.g., in response to different species abundances), the inclusion/exclusion of resources is biased toward the small-body-size end (Fig. 3.1). This explains the emergence of some commonly observed empirical food-web structures from the OFT diet choice mechanism. For example, the generated web can be nested when consumers' diets are rather broad, or be modular when the diets are narrow and the species body-mass distribution favours the formation of size-specific modules (Fig. 3.1 & 3.2; also, Section B.3). The OFT-predicted food webs are also more nested when the time cost for failed attacks is low, and less nested when time cost is high. This could generate testable predictions for future empirical work. For example, to test whether food webs in environments where the foraging requires the consumers to spend much time chasing and subjugating the resources are indeed less nested than in the opposite condition.

In nature, abundances of species are most likely not fixed, but instead fluctuating (e.g., Wolda 1978; Colebrook 1985). The abundance-dependence of OFT diet choice (and adjustment) thus makes the food-web structure a dynamical property that changes over time, and has a mutual influence with species' population dynamics. Our understanding of empirical food webs has been largely based on snapshot-like sampling, and therefore can only reflect an instantaneous

³In other words, a resource that is 10 times smaller than the preferred ratio is more profitable than a resource that is 10 times larger than the preferred ratio.

state but not necessarily the only state of the community. The different structure-changing trajectories of the schemes revealed in the dynamical simulation (Fig. 3.4) imply that the range of food-web structural features that a community can exhibit during the course of its dynamics depends largely on the underpinning behavioural mechanism. Along with the static simulation part, these results point out promising directions for future work. For example, repeatedly sampling the structure of empirical food webs would allow a validation of structural predictions generated by our simulations. Meanwhile, the measured empirical food-web structure has the potential to conversely be used as an index reflecting either the flexibility of species's diets, or the overall condition (e.g., abundance magnitude) of the community at a specific time.

The dynamical simulation revealed that, the abundance-dependent trophic interaction strengths following a Type-II functional response exacerbated species extinctions, and therefore reduced food-web robustness. The OFT diet adjustment was found to mitigate such extinctions and restore food-web robustness, but only when the adjustment is frequent; otherwise it intensifies the species loss. The Type-II functional response has long been known to be a destabilising⁴ mechanism (Oaten & Murdoch 1975), as under its governance, the per-capita predation pressure that a resource suffers from a consumer is positively associated with the resource's abundance (Fig. 3.7). Predation thus suppresses the resource's population growth when it is rare but facilitates the growth when abundant, which is exactly the opposite feedback that is required for stabilising the system (i.e., decreasing population fluctuations). The OFT diet, by allowing consumers to include or exclude resources from their diets, can (to a degree) counteract this destabilising effect of Type-II functional response—when the focal resource becomes rare, the consumer tends to broaden its diet to include other less-profitable resources, thereby the per-capita predation pressure on the focal resource is diluted (Rooney *et al.* 2006) (Fig. 3.7). Indeed, population dynamics saw fewer extinctions in the OF.fast and OF.mid schemes in which consumers were performing (relatively frequent) OFT diet adjustment (Fig. 3.5).

Infrequent OFT diet adjustment, as in the OF.slow scheme in the dynamical simulation,

⁴Here, “stabilise” and “destabilise” are used under a broader sense of stability, which considers the rate of species extinction and the integrity of the whole system. Our use of these terms here is not necessary relevant to the level of the local asymptotic stability (see Table 1.3).

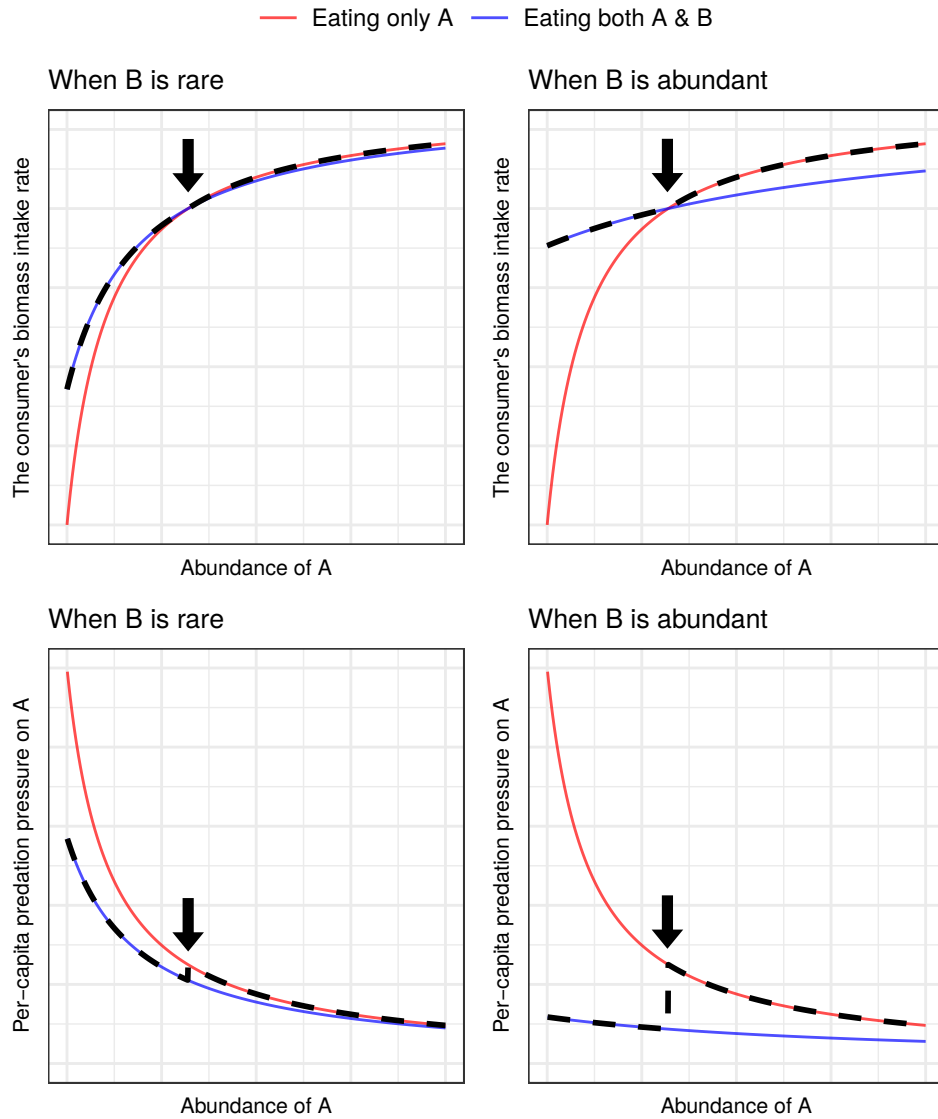


Figure 3.7: **Comparisons of a consumers' biomass intake rate (top) and per-capita predation pressure on the more-profitable resource (bottom) between scenarios with and without optimal-foraging diet adjustment**, illustrated with two resource species, A and B, where A is the more-profitable one. The black dashed lines indicate the scenario with optimal-foraging diet adjustment. The biomass consumption rate follows the multi-species Type-II function, and the per-capita predation pressure on A is quantified by the contribution of A to the consumer's biomass intake rate divided by the numerical abundance of A. The consumer that forages without diet adjustment but feeds "single-mindedly" on A (i.e., red lines) leads to a monotonically decreasing per-capita predation pressure on A (bottom panels), which generates the destabilising effect on A of the Type-II functional response. In contrast, making a diet adjustment to include B when A is rare (i.e., black dashed lines) creates a sudden fall of predation pressure at the threshold abundance of A of the diet adjustment (indicated by arrows), which makes the overall predation pressure pattern less-monotonic, and therefore mitigates partly the destabilising effect. Comparing the bottom-left with bottom-right panel reveals that such mitigation is more effective if the less-profitable resource (B in this case) is abundant.

drove species extinct even more severely than in the Type.II scheme which had no diet adjustment. Notably, in the Type.II scheme, some consumer species may be isolated (as all its previously interacting species have gone extinct) but yet have their abundances drop below our extinction threshold by the end of dynamical simulation⁵. These species were not recorded as extinct, but actually are doomed to extinction without the ability to establish new links to resources. Therefore, the OF.slow scheme may not necessarily lead to “more” extinction than the Type.II scheme, but it certainly accumulates species extinctions faster. It has been shown previously that the rapid predatory switching behaviour of higher-trophic-level predators is needed for regulating the predatory pressure among resources and stabilising different resource channels in the system (Rooney *et al.* 2006). Therefore, too-infrequent diet adjustment (in a sense of failing to catch up with the pace of species’ population dynamics) may lose its stabilising ability, but incurs extra predatory pressure on the remaining intermediate- or small-sized species. This may facilitate species extinction especially when the system is already fragile and with low species abundances (Fig. 3.3). Among studies on adaptive foraging in food webs, this study presents the first model that adopts an OFT framework throughout—including the establishment of initial trophic links and the diet adjustment during the course of population dynamics. While most previous studies suggested that adaptive foraging positively contributes to species persistence in food webs (e.g., Kondoh 2003; Heckmann *et al.* 2012), some reported the opposite (Gilljam *et al.* 2015). Our results indicate that both outcomes are possible, as the stabilising/destabilising effect depends on how well species can achieve OFT foraging by making frequent diet adjustments.

By mapping species’ identities (i.e., their body masses and trophic roles) to the extinction outcomes (Fig. 3.3 & 3.6), we found that not all species shared the same extinction risk. Basal resources, with their positive intrinsic growth rates set in the Lotka-Volterra dynamical model, in general were free from the risk of going extinct. In the long term, large-sized consumers are more susceptible to extinction (Fig. 3.6). Although the OFT diet adjustment allowed the largest very few consumers to persist, the remaining large consumers besides these few

⁵Even though extinction may temporarily isolate some consumers in the schemes with OFT diet adjustment, they will soon form new links to other remaining species once the diet adjustment is carried out. Thus, the isolated state does not last long.

still eventually went extinct, even with frequent diet adjustment (OF.fast scheme in Fig. 3.6). Notably, the ability of large-sized consumers to quickly adjust their diets (OF.fast & OF.mid schemes in Fig. 3.3) seemed to be important for avoiding the early extinction caused by the destabilising effect of a Type-II functional response (Type.II & OF.slow schemes in Fig. 3.3). These discoveries indicate that body size may play a role in influencing how optimal foraging could possibly enhance the robustness of the whole system. Indeed, species with different sizes have distinctive life-history traits, such as birth rate, death rate, and generation time (Brown *et al.* 2004). At a population level, large-sized species have relatively low growth potential, thus the maintenance of high abundances would be difficult, and their population's numerical response would be rather inefficient. At an organism level, a large individual in its relatively long life span would experience more occurrences, and with larger extents, of fluctuations in abundances of those relatively small-sized species with which it interacts. It is therefore reasonable to expect that large-sized species should be more efficient at making functional adjustments, e.g., change their diet behaviourally, in order to adaptively respond to these fluctuations. For small-sized species, on the other hand, such an efficient behavioural diet-adjusting ability may not be as necessary, as their short generation time could allow a fast numerical response, or even a quick evolution in changing diet, for promoting their persistence. In the study of this chapter, the frequencies of OFT diet adjustment were universal, i.e., applied to all species in the community. However, given body size being a fundamental determinant of animal behaviour (Cozzoli *et al.* 2019), as well as the above inference, it would be intriguing for future research to investigate whether there exists an “allometry” of diet adjustment frequency (presumably positively mass-scaled, according to the above deduction) in the real world.

In conclusion, optimal-foraging diet choice has significant consequences for both the structure and dynamics of food webs. The ability of making OFT diet adjustment according to resources' abundances not only benefits consumer organisms, but also can improve the dynamical robustness of the whole food web given an appropriate diet-adjusting frequency. Therefore, such a diet adjustment mechanism would be favoured by selection and could act as a shaping force of food-web properties that we empirically observe. The study of this chapter joins previous works (e.g., Kondoh 2003; Petchey *et al.* 2008) to explore how individual-level foraging

behaviour scales-up its effect to determine community-level phenomena. Especially, it is among the first that reveals the dynamical outcomes of food webs fully under an OFT framework. Taking account of foraging behaviour as the fundamental driver of food-web formation can thus be the path to a more thorough mechanistic understanding of the complex systems in nature.

Chapter 4

Predation risk influences food-web structure by constraining species diet choice

Declaration

This chapter has been published in *Ecology Letters*, with Dr Samraat Pawar, Prof Jason Tylianakis, and PhD candidate Jonathan Zheng (Department of Electrical and Electronic Engineering, Imperial College London) being my coauthors. When writing the content, I received input from all coauthors, as well as the editor and reviewers during the publication process. Part of the empirical data used in this chapter was compiled with the assistance by Molly Edbrooke (Department of Life Sciences, Imperial College London). Parts of Fig. 4.1, Fig. 4.5, and the Pseudocode in the Appendix (Section C.2) are contributed by J. Zheng.

4.1 Abstract

The foraging behaviour of species determines their diet and, therefore, also emergent food-web structure. Optimal foraging theory (OFT) has previously been applied to understand the emergence of food-web structure through a consumer-centric consideration of diet choice. However, the resource-centric viewpoint, where species adjust their behaviour to reduce the risk of predation, has not been considered. We develop a mechanistic model that merges metabolic theory with OFT to incorporate the effect of predation risk on diet choice to assemble food webs. This “predation-risk-compromise” (PR) model better captures the nestedness and modularity of empirical food webs relative to the classical optimal foraging model. Specifically, compared with optimal foraging alone, risk-mitigated foraging leads to more-nested but less-modular webs by broadening the diet of consumers at intermediate trophic levels. Thus, predation risk significantly affects food-web structure by constraining species’ ability to forage optimally, and needs to be considered in future work.

4.2 Introduction

Understanding food-web structure—the arrangement of who-eats-whom interactions—is necessary for understanding biomass (ergo, energy) flows and the stability of ecosystems (May 1972; Allesina & Tang 2012; Rossberg 2013; Gravel *et al.* 2016). The trophic interactions in a food web are, in fact, accumulations of foraging events between individual organisms; all structural properties of food webs therefore emerge from individual foraging behaviours driven by metabolic demands (Brose *et al.* 2008; Petchey *et al.* 2008; Pawar *et al.* 2012; Portalier *et al.* 2019). Although this idea is intuitive, food-web structure, foraging behaviour, and metabolic constraints have historically been studied independently until recently (Abrams 2010; Beckerman *et al.* 2010; Loeuille 2010; Stouffer 2010; Valdovinos *et al.* 2010). To mechanistically understand the emergence of food-web structure, it is therefore important to explore the underpinning, metabolically-driven diet choice of species. To this end, previous work has used optimal foraging theory (OFT; Charnov & Orians 1973; Stephens & Krebs 1986; Krebs *et al.*

1977) combined with metabolic theory (Brown *et al.* 2004) to model the diet choice of consumers in food webs (Beckerman *et al.* 2006; Petchey *et al.* 2008). Optimal foraging theory stochastically models a series of decisions for each consumer, between whether to pursue or ignore each encountered resource item, such that their final diet composition maximises its net energy intake rate.

By using metabolically-constrained search and handling parameters in the classical OFT diet-choice model as the mechanism for trophic link formation, Petchey *et al.* (2008), building on previous work by Beckerman *et al.* (2006), showed that the resulting “Allometric Diet Breadth Model” (ADBM) could help predict links in real food webs. This result highlighted the importance of metabolic constraints (through size-scaling) in determining diet choice, and supported the idea that OFT can help explain food-web structure. The ADBM and its variants has since then been used to predict the effects of temperature (Petchey *et al.* 2010) and behavioural size-dependence (Thierry *et al.* 2011b) on food-web structure. Nevertheless, the predictive abilities of ADBM-type models remain limited, raising doubts about the utility of body size and OFT alone for predicting food-web structure (Allesina 2011). Additional factors may thus be needed to explain how food-web structure emerges from foraging decisions (Berlow *et al.* 2008; Eklöf *et al.* 2013; van Leeuwen *et al.* 2013; Jonsson *et al.* 2018). Furthermore, the ADBM is also limited in its ability to provide mechanistic insights because it “tunes” key foraging parameters (attack rate scaling and upper limit of consumer-resource size-ratio) to maximise fits to empirical data. This results in (mechanistically) unfeasible values of these parameters: varying by more than 20 orders of magnitude and carrying the wrong signs (Petchey *et al.* 2008).

Here, we argue that the ability of OFT-based models like the ADBM to mechanistically predict empirical food-web structure is limited partly because the classical model is consumer-centric, where diets are chosen purely to maximise energy intake rate as the only objective. In reality, all species in food webs (excluding top predators and basal taxa) are both a consumer and a resource, always risking predation while foraging themselves. Indeed, anti-predator behaviour is common—consumers from practically all taxonomic lineages modify their foraging behaviour to mitigate predation risk (Laurila *et al.* 1997; Schmitz *et al.* 1997; DeWitt *et al.*

1999; Altwegg *et al.* 2004; Jousset 2012), with these strategies playing a significant role in determining the forager’s fitness (Lima 1998). Studies have also found that predation-risk-driven behavioural responses of prey can strongly reduce their own consumption rates as predators and influence their diet choice (Lima & Valone 1986; Metcalfe *et al.* 1987; Beckerman *et al.* 1997; Pangle *et al.* 2012; McMahon *et al.* 2018). Thus, most consumers cannot possibly forage optimally (in a strict OFT sense) all the time, but still need to meet their metabolic demands while living in an “ecology of fear” (Brown *et al.* 1999). We therefore propose that predation risk, by modulating optimal foraging (Berlow *et al.* 2008), should be an additional key factor structuring food webs (Beckerman *et al.* 1997; Schmitz *et al.* 1997; Kondoh 2007; Bucher *et al.* 2015). Yet, to our knowledge, no study has investigated how predation risk and metabolic constraints together influence the foraging decisions that generate food-web structure.

In this chapter, we include predation risk and metabolic constraints into the classical OFT diet choice model to study the emergence of food-web structure. Using this “predation-risk-compromise” (PR) model, we assemble food webs *in silico*, and test whether the new model better captures empirically observed food-web structure than the ADBM type approach based on classical OFT (the OF model). We focus our discussion on nestedness and modularity as measures of food-web structure (Table 1.2 & C.3). Empirical food webs are known to be nested and modular (Kondoh *et al.* 2010; Krause *et al.* 2003; Teng & McCann 2004; Montoya *et al.* 2006; Guimerà *et al.* 2010), and both properties have been proposed to promote the dynamical stability of food webs (Krause *et al.* 2003; Thébault & Fontaine 2010; Stouffer & Bascompte 2011; Grilli *et al.* 2016; Gilarranz *et al.* 2017). We show that the PR model outperforms the OF model in capturing empirical food-web structure in terms of these two metrics as well as many others across multiple communities, and quantify the relative importance of optimal foraging vs. predation risk in determining model food-web structure.

4.3 Materials and methods

4.3.1 Foraging models

The OF model derives the optimal diet of an individual consumer that maximises its net energy intake rate according to classical OFT (Charnov & Orians 1973; Krebs *et al.* 1977). We use biomass consumption rate as a proxy for energy intake rate, under the assumption that the energy content per unit biomass of resource and conversion efficiency (i.e., from biomass to energy) of consumer are both approximately constant irrespective of consumer or resource identity (Kondoh 2007; Petchey *et al.* 2008), and independent of body size (Peters 1983; DeLong *et al.* 2010; Lang *et al.* 2017). The total biomass consumption rate of the j^{th} consumer species in a food web can be written as

$$C(D_j) = \sum_{i \in D_j} \left(\frac{\epsilon a_{ij} A_{ij} X_i}{1 + \sum_{k \in D_j} a_{kj} A_{kj} h_{kj} X_k} \right) \quad (4.1)$$

where D_j is the set of species in its diet, ϵ its conversion efficiency (here assumed constant, but further examined in the Discussion), and, for its i^{th} resource species, a_{ij} is mass-specific search rate ($\text{m}^2 \cdot \text{kg}^{-1} \cdot \text{s}^{-1}$), A_{ij} its attack success probability, h_{ij} its mass-specific handling time (s) (the time from pursuing to subjugating the resource), and X_i the resource's biomass abundance (density) ($\text{kg} \cdot \text{m}^{-2}$). Equation (4.1) is a multi-resource extension of the classical (single-resource) Type-II functional response (Holling 1959) (Appendix Section B.1), and is the expected energy intake over a large sample of iterated, stochastically-spaced foraging bouts (Charnov & Orians 1973)¹. The consumer's biomass consumption rate depends on its diet set, as well as the abundances of those resource species. Using eqn (4.1), we use OFT to assign trophic links in a community with given and fixed species abundances (Section C.1.3) as follows. For a consumer, the profitability of each resource species is calculated as its attack success probability divided by mass-specific handling time (Section C.1.1; eqn (C.2)). According to OFT, given

¹Note that for modelling simplicity, eqn (4.1) here is a conceptually identical but mathematically simpler version of eqn (3.1) in Chapter 3 by removing the effect of time cost of failed attacks. Also, we model eqn (3.1) in per-capita units while here eqn (4.1) in mass-specific units (i.e., per-biomass consumer on per-biomass resource); this makes no difference as the two sets of units are inter-convertible. Finally, the parameterisation of the two chapters are conceptually similar but nonidentical; please see Section B.2 and C.1.3, accordingly, for details.

the profitability ranking of resource species, lower-rank resource would not be eaten without higher-rank ones being included in the consumer's diet (Section 1.2.2 and B.1). We therefore calculate, for each consumer species in the given community, the biomass consumption rate across the whole range of diet breadth, i.e., from eating only the most profitable species to sequentially including others ordered by profitability until it eats all species (Section C.1.1). The resource set that produces the highest consumption rate, C_{opt} , constitutes the OF diet (Fig. 4.1A–B).

OF can be seen as a predation-risk-free state of a consumer, where it has the luxury of being “picky” by ignoring not-so-profitable resources to achieve an optimal (maximised) consumption rate. The PR model is an extension of the OF model to include metabolic expenditure and predation risk as additional constraints on (objectives for) consumer foraging decisions as follows. First, we include a minimum mass-specific consumption rate, C_{min} (s^{-1}) that the consumer needs to balance its energy loss to somatic maintenance (Fig. 4.1C) (Rizzuto *et al.* 2018). Second, we introduce the effect of predation risk on every species as follows. First, we quantify realised predation risk (P_{risk}) for every species as

$$P_{\text{risk}} = \left(\frac{\sum X_{\text{real}}}{\sum X_{\text{all}}} \right)^{e_P} \quad (4.2)$$

where $\sum X_{\text{real}}$ is the total biomass of all its realised consumers, $\sum X_{\text{all}}$ is the total biomass of all (including the realised) consumer species, and the exponent e_P determines how P_{risk} increases with $\sum X_{\text{real}}$ (Fig. C.1). Thus, P_{risk} is bounded between 0 and 1 (Fig. 4.1D). Then, for a given species' P_{risk} value, its corresponding risk-compromised consumption rate, C_{risk} , necessarily lies between the optimal (OF) consumption rate C_{opt} and C_{min} (Fig. 4.1C–D), such that:

$$C_{\text{risk}} = C_{\text{min}} + (1 - P_{\text{risk}})(C_{\text{opt}} - C_{\text{min}})$$

Then, the resource set that yields the closest-but-higher consumption rate than this risk-compromised value is the predicted predation-risk-compromise (PR) diet (the diet set above the dashed line in Fig. 4.1D that is closest to it). That is, the P_{risk} value determines where a species lies between two extremes, depending upon its trophic position in the food web. When

there is no risk ($X_{\text{real}} = P_{\text{risk}} = 0$), predator avoidance is unnecessary, and the population can forage to maximise consumption rate (well exceeding its C_{min}). This is essentially equivalent to the classical OFT condition (i.e., the OF model). At the other extreme, where the consumer bears maximum predation risk because all possible species forage on it ($X_{\text{real}} = X_{\text{all}}$, so $P_{\text{risk}} = 1$), the need for predator avoidance outweighs the optimal consumption objective, such that the consumer forages in a way that minimises predation risk, while still meeting the C_{min} threshold. This can be accomplished by taking a diet that requires the least time spent doing risky foraging actions (searching/waiting vs. handling), yielding a consumption rate closest to, or exactly at, the threshold C_{min} . Thus, in the PR model, consumers are simultaneously trying to meet three objectives: foraging optimally, mitigating predation risk, and meeting an energetically-minimum consumption rate. This approach is in the spirit of foraging models that use multiple-objective dynamic programming by Rothley *et al.* (1997).

There are two possible ways that consumers can mitigate risk, depending on which of searching (waiting, if the consumer adopts sit-and-wait foraging) and handling is the riskier action. If handling is less risky than searching, the consumer can accept more resource types (i.e., becomes more generalised), effectively lowering the time allocated to searching/waiting within a foraging bout relative to what OFT would predict (resulting in a “diet-broadening” strategy). Conversely, if searching is less risky than handling, it can pursue only the more profitable resources which require less time to handle for gaining the same amount of energy (i.e., it becomes more specialised), effectively lowering the total time allocated to handling within a foraging bout (resulting in a “diet-narrowing” strategy) (Section C.1.2).

In the following sections, we focus on the diet-broadening strategy because assuming handling being the less risky action is empirically supported (see Section 4.5), and the diet-narrowing strategy also effectively converges to the OF model in our simulation. Simultaneously allowing both strategies converges to the broadening case. For full results of all strategies, see Section C.7. Finally, note that we define P_{risk} (eqn (4.2)) to be monotonic under the assumption that other mechanisms affecting predation risk of a species, such as interference between its consumers, are less important than the effect of increasing the abundance of those consumers *per se*.

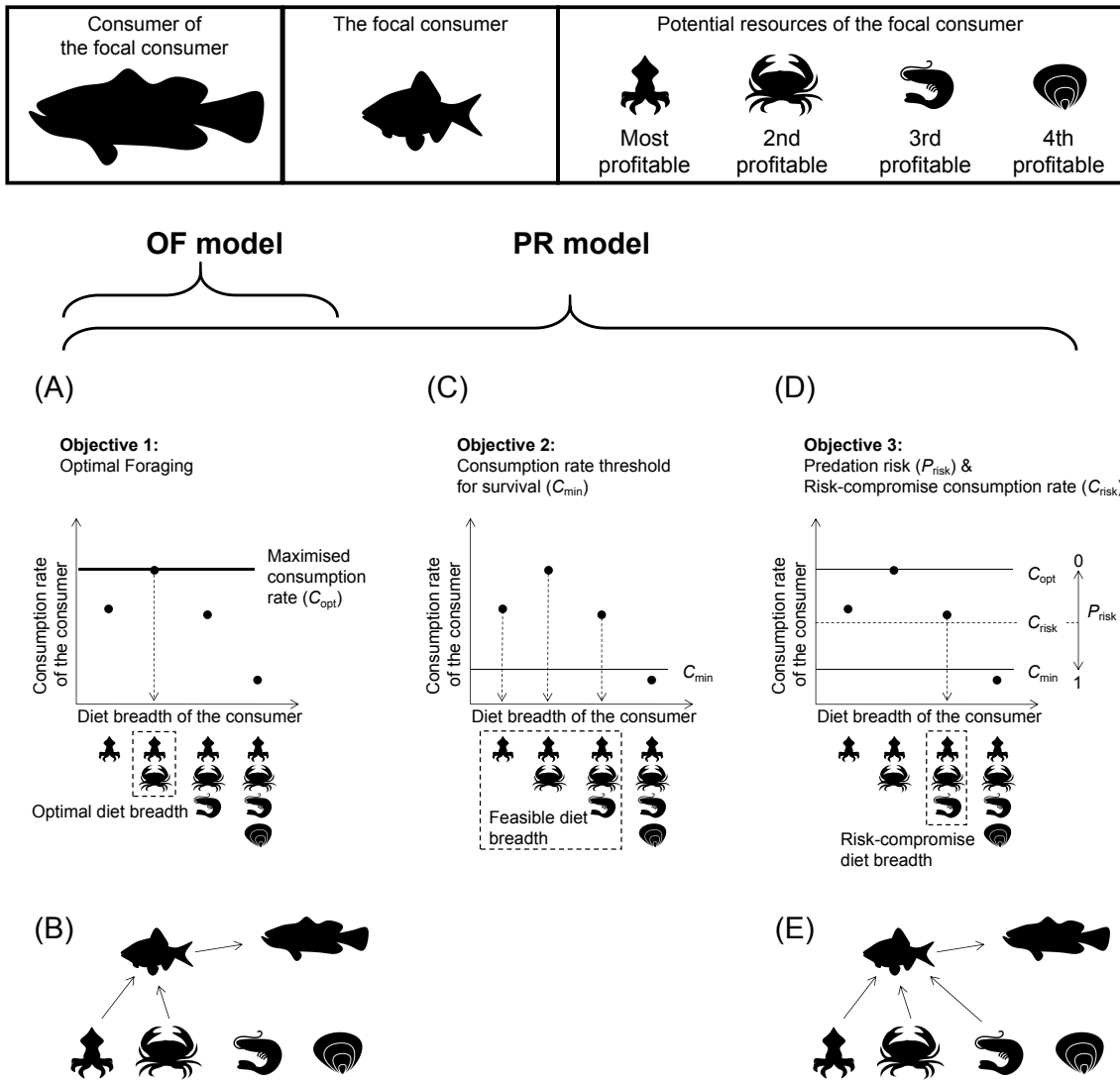


Figure 4.1: Illustration of the Optimal Foraging (OF) and Predation-Risk-Compromise (PR) models for predicting the diet breadth of a focal consumer. Under the OF model (A–B), the predicted diet for a consumer is the one that yields maximum net consumption. Under the PR model (A, C–E) predation risk, P_{risk} , is incorporated as a constraint on optimal foraging, resulting in a diet with a risk-compromise consumption rate (C_{risk} , the point closest to, while still being above, the horizontal dashed line in D) lying somewhere between the OF maximum, C_{opt} , and a minimum metabolically-feasible consumption rate threshold, C_{min} . Both models are applied to all consumer species in a community to assemble model food webs. Note that we focus on the diet-broadening strategy in the PR model, which “propagates” iteratively during food-web assembly, as described in the main text.

4.3.2 Building food webs using the foraging models

We use metabolic scaling theory to parameterise the foraging models (Section C.1.3). In short, X , a , A , and h of eqn (4.1) and the C_{min} of the PR model are specified using body mass-based

scaling rules. These update the ADBM model parameterisations (Petchey *et al.* 2008) with new, empirically-validated relationships. We recognise that there is uncertainty in both the mathematical structure and exact parameterisation of the quantities. Therefore, we test the robustness of our results to variation in these formulations as described in Section 4.3.4.

Given the values of parameters, we generated predicted food webs by applying each of the above two foraging models to every consumer species in a given community. The set of species could either be from an empirical community or a synthetic one, as explained further below. All simulations and analyses were performed using R (ver. 3.4.4) (R Core Team 2013).

To assemble OF webs, we simply apply the OFT diet criteria simultaneously to each consumer species in the communities (eqn (4.1); Fig. 4.1A–B). In contrast, PR webs were assembled using the the following iterative algorithm (pseudocode in Section C.2):

1. Generate an initial web following the OF diet choice rules using eqn (4.1). Notably, this is not the OF web against which the PR web will be compared.
2. Calculate the predation-risk index (P_{risk}) of each species using eqn (4.2).
3. Re-assign resource links for each species according to the diet-broadening strategy (Fig. 4.1C–E).
4. Repeat steps 2–3 until both P_{risk} and the web’s topology do not change anymore.

In step 3 we choose the diet-broadening strategy because using a diet-narrowing strategy effectively reproduces the food-web structure predicted by the OF model (Section C.7). Thus, in each iteration of steps 2–3, predation risk of certain consumers increases, which broadens the diet of those consumers in order to find the best risk-compromised diet, which, in turn, imposes additional predation risk to those newly-consumed species. This results in a sequential broadening of diets across trophic levels in each iteration until a steady state where no more diet broadening (and therefore no more change in predation risk) occurs.

Most food-web topological features, and nestedness and modularity in particular, are connectance-dependent (Thébault & Fontaine 2010). Therefore, to generate PR and OF webs

with comparable connectance to the empirical web, we manipulated the magnitude of handling time (h_0 ; Section C.1.3) while generating the model webs, keeping species' abundances fixed (Section C.3). We choose to manipulate handling time instead of abundance to control food-web connectance because the aim of our foraging models is to generate a predicted food web based on given information, and abundance across a wide range of species is arguably better-quantified empirically (i.e., measured or estimated) than handling time.

We note that the aim of this study is not to make the best model to reproduce food webs, but to quantify the effect of predation risk and maintenance metabolic rate constraining optimal foraging in food webs. We therefore focus on the difference between the foraging models *per se*, and do not compare these with existing web-generating models such as the Cascade (Cohen & Newman 1985) and Niche (Williams & Martinez 2000) models and their variants. This is also the reason why our food-web models differ fundamentally from the ADBM and are purely mechanistic—we do not tune free parameters to maximise the fit of the OF or PR webs to their empirical counterparts. Tuning parameters would also prevent us from directly comparing OF and PR models for each set of parameterisations. Indeed, this lack of tuning sets our approach apart from all other previous food web-generating models such as the Niche (Williams *et al.* 2010) or Matching models (Rossberg *et al.* 2006).

4.3.3 Comparing ability of the foraging models to capture empirical food-web structure

To compare the ability of the OF and PR models to capture real-world food-web structural properties, we used twelve terrestrial and aquatic empirical food webs with nodes well resolved to the species level (Section C.5). Because of the size-ratio biased (i.e., large-eats-small) nature of the allometric constraints we use (also see Petchey *et al.* 2008), we confined our study to carnivorous and herbivorous interactions, excluding pathogenic, parasitic, and symbiotic interactions from each empirical food web.

Based on four attributes of each empirical food web—species richness, identities of basal

species, species' body masses, and connectance—we generated fifty OF- and PR-predicted food-web counterparts each. The parameters X , a , A , h , and $C_{\min}$ used for web-generation were specified as above-mentioned but with the constant and exponent(s) re-sampled from a normal distribution with means equal to the specified values and standard deviation as one tenth of the respective mean. This allowed us to account for parameter uncertainty. The preferred body-size ratio, R_p , was set to be the observed median resource-consumer body-mass ratio of each empirical web.

The connectance for the OF and PR model webs was matched to the empirical value by manipulating h_0 value as mentioned above. The consumption rate threshold, $C_{\min}$, of the PR model automatically set an upper bound for h_0 , preventing it from being biologically unfeasible. When h_0 becomes too large, even the optimal consumption rate for certain species falls below $C_{\min}$, which is unfeasible and a PR food web cannot be generated. This also imposes a lower-bound on the connectance that PR food webs can achieve. During the simulation of PR food webs, we began by assuming a linear relationship between predation risk of the focal consumer and the total biomass of its predators (i.e., e_P in eqn (4.2), equals one). Whenever the combination of empirical community attributes and the parameter values failed to produce a PR counterpart with acceptably close-to-empirical connectance (i.e., within 10%), we lowered the extent of the diet-broadening effect by increasing e_P by 0.25 and re-assembled the PR food web (Section C.1.3). This process was repeated until an acceptable PR food web was produced. The summary of connectance and e_P values of the fifty replicates of each empirical community can be found in Table C.4 and shows that the mean value of e_P was typically not much larger than one.

Nestedness and modularity of empirical and model food webs were measured using the NODF and modularity indices, respectively (Table C.3). We quantified how well the two foraging models captured these features of empirical food webs by calculating their absolute deviations from the empirical value. The comparison of performance was made by collapsing the fifty replicates of the twelve communities to 600 paired observations (paired by identity of replicates, as for each replicate the OF and PR web are generated with the same set of re-sampled parameters), then checking whether the deviations are smaller in PR than in OF.

These paired observations were then compared using a linear mixed model (LMM, using the `lmer` function of the R package `lme4` (Bates *et al.* 2014)), where the type of model (OF vs. PR) was set as the fixed effect, and community and iteration as nested random effects. To test if the performance results were consistent across different communities, we also conducted a community-specific comparison of the above-mentioned deviations using a paired-Wilcoxon test. Along with nestedness and modularity, we also analysed how well the two models captured several additional metrics that are commonly used in the literature to quantify food-web structure (results in Section C.7).

4.3.4 Synthetic food webs

We also generated synthetic food webs to gain further insights into the differences in food-web structures generated by the OF and PR models, the mechanisms generating these differences, and to test their structural sensitivity. For this, we assembled and compared synthetic food webs based on the OF model, PR model, and a null model where the links are randomly assigned. Structural differences between OF and null food webs allow us to identify structural signatures of optimal foraging *per se*, while differences between OF and PR webs allow us to understand the additional structural effects of predation risk.

To test the sensitivity of our results to the structures of the metabolic models used for the foraging parameters and in food-web attributes, we repeated the above simulations and comparisons across fourteen schemes (Table C.2). Each of these schemes is a unique combination of food-web attributes (species richness, proportion of basal species, mean and variation of species body masses) and parameters of foraging models (X , a , A , h , and e_P ; eqns (4.1) & (4.2)). Note that scheme 1 served as a baseline, with all others varying one attribute or parameter at a time. For further details about schemes, see Section C.1.3.

Thus, we independently simulated fifty synthetic communities for each scheme based on scheme-dependent attributes and parameters. For each simulation, a given number of species were generated, and a designated number of these were randomly picked to be basal species. Species body masses were randomly drawn from a log-normal distribution (Preston 1948; Engen

& Lande 1996; Pawar 2015) with scheme-dependent mean and standard deviation, which were considered to cover a range that is representative of empirical values (Table C.4). Biomass densities of species were then derived based on a scheme-dependent scaling exponent. Across the three derived food webs (OF, PR, and null) for each synthetic community, the total number of links and the identities of basal species were kept the same. Also, cases where extra basal species (i.e., additional species with no resource other than the pre-picked basal species) or isolated basal species (i.e., basal species with no species consuming them) were by chance produced were discarded and replaced with new simulations. As the parameters were kept constant under each scheme, the variation among replicates here is due to the difference in species composition among synthetic communities. Structure quantification was done in the same way as described in the previous section. For each scheme, we compared the model-generated nestedness and modularity by LMM with the type of model (i.e., OF vs. PR vs. null) as the fixed and iteration as the random effect.

4.4 Results

In general, the PR model predicts the two key empirical food-web features better than the OF model. For nestedness, the PR model deviates significantly less from empirical networks than does the OF model (Fig. 4.2), though empirical food webs tend to be more nested than the counterparts predicted by either foraging model (Fig. 4.3A). The PR model produces closer-to-empirical nestedness in nine out of twelve empirical communities (Fig. 4.3A). In terms of modularity, the deviations of the PR model are again significantly smaller than those of the OF model (Fig. 4.2). How model-predicted webs differed from the empirical webs was community-dependent (Fig. 4.3B). Here again, the PR model performs better in nine out of twelve empirical communities (Fig. 4.3B).

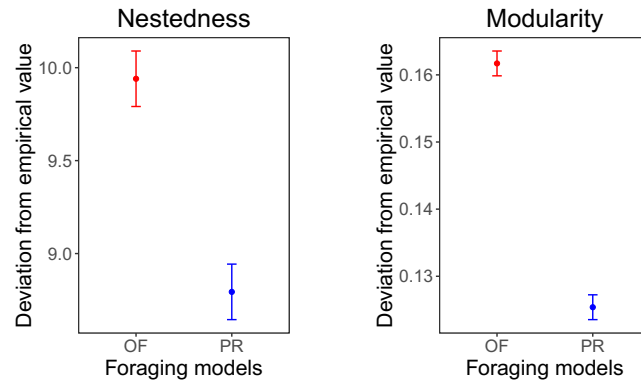


Figure 4.2: **Performance of the Optimal Foraging (OF) and Predation-Risk-Compromise (PR) models in capturing nestedness and modularity of empirical food webs.** The absolute deviations from the empirical value of both foraging models are shown as mean $\pm$ 95% CI (LMM fixed-effect uncertainty only). The PR model has deviations significantly smaller than those of the OF model in both nestedness and modularity measurements ($p < 0.001$ in both cases). Note that empirical nestedness reads 21.29 ± 14.30 and modularity 0.18 ± 0.15 (mean $\pm$ SD). The absolute deviations of nestedness are not directly comparable with those of modularity. For results using standardised values, see Fig. C.3

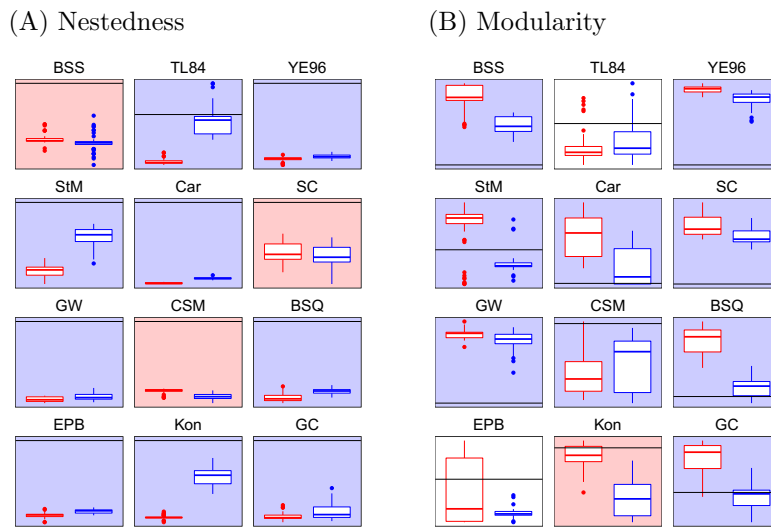


Figure 4.3: **Comparison of nestedness and modularity of empirical food webs and their model (OF and PR) counterparts.** Community name abbreviations are in Table C.4. The red and blue colours refer to OF and PR food webs, respectively. The black horizontal line presents the empirical value, whereas the box plots present the model-generated values. The background of the plots are also coloured in red or blue shade to indicate which of the OF and PR value is significantly closer ($p < 0.05$, no shading if not significant) to the empirical one, according to a paired-Wilcoxon test on the deviations from the empirical values. Out of twelve empirical communities, the PR model produces closer-to-empirical nestedness (A) and modularity (B) values in nine communities for each metric, indicating its superior performance. As the relative, rather than absolute, values matter here, we have omitted the y-axes scales for simplicity (as in Fig. 4.4 and Fig. C.6–C.9.)

Our analysis of synthetic food webs demonstrates that the structural features generated by the foraging models are largely insensitive to variation in food-web attributes or specification of the mathematical structure of the foraging parameters (Fig. 4.4). The OF model tends to produce more-nested synthetic food webs than the null model in practically all schemes, and the PR model consistently generates more-nested food webs than the OF model (Fig. 4.4A). In contrast, the modularity of model-generated synthetic webs, in comparison to null webs assembled at random, did depend on the scheme. Nevertheless, the differences between the OF and PR model predictions *per se* remain robust across schemes, with OF food webs nearly always being more modular (Fig. 4.4B).

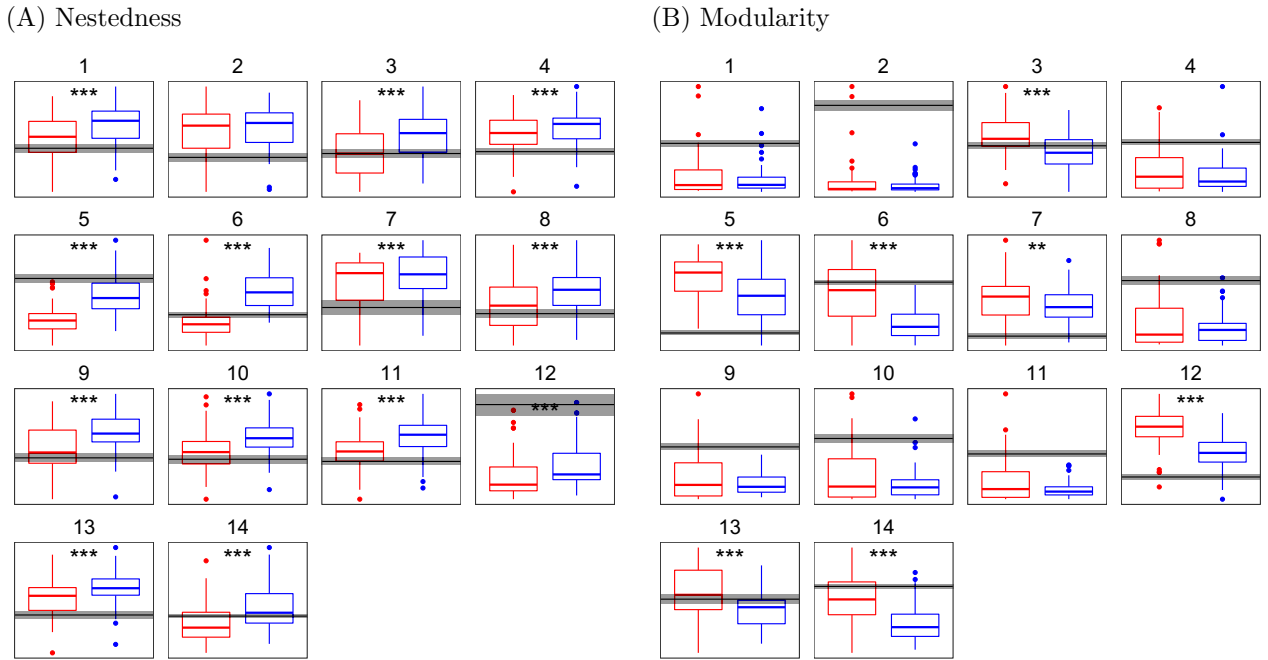


Figure 4.4: **Summary of nestedness and modularity of OF, PR, and null food webs.** Scheme IDs are indicated on the top of each plot (key in Table C.2). Red and blue colours refer to OF and PR food webs, respectively. The black horizontal line with shade presents the mean $\pm$ 95% CI of null food webs observations, whereas the box plots present the model-generated observations. The asterisks indicate whenever the OF/PR values are significantly larger than the other (*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$. LMM results may be based on transformed data to meet model assumptions, see Section C.6). There is a tendency for PR webs to be more nested than the OF webs (A), whereas the reverse is true for modularity (B).

Besides the focal structural measures of nestedness and modularity, we also measured several other food-web structural metrics. The PR model also better captured empirical values

than the OF model in the level of clustering, and variation in resource-consumer body-size ratios. Synthetic webs also showed a systematic and robust difference between the two models for all metrics. For further details, see Section C.7.

4.5 Discussion

Understanding the mechanisms and constraints that lead to the typically non-random structures of food webs remains a central challenge in ecology (May 1973; McCann 2000; Allesina & Tang 2012; Rossberg 2013). We have shown that predation risk constrains optimal foraging in ways that have significant consequences for food-web structure. Specifically, an assembly model that incorporates predation risk (PR) generates more nested but less modular food webs than by optimal foraging (OF) alone, providing a better fit to the empirical data for both of these measures (Fig. 4.2–4.3). In addition, PR also causes other food-web features to deviate systematically from those produced by the consumer-centric OF model (Section C.7).

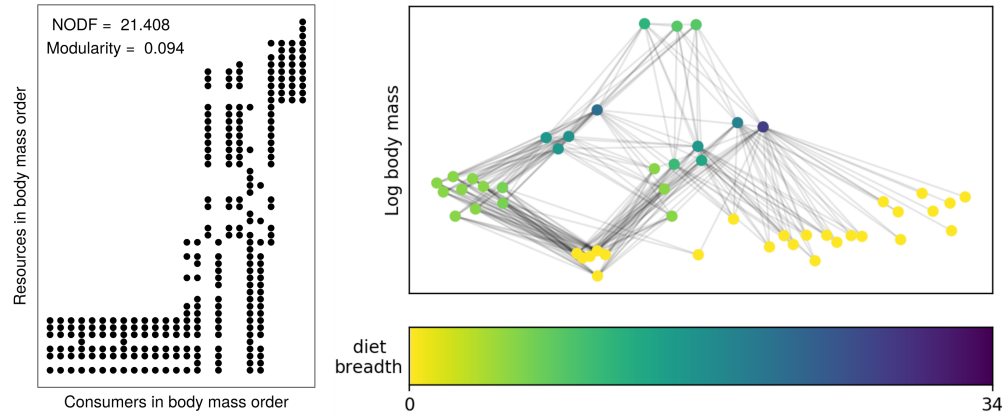
Under both OF and PR assembly, the trophic level of consumers increases with their body mass, and in-degree (diet breadth) has a dome-like relationship with body mass (Fig. C.6 & C.7) because the preferred body-size ratio (R_p) is fixed. However, predation risk results in a broader diet at intermediate trophic levels than OF alone (Fig. 4.5B–C), which is also more empirically realistic (Fig. 4.5A). Furthermore, nestedness quantifies how much the diet of some consumers are subsets of the others, so it increases with the average diet overlap among species. The risk-driven increase in diet breadth of intermediate trophic-level (also intermediate-sized) consumers, effectively increases diet overlap, and therefore also nestedness. Thus, the predation-risk constraints produce webs that more closely match the higher-than-random nestedness of empirical food webs. Modularity, on the other hand, is essentially a measure of compartmentalisation—the degree to which species’ can be rearranged as highly connected groups with few inter-group connections. A food web has high modularity if the diet matrix can be arranged in distinct blocks. Thus, the diet-broadening effect of predation risk at intermediate trophic levels may increase the diet overlap within groups, making them more

strongly connected, effectively increasing modularity. However, it may also blur the distinction among groups, effectively decreasing modularity. Therefore, the change in modularity produced by PR is less predictable than nestedness, and largely depends on the body-size structure of the community (Fig. 4.4B).

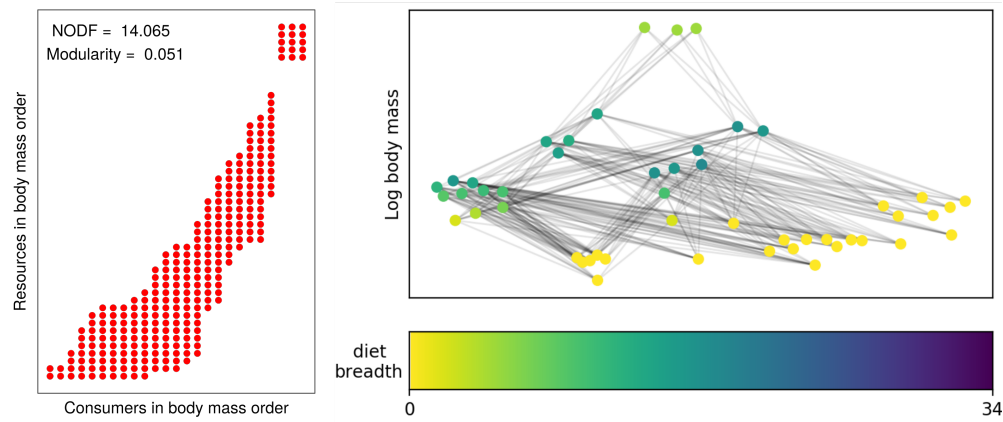
Overall, incorporating predation risk improves the ability of OFT-based assembly models to predict food-web structure, especially nestedness and modularity. This improvement is not tremendous, but is nevertheless significant, not just statistically, but also because of the new insights it provides into the mechanistic basis of food-web structure. Although we compared empirical and model-generated food-web structures using a particular mechanistic model structure, our study of synthetic food webs shows that our results are robust to variation in model structures and parameterisations. The superior fit of the PR model to the empirical data does not guarantee that the way in which our specific model of predation risk operates is mirrored in the real world, but, with the behavioural evidence we discuss below, the mechanisms we modelled likely occur to some extent in nature. Nevertheless, the PR-predicted food-web structures still show considerable discrepancies from empirical webs. In particular, empirical food webs are consistently much more nested than model-predicted webs. There may be a number of reasons for these discrepancies, and our general framework can be extended in multiple ways to arrive at more precise models for predicting trophic links in real food webs.

First, the conversion coefficient (ϵ ; eqn (4.1)), the dimensionality (Pawar *et al.* 2012) of search rate (a ; Section C.1.3), and preferred body-size ratio (R_p ; Section C.1.3) are each assumed to be constant across species. However, all of these likely vary in the real world. Incorporating more detailed information on all these parameters, if available, would be expected to improve the models' predictive performance. R_p , in particular, determines the shape of attack success probability (A ; Section C.1.3) and handling time (h ; Section C.1.3) across the spectrum of resource-consumer body-size ratios. This, in turn, influences the degree of diet overlap among species and therefore the web's nestedness. Indeed, comparing scheme 12 to scheme 1 (Table C.2) of the synthetic food webs as an example, we show that the way null webs differ from the OF and PR webs in nestedness is mainly affected by the shape of the chosen handling time function (eqn (C.9) vs. eqn (C.11); Fig. 4.4A). The literature also indicates that ϵ

(A) Empirical food web (TL84)



(B) Optimal foraging food web



(C) Optimal foraging with predation risk food web

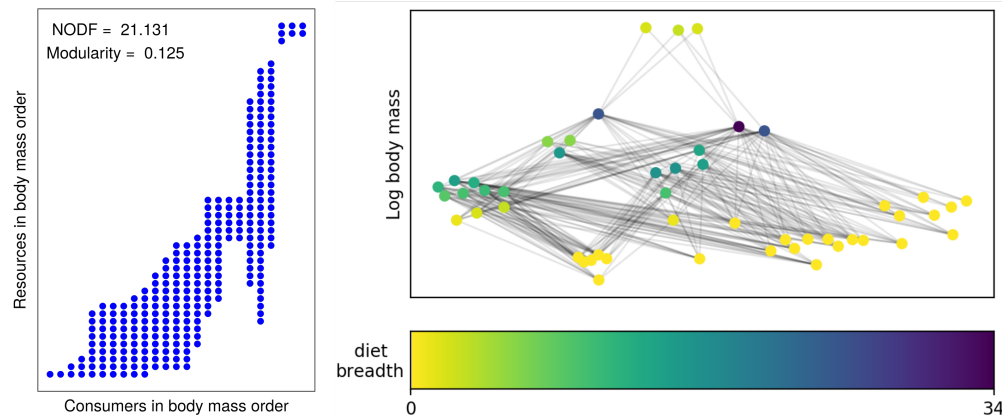


Figure 4.5: **Illustration of how predation risk affects nestedness and modularity of food webs by diet broadening at intermediate trophic levels.** The size-ordered diet matrix and corresponding network of empirical web TL84 (A) is shown, along with its OF (B) and PR (C) counterparts generated from a single model simulation. Each dot in the diet matrix indicate a trophic interaction between a consumer (column) and a resource (row) species. Each network representation was produced by a visualisation algorithm (Zheng *et al.* 2018); species' nodes are colored by diet breadth (darker nodes have broader diet).

differs between feeding groups (Lang *et al.* 2017), with the value for carnivores about twice that of herbivores. We investigated this difference by assigning resource-type-specific ϵ to consumers, and this does change the generated food-web structure, but the main finding—the difference between OF and PR predictions—is qualitatively unchanged (Section C.7).

Second, when assembling food webs, we allowed all species in the community to be a potential resource of each consumer. However, in reality, species may have foraging or anti-predator traits, or spatio-temporal differences in phenology (Holomuzki 1986; Tollrian 1995; Relyea 2001; Turner & Montgomery 2003; Mikolajewski *et al.* 2010; Eklöf *et al.* 2013) that essentially forbid certain links. These constraints, which may not necessarily covary with body size, could possibly be better captured by food-web models based on phylogenetic relatedness (Cattin *et al.* 2004; Naisbit *et al.* 2012), which encodes such information. Here, we adopt a size-driven mechanistic modelling approach to focus on our aim, which is to explore how our understanding of food-web structure can be improved by including metabolic and predation-risk constraints into OFT, but necessarily ignore these other constraints.

Third, the form of the predation-risk index (P_{risk}) function (eqn (4.2)) could also be refined. We have assumed that the risk to a focal species increases monotonically with the number of its realised consumer species and their abundances, with the rationale that other mechanisms affecting predation risk are less important than consumer abundance itself. More work on the mechanistic basis of the predation risk function may lead to more accurate PR assembly models. For example, at high consumer densities, interference among consumers is expected to increase (Skalski & Gilliam 2001), possibly leading to a non-monotonic predation-risk index.

Lastly, animals may respond to predation risk by decreasing total foraging time (Lima & Dill 1990; Beckerman *et al.* 1997) and pay the cost of predator evasion through an increased metabolic rate (e.g., Hawlena & Schmitz 2010). These can practically be incorporated into the PR model by switching C_{min} from a fixed value to a risk-dependent variable, such that if the increasing predation risk results in the total foraging time of a consumer being cut by half (or its metabolic rate being doubled), its C_{min} should also become twice as large according to the energy balance concept. Moreover, it is also possible that a risk-driven response of animals

leads to a re-ranking of their profitabilities (e.g., forming a defensive group, thereby lowering the consumer’s attack success) which would, in turn, influence the OFT-based diet predictions. Such nuanced behaviours highlight the potential of extending the PR model.

Although the empirical webs we used are all relatively well-sampled (Section C.5), food webs are known to be under-sampled generally (i.e., existent links are not detected), which leads to poor estimates of food-web metrics (Goldwasser & Roughgarden 1997; Martinez *et al.* 1999; Banašek-Richter *et al.* 2004; Tylianakis *et al.* 2010; Wood *et al.* 2015). However, the two features we focus on—nestedness and modularity—have been shown to be robust to such artefacts (Nielsen & Bascompte 2007; Tylianakis *et al.* 2010; Rivera-Hutinel *et al.* 2012; Vizentin-Bugoni *et al.* 2016). More importantly, there is no reason to expect that sampling artefacts are likely to bias construction of PR counterparts more than OF ones, and our results should hold qualitatively even as higher quality food-web data become available. A related food-web sampling issue is the common practise of using the average adult state as being representative of a species’ role in the ecosystem. In reality, individuals of a species vary in body size, and often forage differently across life stages. Omitting such intraspecific variation or ontogenetic shifts in diet could fundamentally bias our understanding of empirical food-web structure (Clegg *et al.* 2018). In the study here, we have also ignored such diet variation in both our modelling and empirical validation due to limits on the resolution of empirical data. Nonetheless, our models could also be applied to webs resolved to the ontogenetic level if data are available—the same assembly algorithm can be used.

Predation risk is also likely to have consequences for food-web dynamics and stability (Kondoh 2007), which we have not explored here. That is, we fixed species biomass abundances to generate food-web structures. The purely structural findings of this study, though, should also have dynamical implications given that nestedness and modularity are associated with stability, and the influence of predation risk on stability is a key direction for future work. Moreover, our model can be extended to tackle population dynamics by setting biomass abundance as a variable, and letting species adjust their diet in an abundance-dependent manner (adaptive foraging, e.g., Kondoh 2003). Note that predation risk in such cases can also be an abundance-dependent dynamical feature of species.

Our results also provide novel insights for foraging ecology. Firstly, the diet-broadening (instead of diet-narrowing) strategy implicit in our PR model is consistent with empirical evidence that consumers tend to broaden their diet by taking less-profitable resources (Lima & Valone 1986; Metcalfe *et al.* 1987; Rothley *et al.* 1997). That the PR model, through this diet-broadening strategy, results in food-web nestedness and modularity closer to reality than the OF model (same as diet-narrowing; Section C.7), suggests that searching/waiting may be indeed riskier than handling across food webs—likely because animals can hide or be camouflaged while handling food (Charnov & Orians 1973). Secondly, most empirical tests of OFT indeed show that the classical model frequently under-predicts diet breadths (Krebs *et al.* 1977; Elner & Hughes 1978; Mittelbach 1981; Sih & Christensen 2001). This discrepancy has been proposed to be due to consumers’ imperfect foraging information. Our study suggests that predation risk could also give rise to such broader-than-optimal diets. We encourage future work to validate this risk-driven diet-broadening effect via empirical experiments. Thus, our results suggest that not just OFT-based food-web assembly rules, but also OFT itself needs to be revisited by incorporating predation risk. This may re-vitalise OFT, which has gradually faded from the research focus of ecologists.

In conclusion, the study of this chapter answers the call to add further dimensions beyond body size (Allesina 2011; Eklöf *et al.* 2013; Jonsson *et al.* 2018), including non-trophic effects (Terry *et al.* 2017), into food-web models. It shows that predation risk could, in principle, be a significant factor affecting food-web assembly and the emergent structure. Many models have been proposed to predict empirical food-web structure over the last three decades (Cohen & Newman 1985; Williams & Martinez 2000; Beckerman *et al.* 2006; Petchey *et al.* 2008), but few have formally incorporated predation risk (Kondoh 2007). The field has also not yet reached an effective synthesis of metabolic and foraging theories. This study joins the recent work of Portalier *et al.* (2019) to provide the first major advances in that direction since the ADBM (Petchey *et al.* 2008). Food webs represent the roles of species as both consumers and resources, and considering the joint constraints on foraging behaviour of these dual roles (Naisbit *et al.* 2012) is a necessary step towards truly capturing the complexity of real ecosystems.

Chapter 5

Conclusions and directions for future work

5.1 Summary of thesis achievements

The aim of this thesis was to investigate the behavioural components of foraging that may serve as the underpinning mechanism of the emergence of food-web properties at the scale of communities, and to provide mechanistic understanding of how it may happen. To achieve this, we modelled species foraging, food-web formation, and food-web dynamics using a conceptual framework that was jointly based on Metabolic Theory of Ecology (MTE; Brown *et al.* 2004) and Optimal Foraging Theory (OFT; Charnov & Orians 1973). The MTE posits that most observed patterns in ecology are fundamentally governed organismal metabolic rate. Therefore, with its well-established, metabolic rate-derived scaling rules, it allows realistic modelling of parameters regarding species behaviour (in foraging and other aspects) and dynamics. The OFT, meanwhile, posits that consumer species forage in an abundance-dependent manner, where their diet should be the set of resources that provide the maximised energy (biomass) intake rate. It thus allows the explicit modelling of species' diet choice behaviour. Both theories are well-defined and can be connected via the foraging-relevant behavioural parameters.

We began our study with the behavioural mechanisms that influence the most fundamental

aspect of foraging—that is, how consumers and resource encounter each other. In the first research chapter (Chapter 2), we examined how foraging strategy (i.e., whether the consumer forages as grazing, sit-and-wait, or active-capture) and foraging dimensionality (i.e., whether the consumer forages on a 2D plane or within a 3D volume) could affect species coexistence (here, mathematical equilibrium feasibility) in food webs with various topological and body-size structures. We showed via simulations that these behavioural properties interact with food-web structure to determine the system’s feasibility. Food webs dominated by large-eat-small foraging (consumers eating smaller resources) were more feasible when they had many top consumers and when 2D grazing or sit-and-wait interactions were common. The simulation-derived prediction on foraging strategy indeed was associated with dominance of large-eat-small foraging in empirical food webs. “Being feasible” thus may be a critical constraint that has shaped the properties of food webs in nature.

Although Chapter 2 looked at feasibility (the avoidance of extinction), we did not explicitly examine the dynamics that lead to extinction. Moreover, we explored behavioural attributes of species’s foraging, but not their foraging “decisions”. Therefore, to extend our understanding of behavioural influences on food-web structure and dynamics, we examined in the second research chapter (Chapter 3) the effects caused by species’ diet choice. By modelling species’ diet choice using the MTE-OFT joint framework, we showed that both community properties (i.e., species mass distribution and their overall abundance) and consumers’ behavioural properties (i.e., their preferred resource-consumer body-size ratio, and the time cost they need to spend on failed foraging attacks) influenced the structure of food webs that emerge from the OFT diet choice mechanism. This included the emergence of some commonly observed structural features in empirical food webs, e.g., being nested or modular. Furthermore, the abundance-dependent diet choice mechanism made food-web structure itself a dynamical property that varies over time. In this case, food-web structure and species abundances constantly and mutually influence each other and, thus, determine the dynamical consequences of the community. The diet choice that matches predictions of OFT could increase robustness of communities (i.e., decrease extinction rate) by mitigating the destabilising effect caused by Type-II functional response-driven trophic interaction strengths. However, this mitigation occurs only when species’ abundance-dependent

diet adjustment was frequent enough; a too-infrequent diet adjustment reduced the robustness instead. Diet choice as predicted by OFT can therefore be an underpinning mechanism that governs the formation of diversity and complexity of we observed in real-world food webs.

Besides the frequency of diet adjustment, species' ability to forage optimally can be constrained in other aspects. Especially, considering that most species play dual roles in a food web, i.e., as consumer and resource at the same time, foraging under the risk of being predated should be the norm in nature. Predation risk is thus likely to be a key constraining factor on foraging behaviour. We thus explored this possibility in the last research chapter (Chapter 4). By taking the dual-role perspective, we modelled how species' diet choice deviates from OFT prediction due to constraints of both predation risk and metabolism. As such, we developed the previously consumer-centric MTE-OFT joint framework into a new "Predation-Risk-Compromise (PR) Model". We then further looked into the food-web structural consequences caused by such a diet choice mechanism. Compared with OFT-driven food webs (without predation-risk considerations), the risk-mitigated foraging of the PR model led to more-nested while less-modular food-web structure by broadening the diet of consumers at intermediate trophic levels. Further, empirical validation showed that the PR model indeed outperformed the pure OFT model in capturing key structural properties, i.e., nestedness and modularity, in empirical food webs. Thus, predation risk can significantly mediate species' ability to forage optimally and therefore affect food-web structure. This previously-missing piece should to be considered in future food-web studies.

5.2 Prospects for future work

The most straightforward direction for future studies would be to find empirical evidence for both the assumptions that we applied in the modelling of this study, as well as the predictions that emerged from our simulations. For example, in Chapter 2, we assumed that species should exhibit positive mass-scaled intraspecific interference strengths, and predicted that food webs with very few top consumers and weak large-eat-small body-size structure should have

species with intrinsic growth rates, interaction strengths, and interference strengths that deviate from the mass-scaling rules we used (so as to have achieved food-web feasibility). To test these, innovative empirical studies that measure these components within food webs would be required. In Chapter 3, the simulation suggested that low species abundances and low time cost for failed attacks contribute to food-web nestedness, while the opposite condition enhances modularity. Also, infrequent diet adjustment may counter-intuitively impede the robustness of the community. Such predictions could be validated by the combination of empirical food-web data, population-size data, and behavioural data of the species within the food web. In Chapter 4, we proposed that whether predation risk broadens or narrows the diet of a consumer depends on which of the searching and handling is the riskier action, and deduced that the broadening is likely to be the majority of cases in nature. Behavioural experiments that quantify the risk while performing different actions, and measures the predation risk-driven diet change across taxa, may be able to provide relevant evidence. Some other ideas of prospective research are expanded in the Discussion section of each chapter.

Another direction of future research would be to extrapolate some key ideas presented in this thesis, or to explore other potentially influential factors using similar approaches. For example, we have developed a model to describe the how predation risk can constrain species diet choice, and thereby to significantly influence the emergent food-web structure. The further application of this model to investigate the food-web dynamical consequences caused by such predation risk-compromise foraging would be a promising extension of our work. Also, there can be other factors beside predation risk that constrain species from fully complying with optimal foraging, such as the necessity of having diet that covers certain essential nutrients, or the satiation of organisms. These effects could be modelled and explored using a similar multiple-objective approach (Rothley *et al.* 1997) to that which we used for studying predation risk.

Finally, the MTE-OFT joint framework provides an integral theoretic tool which can be applied to tackle—beyond what has been done in this thesis—high-profile ecological questions of the present era. For instance, the ability of the framework to predict extinctions during food-web dynamics can be combined with the modelling of processes where new species emerge, such

as species invasion or speciation. Such work would allow the prospecting of behavioural-driven food-web consequences at even longer time scales—those of community assembly (Pawar 2009) or evolution. Also, in this thesis we adopted mostly the body-mass scaling part of MTE, while another key feature of MTE is that it mechanistically describes how temperature can affect organismal metabolic rate and, therefore, also influence all behaviour-relevant components that we have looked at in this study. As long as not all species behaviourally respond identically to the the varying temperature—due to mechanisms such as the difference in their thermoregulation or mis-matches in their metabolic rate activation energy (Dell *et al.* 2014), it is to be expected that behaviourally-driven food-web structure and dynamics can thus be largely influenced by temperature (Petchey *et al.* 2010; Rall *et al.* 2010). By plugging-in the temperature effect into the MTE-OFT joint framework, it could be used to predict the food-web outcomes under different temperatures, and generate insights about how ecosystem functions are affected by temperature accordingly. Such a research direction is of immense importance especially given ongoing global climate change and rapid biodiversity loss.

5.3 Conclusion

To sum up, in this thesis we sequentially investigated the effects of different aspects of foraging behaviour on influencing food-web structure and dynamics. The discoveries of each chapter collectively improve our mechanistic understanding of how complex food webs could emerge from foraging behaviour of the individuals within. While we showed that the effects of behaviour can be scaled up to determine ecological properties at the food-web level, such scaling up are mostly not simply additive, but instead context-dependent (e.g., the effect of diet choice on food-web topology depends on species abundances) or interacting with each other (e.g., the effect of foraging strategy on feasibility depends on food-web topology). Therefore, to fully understand food webs, knowing how they have reached their current states and predicting how they will change in the future, it is necessary to embrace multiple scopes at once. That is, one should dig down to the underpinning behavioural drivers when exploring food-web phenomena, meanwhile keep a large-scaled view point at the whole web and consider the context

within which these behaviours and interactions happen. The present thesis reveals previously unrecognised connection between foraging behaviour and food-web properties, and lays a firm quantitative foundation for future work in such a direction.

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Appendix A

Behaviour moderates the impacts of food-web structure on species coexistence

A.1 Further information of the topological models and synthetic food webs

A.1.1 Topological models' algorithms

Here we explain further the algorithms of the six topological models and how they simulate diet matrices. Several constraints are applied to all models when generating food webs: (1) The smallest five species are fixed to be the basal resource, i.e., they are not consuming any other species, but are consumed by at least one consumer species. (2) Cannibalism (i.e., one species consumes itself) is forbidden, that is, there cannot be any trophic link realised at the diagonal entries of the diet matrix. (3) Mutual consumption between two species is not allowed. (4) The realised connectance of all webs is about 0.1. For constraint (1), choosing the smallest species is a reasonable simplification as we are modelling individual-based (i.e.,

whole-organism) consumption (see Section 2.3.4), and the number of basal species is inspired from empirical data (see Section A.4). For constraints (2)–(4), these eliminate some unwanted biases in the generated food webs, e.g., some models may likely generate more cannibalistic links than others. By following these constraints, we could thus make comparisons with the same standard for all generated webs (i.e., all with the same type of links), and clearly capture the effects caused by our focal factors. For the Cascade and Niche models, we in principle followed the original algorithms proposed in the literature as cited in Section 2.3.2, with slight modifications to fulfill our constraints here. The Nested, Modular-1, and Modular-2 models phenomenologically simulate food webs that exhibit a high degree of corresponding topological structure.

To explain the algorithms, we begin with an all-zero diet matrix, where species are ordered from the smallest to the largest at both columns (left to right) and rows (down to up):

- The Random model is straightforward. It just randomly draws the desired number of entries of the diet matrix that are allowed by the above-mentioned constraints, then turns these entries to one that represents a realised trophic interaction between the consumer (column) and the resource (row).
- The Cascade model is similar to the Random model. It randomly draws the entries, but does so strictly from the lower triangle of the diet matrix, where the consumer’s body mass is sure to be larger than its allowed resource. These entries are then turned to one.
- With the Niche model, to be in line with the original work, each species should be assigned with a “niche value” but such values should be uniformly distributed. We therefore can not directly take the log-normally distributed body masses as the niche value. We thus generate a set of uniformly distributed niche values, then assign these niche values to species according to their body-mass ordering (i.e., the species-wise ordering of body mass and niche value are the same). Then a “radius” is randomly drawn for each consumer species from a beta distribution that leads to the desired connectance, and the corresponding “centre” is uniformly and randomly drawn from the values between radius/2 and the niche value of the focal consumer. For each consumer species, all species

(except itself) fall into the range of its centre $\pm$ radius become its realised resource, and the corresponding diet matrix entries are turned to one.

- The Nested model firstly establishes links such that the largest consumer species eats every other species, whereas the smallest consumer's diet is a certain number (randomly drawn) of the smallest species; the diet breadth of other consumers in between are gradually shrinking along with their body masses by dropping their largest resource(s) so that they fit to the right-most (largest species) and left-most (smallest species) columns of the diet matrix. Up to here, the diet matrix represents a nested but over-connected web. Then the model iteratively removes a link (i.e., turns the entry back to zero) from the top of a randomly drawn consumer column under the constraint that the removal will not make the diet breadth of the focal consumer narrower than its next-smaller one's. The iteration is repeated until the desired connectance is achieved. The resultant web is therefore nested, and the realised links largely aggregate at the bottom-right of the diet matrix.
- The Modular-1 model randomly divides consumers along their body-size order into four continuous-sized groups (four is our arbitrary setting, which we consider an appropriate number of diet blocks to form in a 50-species food web). Each group at first has a diet breadth of one, i.e., all group members share the same single resource. The smallest-sized group eats the smallest species, while the second-smallest-sized group eats the second-smallest species and so on, so the diet of each group is distinct and without overlap with other groups, and the resource body size increases with the groups' body size. Then the model iteratively increases the diet breadth of a randomly drawn group by one, i.e., adding the next-larger resource to the diet. Meanwhile, on the diet matrix, the diet of other groups also shifts upward so the group-wise diet remains non-overlapped. Therefore, for example, when the smallest-sized group of consumer achieve a diet breadth ≥ 5 , the second-smallest-sized group of consumer would no longer consumes basal resource (as we set five smallest species as the basal resources). The process is repeated until the desired connectance is achieved. The resultant diet matrix shows four distinct and compact blocks of realised links in the lower triangle, which is expected with a high bipartite modularity but not necessarily a high unipartite modularity.

- The Modular-2 model does the similar dividing of species into four groups, but then randomly draws 90% of the realised links within the group. That is, the interacting consumers and resources are from the same group. The remaining 10% of the realised links are then drawn randomly at the entries outside the groups, thereby the four groups will not be trophically isolated from each other (but are still connected to form a food web). The resultant diet matrix shows four distinct but not-compact blocks of realised links along the diagonal, which is expected with both high bipartite and unipartite modularity.

The models generate topologically distinct diet matrices with given species body masses as the input. The simulation process of all models embeds stochasticity.

A.1.2 Synthetic food webs

Here we summarise the topological and body-size properties of the synthetic food webs in Table A.1, Fig. A.1, and Fig. A.2. We note especially the accordance of T score order across topological models in Fig. A.1 and the level of importance of being body-size structured in main text Fig. 2.3B. This indicates the role of T score in influencing this importance. Such an accordance remains true when the weighting constant of T score (0.5 in the main text) ranges between 0.3 and 1.1. We note also the qualitative similarity of the changing patterns between the level of LES structure in Fig. A.2 and the web feasibility in main text Fig. 2.3A. We also plot the feasibility of synthetic food webs against their LES and LEL indices, in both model-by-model and pooling-all-webs fashions. It appears that in either way, the LES index is a better indicator of the feasibility, which can be seen from the smaller confidence interval of the regression line(s) (Fig. A.3–A.6). Therefore, among the LES and LEL structures, the former is more tightly related to, and thus is likely the more influential driver of, the feasibility of food webs.

Table A.1: **Guild-relevant topological properties of food webs generated by the topological models (N = 30 each).** The values show the mean $\pm$ standard error. Num.T: the number of species that act as top consumers. Prop.TB: the proportion of links that are top-eat-basal trophic interactions, same for top-eat-intermediate (TI), intermediate-eat-basal (IB), and intermediate-eat-intermediate (II).

Topological model	Num.T	Prop.TB	Prop.TI	Prop.IB	Prop.II
Random	0.33 $\pm$ 0.55	0.0004 $\pm$ 0.001	0.0072 $\pm$ 0.013	0.1095 $\pm$ 0.019	0.8829 $\pm$ 0.026
Cascade	4.67 $\pm$ 1.49	0.0211 $\pm$ 0.009	0.1524 $\pm$ 0.042	0.1651 $\pm$ 0.022	0.6614 $\pm$ 0.053
Niche	4.50 $\pm$ 2.62	0.0066 $\pm$ 0.011	0.1647 $\pm$ 0.097	0.1132 $\pm$ 0.031	0.7155 $\pm$ 0.100
Nested	31.20 $\pm$ 2.75	0.4501 $\pm$ 0.052	0.4940 $\pm$ 0.047	0.0559 $\pm$ 0.011	0.0000 $\pm$ 0.000
Modular-1	27.20 $\pm$ 3.60	0.0428 $\pm$ 0.068	0.5661 $\pm$ 0.149	0.2295 $\pm$ 0.132	0.1616 $\pm$ 0.141
Modular-2	0.60 $\pm$ 0.81	0.0019 $\pm$ 0.004	0.0116 $\pm$ 0.019	0.0978 $\pm$ 0.042	0.8888 $\pm$ 0.048

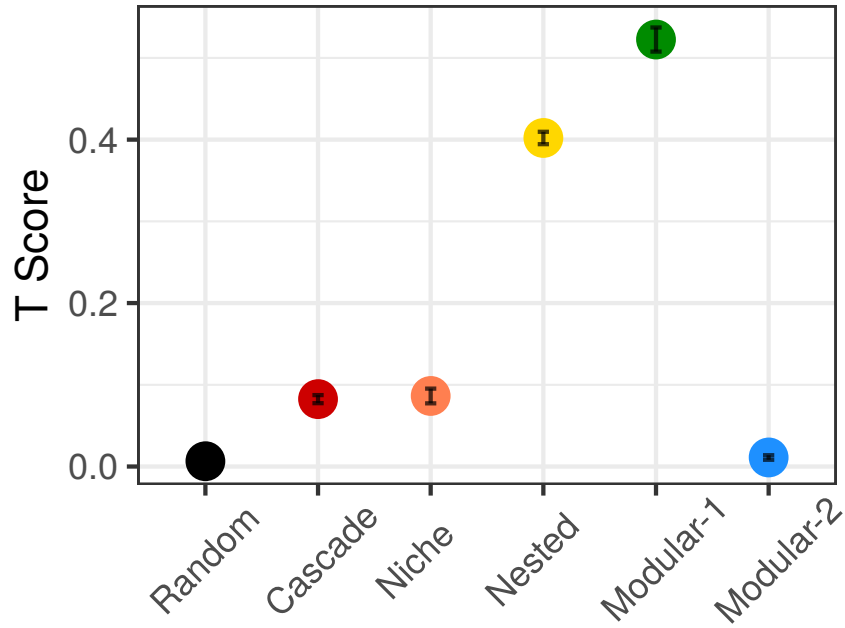


Figure A.1: **The T score of food webs generated by the topological models (N = 30 each).** The error bars represent the standard error.

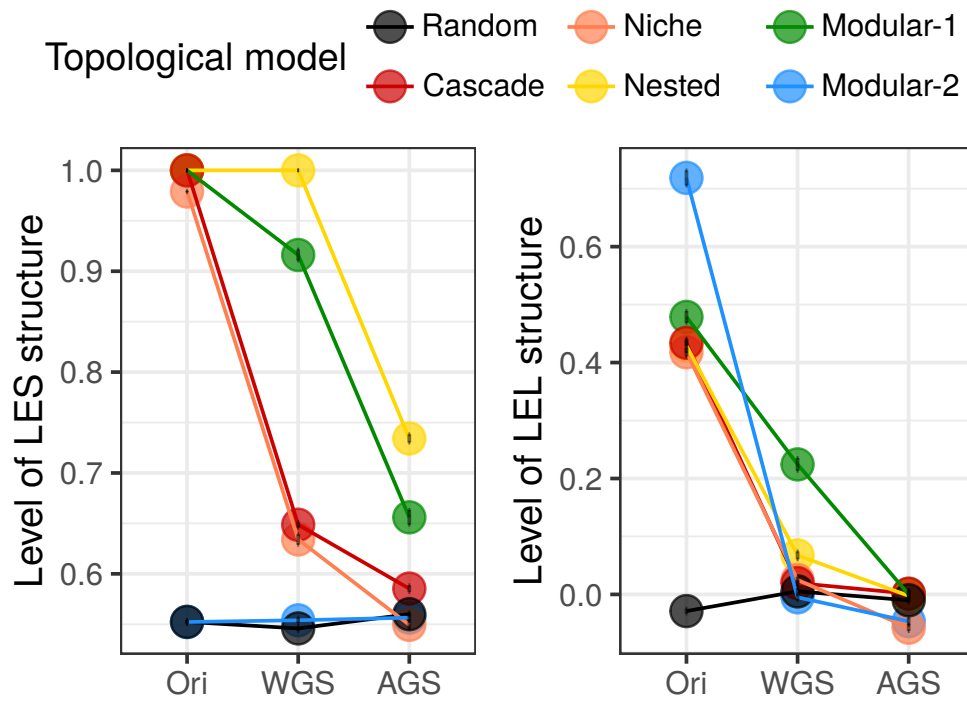


Figure A.2: The level of Large-Eat-Small (LES) and Large-Eat-Large (LEL) body-size structures of food webs generated by the topological models across the three body-size arrangements ($N = 30$ each). The LES and LEL readings are calculated as the corresponding indices as explained in Section 2.3.3. The error bars represent the standard error. Abbreviations Ori, WGS, and AGS stand for the Original, Within-Guild-Shuffled, and Across-Guild-Shuffled body-size arrangements, respectively.

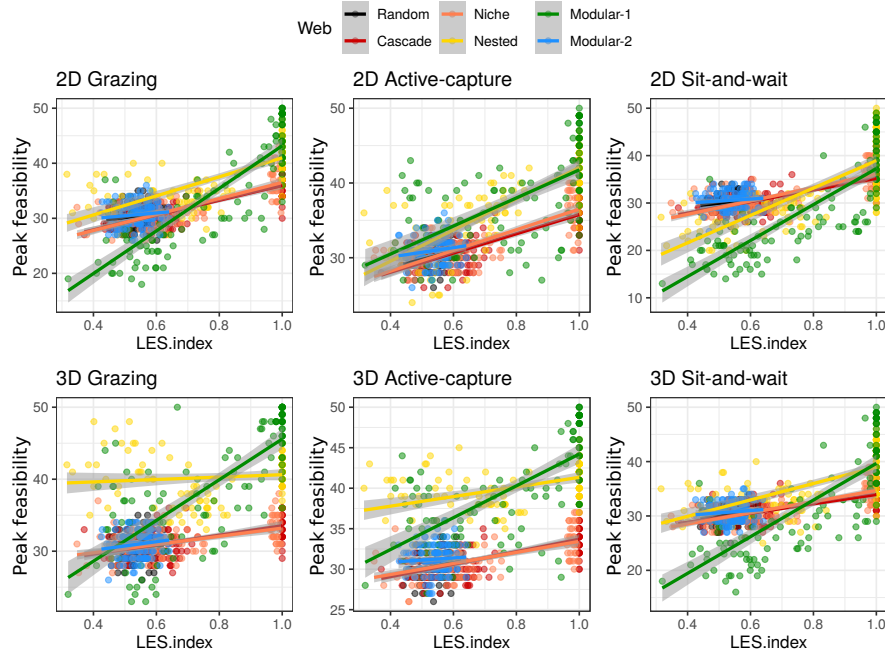


Figure A.3: **Regression (one per model) between feasibility and the LES index of all 3240 synthetic food webs.** Each plot collapses the webs across the three body-size arrangements. Colors indicate the topological models. The shaded areas indicate the 95% confidence interval of the regression.

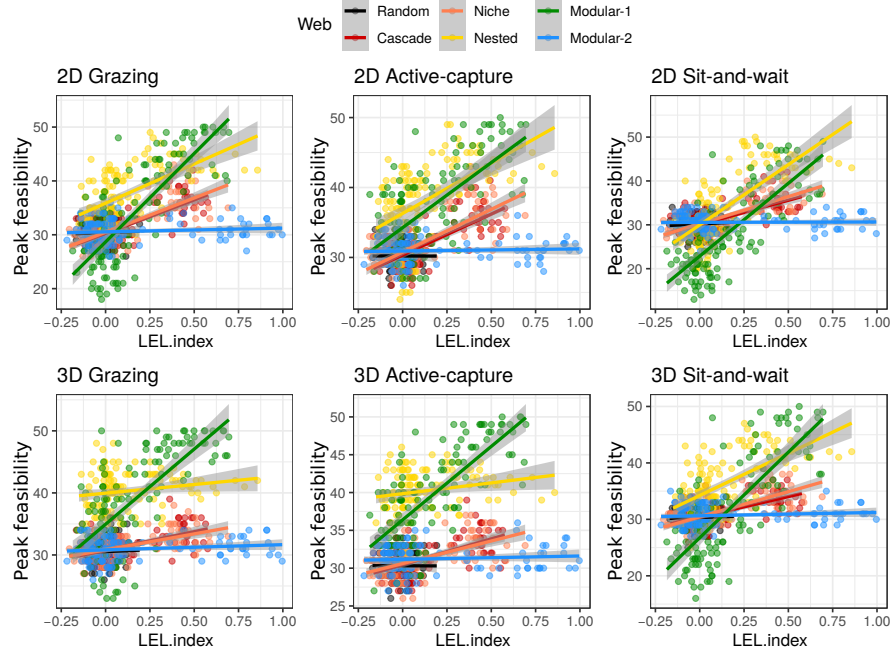


Figure A.4: **Regression (one per model) between feasibility and the LEL index of all 3240 synthetic food webs.** Each plot collapses the webs across the three body-size arrangements. Colors indicate the topological models. The shaded areas indicate the 95% confidence interval of the regression.

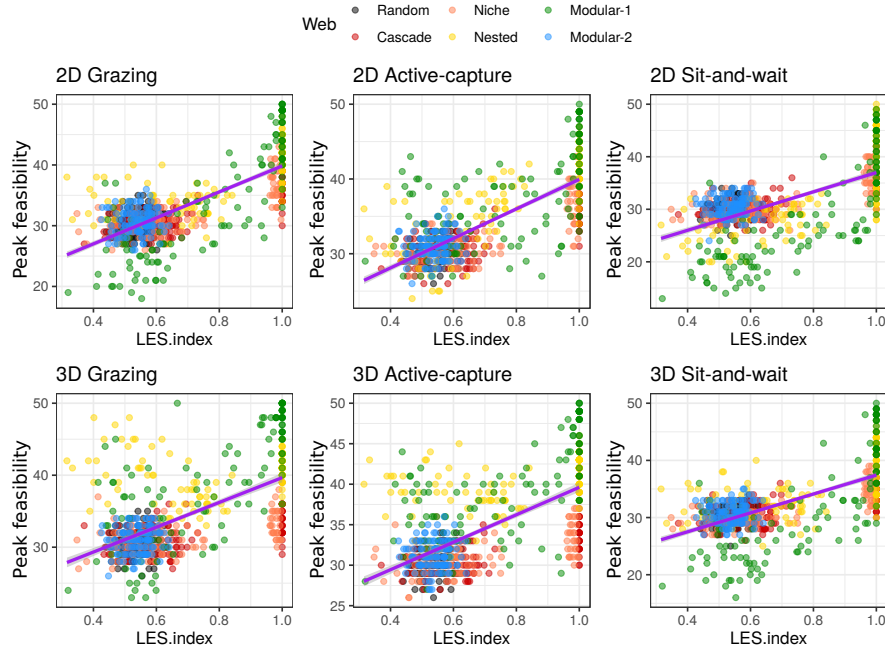


Figure A.5: **Regression between feasibility and the LES index of all 3240 synthetic food webs.** Each plot collapses the webs across the three body-size arrangements. Colors indicate the topological models, whereas the solid purple line is the regression line. The shaded areas indicate the 95% confidence interval of the regression.

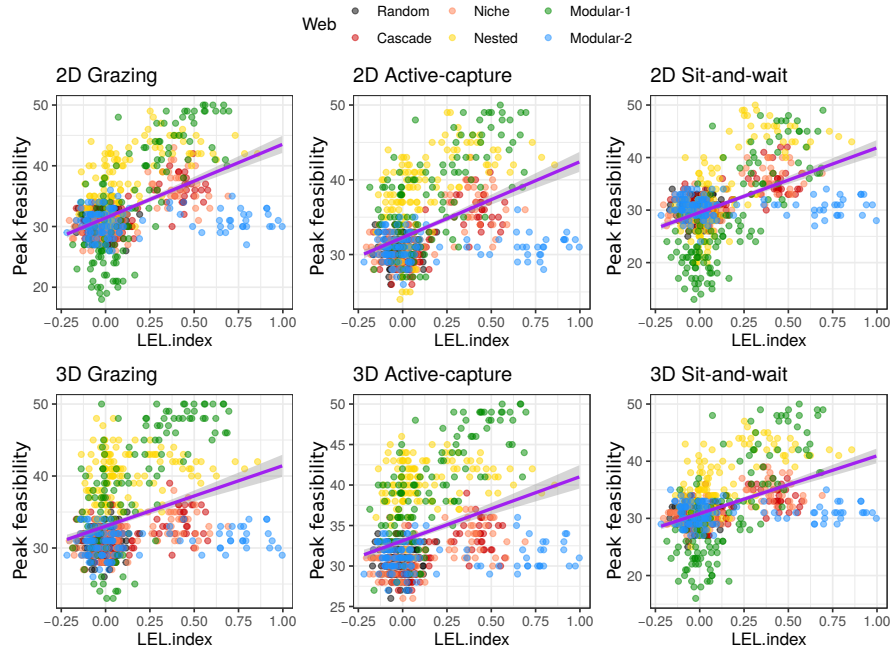


Figure A.6: **Regression between feasibility and the LEL index of all 3240 synthetic food webs.** Each plot collapses the webs across the three body-size arrangements. Colors indicate the topological models, whereas the solid purple line is the regression line. The shaded areas indicate the 95% confidence interval of the regression.

A.1.3 Quantifying modularity and nestedness

We quantified the holistic topological measurements, modularity and nestedness, of the synthetic food webs we generated. If expressing the food web as a consumer-resource bipartite network, modularity reflects the degree of having modules (compartments) where many links establish within but a few between, whereas nestedness reflects the degree to which some species' diet comprises a subset of others'. We focused on specifically these two measurements because they are the most well-reported empirical food-web properties, and have been widely studied for their effects on the system's dynamics.

For quantifying modularity, we used the R package `bipartite` (Dormann *et al.* 2008) with its function `computeModules` taking the synthetic diet matrices as inputs. For quantifying nestedness, we measured the NODF value by using the R package `vegan` (Oksanen *et al.* 2013) with its function `nestednodf` taking the synthetic diet matrices as inputs. Please refer to the manuals of these packages for calculation details.

A.2 Further details of the feasibility index

We here give further details of the feasibility index we used. When solving the equilibrium of the synthetic webs, it appears that the number of feasible species at equilibrium depends on the intraspecific interference strengths. Typically, as the magnitude of interference strength increases, the number of feasible species increases to a peak value before abruptly dropping to the situation where only the five basal resources are feasible (Fig. A.7; also Fig. A.9–A.16). To extract the mathematical optimal performance (i.e., maximum number of feasible species) of the system along a parameter axis (i.e., interference magnitude), we took the peak value as the index of feasibility, and summarised it across all repeats and across topology $\times$ body-size arrangement $\times$ foraging strategy $\times$ dimensionality combinations ($N = 30$ each) as presented in main text Fig. 2.3A. This index gives the highest possible number of feasible species at the analytically-derived equilibrium of each generated web, given a web-specific appropriate magnitude of interference strength.

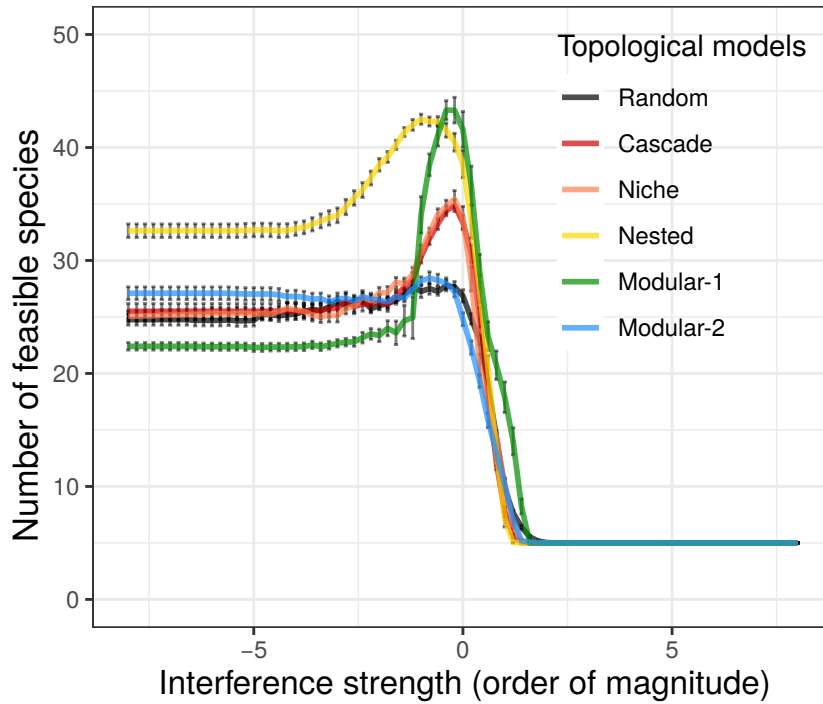


Figure A.7: **The number of feasible species at the equilibrium of synthetic food webs generated by each topological model across magnitudes of interference strength ($N = 30$).** Note the typical peaking pattern of all models. We take the 2D grazing, Original body-size arrangement scenario as the example here, whereas scenarios of other body-size arrangement $\times$ foraging strategy $\times$ dimensionality combinations can be found in the next section. The error bars indicate the standard error.

We recognise that an analytically-derived solution does not equal the true dynamical fate of species. Any non-perfectly-feasible equilibrium still has at least one species with negative equilibrium abundance. As all ordinary differentiation equations of the system are actually inter-dependent, those positive equilibrium abundances are thus derived based on the biologically unrealistic negative value(s). Similarly, in such a system, if numerically simulating the dynamics of the system but not allowing the species abundance (density) to go below zero, then the dynamical outcome will not perfectly mirror the analytical one. Nonetheless, we consider the index to be informative and applicable because of the following reasons.

Firstly, for non-perfectly-feasible equilibria, the number of species with negative equilibrium abundance can be seen as the distance from getting a perfectly-feasible (i.e., all species are feasible) solution. From a perspective regarding the parameters, considering that there exists a multi-dimensional parameter space within which the system could generate perfectly-feasible

equilibria, whereas outside the space there will be infeasible species at the equilibria. If the system, with the given parameter values, generates only one infeasible species at the equilibrium, it is very likely that in the multi-dimensional parameter hypervolume, the system is located at somewhere very close to one of the boundaries of the feasible domain, and requires just a very small change of the parameter value to move into the feasible domain, i.e., to make the non-feasible species feasible. A system with many negative equilibrium abundances, on the other hand, is less likely to be as close to the feasible domain as the previous one (Rohr *et al.* 2016; Grilli *et al.* 2017). Therefore, even though counting the positive equilibrium abundances at the analytical solution does not perfectly reflect the true dynamical outcome of the multi-species system, it still quantifies how far the system is from being perfectly feasible.

Secondly, in practice we made the comparison between the analytical equilibrium abundances and those derived by numerical simulation. This was done by randomly picking 10 replicates from our synthetic food webs of each topological model, with 2D grazing interaction strengths, an arbitrary magnitude of interference strength (a_0) at 1, initial species abundance for all at 10^{-7} , and the intrinsic growth rates as described in Section 2.3.5. The numerical simulation was carried out by the R package `deSolve` (Soetaert *et al.* 2010) with function `ode`. The simulation time was set to 10^8 with 1000 as each step. We then plot the analytical derived final abundances with the numerically simulated ones, and calculate the percentage of times that the dynamical fate (being feasible/infeasible) is consistent in both ways. The results are in Fig. A.8. It can be seen that even though the analytical and numerical solutions of equilibrium are not perfectly matching to each other, they largely converge, not only qualitatively, but also quantitatively in species abundances of those feasible ones. The accordance of species fates between the two methods ranged from 0.734 to 0.956 (Fig. A.8). Therefore, as in this study we just need information on the number of feasible species at the equilibrium, using the analytical solution would be arguably a very reasonable proxy of the true dynamical outcome.

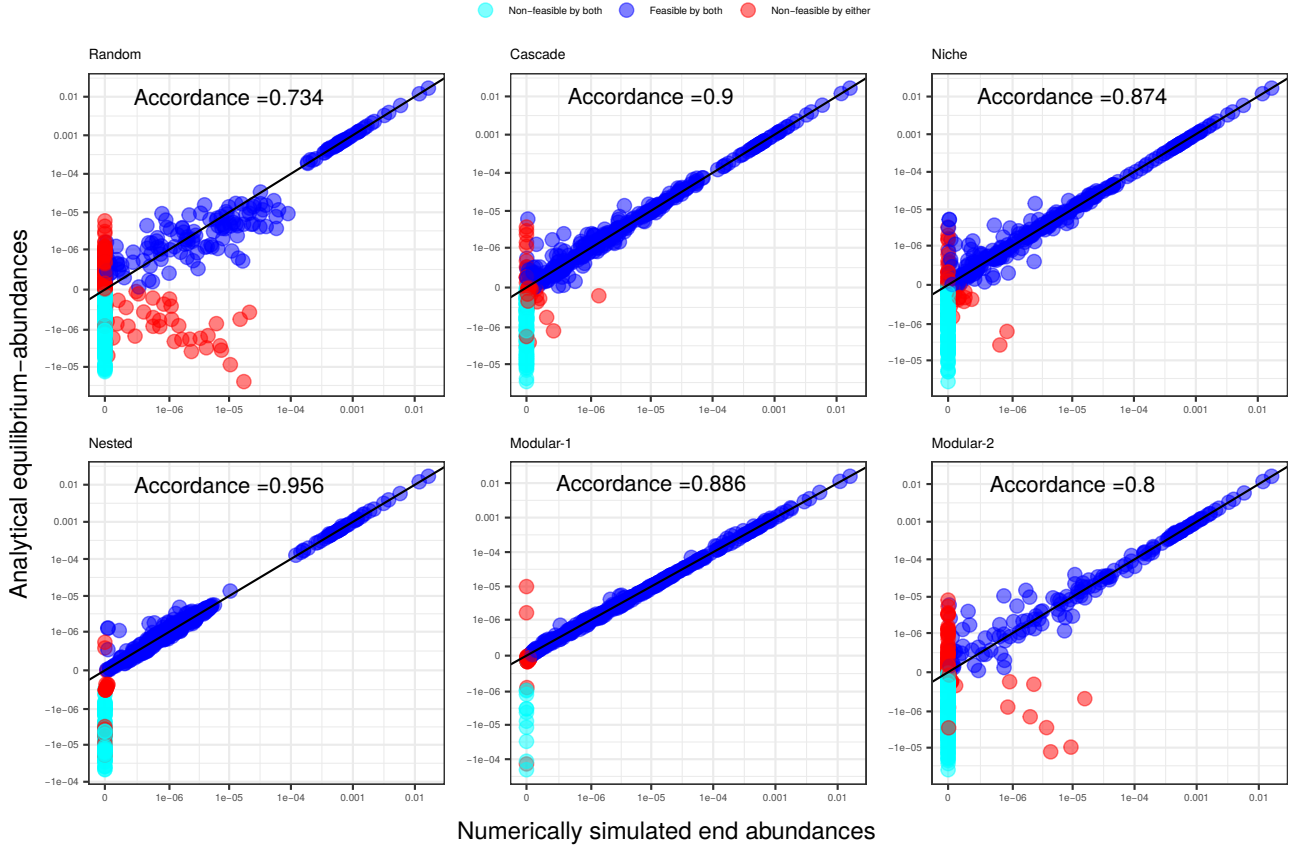


Figure A.8: **The analytical equilibrium abundances and numerically-simulated final abundances of the same species ($N = 10$ webs, 50 species each).** We collapsed the webs so each point is a species coming from a certain replication, and there are 500 points in total per plot. The solid black line indicates the $x = y$ line. Note that the axes are presented in a bi-symmetrical log-transformed fashion. The accordance indicated on the top shows the percentage of species where its dynamical fate (being feasible/infeasible) is consistent (i.e., blue and cyan points) in both methods.

A.3 Additional simulation results: other interference scaling exponents and a preferred body-mass ratio

In this section, we present the simulation results from several parameter settings other than the one we used in the main text (Chapter 2), all as figures below. This includes the using of neutral and a negative (i.e., 0 and -0.5, respectively) interference strength scaling exponents, as well as adding a universal preferred body-size ratio to all consumers when assigning the trophic interaction strengths. Other parameters remain the same as the settings in the main

text. We show how the number of feasible species at the equilibrium of the synthetic food webs fluctuates across magnitudes of interference strength (in correspondence with Fig. A.7), and how feasibility varies across all scenarios we checked (in correspondence with main text Fig. 2.3). For ease of making comparisons, we include also the results that have already been presented in the main text (Section 2.4). We indicate the exact parameter setting in the figure caption.

For adding a preferred resource-consumer body-size ratio effect to the interaction strengths, we multiplied the interaction strengths (derived by the scaling rules considering the foraging strategy and dimensionality, as described in Section 2.3.4) by an additional term as

$$\left(\frac{1}{1 + \left(\log \frac{1}{P.R.} \frac{m_R}{m_C} \right)^2} \right)^{exp_{P.R.}},$$

where $P.R.$ stands for the preferred resource-consumer body-size ratio, which we set to 0.1. m_R and m_C are the body mass of the resource and the consumer of the interaction, respectively. $exp_{P.R.}$ is the exponent that determines how strong the effect of the preferred body-size ratio is, which we set to 2. This term by itself is a dome-shaped function, peaks at one when the resource-consumer body-size ratio of the focal interacting pair exactly equals the preferred ratio. When the realised ratio deviates from the preferred ratio in either direction, the output of the term decreases symmetrically on a log scale (i.e., 10-times larger and 10-times smaller realised ratios lead to identical output values, which are smaller than one). $exp_{P.R.}$ controls the steepness of the dome. Therefore, the multiplying of this term to the interaction strengths provides an additional shrinking to the strengths due to the deviation from the preferred ratio of each realised resource-consumer pair.

In general, we observed the trend that feasibility peaks at an intermediate magnitude of interference were robust across all schemes. The peak value was the highest in the case where interference was positively mass-scaled. The pattern that this peak value, i.e., the feasibility index, of each topological model changes with the three body-size arrangements was rather consistent across all schemes. The ordering of the importance of being body-size structured across topological models was roughly consistent, as the importance was higher

in models with more top consumers. The way that such importance varies across foraging strategy $\times$ dimensionality combinations depended on the interference scaling exponent and also was influenced by whether a preferred ratio effect is embedded.

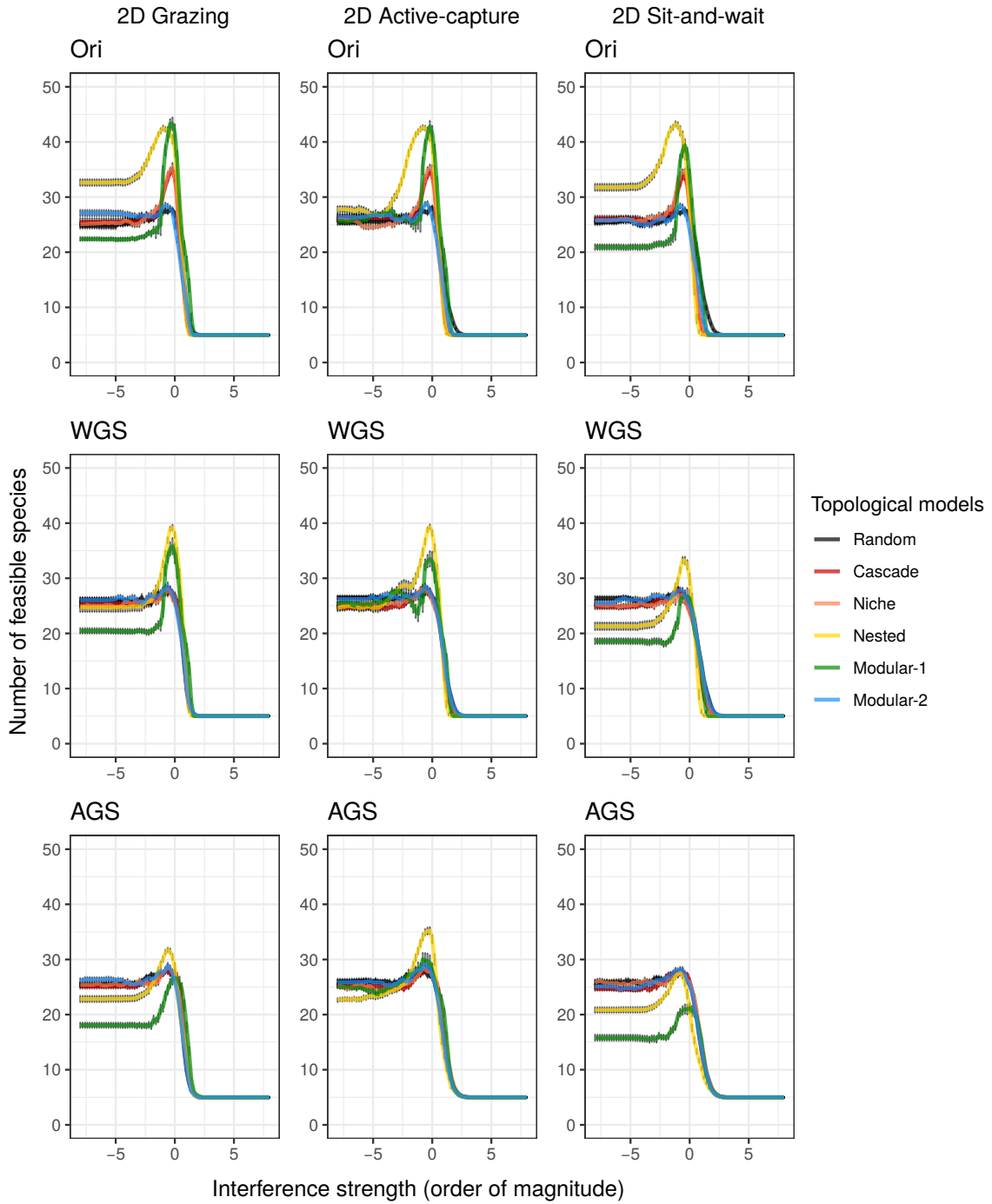


Figure A.9: **The number of feasible species at the equilibrium of synthetic food webs generated by each topological model across magnitudes of interference strength ($N = 30$), with interference strength exponent equals 0.5 and 2D foraging dimension.** Abbreviations Ori, WGS, and AGS stand for the Original, Within-Guild-Shuffled, and Across-Guild-Shuffled body-size arrangements, respectively.

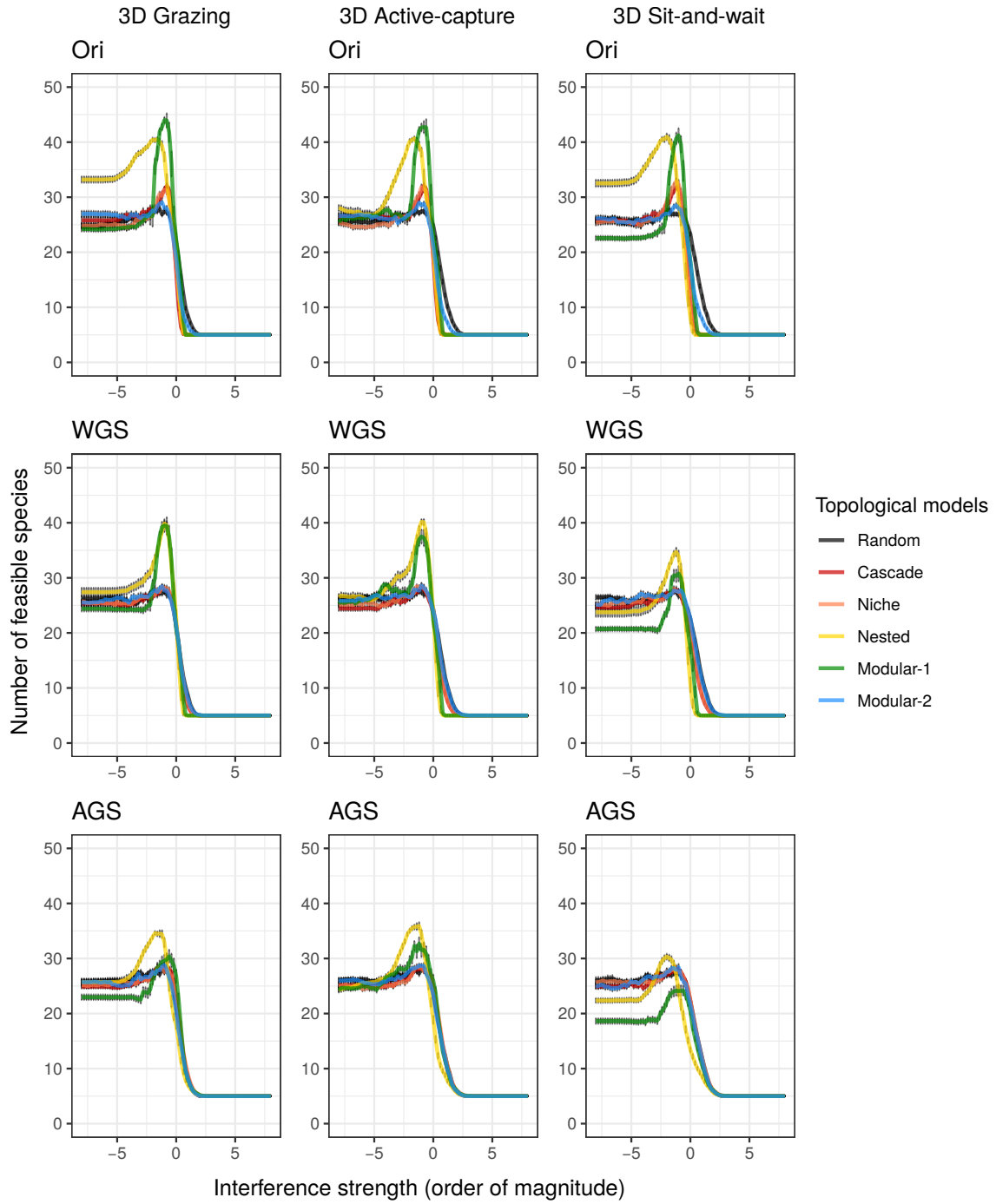


Figure A.10: **The number of feasible species at the equilibrium of synthetic food webs generated by each topological model across magnitudes of interference strength ($N = 30$), with interference strength exponent equals 0.5 and 3D foraging dimension.** Abbreviations Ori, WGS, and AGS stand for the Original, Within-Guild-Shuffled, and Across-Guild-Shuffled body-size arrangements, respectively.

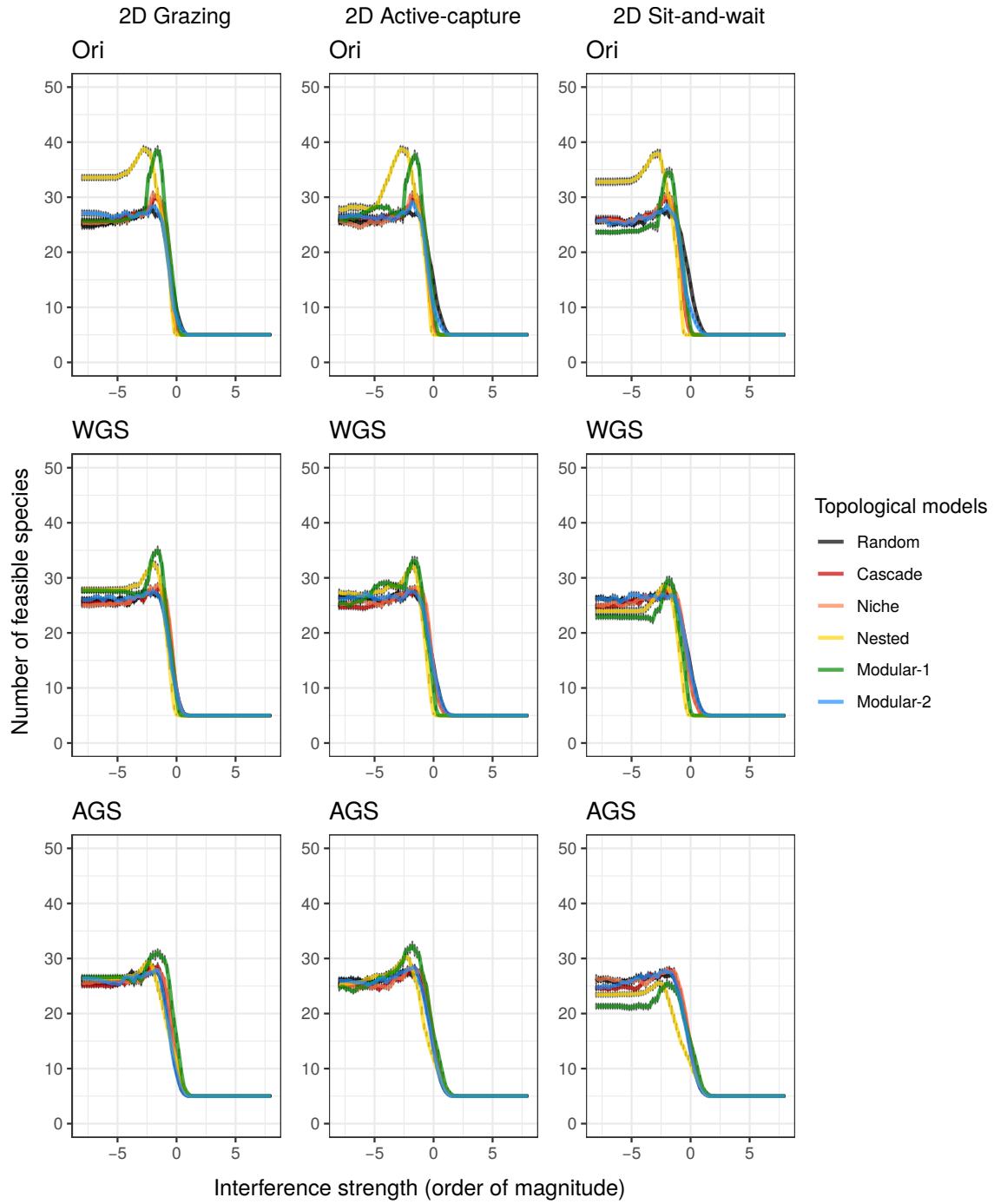


Figure A.11: The number of feasible species at the equilibrium of synthetic food webs generated by each topological model across magnitudes of interference strength ($N = 30$), with interference strength exponent equals 0 and 2D foraging dimension. Abbreviations Ori, WGS, and AGS stand for the Original, Within-Guild-Shuffled, and Across-Guild-Shuffled body-size arrangements, respectively.

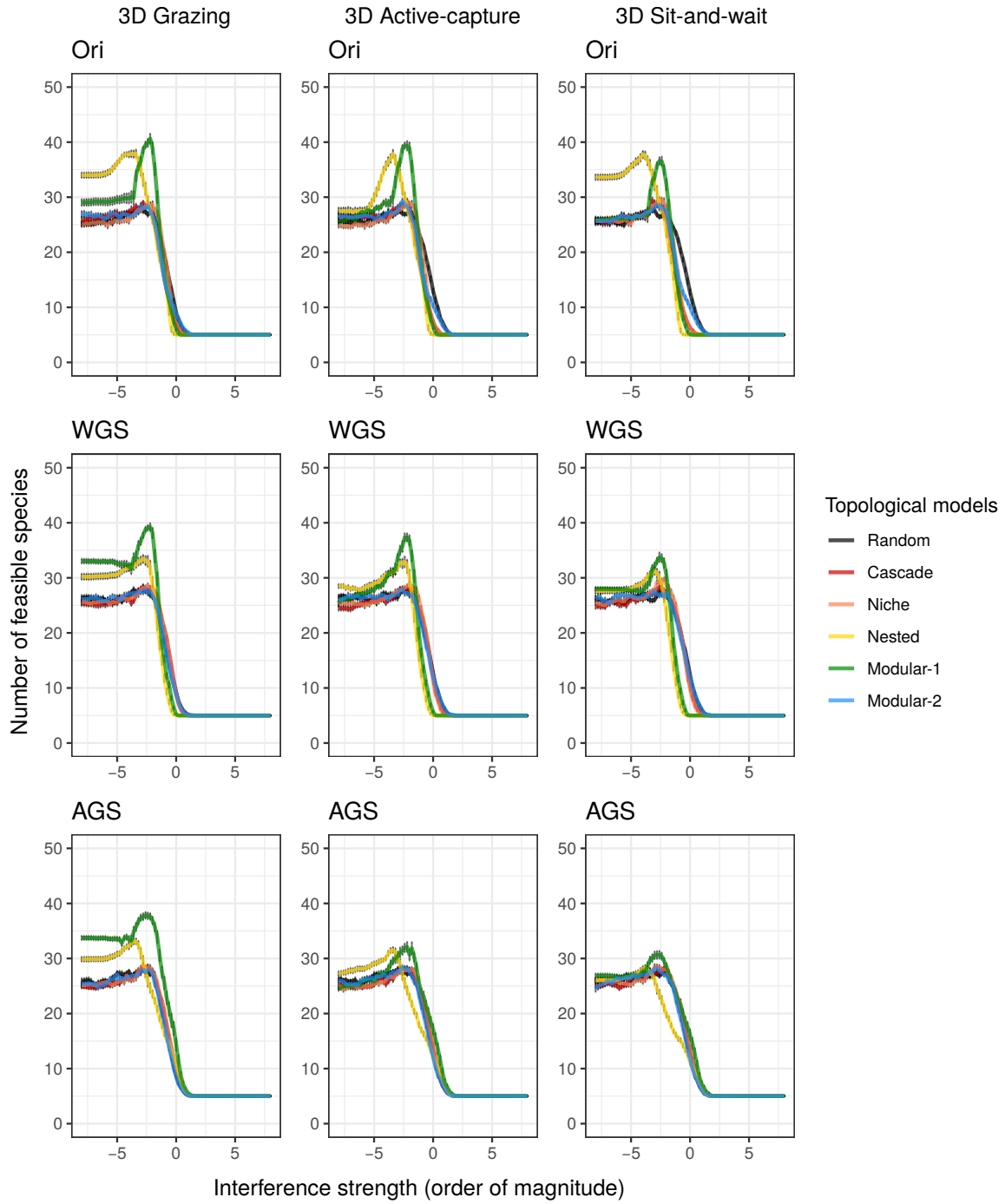


Figure A.12: **The number of feasible species at the equilibrium of synthetic food webs generated by each topological model across magnitudes of interference strength ($N = 30$), with interference strength exponent equals 0 and 3D foraging dimension.** Abbreviations Ori, WGS, and AGS stand for the Original, Within-Guild-Shuffled, and Across-Guild-Shuffled body-size arrangements, respectively.

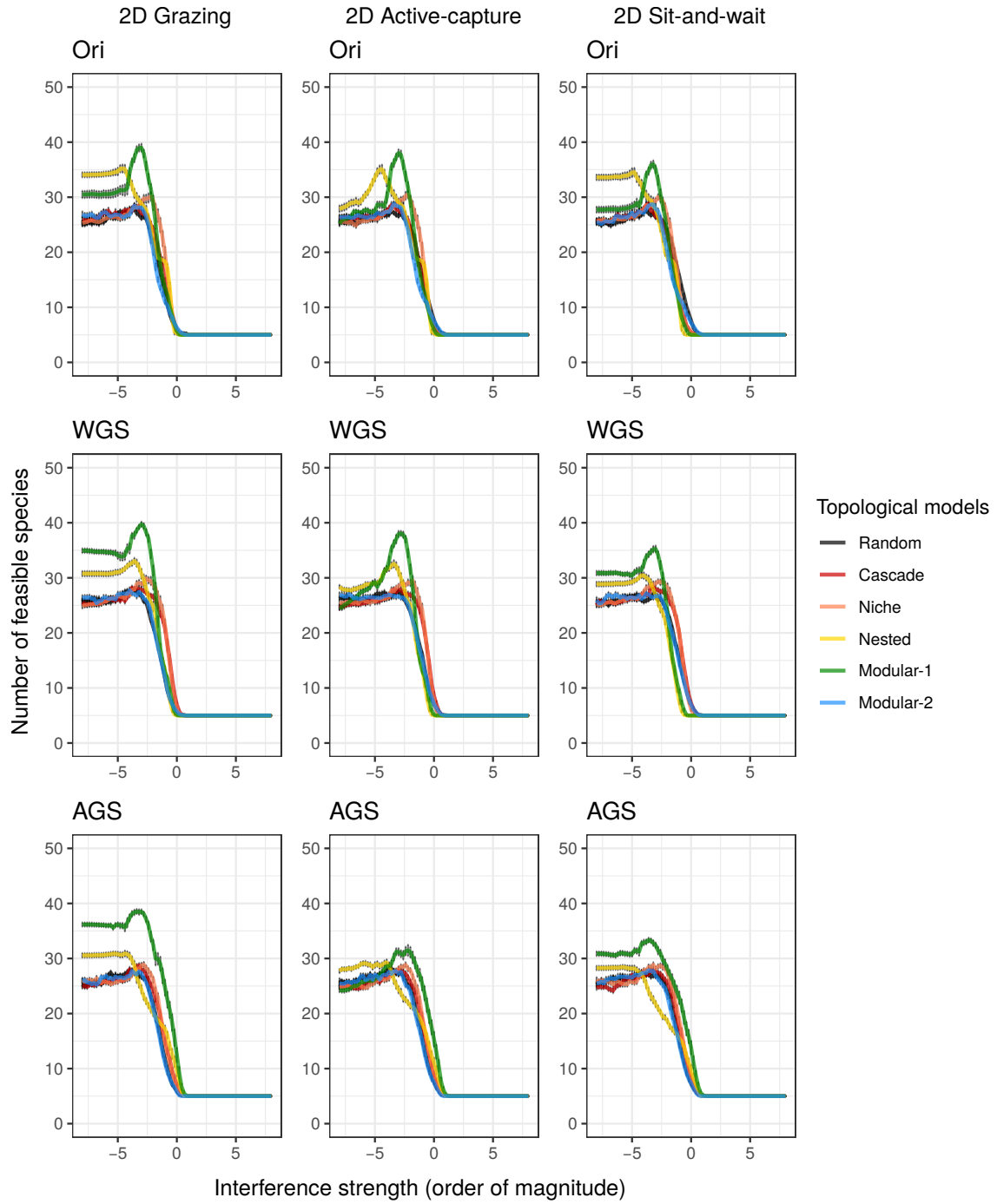


Figure A.13: **The number of feasible species at the equilibrium of synthetic food webs generated by each topological model across magnitudes of interference strength ($N = 30$), with interference strength exponent equals -0.5 and 2D foraging dimension.** Abbreviations Ori, WGS, and AGS stand for the Original, Within-Guild-Shuffled, and Across-Guild-Shuffled body-size arrangements, respectively.

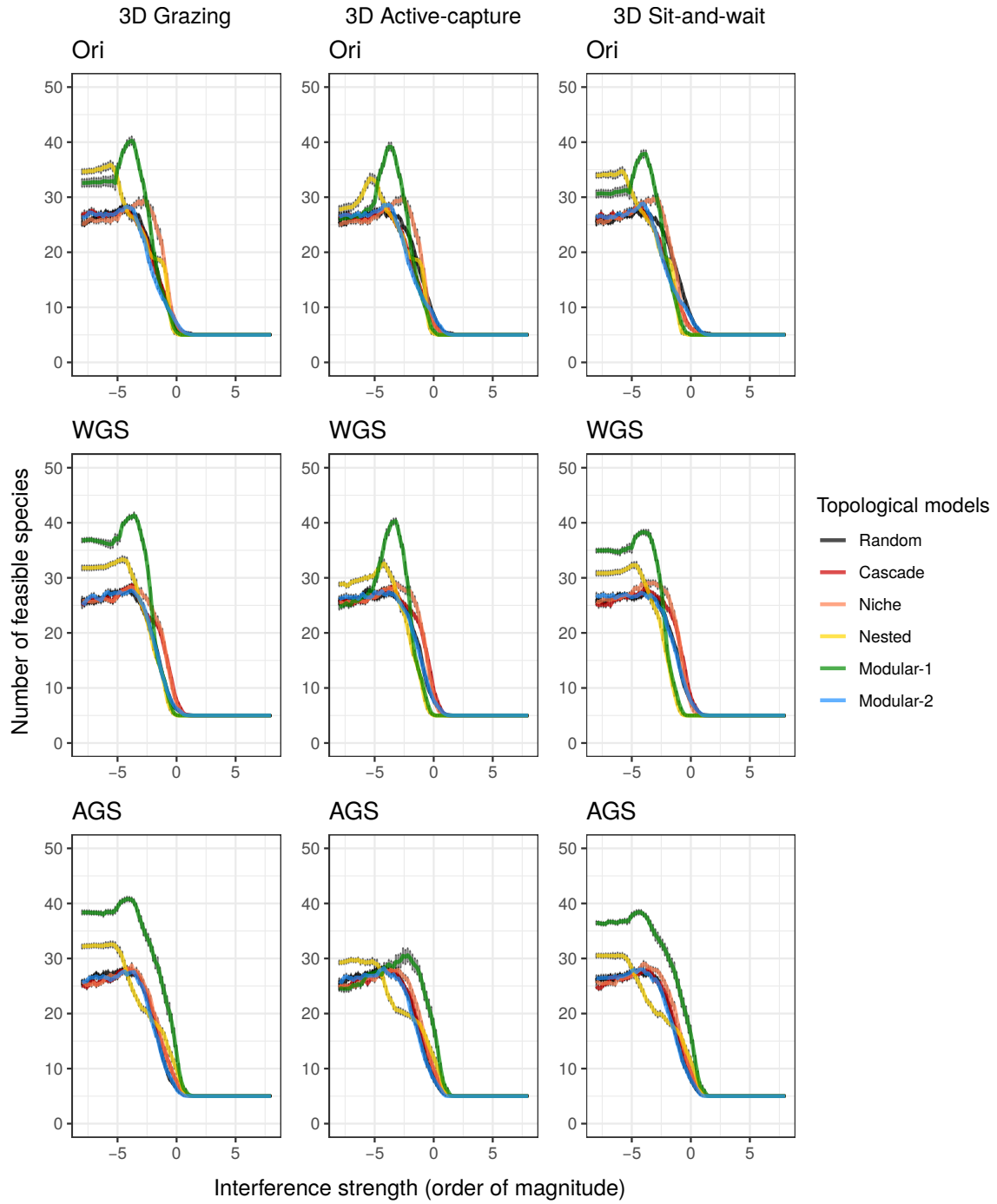


Figure A.14: **The number of feasible species at the equilibrium of synthetic food webs generated by each topological model across magnitudes of interference strength ($N = 30$), with interference strength exponent equals -0.5 and 3D foraging dimension.** Abbreviations Ori, WGS, and AGS stand for the Original, Within-Guild-Shuffled, and Across-Guild-Shuffled body-size arrangements, respectively.

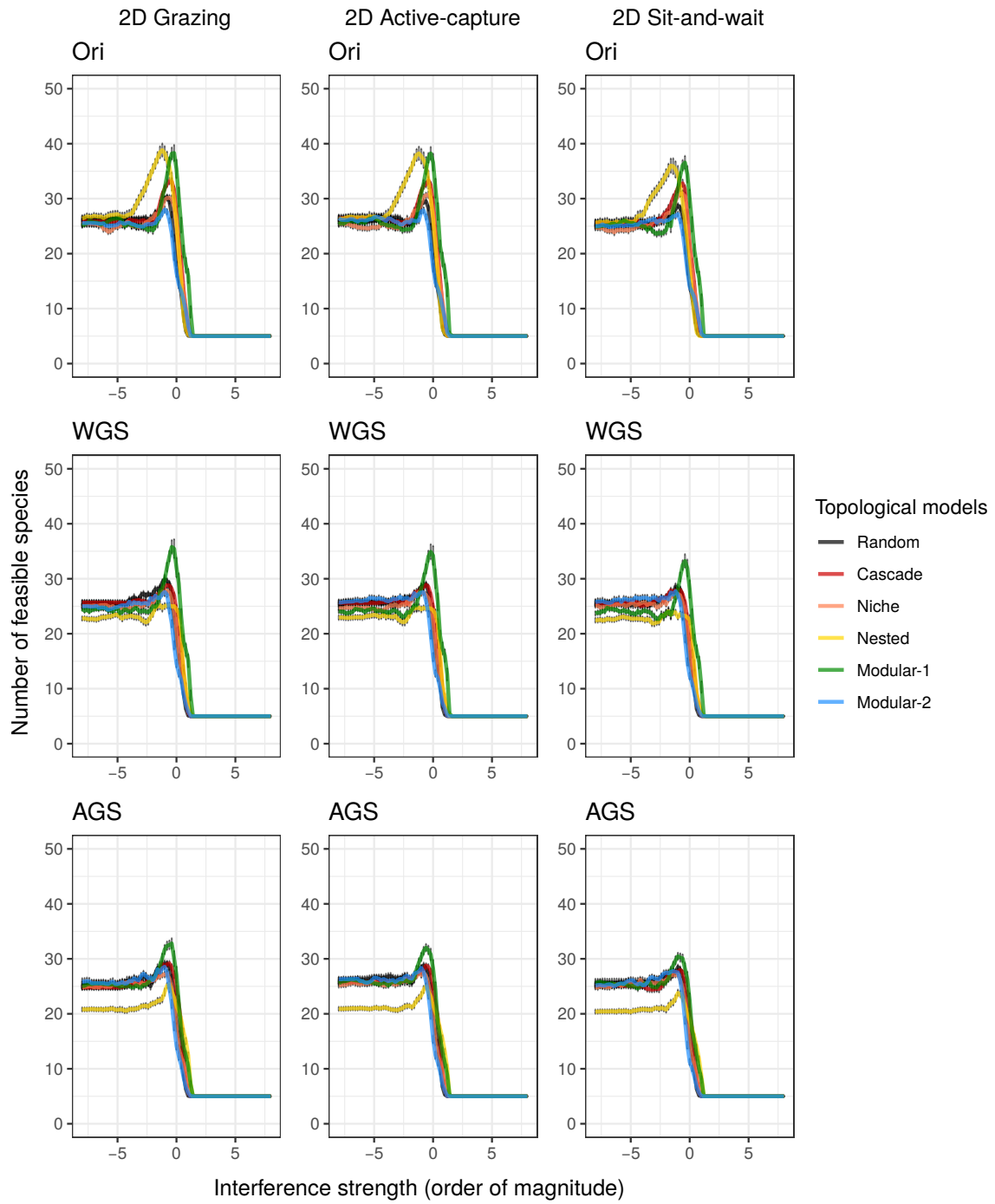


Figure A.15: The number of feasible species at the equilibrium of synthetic food webs generated by each topological model across magnitudes of interference strength ($N = 30$), with the preferred body-size ratio effect and 2D foraging dimension. Abbreviations Ori, WGS, and AGS stand for the Original, Within-Guild-Shuffled, and Across-Guild-Shuffled body-size arrangements, respectively.

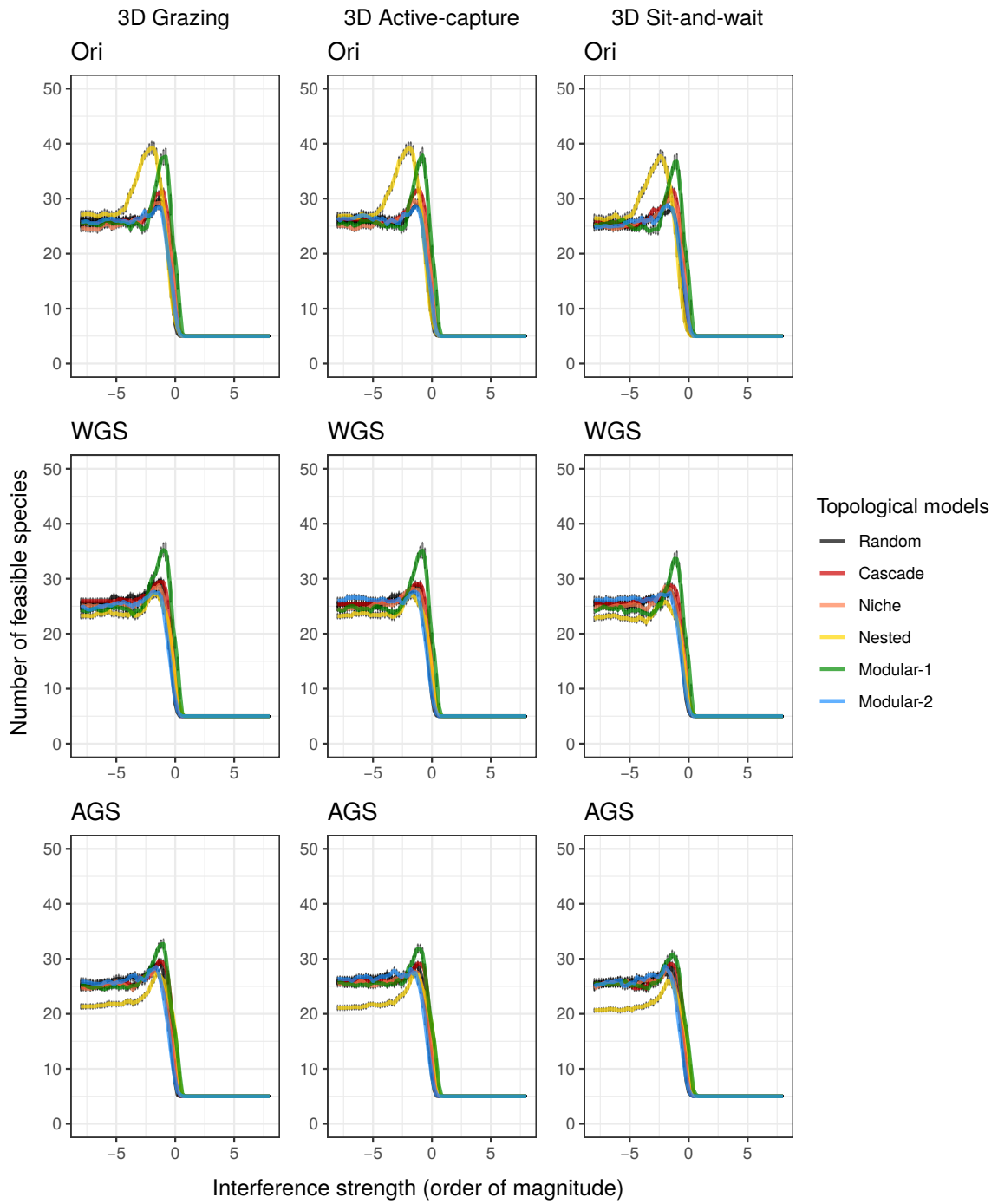


Figure A.16: **The number of feasible species at the equilibrium of synthetic food webs generated by each topological model across magnitudes of interference strength ($N = 30$), with the preferred body-size ratio effect and 3D foraging dimension.** Abbreviations Ori, WGS, and AGS stand for the Original, Within-Guild-Shuffled, and Across-Guild-Shuffled body-size arrangements, respectively.

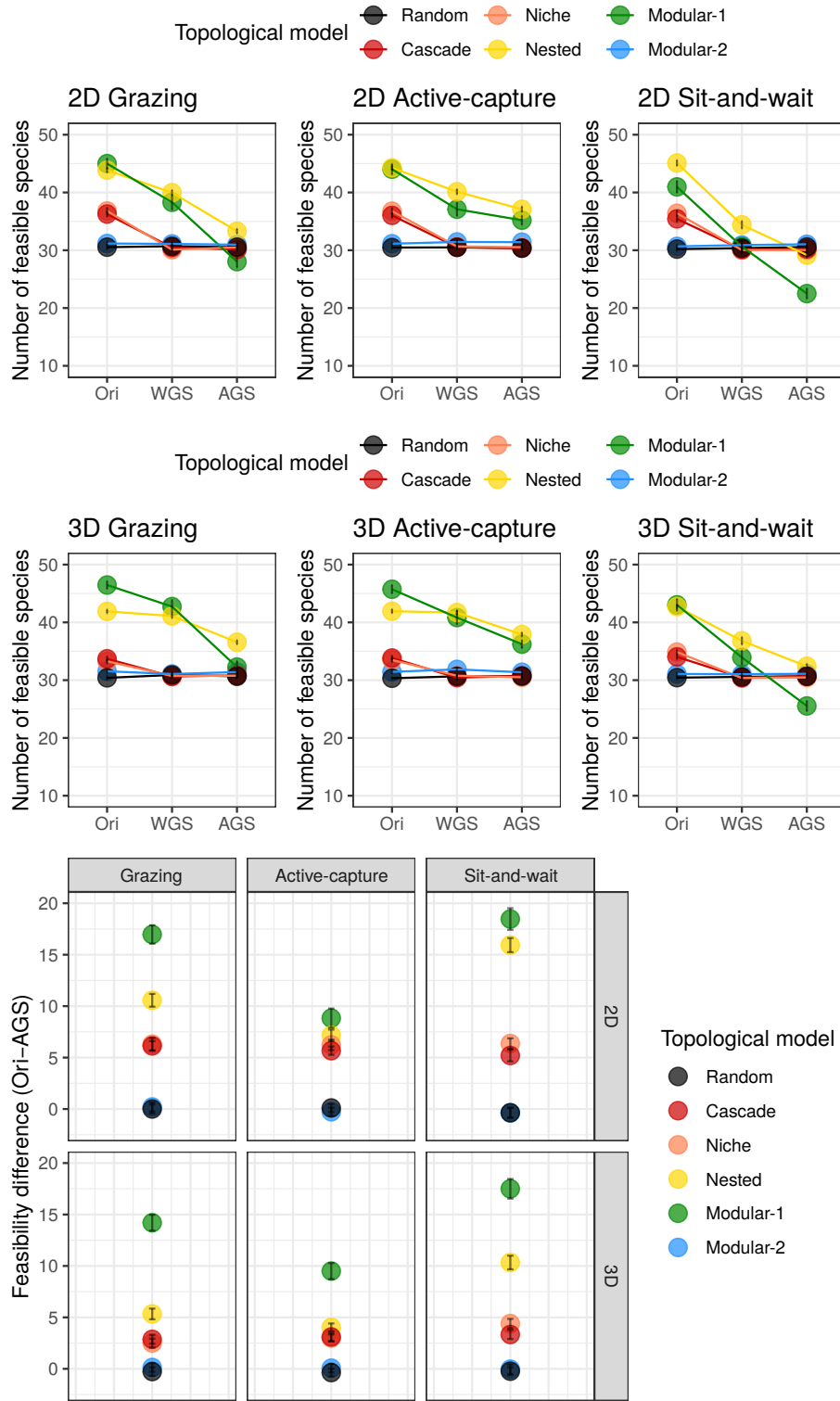


Figure A.17: The feasibility index readings, and the difference in feasibility index between the Original and the Across-Guild-Shuffled arrangements (i.e., $\text{Ori} - \text{AGS}$), of synthetic food webs of all topology $\times$ body-size arrangement $\times$ foraging strategy $\times$ dimensionality combinations, with interference strength exponent equals 0.5. Abbreviations Ori, WGS, and AGS stand for the Original, Within-Guild-Shuffled, and Across-Guild-Shuffled body-size arrangements, respectively. These are the results presented in the main text (Section 2.4).

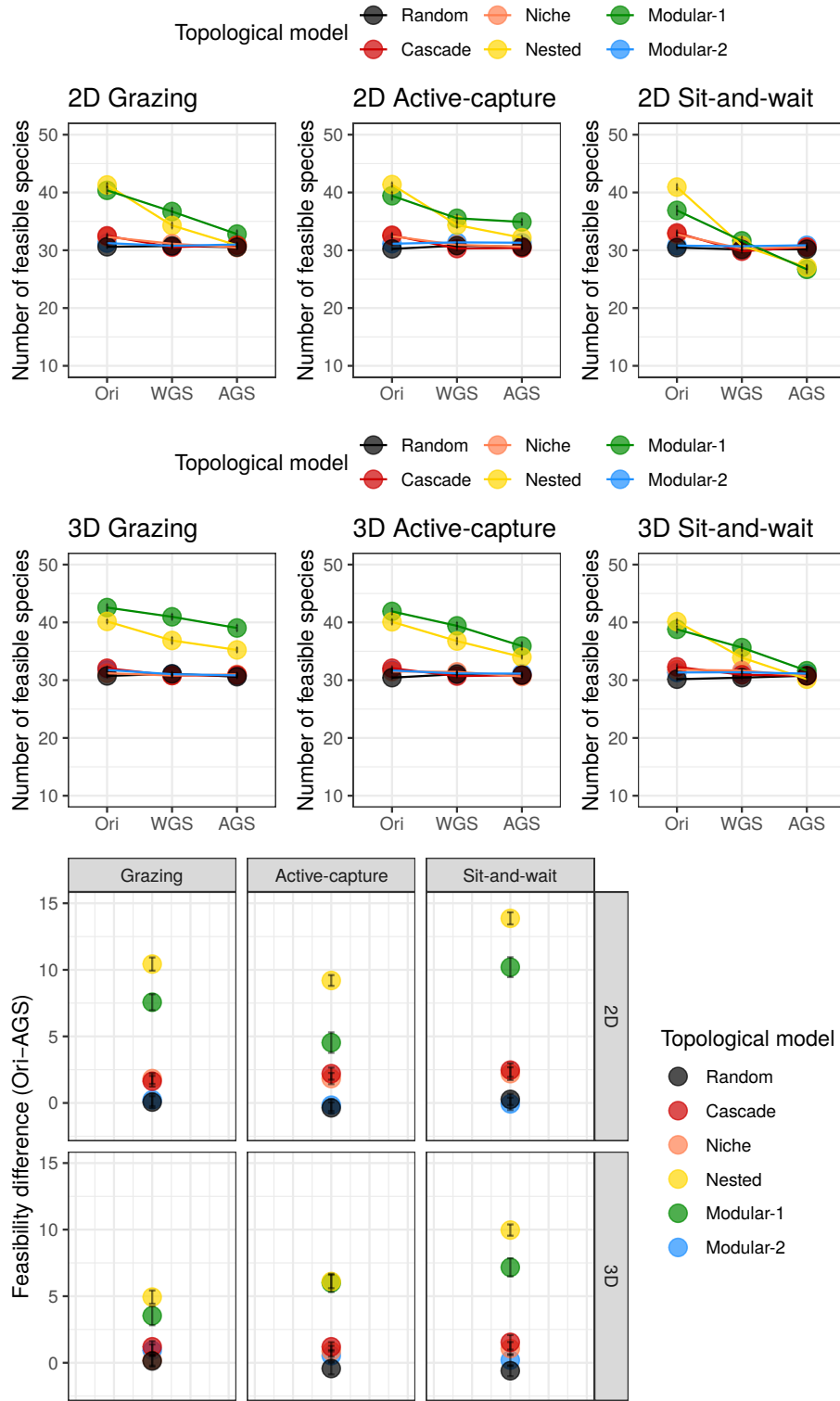


Figure A.18: The feasibility index readings, and the difference in feasibility index between the Original and the Across-Guild-Shuffled arrangements (i.e., $\text{Ori} - \text{AGS}$), of synthetic food webs of all topology $\times$ body-size arrangement $\times$ foraging strategy $\times$ dimensionality combinations, with interference strength exponent equals 0. Abbreviations Ori, WGS, and AGS stand for the Original, Within-Guild-Shuffled, and Across-Guild-Shuffled body-size arrangements, respectively.

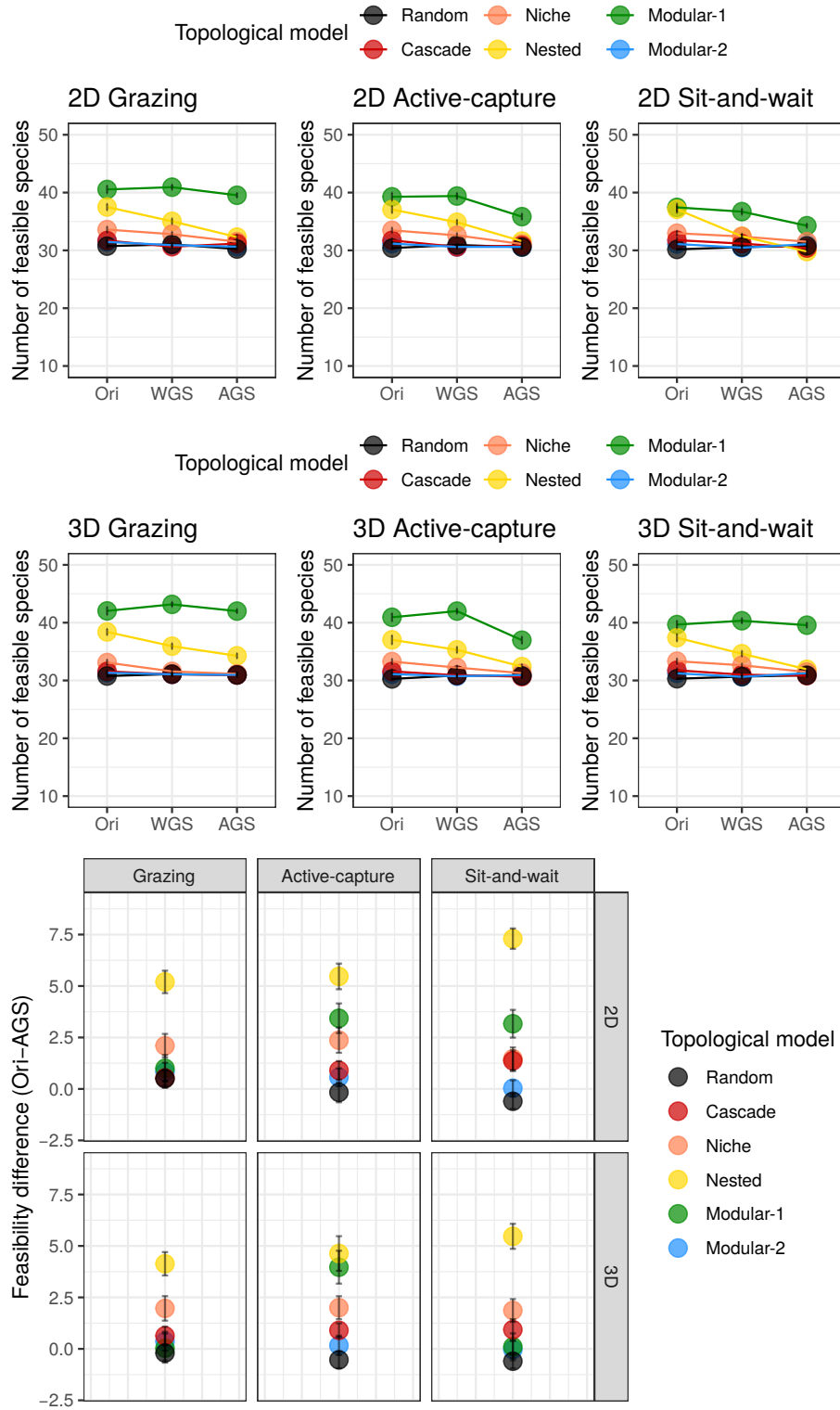


Figure A.19: The feasibility index readings, and the difference in feasibility index between the Original and the Across-Guild-Shuffled arrangements (i.e., Ori – AGS), of synthetic food webs of all topology $\times$ body-size arrangement $\times$ foraging strategy $\times$ dimensionality combinations, with interference strength exponent equals -0.5. Abbreviations Ori, WGS, and AGS stand for the Original, Within-Guild-Shuffled, and Across-Guild-Shuffled body-size arrangements, respectively.

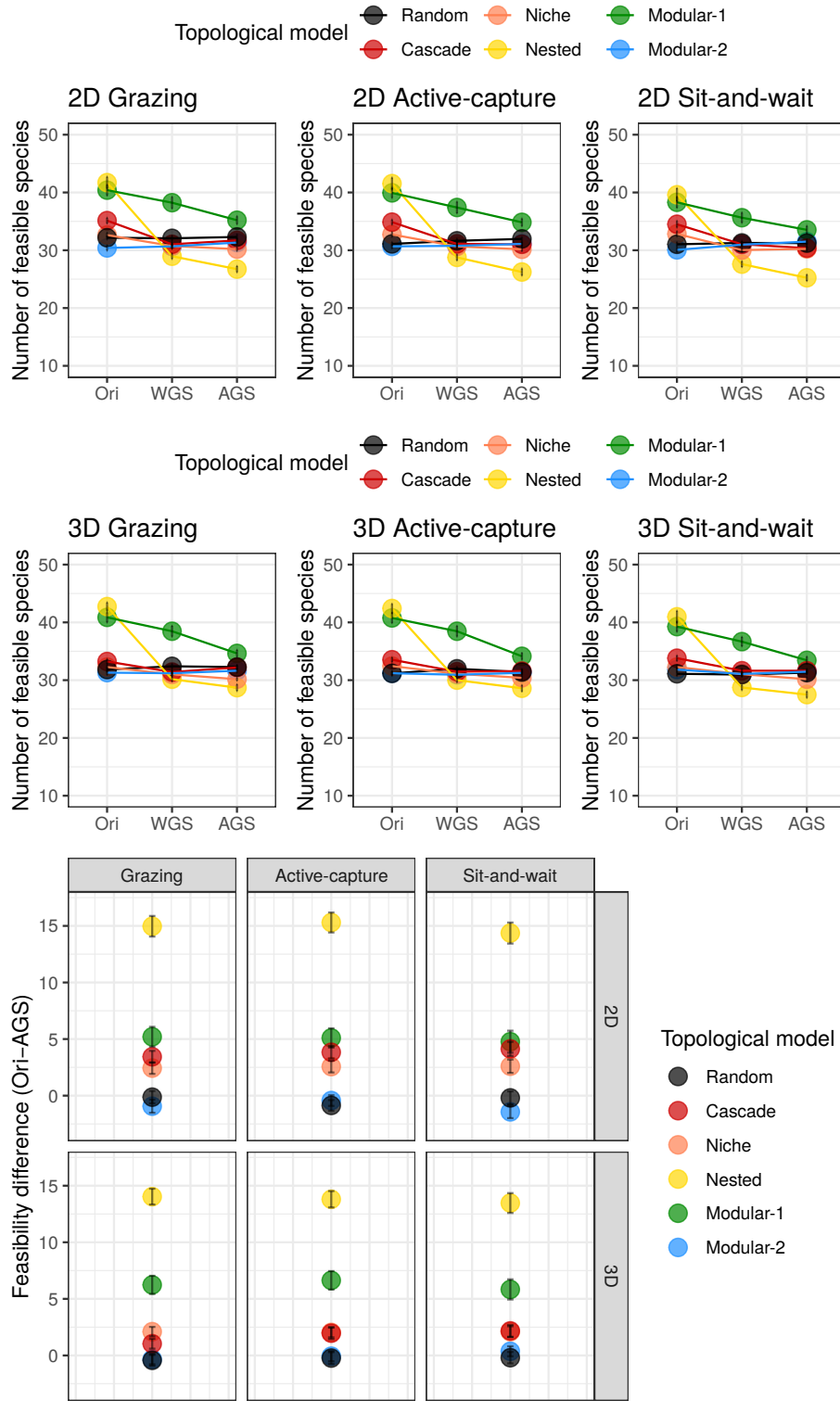


Figure A.20: The feasibility index readings, and the difference in feasibility index between the Original and the Across-Guild-Shuffled arrangements (i.e., $\text{Ori} - \text{AGS}$), of synthetic food webs of all topology $\times$ body-size arrangement $\times$ foraging strategy $\times$ dimensionality combinations, with the preferred body-size ratio effect. Abbreviations Ori, WGS, and AGS stand for the Original, Within-Guild-Shuffled, and Across-Guild-Shuffled body-size arrangements, respectively.

A.4 Further information on the empirical food webs

The empirical food-web data we used in this study come from the open-access dataset in the work by Brose *et al.* (2019). Below we list the names of the 74 food webs we used for analysis, and explain the criteria for selecting them using notations in accordance with the original dataset. We also present the summaries of some focal properties of these empirical webs that have not been shown in the main text. For further information about the dataset *per se*, please refer to the Brose *et al.* 2019 work.

From all food webs of the dataset, we selected the ones that include basal resource species as nodes (i.e., at least one link of the web has `res.metabolic.type` coded as `primary producer`) and all nodes have clear, strictly positive body masses. As we were modelling the trophic interaction among species, the basal resources in the web should themselves be species rather than organic particles or similar. Also, our prediction emerged from mass-scaling rules of interaction strengths on individual-based (i.e., whole-organism) consumption (see Section 2.3.4 and corresponding citations there); therefore it would not be sensible to test our predictions against the strengths of non-individual-based (i.e., the consumer eats just a part of a resource individual) and non-predacious (e.g., parasitic) interactions. We thus discarded interactions of other types but only focused on those whose `interaction.type` were coded as `predacious`, `herbivorous`, and `fungivorous`, and further discarded webs that have total node number below 30 (considered too small to reflect the effect of food-web structures), and those have less than 50% of the links being individual-based interaction (i.e., `interaction.classification` coded as `ibi`).

The selecting procedure left us with 74 webs (names as appeared in the original dataset): Ythan Estuary, Kongsfjorden, Alford lake, Chub pond, Grass lake, Horseshoe Lake, Long Lake, Loon Lake, Lower Sister Lake, Razorback Lake, Safford Lake, Stink Lake, Whipple Lake, Weddell Sea, Caribbean Reef, FloridaIslandE2, FloridaIslandE7, FloridaIslandE9, Lough Hyne, CGP3, CR1P1, CR1P2, CR1P3, CR1P4, CR2P1, CR2P2, CR2P3, CR2P4, F1P1, F1P2, F1P3, F1P4, F2P1, F2P2, F2P3, F2P4, FXAP1, FXAP2, FXAP3, FXBP1, FXBP2, FXBP3, FXBP4, GJAP1, GJAP2, GJBP1, GJBP2, L1P1, L1P2, L1P3, L1P4, L2P1, L2P2, L2P4, L3P1, L3P3,

L3P4, L4P1, L4P2, L4P3, L4P4, MBP1, MBP3, PC2P2, RV1P1, RV1P2, RV1P3, RV1P4, RV2P1, RV2P2, RV2P3, RV2P4, WP1, WP3.

Notably, applying the above selecting criteria effectively left mostly aquatic food webs after selection. Along with our modelling of individual-based consumption (see Section 2.3.4), the discoveries of this study, from both the simulation and empirical parts, may reflected better the situation of aquatic than other types of food webs.

The topological, body-size, and behavioural properties (as defined in the main text) of food webs in each type of ecosystems are summarised below in Fig. A.21 and Fig. A.22. We note especially that the T score is the highest in marine food webs (Fig. A.21), and there is a strong correlation between the proportion of 3D links and the proportion of active-capture links (Fig. A.22). We also note that, the proportion of basal resource out of all species is about 0.05 in terrestrial systems and 0.29 in aquatic ones, roughly the same before (i.e., with the original dataset) and after food-web selection (i.e., with the 74 webs we used). We therefore took a middle-ground value 0.1 for this proportion when conducting the simulation part of this study (see Section 2.3.2).

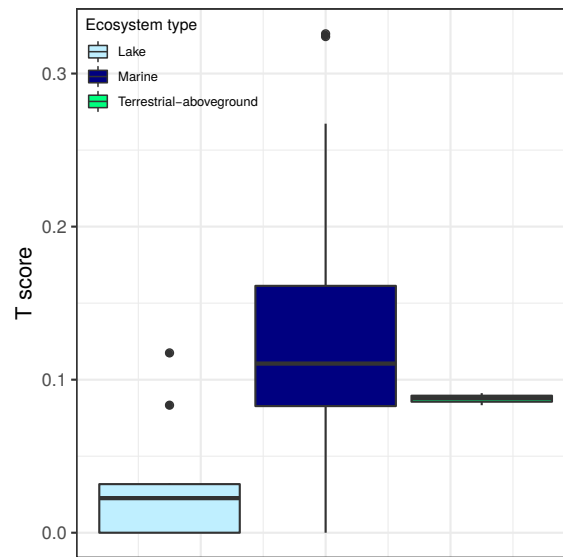


Figure A.21: **The T score of the empirical food webs of the three ecosystem types as box plots.** The T score of each web is calculated as explained in Section 2.3.6

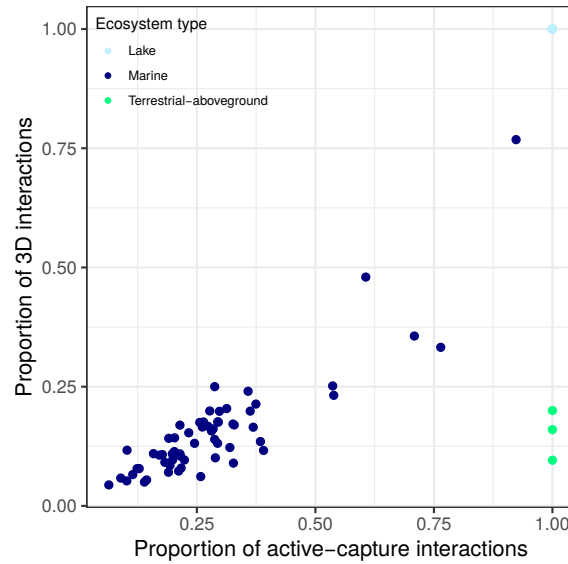


Figure A.22: The proportion of active-capture and 3D interactions, respectively, in the empirical food webs across the three ecosystem types. We note the obvious positive correlation between the two measurements.

A.5 Additional analyses: other regression models for the empirical validation

In addition to the linear (and mixed-model) regression analysis of the empirical food webs' LES/LEL body-size structure as presented in the main text (Table 2.1), we show here the results with other regression models. These include the analyses using each of the predicting food-web properties—namely the T score, the proportion of active-capture interactions, and the proportion of 3D interactions—as the single predictor (Table A.2–A.4), as well as the analysis excluding the proportion of 3D interactions from the predictors (Table A.5). In general, from the results of these analyses, we can see that the sign and significance of the effects of the T score and the proportion of active-capture interactions on the LES structure are qualitatively consistent with the results presented in the main text (Section 2.4), while the effect of the proportion of 3D interactions is less so. The former two effects are thus rather convincing due to their robustness across regression models.

As the three terrestrial aboveground food webs do not follow the strong positive correlation

between the proportion of active-capture vs. 3D interactions that we observed in the webs of marine and lake ecosystems (Fig. A.22), we also performed the regression analysis with these three outlier-like points removed. The results remain qualitatively the same (Table A.6) as using all 74 food webs.

Table A.2: **The results of the linear (mixed-model) regression analyses with the T score as the only predictor (N = 74).** The sign of the estimated effect indicates whether the predictor has a positive/negative contribution to the level of the Large-Eat-Small (LES)/Large-Eat-Large (LEL) structure.

For LES & LEL body-size structure				
	Estimated effect	SE	t value	P value
<i>Model: Level.LES ~ T.score</i>				
Intercept	0.85	0.016	53.53	< 1e-10
T.score	0.30	0.122	2.46	0.02
<i>Model: Level.LES ~ T.score, ecosystem type as random intercept</i>				
Intercept	0.78	0.084	9.29	0.01
T.score	0.26	0.104	2.54	0.01
<i>Model: Level.LEL ~ T.score</i>				
Intercept	0.40	0.026	15.28	< 1e-10
T.score	-0.31	0.242	-1.30	0.20
<i>Model: Level.LEL ~ T.score, ecosystem type as random intercept</i>				
Intercept	0.40	0.030	13.36	0.02
T.score	-0.37	0.258	-1.44	0.19

Level.LES/LEL: the level of this body-size structure, with corresponding index as described in Section 2.3.3

Table A.3: **The results of the linear (mixed-model) regression analyses with the proportion of active-capture interactions as the only predictor (N = 74).** The sign of the estimated effect indicates whether the predictor has a positive/negative contribution to the level of the Large-Eat-Small (LES)/Large-Eat-Large (LEL) structure.

For LES & LEL body-size structure				
	Estimated effect	SE	t value	P value
<i>Model: Level.LES ~ Prop.Act</i>				
Intercept	0.92	0.014	67.78	< 1e-10
Prop.Act	-0.11	0.026	-4.12	< 0.01
<i>Model: Level.LES ~ Prop.Act, ecosystem type as random intercept</i>				
Intercept	0.90	0.078	11.48	< 0.01
Prop.Act	-0.13	0.045	-2.88	< 0.01
<i>Model: Level.LEL ~ Prop.Act</i>				
Intercept	0.34	0.026	13.02	< 1e-10
Prop.Act	0.08	0.047	1.61	0.11
<i>Model: Level.LEL ~ Prop.Act, ecosystem type as random intercept</i>				
Intercept	0.12	0.124	1.00	0.45
Prop.Act	0.27	0.079	3.44	< 0.01

Level.LES/LEL: the level of this body-size structure, with corresponding index as described in Section 2.3.3.

Prop.Act: the proportion of active-capture interactions.

Table A.4: **The results of the linear (mixed-model) regression analyses with the proportion of 3D interactions as the only predictor (N = 74).** The sign of the estimated effect indicates whether the predictor has a positive/negative contribution to the level of the Large-Eat-Small (LES)/Large-Eat-Large (LEL) structure.

For LES & LEL body-size structure				
	Estimated effect	SE	t value	P value
<i>Model: Level.LES ~ Prop.3D</i>				
Intercept	0.88	0.012	72.55	< 1e-10
Prop.3D	-0.01	0.029	-0.51	0.61
<i>Model: Level.LES ~ Prop.3D, ecosystem type as random intercept</i>				
Intercept	0.81	0.093	8.72	< 0.01
Prop.3D	-0.03	0.065	-0.50	0.62
<i>Model: Level.LEL ~ Prop.3D</i>				
Intercept	0.35	0.021	16.63	< 1e-10
Prop.3D	0.07	0.044	1.54	0.13
<i>Model: Level.LEL ~ Prop.3D, ecosystem type as random intercept</i>				
Intercept	0.11	0.129	0.88	0.45
Prop.3D	0.40	0.093	4.27	< 0.01

Level.LES/LEL: the level of this body-size structure, with corresponding index as described in Section 2.3.3.

Prop.Act: the proportion of active-capture interactions.

Table A.5: The results of the linear (mixed-model) regression analyses with the T score and the proportion of 3D interactions as predictors (N = 74). The sign of the estimated effect indicates whether the predictor has a positive/negative contribution to the level of the Large-Eat-Small (LES)/Large-Eat-Large (LEL) structure.

For LES & LEL body-size structure				
	Estimated effect	SE	t value	P value
<i>Model: Level.LES ~ T.score + Prop.Act</i>				
Intercept	0.91	0.025	36.00	< 1e-10
T.score	0.07	0.135	0.53	0.60
Prop.Act	-0.10	0.030	-3.21	< 0.01
<i>Model: Level.LES ~ T.score + Prop.Act, ecosystem type as random intercept</i>				
Intercept	0.86	0.084	10.30	< 0.01
T.score	0.19	0.107	1.79	0.08
Prop.Act	-0.10	0.046	-2.21	0.03
<i>Model: Level.LEL ~ T.score + Prop.Act</i>				
Intercept	0.35	0.054	6.47	< 0.01
T.score	-0.11	0.322	-0.33	0.74
Prop.Act	0.06	0.063	0.98	0.33
<i>Model: Level.LEL ~ T.score + Prop.Act, ecosystem type as random intercept</i>				
Intercept	0.15	0.131	1.14	0.37
T.score	-0.15	0.304	-0.48	0.63
Prop.Act	0.25	0.087	2.93	< 0.01

Level.LES/LEL: the level of this body-size structure, with corresponding index as described in Section 2.3.3.

Prop.Act: the proportion of active-capture interactions.

Table A.6: **The results of the linear (mixed-model) regression analyses without terrestrial food webs (N = 71).** The sign of the estimated effect indicates whether the predictor has a positive/negative contribution to the level of the Large-Eat-Small (LES)/Large-Eat-Large (LEL) structure.

For LES body-size structure				
	Estimated effect	SE	t value	P value
<i>Model: Level.LES ~ T.score + Prop.Act + Prop.3D</i>				
Intercept	0.91	0.021	43.73	< 1e-10
T.score	0.22	0.101	2.18	0.03
Prop.Act	-0.30	0.077	-3.95	< 0.01
Prop.3D	0.27	0.071	3.80	< 0.01
<i>Model: Level.LES ~ T.score + Prop.Act + Prop.3D, ecosystem type as random intercept</i>				
Intercept	0.85	0.069	12.25	0.04
T.score	0.24	0.098	2.40	0.02
Prop.Act	-0.38	0.083	-4.51	< 0.01
Prop.3D	0.45	0.113	3.93	< 0.01
For LEL body-size structure				
	Estimated effect	SE	t value	P value
<i>Model: Level.LEL ~ T.score + Prop.Act + Prop.3D</i>				
Intercept	0.33	0.057	5.80	< 0.01
T.score	-0.13	0.333	-0.38	0.70
Prop.Act	0.26	0.195	1.34	0.18
Prop.3D	-0.18	0.183	-1.00	0.32
<i>Model: Level.LEL ~ T.score + Prop.Act + Prop.3D, ecosystem type as random intercept</i>				
Intercept	0.12	0.198	0.61	0.64
T.score	0.03	0.309	0.09	0.93
Prop.Act	-0.10	0.205	-0.46	0.64
Prop.3D	0.52	0.261	2.00	0.05

Level.LES/LEL: the level of this body-size structure, with corresponding index as described in Section 2.3.3.

Prop.3D: the proportion of 3D interactions.

A.6 Linear vs. non-linear functional responses

In this section, we present the theoretical and empirical rationale for our sole focus on Type I functional responses in this study. Note that the Type-I functional response is also an important simplification that allows us to analytically solve the dynamical Lotka-Volterra system for feasibility (see Section 2.3.5).

A.6.1 Theoretical rationale

Regarding interspecific (trophic) interaction, Pawar *et al.* (2012) have shown that, with both metabolically-constrained modelling prediction and empirical evidence, the scaling of consumers' consumption rates to their body masses is similar whether resources are abundant or scarce, and is thus relatively unconstrained by handling time. In other words, although the consumption rate of each consumer may gradually become less sensitive to the increasing of its resource abundance (e.g., enters the saturating phase of a Type-II functional response), the pattern of consumption rates across consumers does not scale like handling time, but mostly be constrained by search rate (and its scaling to consumer's body mass) instead. Note that, mathematically, given species intrinsic growth rates are fixed, it is the pattern of interaction matrix's entries rather than their actual sizes that determines feasibility. That is, the equilibrium abundances ($\hat{\mathbf{n}}$, as a vector) can be expressed as

$$\hat{\mathbf{n}} = -\mathbf{A}^{-1}\mathbf{b},$$

where $\mathbf{A}$ is the interaction matrix (interspecific interaction strengths on off-diagonal and intraspecific interference strengths on diagonal) and $\mathbf{b}$ the vector of species intrinsic growth rates. With fixed $\mathbf{b}$, multiplying any positive constant to $\mathbf{A}$ does not affect the signs of $\hat{\mathbf{n}}$. The above implies that the feasibility of the system is thus mostly driven by the scaling of consumers' search rate, which is approximately linear. Indeed, Pawar *et al.* (2012) have tested their model with handling time across five order of magnitudes (0— 10^4), and the feasible coexistence regions (of resource and consumer masses) remain the same regardless the size of handling time.

Consistent with this, Tang *et al.* (2014) have shown numerically that, with empirical food-web topologies and mass-scaled predetermined equilibrium abundances (all positive and thus the system is feasible), species' interaction strengths are almost identical whether estimated by Type-I or Type-II functional responses. Introducing the constraining effect of handling times thus does not significantly alter the entry values of the interaction matrix, nor affect the dynamical properties of the food web, because intraspecific interference overrides the effect of any non-linearity in functional responses.

Indeed, Barabás *et al.* (2016) have shown that intraspecific interference has a dominant influence on feasibility in large Lotka-Volterra systems. The size of the parameter space allowing feasibility always increases with intraspecific interference strength (within their range of exploration) regardless of the interspecific interaction structure. Biologically, this implies that for large communities to be feasible, the interference strengths should generally be large enough to prevent species abundances from reaching high levels (where effects of interspecific interaction structure and any functional response non-linearities therein would become prominent instead). That is, intraspecific interference generally overrides the effects of functional responses because low species abundances prevent the effect of handling-time constraints (of non-linear Type-II or III functional responses) on consumption rates from kicking in. We note that this issue has not been explored till recently because only after Tang *et al.* (2014) introduced nonlinear functional responses into the Lotka-Volterra type models did the effects of intraspecific interference vs. non-linear functional responses on large food webs' dynamics start to be directly compared. Hitherto, non-linear functional responses and intraspecific interference were studied in separate modelling frameworks: the former in food-web extensions of the Rosenzweig-MacArthur model (Brose *et al.* 2006b), and the latter in Lotka-Volterra type models.

A.6.2 Empirical rationale

Here we provide evidence that in nature, resource species' abundance (density) is generally not high enough to saturate consumer species' consumption rate due to handling time constraints (as in Type-II or III functional responses).

We used the FoRAGE dataset compiled by Uiterwaal *et al.* (2018), which includes the largest current compilation of empirical functional response data worldwide. Among the 2083 standardised functional response datasets, we identified 48 “natural” ones, where foraging happened in the field but not in the lab (i.e., identified as “Field” or “In the field” in the FoRAGE dataset), and the resource population size was estimated by field surveys instead of being manipulated (e.g., with cages/enclosures) (i.e., “NaturalDensity” identified as “Y” in the FoRAGE

dataset). We then fitted both a linear model and a Type-II functional response model,

$$y = \frac{ax}{1 + axh},$$

to the relationship between consumer's foraging rate (y) and resource density (x) (i.e., the functional response curve) using R version 3.4.4 (R Core Team 2013) with package `minpack.lm` (Elzhov *et al.* 2010). We then evaluated the quality of both models' fitting by comparing their AIC and BIC values across all 48 functional responses.

The results are shown in Fig. A.23. In more than half of the cases (26/48 if evaluated with AIC, and 28/48 with BIC), the linear model actually outperformed the Type-II function. This indicates that for modelling sampled foraging rates in natural population densities, using a Type-I function is in general no worse than using a Type-II one. Furthermore, in most of the datasets, the data points showed a clear biased (over-representation) towards the low end of the resource density axis, indicating that in nature, resources rarely reach high levels. In this sense, most of the the sampled foraging rates in natural population sizes should remain in the ascending (low-density) section of the functional response curve, where a Type-I function is especially applicable for describing these rates. To validate this idea, we further conducted the following analysis. We first kept 90 percent of data from each functional response dataset by dropping the 10 percent with highest resource densities. We then evaluated which of the above fitted models explain better the remaining 90 percent of data by checking which model has a smaller residual sum of squares (RSS). Indeed, in 39/48 cases, the linear model showed lower RSS than the Type-II model (Fig. A.24), indicating the superior explanation of data variance of the former. This supports the idea that natural resource densities are rarely high enough to allow handling time constraints to come into play.

The above results indicate that using the Type-I functional response is appropriate for modelling foraging rates typically observed under natural conditions, where resources are relatively rare, and consumption rate is mainly limited by searching rather than handling. The Type-I functional response is therefore appropriate for generating predictions about food web feasibility based on empirical species abundances as in the present study.

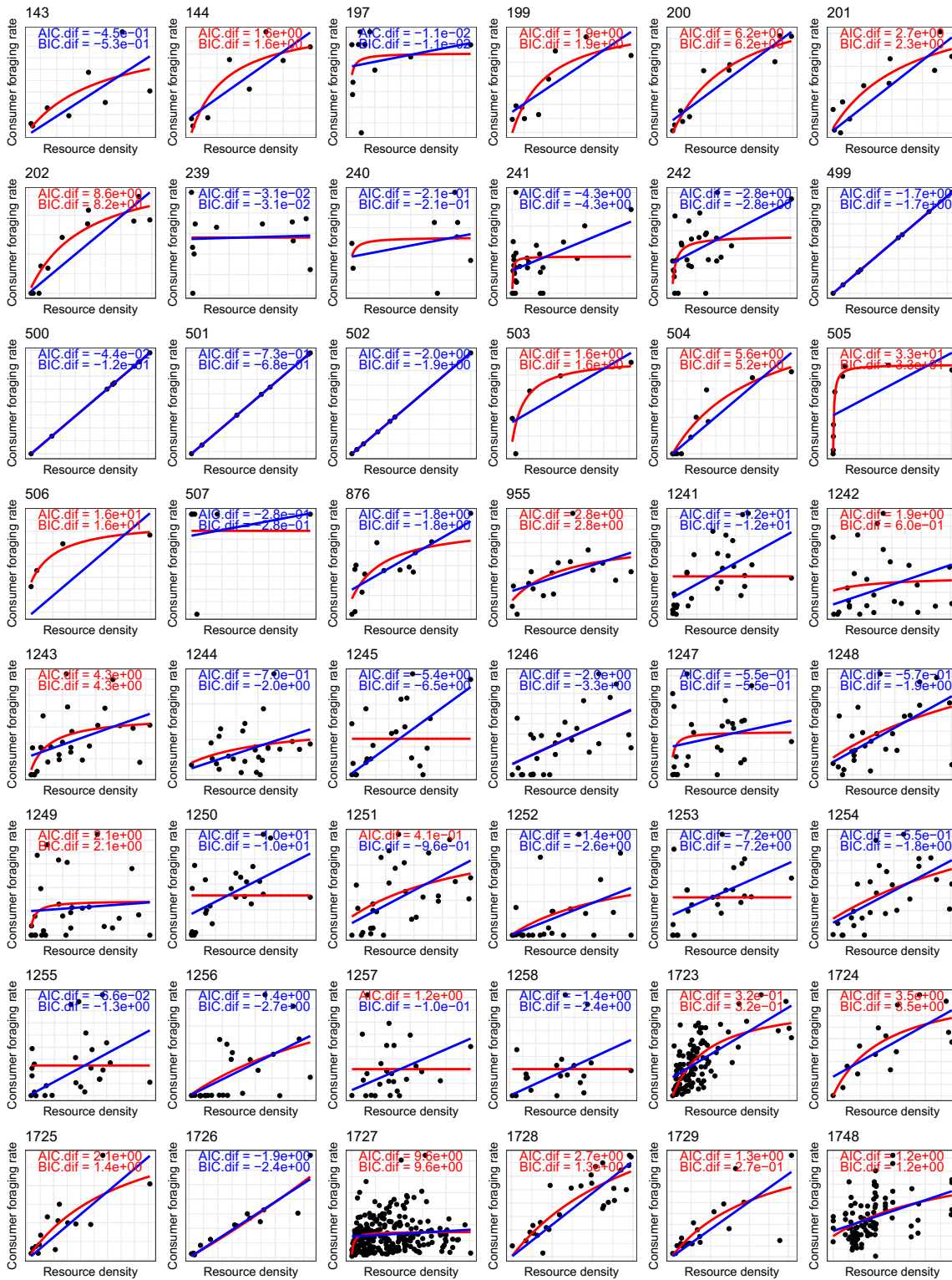


Figure A.23: **The potential functional responses of 48 empirical consumer-resource interactions.** Each data point represents a measured foraging rate at a given resource density. The blue/red are the regression lines/curves of the linear model/Type-II functional response model, respectively. The AIC.dif/BIC.dif show the difference in AIC/BIC readings between the two models (linear minus Type-II), where a negative value indicates the linear is the better model, while a positive value the opposite (blue/red colours are used to indicate the better model in accordance with the fitted curves). The number on the top of each subplot gives the case ID as in the FoRAGE dataset. For simplicity we dropped the ticks and values of both axes. For further details regarding the data, please check the FoRAGE dataset (Uiterwaal *et al.* 2018)

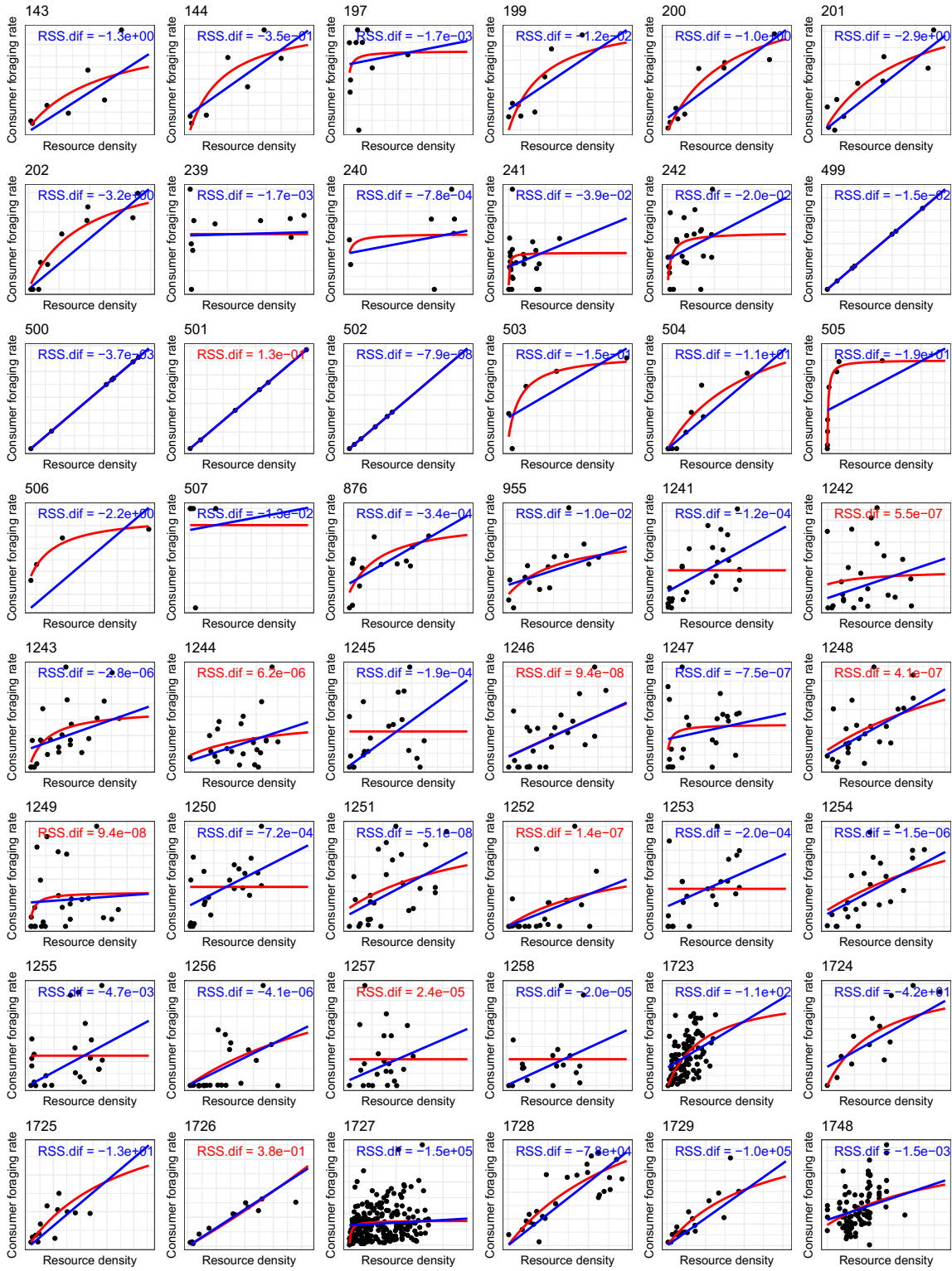


Figure A.24: The abilities of fitted models to explain variance in functional responses with 90 percent of sampled data towards the low end of the resource density axis. All annotations are the same as in Fig. A.23, except that only the remaining 90 percent of data are shown, and we here compared the residual sum of squares (RSS) instead of AIC/BIC. The RSS.dif shows the difference in RSS readings between the two models (linear minus Type-II), where a negative value indicates the linear model explain better the data variance, while a positive value the opposite (blue/red colours are used to indicate the better model in accordance with the fitted curves).

Appendix B

The effects of optimal-foraging diet choice on food-web structure and dynamics

B.1 The mathematical concept of optimal foraging diet choice

Here we explain the mathematical concept of the classical optimal foraging theory (OFT). For simplicity, we first consider the case where a focal consumer preys on a single resource species, with per-capita units. Given the total searching time (T_s , the total time spent searching for resource items within a certain period of time, say, a foraging bout) and encounter rate (λ) between the consumer and the resource, we can derive the total number of resource items that a consumer can encounter per bout (R_{tot}) as:

$$R_{\text{tot}} = \lambda T_s , \tag{B.1}$$

with

$$\lambda = a' R , \tag{B.2}$$

where a' is per-capita search rate and R the numerical density of the resource. In the original OFT work (Charnov & Orians 1973), it is assumed that once a resource item is encountered, it is captured instantly and successfully by the consumer, i.e., attack success probability (A in Chapter 3 & 4) equals one. However, we relax this assumption by explicitly including the A_{ij} term (with values generated by body-mass considerations) in our models and investigating its effect, rather than implicitly assuming it equals one. The total time spent foraging (T_{tot} , the length of a bout) is then

$$T_{\text{tot}} = T_s + T_s \lambda h' , \quad (\text{B.3})$$

where h' is the per-capita handling time: the time taken by the consumer for pursuing, subjugating and ingesting one resource item. T_{tot} is nothing but the sum of searching time and handling time dealing with all captured resource items within a bout. Then, the per-capita intake rate during a foraging bout is the total number of resource items eaten (eqn (B.1)) divided by the total foraging time (eqn (B.3)):

$$\frac{R_{\text{tot}}}{T_{\text{tot}}} = \frac{T_s \lambda}{T_s + T_s \lambda h'} . \quad (\text{B.4})$$

By cancelling T_s out from both the numerator and denominator, and replacing λ with eqn (B.2), we get

$$\frac{R_{\text{tot}}}{T_{\text{tot}}} = \frac{a' R}{1 + a' R h'} . \quad (\text{B.5})$$

This is the classical type-II functional response (Holling 1959) in per-capita units. Using this functional response equation, OFT stochastically models a series of decisions of the consumer, who either pursues or ignores each encountered resource item (of different types) such that its final diet composition maximises its net energy intake rate when averaged across many (sufficient from a sampling perspective) bouts. To illustrate this diet choice mechanism, let's introduce another resource species into the system. We now have two resources species, 1 and 2, identified by subscripts in the following equations. The profitability of the i^{th} resource species is how fast the consumer can gain energy from that item once it has been encountered. Let E_i

be its energy content. Then, its profitability (p_i) is:

$$p_i = \frac{E_i}{h'_i} . \quad (\text{B.6})$$

Note again that this is assuming attack success probability $A = 1$.

Now, let resource 1 be the more profitable resource among the two, such that:

$$p_1 > p_2, \text{ i.e., } = \frac{E_1}{h'_1} > \frac{E_2}{h'_2} . \quad (\text{B.7})$$

We can calculate the consumer's energy intake rate (henceforth, consumption rate, C') by multiplying eqn (B.5) by E , under three possible diet choice scenarios: eating only the more-profitable resource 1, eating only the less-profitable resource 2, or eating both:

$$\begin{aligned} C'_1 &= \frac{a'_1 R_1 E_1}{1 + a'_1 R_1 h'_1} \\ C'_2 &= \frac{a'_2 R_2 E_2}{1 + a'_2 R_2 h'_2} \\ C'_{12} &= \frac{a'_1 R_1 E_1 + a'_2 R_2 E_2}{1 + a'_1 R_1 h'_1 + a'_2 R_2 h'_2} . \end{aligned} \quad (\text{B.8})$$

Given that resource 1 is more profitable (eqn (B.7)), C'_2 is necessarily smaller than C'_{12} . Therefore, the consumer cannot achieve optimal (maximum) intake rate by eating only the less-profitable resource 2, and must always include the more-profitable resource 1 in its diet. The choice that the consumer needs to make then is whether or not to also include resource 2 into its diet. The criterion for resource 2 to be included is $C'_{12} > C'_1$, which can be re-written as:

$$a'_1 R_1 < \frac{E_2}{E_1 h'_2 - E_2 h'_1} , \quad (\text{B.9})$$

because a' , E , and h' are species-specific fixed values, the inclusion of resource 2 (the less-profitable resource) into the consumer's diet depends only on R_1 , i.e., the density (or say abundance) of resource 1. Note the fact that the abundance of resource 2 itself is not relevant to its inclusion or not—only when resource 1 is rare enough should the consumer start to prey on resource 2.

From the above, we can summarise three diet-choice rules from classical OFT: (i) The most profitable resource species is always included in the consumer’s diet regardless of its abundance. (ii) It is not because of the abundance of the less-profitable resource, but the rarity of the more-profitable resource, that the consumer includes the former into its diet. (iii) There is no way that the consumer “skips” species along the profitability ranking, that is, not eating the more-profitable resource but eating the less-profitable ones. All these rules also apply to our multi-species optimal-foraging diet choice model as described in Chapter 3.

B.2 Parameterisation of the search rate, attack success probability, and handling time

Here we describe how some foraging parameters of the optimal-foraging diet choice model, namely the search rate (a_{ij}), attack success probability (A_{ij}), and handling time (h_{ij}) are specified in Chapter 3. All quantities are in per-capita SI units.

Search rate

For the per-capita consumer’s search rate (a , units of area/time or volume/time), we follow literature (Pawar *et al.* 2012; Tang *et al.* 2014; Rizzuto *et al.* 2018) and adopt the mass-scaling rule that has been described in eqn (2.1) in Chapter 2. Notably, as we focus on the emergent properties of simulated OF webs in this chapter, and our preliminary test shows that using mass-scaling rules of different foraging strategies/dimensions does not qualitatively influence how the simulated OF webs respond to the key factors we manipulated, we therefore adopt only the mass-scaling rule of 2D active-capture throughout this chapter for saving simulation effort. That is, for species j searching for i ,

$$a_{ij} = -1.07 \times m_j^{0.21} m_i^{0.21} \sqrt{m_j^{0.42} + m_i^{0.42}} , \quad (\text{B.10})$$

where m is the species' body mass (in kg, the same hereinafter). We pick active-capture because it represents a more general form of searching, whereas the other two strategies can be seen as the special cases where the resource/consumer is immobile.

Attack success probability

We phenomenologically model the attack success probability of species j attacking i as:

$$A_{ij} = \left(\frac{1}{1 + \left(\log_{10} \left(R_p \frac{m_j}{m_i} \right) \right)^2} \right)^{0.2}, \quad (\text{B.11})$$

where R_p is the preferred resource-consumer body-size (body mass) ratio. This imposes a dome-shaped change in success probability (bounded between zero and one) with resource-consumer body-size ratio with its breadth controlled by the exponent 0.2. The success probability peaks at one when the size ratio of the focal interacting consumer-resource pair equals R_p . Because size ratios tend to be log-normally distributed, the $\log_{10}$ transformation guarantees that the decline is symmetric on either side of this ratio. This model (eqn (B.11)) captures the biologically-realistic feature of attack success that the consumer's attack is more likely to succeed when the resource's body size is appropriate, and less likely when the prey is too large or too small (*sensu* Caparroy *et al.* 2000; Vucic-Pestic *et al.* 2010; Pawar 2015).

Handling time

According to Pawar *et al.* (2012), the consumer's per-capita handling time for a resource item is positively associated with the body size of the resource while negatively associated with the consumer's. Therefore, we express handling time (h) of consumer species j handling resource species i as

$$h_{ij} = h_0 \frac{m_i^{1.25}}{m_j^{1.1}}, \quad (\text{B.12})$$

where h_0 is a constant that reflects the overall magnitude of handling time. Indeed, this captures the nature that for the same consumer, handling larger resource items takes more time than handling small ones, while for the same resource, a larger consumer could handle it much quicker. The 1.1 scaling exponent for the consumer's mass is chosen based on Pawar *et al.* (2012); the 1.25 scaling exponent (slightly larger than one) for the resource's mass is set based on the consideration that the required handling time should increase with resource's body mass superlinearly, such that handling a 10-kg resource item is more time-costly than handling ten 1-kg items, as the former needs extra time to be dismantled into smaller pieces.

B.3 Further details of simulations and additional results

B.3.1 Static simulation

We simulated four distinct synthetic species pools, each had specific body-mass distribution. From these pools, we drew 50 species each time as the synthetic community that was then wired (by establishing trophic links using the OFT model) into OF webs. These pools were called small, intermediate, large, and broad pool, respectively, describing the body-mass ranges (in kg) that they each covered. The broad pool was constituted by 100000 synthetic species and with their body masses randomly drew from a log-normal distribution that covered the range $\sim 10^{-7}$ – 10^3 ; this is the same pool that we used in the simulations of Chapter 2. The rest three pools were smaller (each had 10000 species) and covered a narrower range: the small ranged $\sim 10^{-5}$ – 10^2 ; the intermediate ranged $\sim 10^{-3}$ – 10 ; the large ranged $\sim 10^{-1}$ – 10^3 . Therefore, synthetic communities drawn from one of these pools (or the combination of pools), as the four mass distribution schemes depicted in main text Section 3.3.2, adopted the corresponding specific body-mass distribution.

In the main text, we showed only the diet matrices of generated food webs of the Broad mass distribution scheme. Here we provide the diet matrices of the other three mass distributions schemes, for ease of making comparison among. Note that here all matrices are also derived

from one replicate (i.e., the same community) as in Fig. 3.1 of the main text, but the patterns are representative. We can learn from the below Fig. B.1 and Fig. 3.1 and 3.2 of the main text that body mass *per se* did not influence the food-web properties generated by OFT, as the Small and Large schemes showed almost identical outcomes. In contrast, it was the species body-mass difference within the community—such as how much they differ from each other, and whether they aggregate into discrete body-size groups—that influenced more. The Discrete scheme, with artificial exaggerating of discrete body-mass grouping of species, indeed tend to be the most modular one among all. Notably, the ways that other factors (namely the abundance magnitude, the preferred body-size ratio, and the time cost for failed attacks) affect the generated food web were rather consist across the mass distribution schemes. This allowed us to expand details of the other factors by focusing on only one mass distribution scheme, as we did in the main text.

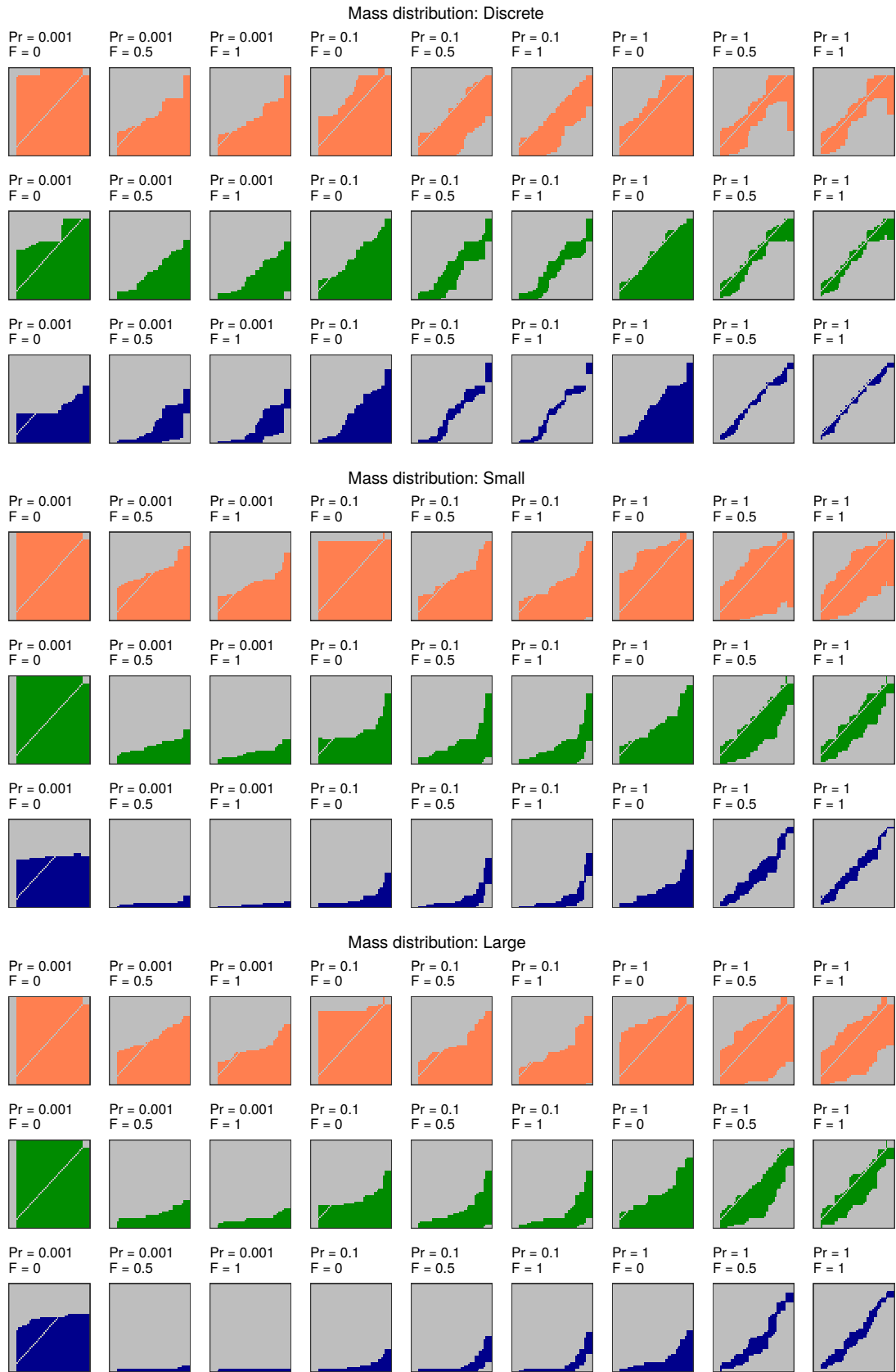


Figure B.1: Diet matrices of generated food webs in the static simulation (Discrete, Small, and Large mass distribution schemes). All notations are in line with Fig. 3.1.

B.3.2 Dynamical simulation

In the main text (Section 3.4), we provided the results of the dynamical simulation across the whole time span of integration. However, in the Type.II and OF.slow schemes, many species quickly went extinction in the early stage of numerical integration. Thus, there already exists obvious differences in food-web structure and species extinction between the first two ($t = 0$ and $2.5e7$) focal time points at which we visualised our results (Fig. 3.3–3.6). For not missing the dynamical responses at this early stage of food-web dynamics, we also checked these results at a finer time scale. We looked into the first one-fifth of the integration time span, and visualised them as Fig. B.2–B.5 below. In general, except more detailed trajectories of food-web structural fluctuation can be observed from Fig. B.3, other results remained qualitatively the same as viewing the whole integration time span.

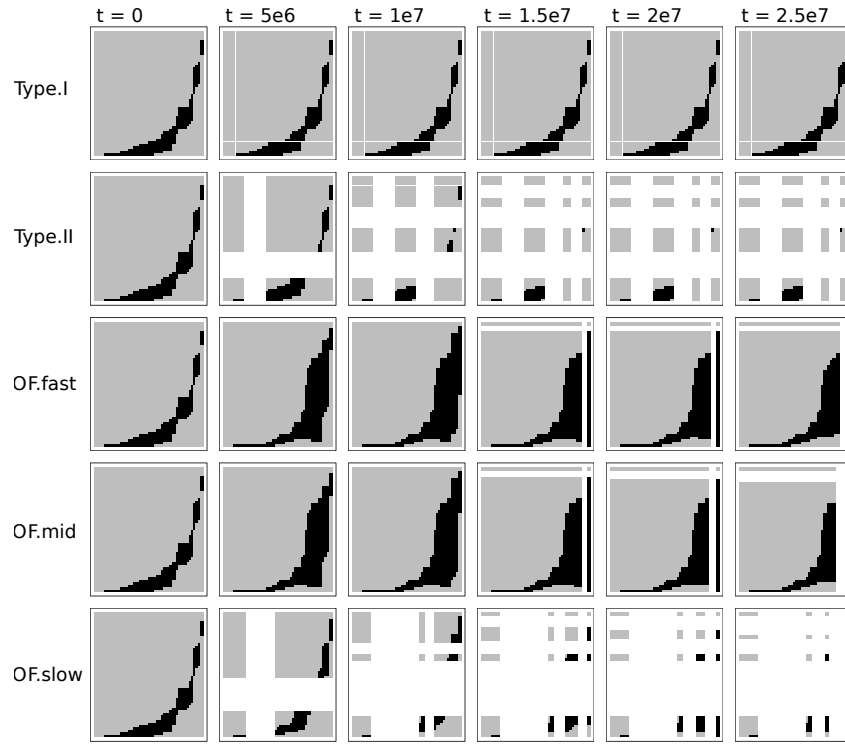


Figure B.2: **Diet matrices of a generated food web over time, zooming into the early dynamics.** Here all matrices are derived from the same replicate as presented in Section 3.4 of the main text. All annotations are in accordance with Fig. 3.3, while the time interval here captures the first one-fifth of the total integration time span.

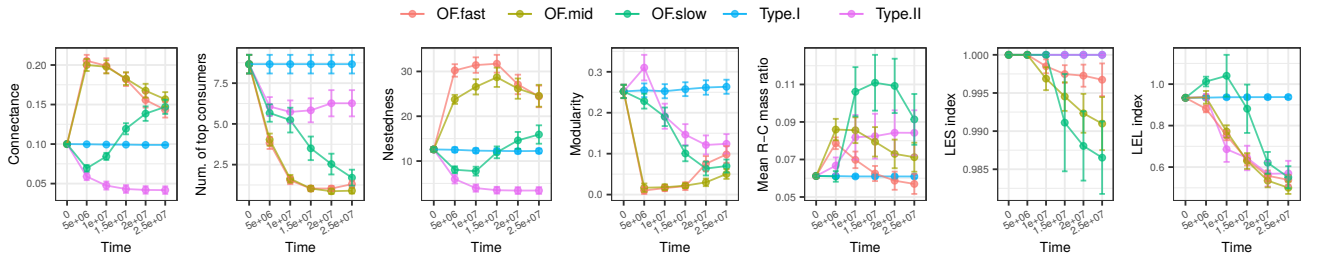


Figure B.3: **Structural measures of the generated food webs ($N = 30$) in the dynamical simulation, zooming into the early dynamics.** The error bars indicate the standard error. All annotations are in accordance with Fig. 3.4, while the time interval here captures the first one-fifth of the total integration time span.

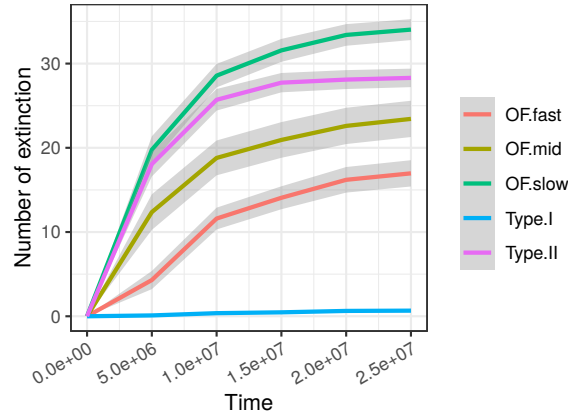


Figure B.4: The robustness (quantified as cumulative extinctions over time) of generated food webs ($N = 30$) in the dynamical stimulation, zooming into the early dynamics. All annotations are in accordance with Fig. 3.5, while the time interval here captures the first one-fifth of the total integration time span.

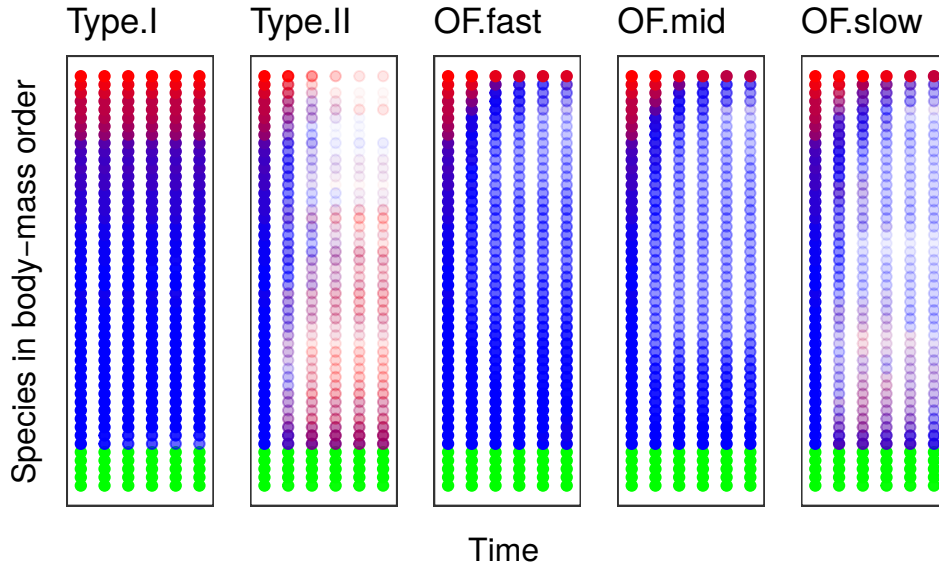


Figure B.5: Species body masses, trophic roles, and dynamical fate (extinct or not) within generated food webs ($N = 30$), zooming into the early dynamics. The six columns of each panel, from left to right, correspond to the time points that are tick-marked in Fig. B.4. All annotations are in accordance with Fig. 3.6, while the time interval here captures the first one-fifth of the total integration time span.

Appendix C

Predation risk influences food-web structure by constraining species diet choice

C.1 Further details of the foraging models

Here we explain how we use classical optimal foraging theory (OFT) on species diet choice in this paper to obtain the OF and PR models, and how we parameterise these models.

C.1.1 The OF model

The OF model of this chapter is conceptually identical to the model we used in Chapter 3 which was an multi-species extension of the classical optimal-foraging model (Section B.1). In this chapter, we decide to use biomass as the currency of energy, which potentially allows an easier merging with metabolic theory. All parameters are therefore converted to mass-specific (i.e., per-biomass consumer on per-biomass resource) units. Also, we simplify the model by removing the effect of time cost of failed attacks (see Chapter 3; we set $F = 1$ here to emphasise the effect of attack success probability) but instead additionally include

attack success probability and handling time of different mathematical forms. Details are provided below. The critical assumptions we make are that the energy content per unit biomass of resource, and conversion efficiency (i.e., from biomass to energy) of consumer, are both approximately constant irrespective of consumer or resource identity, and independent of body size (Section 4.3.1), which are in line with Chapter 3.

Following eqn (3.2) with F set to one, the profitability (p_{ij}) of an i^{th} resource species item (i.e., individual) to a j^{th} consumer can be written as:

$$p_{ij} = \frac{A_{ij}m_i}{h'_{ij}}, \quad (\text{C.1})$$

where m_i is the energy content of the resource item, A_{ij} the attack success probability, and h'_{ij} the per-capita handling time. We then divide both the numerator and denominator of eqn (C.1) by m_i to convert it to profitability per unit resource biomass, and further convert it to consumer mass-specific profitability by multiplying the denominator by its body mass, m_j , to get:

$$p_{ij} = \frac{A_{ij}}{h_{ij}}. \quad (\text{C.2})$$

Here, h_{ij} is thus now resource mass-specific handling time (cf. h'_{ij} in above equations). Note that the above conversion does not change the relative profitabilities of resource species with respect to a focal consumer (i.e., resource profitabilites rank using eqn (C.1) or (C.2) is identical). This value is also assumed to be independent from the effect of predation risk or any other factor.

In this chapter, we again use biomass consumption rate (eqn 4.1) as a proxy for energy intake rate, in accordance with Chapter 3. Eqn (4.1) is a multi-resource extension of the classical (single-resource) Type-II functional response, and is the expected energy intake over a large sample of iterated, stochastically-spaced foraging bouts (Charnov & Orians 1973). Here again we include an explicit attack success probability, A , in comparison to the classical optimal foraging model with implicit $A = 1$. We also note that $A = 1$ is included as scheme 10 in our synthetic food-web analysis (see main text and Section C.1.3 below), so this study covers the classic optimal foraging model structure as well. Just like the classical model (eqn (B.8)–(B.9)),

the OF model determines the optimal diet by searching through all possible diet breadths along the profitability ranking (i.e., rule (iii) at the end of Section B.1) and identifying the D_j that maximises eqn (4.1), which presents the optimal diet.

C.1.2 The PR Model

As explained in the main text (eqn (4.2) & C_{risk}), the PR model extends the OF model by imposing predation risk and metabolic constraint (minimum consumption rate) on consumers' diet choice decisions. Given a risk of predation (eqn (C.14)) and a minimum consumption rate (eqn (C.13)), consumers can either narrow or broaden their diet. Narrowing the diet entails taking fewer resource species than the optimal set, i.e., fewer more energy-rich items that require less handling time overall. Broadening the diet entails taking more resource species than the optimal set, i.e., more energy-poor items that require more handling time overall. Under the assumption that handling is less risky than searching or waiting for prey, diet broadening in the PR model in effect results in a re-allocation of time within a foraging bout from searching/waiting to handling. That is, accepting less-profitable resources makes encounters with acceptable resource items more frequent, but the set of accepted items needs a longer time to handle overall. To make this explicit, consider the two-species OFT scenario stated in Section B.1. From eqns (B.3) and (B.8), the total time spent foraging on resource 1 ($T_{\text{tot}, 1}$) versus on both resource 1 and 2 ($T_{\text{tot}, 12}$) are, respectively,

$$\begin{aligned} T_{\text{tot}, 1} &= T_s + T_s a'_1 R_1 h'_1 \\ T_{\text{tot}, 12} &= T_s + T_s (a'_1 R_1 h'_1 + a'_2 R_2 h'_2) . \end{aligned} \tag{C.3}$$

In eqn (C.3), given a fixed bout length (i.e., $T_{\text{tot}, 1} = T_{\text{tot}, 12}$), the T_s in $T_{\text{tot}, 12}$ must be smaller than the T_s in $T_{\text{tot}, 1}$ (i.e., less total searching/waiting time within a bout due to accepting resource 2), and meanwhile necessarily $T_s(a'_1 R_1 h'_1 + a'_2 R_2 h'_2)$ in $T_{\text{tot}, 12}$ is larger than $T_s a'_1 R_1 h'_1$ in $T_{\text{tot}, 1}$ (i.e., more total handling time within a bout due to accepting resource 2).

The diet narrowing strategy involves the same logic applied in the opposite direction under the assumption that handling is riskier than searching/waiting. By such time-reallocation, the

consumer reduces time spent performing riskier actions. Note that it is biologically possible that the consumer could change the bout length (T_{tot}) as a response to predation risk, which we have addressed in Section 4.5. Basically, it would not affect the diet breadth changing mechanism described here.

C.1.3 Foraging model parameterisation and structural schemes

Here we describe how the parameters of the OF and PR models—species biomass abundance (X_i), search rate (a_{ij}), attack success probability (A_{ij}), handling time (h_{ij}), minimum consumption rate $C_{\min}$ and the predation risk index in the PR model—were specified. All quantities were eventually converted into mass-specific SI units (for values, see Table C.1).

To quantify the model’s sensitivity to variation in food-web attributes (species richness, proportion of basal species, mean and variation of species body masses) and specification of the foraging parameters, we developed schemes where these aspects were manipulated. Scheme 1 serves as a baseline. We describe its specification here, whereas each of the other schemes change one attribute or parameter with respect to scheme 1. These other schemes are detailed in Table C.2.

Biomass abundance (density)

Maximum species abundances generally follow Damuth’s law (Damuth 1981; Peters 1983), with larger species having lower numeric densities. By multiplying eqn (3.3) by m_i we can convert it into the scaling equation for species biomass density (in mass/area or mass/volume),

$$X_i = X_0 m_i^{0.25} . \quad (\text{C.4})$$

We note that the X_0 (a constant 10^{-4} we used here in this chapter) and exponent (0.25) shown in eqn (C.4) fall within the range of empirically-calculated values (Table C.4). Indeed, in the case where we generated OF and PR counterparts of empirical food webs (Section 4.3.3) we

did have empirical species biomass densities in seven webs (Table C.4). However, because not all empirical webs had such data, for consistency we assigned biomass densities in all using Damuth's law. Eqn (C.4) was applied with re-sampling variations in constant and exponent values in Section 4.3.3, and without such variation in Section 4.3.4, as described in the main text. Preliminary analysis shows that using empirical biomass density values for X_i did not qualitatively change any of the results.

Search rate

For mass-specific consumer j 's search rate on resource species i (a_{ij} , units of area/time or volume/time), we again follow eqn (2.1) based on previous studies (Pawar *et al.* 2012; Tang *et al.* 2014; Rizzuto *et al.* 2018) but divided the value by the consumer's body mass (m_j) to convert it to mass-specific units. That is,

$$a_{ij} = \begin{cases} -1.07 \times m_j^{-0.58} m_i^{0.21} & \text{in 2D grazing} \\ -2.72 \times m_j^{-0.37} m_i^{0.42} & \text{in 3D grazing} \end{cases}. \quad (\text{C.5})$$

Notably, we focus on using the equations of "grazing" strategy (in both 2D and 3D foraging dimensions) throughout this chapter because it has been shown that the effect of foraging strategy is relatively small compared with the effect of foraging dimensionality (Pawar *et al.* 2012), and also because the majority of trophic interactions in the twelve empirical food-web data that we used in this chapter were grazing.

Attack success probability

We phenomenologically model the attack success probability of species j attacking i as:

$$A_{ij} = \frac{1}{1 + 0.25e^{-m_j^{0.33}}} \left(\frac{1}{1 + \left(\log_{10} \left(R_p \frac{m_j}{m_i} \right) \right)^2} \right)^{0.2}, \quad (\text{C.6})$$

where R_p is the preferred resource-consumer body-size (body mass) ratio, and e is Euler's number. In comparison to the attack success probability used in Chapter 3 (see eqn (B.11)), eqn (C.6) includes an additional component (first component in the right-hand side) that is bounded between 0.8 and 1 (with the lower bound set by the constant 0.25) and describes an monotonic increase of success probability with m_j , with the curvature regulated by the constant 0.33. That is, besides capturing the biologically-realistic feature where the consumer's attack is more likely to succeed when the prey's body-size is appropriate (at the preferred body-size ratio), eqn (C.6) also describes a condition where large consumers tend to have higher success probability than small consumers (*sensu* Caparroy *et al.* 2000). We note that, however, modelling A as in eqn (B.11) and in other forms are included as schemes 8–10 in our synthetic food-web analysis (see Section C.1.3 below), and it turned out that the mathematical form of A did not qualitatively affect the results of this chapter (Section C.7).

Handling time

According to Pawar *et al.* (2012), the consumer's per-capita handling time for resource biomass (i.e., the conventional per-capita handling time h' divided by resource body mass) is

$$h''_{ij} \propto m_j^{-\beta} , \quad (\text{C.7})$$

where β the scaling exponent of basal metabolic rate (Savage *et al.* 2004, 2007; Pawar *et al.* 2012). To make it mass-specific (i.e., per-biomass consumer on per-biomass resource), we multiply eqn (C.7) by m_j to get

$$h_{ij} \propto m_j^{1-\beta} . \quad (\text{C.8})$$

where h_{ij} is mass-specific handling time. Furthermore, handling time should also be subject to biomechanical constraints imposed by resource-consumer body-size ratio. Therefore, we express handling time as

$$h_{ij} = h_0 m_j^{1-\beta} H \left(\frac{m_i}{m_j} \right) . \quad (\text{C.9})$$

where h_0 is a constant. H is a U-shaped function which captures the fact that consumer should more easily handle a captured resource within an appropriate (preferred) size range with a peak at a particular, optimal resource-consumer body-size ratio. Just like A (eqn (C.6)), handling time should be the lowest at a preferred body-size ratio and increase with deviation from that ratio. We use the inverse of a Gaussian probability density function, standardising the lowest point to 1, to capture this behaviour. For the preferred ratio, the same R_p as in attack success rate is used.

Another handling time parameterisation that also takes into account the body-size ratio influence, but with different logic and assumptions, can be found in the study by Petchey *et al.* (2008) on ADBM. Their “ratio handling time function” is

$$h'_{ij} = \begin{cases} \frac{h_0}{L - \frac{m_i}{m_j}} & \text{if } \frac{m_i}{m_j} < L \\ \infty & \text{otherwise.} \end{cases} \quad (\text{C.10})$$

Here h'_{ij} is consumer per-capita handling time on resource individual. h_0 again is a constant. L is the largest consumable resource-consumer body-size ratio, beyond which the resource is considered too large to be consumed (i.e., with infinite handling time). A lower limit of handling time is set because no matter how small the resource item is ($\frac{m_i}{m_j} \rightarrow 0$), the consumer still needs a certain amount of time to handle it ($\frac{h_0}{L}$). Multiplying eqn (C.10) by $\frac{m_i}{m_j}$ to convert it into mass-specific sense (i.e., per-biomass consumer on per-biomass resource), we get

$$h_{ij} = \begin{cases} \frac{h_0 m_j^2}{L m_j m_i - m_i^2} & \text{if } \frac{m_i}{m_j} < L \\ \infty & \text{otherwise.} \end{cases} \quad (\text{C.11})$$

Both types of handling time parameterisations, i.e., eqn (C.9) and (C.11), are included in the simulation schemes of this study (Table C.4). That is, in comparison to the handling time used in Chapter 3 (eqn (B.12)), we explore here in this chapter the conditions where, for a consumer, handling time does not monotonically increase with the resource’s body size.

Consumption rate threshold and predation-risk index in the PR model

To maintain itself and survive, the energy intake of an individual should at least balance the continuous energy loss due to maintenance metabolism. This corresponds to the basal (survival/maintenance) metabolic rate (BMR, in energy/time) of an individual (Belovsky 1981; Peters 1983; Brown *et al.* 2004; Rizzuto *et al.* 2018)

$$\text{BMR} = B_0 m^\beta, \quad (\text{C.12})$$

where B_0 is a coefficient that depends on taxon and temperature. In this study, as we used biomass density as the currency of energy, a basic biomass consumption rate threshold ($C'_{\min}$) for individual consumer's survival could be drawn in proportion to BMR ($C'_{\min} \propto \text{BMR}$). Dividing eqn (C.12) by m to make it mass-specific, $C_{\min}$ (in 1/time) for species i can then be expressed as

$$C_{i, \min} = C_0 m_i^{\beta-1}, \quad (\text{C.13})$$

where C_0 is a normalization constant. Biologically, this term (eqn (C.13)) is the mass-specific biomass loss rate due to maintenance metabolism.

The amount of predation risk that a focal species experiences is quantified as a predation-risk index (P_{risk}), which is positively determined by the ratio of the total biomass of its realised consumers ($\sum X_{\text{real}}$) and the total biomass of all consumer species ($\sum X_{\text{all}}$)

$$P_{\text{risk}} = \left(\frac{\sum X_{\text{real}}}{\sum X_{\text{all}}} \right)^{e_P}, \quad (\text{C.14})$$

where P_{risk} is bounded between 0 and 1 and is directly used for drawing a reference consumption rate for the diet broadening/narrowing effect described in the main text; e_P is an exponent that determines how P_{risk} increases along with the increasing $\sum X_{\text{real}}$, as shown in Fig. C.1. Compared to the $e_P = 1$ case, P_{risk} will be smaller for the same $\sum X_{\text{real}}$ if $e_P > 1$, where the diet broadening/narrowing effect of the focal consumer species is thereby less sensitive to the change in the number (and thus $\sum X_{\text{real}}$) of its consumers (Fig. C.1). This index is based on

the rationale that, from a resource's point of view, the predation risk it suffers should increase with the number of consumer species in the environment that are preying on it, as well as the abundances of those consumers. We also note that by our assumption of allowing intraguild predation and cannibalism, all species share the same $\sum X_{\text{all}}$ value and therefore this predation-risk index presents a standardised evaluation of risk which could be compared among species. Species with fewer realised consumer species are likely to have lower P_{risk} than those with many.

In Section 4.3.3, we simulated model-generated counterparts of empirical food webs with given parameter values and $e_P = 1$. Regarding controlling the connectance (see the main text and Section C.3), sometimes, for a replicate, even the largest h_0 , based on which all species barely fulfil the C_{min} requirement (i.e., even larger h_0 leads to unfeasible species), is already used, the generated PR web is still over-connected. This can be seen as species being too sensitive to predation risk such that their diet broadens too fast. We therefore increased e_P by 0.25 to slightly weaken the diet-broadening effect (Fig. C.1) in such cases. This process was repeated until a PR web with acceptable connectance was successfully generated. The simulated connectance values, along with the e_P used to achieve them, is summarised in Table C.4. In Section 4.3.4, we did not limit the connectance of generated food webs, but just made sure that the three webs (i.e., the OF, PR, and null ones) share the same connectance. The values of e_P were therefore kept as scheme-dependent values (Table C.4).

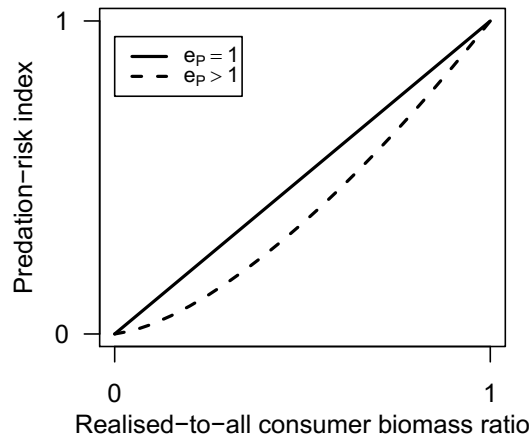


Figure C.1: The effect of e_P on how predation-risk index (P_{risk}) is evaluated from the total realised-to-all consumer biomass ratio ($\sum X_{\text{real}} / \sum X_{\text{all}}$).

Table C.1: Summary of parameters used in this chapter. Note that most of our foraging model parameters are derived from the underlying parameters listed in this table. These are further described in the text of this section.

Parameter	Definition	Value used	Unit	Reference
X_0	Biomass s.c.	10^{-4}	$\text{kg}^{0.75} \cdot \text{m}^{-2}$ for 2D; $\text{kg}^{0.75} \cdot \text{m}^{-3}$ for 3D	Pawar <i>et al.</i> 2012
R_p	Globally preferred body size ratio by consumers	0.1 for synthetic food webs; Median of empirical ratios for empirical food-web counterparts.		
β	Resting metabolic rate s.e.	0.75		Savage <i>et al.</i> 2007; Ritchie 2009; Pawar <i>et al.</i> 2012
h_0	Mass-specific handling time s.c.	Varied	$\text{s} \cdot \text{kg}^{-0.25}$	
L	The largest consumable body size ratio	1	$\text{kg}^{1-\beta} \cdot \text{s}^{-1}$	
C_0	Consumption rate threshold s.c.	4.15×10^{-8}	$\text{kg}^{0.25} \cdot \text{s}^{-1}$	Pawar <i>et al.</i> 2012
e_p	Predation-risk index exponent	Scheme dependent		

In the above table, s.c.: Scaling constant; s.e.: Scaling exponent.

Table C.2: Schemes of generating synthetic food webs that we studied in this chapter. Each scheme stands for a specific combination of mathematical structure of food-web parameters (S , B , M_{mean} , M_{sd} , e_B) and foraging parameters (a , A , h , e_P). Scheme 1 presents a baseline settings for these parameters, whereas each of the following schemes vary one parameter from scheme 1 while keeping others the same.

Scheme	S	B	M_{mean}	M_{sd}	e_B	a	A	h	e_P
1	50	0.1	10^{-5}	10	0.25	2D of eqn (C.5)	Eqn (C.6)	Eqn (C.9)	1
2	150								
3		0.4							
4			10^{-10}						
5				10^3					
6					0				
7						3D of eqn (C.5)			
8							Only 2 nd component of eqn (C.6)		
9							Only 2 nd component of eqn (C.6)*		
10							1		
11								Eqn (C.9)**	
12								Eqn (C.11)	
13									0.5
14									2

In the above table, S : Species richness; B : Proportion of basal species; M_{mean} and M_{sd} : Mean and standard deviation of the log-normal distribution from which species body masses were drawn; e_B : Biomass scaling exponent; a : Search rate; A : Attack success probability; h : Handling time; e_P : Predation-risk index exponent (eqn (C.14)).

*: The dome-shaped component of eqn (C.6), but with the exponent changed from 0.2 to 1 so that the dome becomes steeper.

**: The standard deviation of the inverse Gaussian probability density function, H of eqn (C.9), changed from 1 to 1.1 so that the U-shape becomes less steep.

C.2 Pseudocode for the OF and PR assembly processes

Here we present the pseudocode for our assembly algorithm. Note that this entire process is repeated for multiple values of handling time h in order to achieve a preset connectance. Stopping after line 3 results in an OF web, while continuing results in a PR web. An explanation for the various values of C on line 7 is in Fig. 4.1 of the main text. This pseudocode is contributed by Jonathan Zheng.

input : Set of species $S = \{1 \dots n\}$, their biomasses $m_{\{i \in S\}}$, set of basal species $B \subset S$

output: PR food web diets $D_{\{i \notin B\}}$

```

1 foreach consumer species  $i \notin B$  :
2   Order other species by profitability defined by eqn (C.2)
3   Initialise diet  $D_i$  by adding species in descending order until eqn (4.1) is maximised
4 until all  $D_i$  do not change :
5   foreach consumer species  $i \notin B$  :
6     Calculate  $P_{i,\text{risk}}$  using eqn (4.2)
7     Risk-compromised consumption  $C_{\text{risk}} = C_{\text{surv}} + (1 - P_{\text{risk}})(C_{\text{opt}} - C_{\text{surv}})$ 
8     Re-assign diet  $D_i$  by broadening to the closest  $C(D_i) \geq C_{\text{risk}}$ 

```

C.3 Controlling the connectance of OF and PR webs via handling time magnitude

In this section, we explain how the connectance of an OFT-generated web is determined by species abundances and handling time, as these are the key factors that influence species' diet breadths under the OFT diet-choice rule. We then show how, for both the OF and PR model in this chapter, we controlled the model-generated webs by manipulating the magnitude of handling time.

The OFT diet decision is essentially resource-abundance-dependent, where only when the abundance of more-profitable resources are collectively rare enough will the consumer broaden its diet to include the less-profitable ones (see Section B.1). Given species' abundances follow the Damuth's law (eqn (3.3) & (C.4)), the scaling constant X_0 determines the magnitude of abundance of all species. With a larger X_0 , every species in the food web is more abundant, and thus for each consumer its optimal diet breadth becomes narrower toward focusing on only the more-profitable resources. The other way round is also true. Therefore, all species' diet breadths and the resultant food-web connectance can be determined by the given X_0 .

Likewise, as the magnitude of handling time is increased by giving a larger h_0 value (see Section B.2 & C.1.3), the consumer's consumption rate for every possible diet breadth decreases due to the larger denominator of eqn (3.1) & (4.1). At the same time, the maximum consumption rate shifts to be at a narrower diet set, which means that the optimal diet breadth becomes narrower. This is purely a mathematical outcome of the multi-resource Type-II functional response. Under the OFT diet-choice rule where consumer take the optimal diet set, assigning a large-enough h_0 guarantees that the focal consumer will definitely consume only the most profitable resource (Fig. C.2 rightmost), whereas a small-enough h_0 make the consumer eat everything (Fig. C.2 leftmost).

Extrapolating the above to all consumer species in the community, the food-web connectance will be higher if all consumers have broader diet, and lower in the opposite condition. The connectance of OFT-generated food web can thus be controlled by the chosen value of X_0 and h_0 . Here in this chapter, we decide to fix X_0 and manipulate h_0 (see Section 4.3.2) for generating the desired connectance with the OF and PR model (as PR starts with an OF-derived initial web). Given the same set of species and parameters, the two models reach the same connectance with different h_0 values, where the PR needs a larger one due to the diet-broadening strategy. We thus control the connectance of output food webs via assigning proper h_0 values as described in the main text, so that the structural comparison could be conducted with webs that share the same connectance.

Note that we set the connectance of the PR web first then match the connectance of

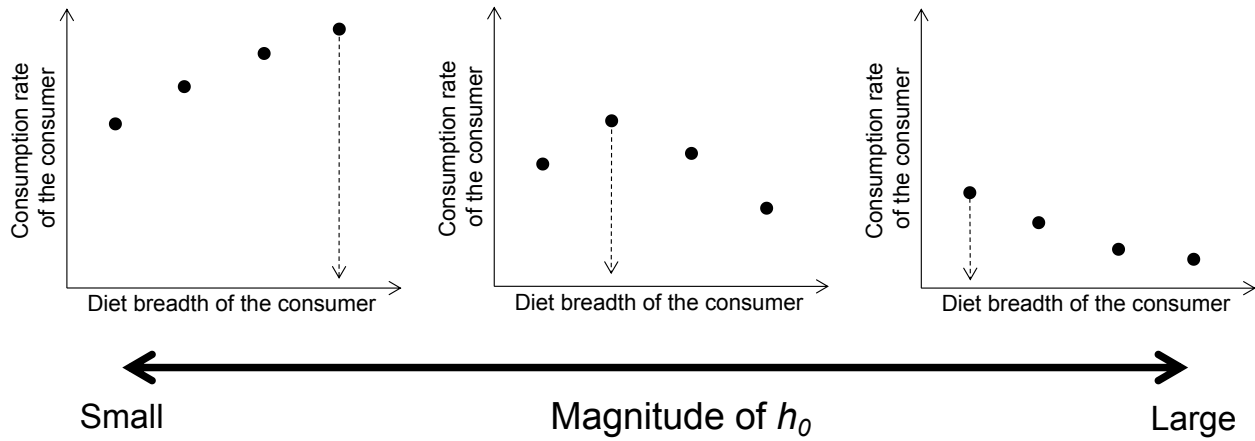


Figure C.2: Illustration of how consumption rate of the consumer is influenced by the magnitude of h_0 . With larger h_0 , the handling time of every resource-consumer pairs increase evenly. For a focal consumer, this results in a decrease in consumption rate across all possible diet breadth (i.e., all points move downward), meanwhile the optimal diet becomes narrower (i.e., the peak shift leftward).

OF/null web with it. The reason is that, in the PR assembly, species' diet breadths and predation-risk index values iteratively change each other until they reach a steady state. Thus, the connectance of PR food webs responds less smoothly but step-wise to variation in h_0 . It is therefore more difficult to generate a PR web with exactly the desired connectance. The OF assembly, on the other hand, can easily achieve a desired connectance by assigning a proper h_0 value. The null webs are randomly connected and we can directly assign their connectance. Therefore, matching the connectance of the latter two to the PR value is a practical way to have them share the same connectance.

C.4 Measurement of structural features

We summarise the food-web metrics used in this study in Table C.3.

We note that in this study we focus on nestedness and modularity because these are arguably the most well-reported empirical food-web properties, as stated in main text, and also because such structural features quantify the pattern of how trophic links are distributed among species, which directly reflects species' diet choice.

Table C.3: Food-web structural metrics used in this chapter.

Metric	Quantifying measurement	Reference
Nestedness	NODF: use <code>nestednodf</code> function of the R package <code>vegan</code> (ver. 2.5-2).	Johnson <i>et al.</i> 2013; Oksanen <i>et al.</i> 2018 (vegan); Ulrich & Gotelli 2007
Modularity (Compartmentalisation)	Modularity index: use <code>cluster_walktrap</code> function with <code>modularity</code> function of the R package <code>igraph</code> (ver. 1.2.1).	Csardi & Nepusz 2006 (igraph); Krause <i>et al.</i> 2003
Clustering (Transitivity)	Clustering coefficient: use <code>transitivity</code> function of the R package <code>igraph</code> (ver. 1.2.1).	Csardi & Nepusz 2006 (igraph); Opsahl & Panzarasa 2009
Coherence	Incoherence index: the SD of the distribution of trophic distance of all linkages. The trophic distance is the difference in trophic level between the consumer and the resource of a linkage. Note that this index has a lower bound of 0 and is inversely reflecting the level of coherence.	Johnson <i>et al.</i> 2014
Trophic similarity	The web-averaged species-pair similarity, which is the number of shared consumers and resources of the focal pair divided by their total number of consumers and resources in combination.	Williams & Martinez 2000
Trophic level	Prey-averaged levels: the level of a species is the average level of all its resources plus 1. The level of basal species are assigned as 1.	Williams & Martinez 2004
In-degree (generality)	Directly count the number of resource of a consumer.	
Connectance	Number of linkages divided by the square of species richness.	Dunne <i>et al.</i> 2002a,b

C.5 Empirical food-web data

We compiled data on 12 empirical food webs from published works (Table C.4). These webs were all resolved to the species level. For CSM, BSQ, and EPB, the original data partly includes life-stage level resolution on trophic interactions among species. We collapsed these 3 webs to species level to stay in accordance with the other webs, by summing up the biomass and diet of any species across all its life stages. We included only carnivorous and herbivorous links. The number of species in these webs ranges from 28 to 251, and web connectance ranges from 0.018 to 0.294. Note that we present the biomass scaling relationship of the seven webs for which we have information on empirical biomass densities, but in our work we reassign the biomass densities of all using Damuth's law as described in Section C.1.3.

Table C.4: Summary of the empirical food web datasets used in this chapter.

Name (abbr.)	No. nodes	No. consumers	No. linkages	Environment	Empirical C	Simulated C	Median RC	e_P	Empirical c_B	Empirical e_B	Reference
Bahia San Quintin (BSQ)	170	115	1290	Mixed	0.055	$0.056 \pm 4.4E-4$	5E-4	1.115 ± 0.086	1E-4.754	0.134	Hechinger <i>et al.</i> 2011
Broadstone Stream (BSS)	28	9	138	Freshwater	0.176	0.170 ± 0.002	0.081	1.075 ± 0.068	1E-3.525	0.236	Woodward <i>et al.</i> 2005
Caribbean (Car)	248	241	3241	Marine	0.053	$0.053 \pm 5.3E-5$	0.012	1	1E-3.526	0.011	Bascompte <i>et al.</i> 2005
Carpinteria Salt Marsh (CSM)	154	111	1303	Mixed	0.068	$0.068 \pm 1.4E-5$	1.4E-3	1	1E-4.482	0.214	Hechinger <i>et al.</i> 2011
Estero de Punta Banda (EPB)	203	145	2368	Mixed	0.075	$0.075 \pm 7.5E-5$	4.9E-4	1	1E-4.753	0.090	Hechinger <i>et al.</i> 2011
Grand Caracae (GC)	87	49	608	Marsh	0.08	$0.081 \pm 5.4E-4$	0.263	1.065 ± 0.031	--	--	Brose <i>et al.</i> 2005
Gearagh Woodland (GW)	105	91	357	Terrestrial	0.032	$0.033 \pm 3.1E-4$	0.31	2.105 ± 0.126	1E-2.200	0.812	McLaughlin <i>et al.</i> 2010
Kongsfjorden (Kon)	251	91	1144	Marine benthic	0.018	$0.018 \pm 1.2E-4$	0.014	1.205 ± 0.068	--	--	Renaud <i>et al.</i> 2011
Skipwith Common (SC)	33	18	320	Freshwater	0.294	$0.289 \pm 4.7E-3$	0.166	1.456 ± 0.238	--	--	Brose <i>et al.</i> 2005
St. Marks (SIM)	96	69	783	Estuarine	0.085	$0.088 \pm 8.1E-4$	0.006	1.285 ± 0.073	--	--	Christian & Luczkovich 1999
Tuesday Lake 1984 (TL84)	50	25	269	Freshwater	0.108	0.108 ± 0.001	6E-4	1.035 ± 0.061	1E-3.748	0.103	Jonsson <i>et al.</i> 2004
Ythan Estuary 1996 (YE96)	79	59	264	Estuarine	0.042	$0.044 \pm 5.2E-4$	2.1E-4	1.355 ± 0.171	--	--	Huxham <i>et al.</i> 1996; Leaper & Huxham 2002

In the above table, C: connectance; RC: resource-consumer body-size ratio; e_P : predation-risk index exponent; c_B : biomass scaling constant; c_B : biomass scaling constant; e_B : biomass scaling exponent. For simulated C and e_P , mean $\pm$ 95% CI of the 50 simulations are shown.

C.6 Further details on data analyses

The measurements in this study (including those of additional results, see the next section), except TL-Mass (trophic level to $\log_{10}$ consumer body mass relationship) and ID-Mass (in-degree to $\log_{10}$ consumer body mass relationship), were analysed using linear mixed model (LMM) and paired-Wilcoxon tests to check for the difference among models. For the empirical part we focused on the absolute deviations from the empirical value and took these as the observations to evaluate model predictive performance. For the overall comparison of model performances (i.e., results in Fig. 4.2 of the main text), we used LMM with the type of model (i.e., OF and PR) as the fixed effect, and community (i.e., the 12 empirical ones) and iteration (50 for each community) as nested random intercept effects. For the community-based comparison, deviations are paired by iterations and analysed using a Wilcoxon test.

For the synthetic part, on the other hand, we directly compare the measurements to show the structural difference among models. Just as the corresponding observations (i.e., among models but from the same iteration) in the empirical part were derived from the same set of re-drawn parameters, in the synthetic part they were derived from the same synthetic community, and thus were not independent to each other. We thus set the type of model (i.e., OF, PR, and null) as the fixed effect, but the identity of iteration as a random intercept effect in the synthetic part, and reported the significance of difference between the OF and PR models. Notably, the measurement here may be transformed to meet the normality assumption of LMM. We first checked residual (i.e., of LMM model) normality of original readings using a Shapiro-Wilk test, and if it was violated, we further applied 4 transformations and picked the one that gave the largest p-value of normality tests for analysis. Possible data types are: Original, Square-root transformed, Log transformed ($\log_{10}(\text{value})$ or $\log_{10}(\text{value} + 1)$ if there is zero in the values), Reverse transformed ($-1/\text{value}$ or $-1/(\text{value} + 1)$ if there is zero in the values), and Arcsine-square-root transformed (if the original values are not bounded between 0 and 1, they are standardised by dividing by the maximum reading (or 100 in NODF case), then taking the $\sin^{-1}\sqrt{\text{value}}$). The final adopted data type of the LMM analysis is indicated in Fig. C.7–C.9.

For TL-Mass, LMM were applied to visualise the relationship, where we took species body

mass in $\log_{10}$ scale and the type of model as fixed effects with interaction, with the identity of iteration as a random effect. The random effect was set to be either on the intercept, the slope, or both, depending on which structure yielded the smallest AIC. For ID-Mass, as the relationship was not linear, we used a generalized additive mixed model (GAMM) to visualise the relationship. The type of model was set as a linear fixed predictor, while species body mass in $\log_{10}$ scale of each model type was set as a smooth predictor, and the identity of iteration as a random smooth.

The LMM was done by using `lmer` function of R package `lme4` (ver. 1.1-17, Bates *et al.* 2014). The GAMM was done by using `gam` function of R package `mgcv` (ver. 1.8-24, Wood 2017). Paired-Wilcoxon and Shapiro-Wilk tests were conducted using R-inbuilt functions.

C.7 Additional results

Here we firstly present the same result of Fig. 4.2 of the main text, except with standardised absolute deviation (Fig. C.3). The results are qualitatively the same. We note that we were not comparing the deviation between nestedness and modularity, but between the two foraging models. As long as the deviations are paired-calculated with empirical values, we can judge if it is statistically different from 0 and if any of the OF/PR have smaller deviations (as an indication of better predictive performance), so standardisation is not necessary. However, using standardised values provides hints of how large the deviations are, relative to the empirical value.

We assumed a globally-constant conversion efficiency ϵ for all consumer species in all our simulations. However, this assumption might, arguably, not be true, as previous work has shown that conversion efficiency is lower for plant-eating herbivores than for prey-eating predators (Yodzis & Innes 1992). To check the effect of such differences in ϵ on our findings, we repeated the major analyses with all consumers' ϵ being set to 0.4 toward any basal species as the resource, and 0.8 toward any non-basal species as the resource (Yodzis & Innes 1992; Lang *et al.* 2017). Profitability of resources was evaluated accordingly with these efficiencies.

The results corresponding to those of Fig. 4.2 and Fig. 4.5 of the main text are shown here as Fig. C.4 and Fig. C.5. From the results, we can tell that this difference in ϵ according to resource type leads to noninterval food webs, such that the diet of some consumers becomes discontinuous in resource body-mass space (Fig. C.5). This is due to the fact that the ϵ toward basal species is smaller, making them less-profitable to the consumer, thus under the optimal foraging diet prediction they tend to be replaced by non-basal resources with smaller body size. Nonetheless, our main findings regarding the better performance of the PR model on capturing empirical nestedness and modularity, and the broader diet of intermediate-sized consumers of the PR model, are not qualitatively affected by this ϵ setting change.

Besides the focal structural measures of nestedness and modularity, we also measured several other food-web structural metrics and performed the same comparisons as described in Sections 4.3.3 and 4.3.4 of the main text. We note that the metrics we measured cover much of the same structural information as in the previous works, such as the ADBM studies (Beckerman *et al.* 2006; Petchey *et al.* 2008). The results of these are as shown in Fig. C.6–C.9, and the relevant terminology definitions and quantifying method can be found in Table 1.1–1.2 and C.3, respectively.

The PR model predicts clustering closer to the empirical value, while for coherence and trophic similarity there is no obvious superiority of predicting performance (Fig. C.6). The synthetic part shows that the PR food webs are consistently more clustered, more coherent, and have higher similarity among nodes than OF food webs (Fig. C.7).

For the resource-consumer body-size ratio-related features, we compared the median and standard deviation of resource-consumer body-size ratio distribution among the models. These features provide insights into how different-sized species and linkages are distributed within the food web. For the comparison with empirical food webs, there is no obvious pattern for the median of the ratio. For the standard deviation of the ratio distribution, empirical food webs tend to adopt higher value than the models' prediction. The PR model outperforms OF in 9 out of 12 empirical communities (Fig. C.6). For the comparison among synthetic food webs, because of the body-size constraints embedded in A and h , both foraging models

produced more constrained ratio distributions than the null webs, that is, with much smaller standard deviation. The comparison between the two foraging models showed that the PR model tended to produce food webs with higher median resource-consumer body-size ratio and higher standard deviation of that ratio, i.e., a wider and flatter ratio distribution, than the OF model (Fig. C.7).

With regard to node-level features, we checked the relationships of consumer species' trophic level and in-degree against their $\log_{10}$ body mass (TL-Mass and ID-Mass, respectively) to inspect how these two node-level features varied with body mass. In-degree is the number of resources of a node, which directly reflects the diet breadth of species, so was considered as an important node feature in the diet-predicting context of this study. In general, empirical food webs tend to adopt a positive TL-Mass relationship and a dome-like ID-Mass relationship—not perfectly humped, but qualitatively higher in the middle than in the ends (Fig. C.6), and the model-predicted webs reflect such a characteristic (Fig. C.6 & C.7).

As stated in the main text, biologically, a species can either broaden or narrow its diet breadth as a response to predation risk, and we mainly focused on the former. We also conducted the same simulation using the PR model which is set to have the diet-narrowing effect. In a food web, however, if the consumers' diet become narrower, the resources species' predation risk will decrease, which will lead to further diet narrowing of these resource species and lower the predation risk downstream. This is exactly the opposite of the positive feedback between diet breadth and predation risk that happens in diet-broadening case (as described in the main text), so the effect of predation risk tends to mitigate itself here. As a result, the predicted food webs of diet-narrowing PR model converges to OF, and the structural outcomes of the two models are almost identical (Fig. C.8). If allowing the PR model to select the diet that gives the closest consumption rate to the risk threshold C_{risk} (i.e., could either be broadening or narrowing), because the diet-narrowing effect again diminishes, the results of this either-direction PR model (Fig. C.9) largely converges to the diet-broadening case (Fig. C.7).

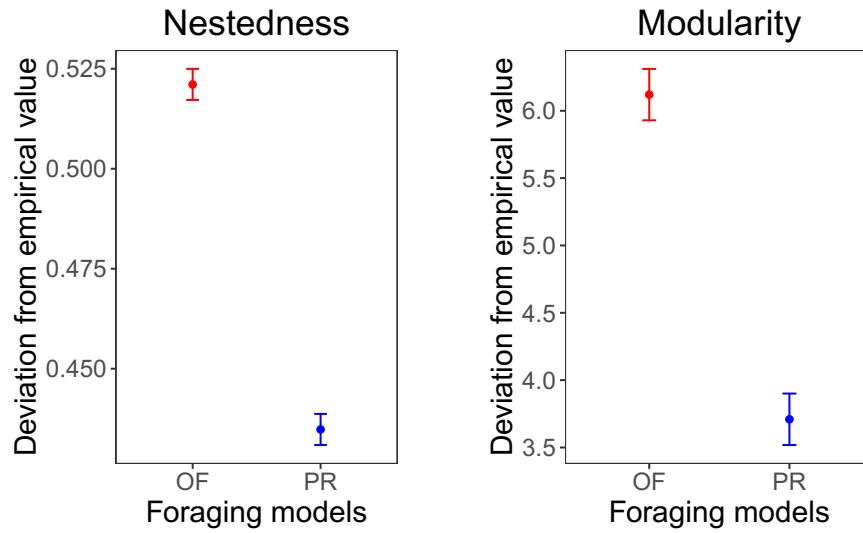


Figure C.3: Performance of the Optimal Foraging (OF) and Predation Risk-Compromise (PR) models in capturing nestedness and modularity of empirical food webs. This figure is identical to Fig. 4.2 except that we evaluate here the performance using standardised absolute deviations from the empirical value of both foraging models, which is the absolute value of the difference (of NODF and modularity index) between the model-generated web and the empirical web, divided by the reading of the empirical web. These are shown as mean $\pm$ 95% CI (LMM fixed-effect uncertainty only). The PR model has deviations significantly smaller than those of the OF model in both nestedness and modularity measurements ($p < 0.001$ in both cases), indicating a better predictive ability.

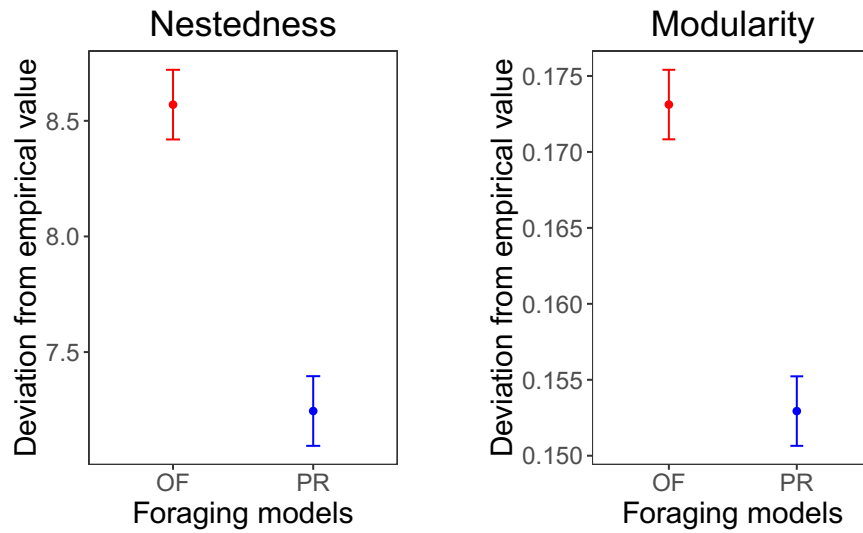


Figure C.4: Performance of the OF and PR models in predicting nestedness and modularity of empirical food webs but with conversion efficiency set to 0.4 toward basal resource and 0.8 toward non-basal resource. All notations are the same as in Fig. 4.2 of the main text.

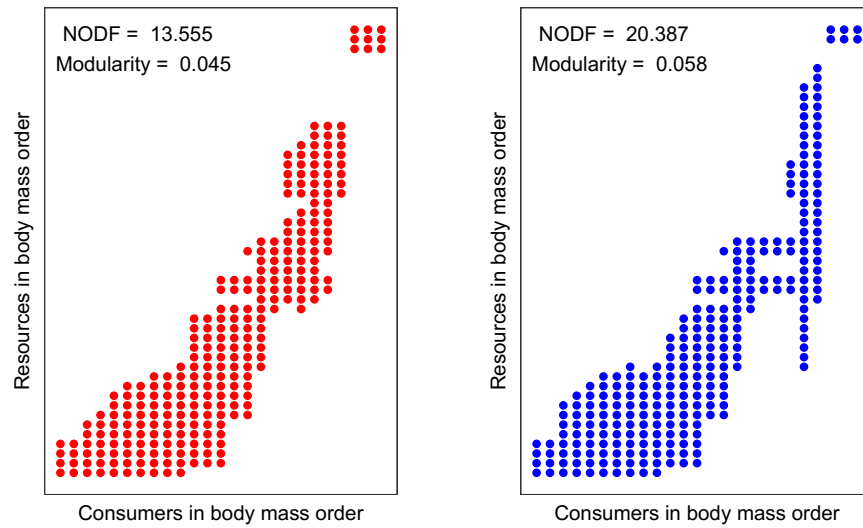


Figure C.5: The size-ordered diet matrix of OF- and PR-predicted counterparts (red and blue, respectively) of empirical community TL84 from a single model simulation, with conversion efficiency set to 0.4 toward basal resource and 0.8 toward non-basal resource. All notations are the same as in Fig. 4.5 of the main text.



Figure C.6: Summary of the structural features (as columns) of empirical food webs (as rows) and their OF and PR counterparts. Nest: level of nestedness (as NODF); Modu: level of modularity (as modularity index); Clus: clustering coefficient; Incohe: Incoherence index; Simi: web-averaged species-pair similarity; TL-Mass: Trophic level to $\log_{10}$ consumer body mass relationship; ID-Mass: In-degree to $\log_{10}$ consumer body mass relationship. Food-web name abbreviations are in accordance with Table C.4. Red, blue, and black colour refer to OF, PR, and empirical food webs, respectively. The solid line present the mean or regression line, with corresponding shade present the 95% CI. The box plots present the model-generated values. Except in TL- and ID-Mass, the background of the plots are coloured in red/blue shade to point out which of OF and PR measurement mean values is significantly closer ($p < 0.05$) to the empirical value based on paired-Wilcoxon tests.

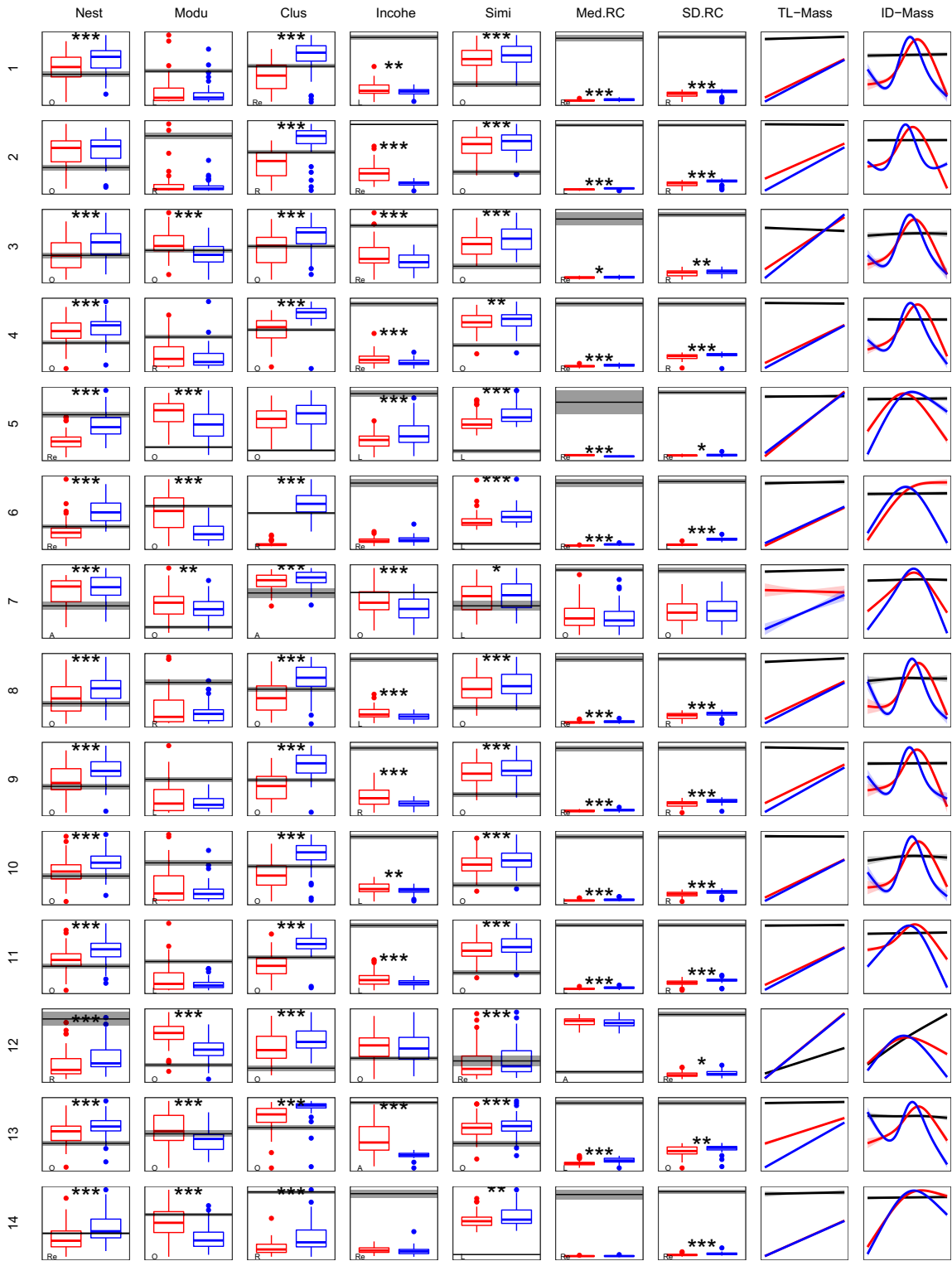


Figure C.7: Summary of the structural features (as columns) of the OF, PR, & null food webs across all schemes (as rows). Measurement abbreviations are in line with Fig. C.6. Red, blue, and black colour refer to OF, PR, and null food webs, respectively. The solid line with corresponding shade presents the mean $\pm$ 95% CI of observations or the regression line, whereas the box plots present the model-generated observations. The asterisks indicate whenever the OF/PR values are significantly larger than the other (*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$. LMM results). Adopted data type is indicated at the bottom left of the plots: O(original), R(square-root), L(log), Re(reverse), and A(arcsine square-root). Across schemes, there are consistent structural differences between OF and PR food webs despite of the variation in model mathematical structure and parameters.

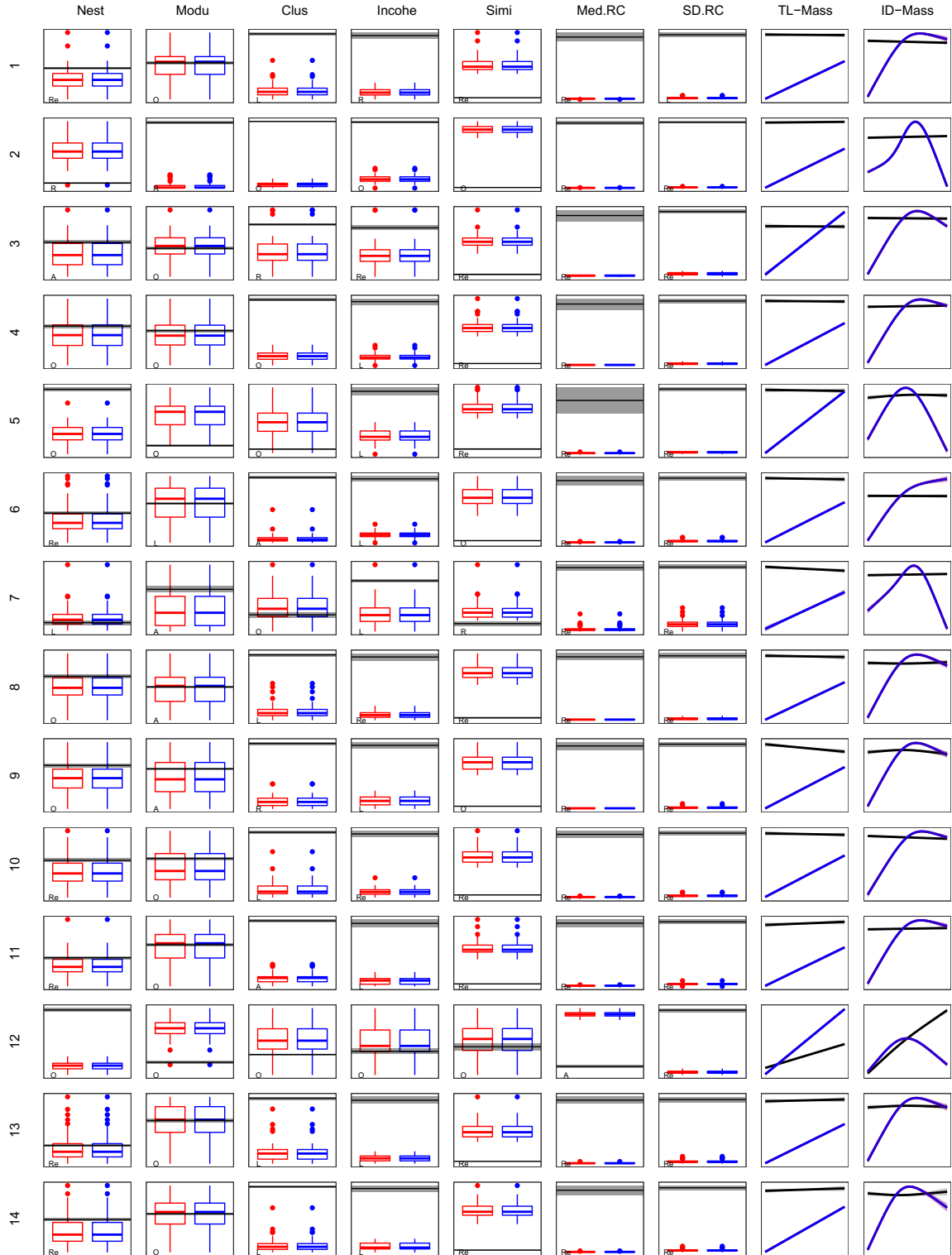


Figure C.8: Summary of the structural features (as columns) of the OF, PR, and null food webs across all schemes (as rows), where in the PR model the predation risk is set to have diet-narrowing effect. All notations are in line with Fig. C.7. As the PR in this case largely converge to the OF, the results show no difference between the two.

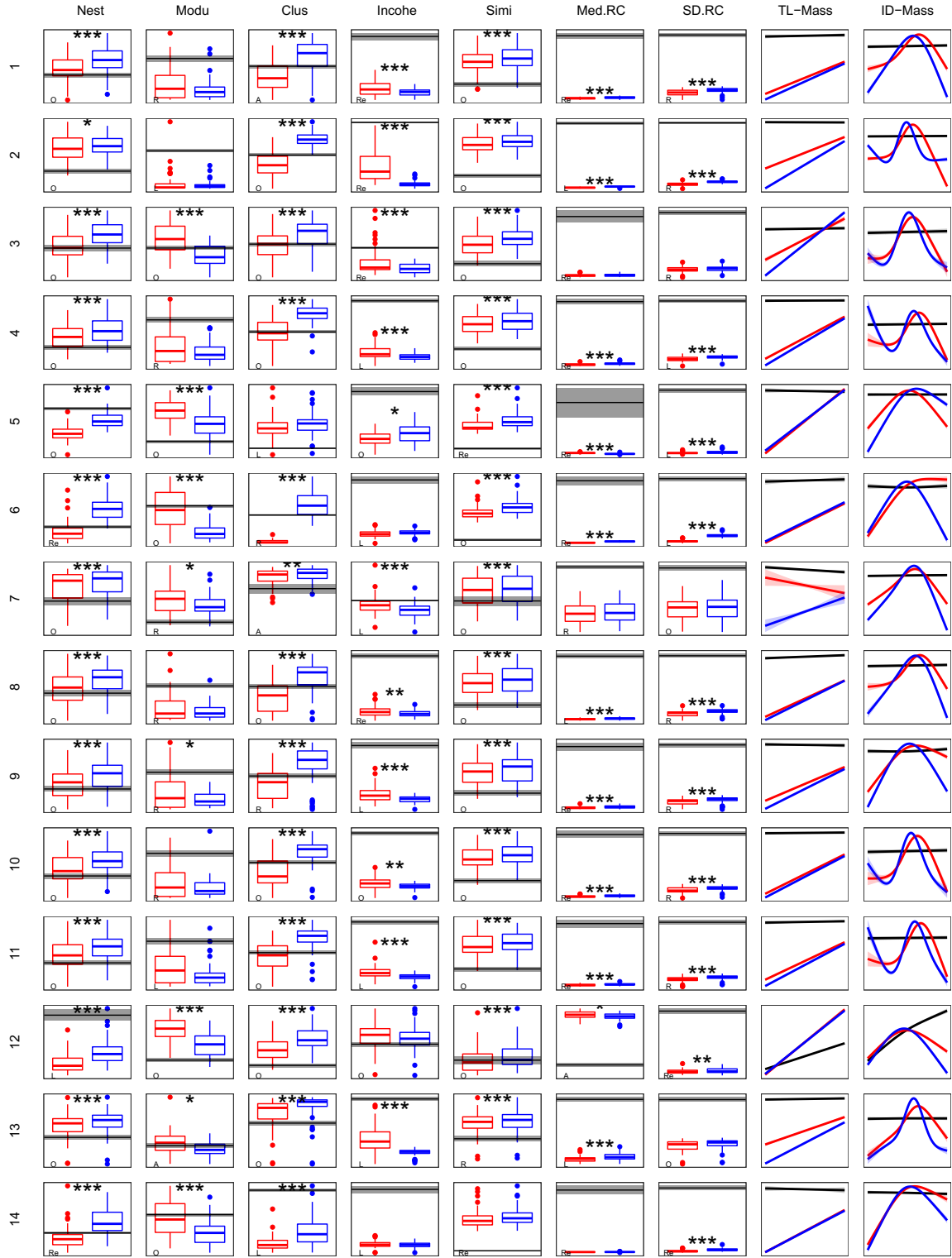


Figure C.9: Summary of the structural features (as columns) of the OF, PR, & null food webs across all schemes (as rows), where in the PR model the predation risk is set to have either diet-narrowing or diet-broadening effect depending on which gives the closer consumption rate to the reference value. All notations are in line with Fig. C.7. The results are largely the same with pure diet-broadening case as in Fig. C.7.