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Interaction Strengths and Net Effects in Food Web Models

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**This thesis is presented to the National University of Ireland, Cork,
in candidature for the degree of Doctor of Philosophy**

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Declaration

I hereby declare that the work presented in this PhD thesis is my own work and has not been previously submitted for another degree at any other university or institution.

Catherine Palmer

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ABSTRACT

Understanding how dynamic ecological communities respond to anthropogenic drivers of change such as habitat loss and fragmentation, climate change and the introduction of alien species requires that there is a theoretical framework able to predict community dynamics. To do this requires that we understand how component individual species populations respond to environmental change and how these species populations interact with one another. At present there is a lack of empirical data that can be used to inform and test predictive models, which means that much of our knowledge regarding the response of ecological communities to perturbations is obtained from theoretical analyses and simulations.

This thesis is composed of two strands of research: an empirical experiment conducted to inform the scaling of intraspecific and interspecific interaction strengths in a three species food chain and a series of theoretical analyses on the changes to equilibrium biomass abundances following press perturbations. Both strands of research are conducted within the Lotka-Volterra model framework. The experiment presented in Chapter 2 is a consequence of the difficulties faced when parameterising the intraspecific interaction strengths in a Lotka-Volterra model. A modification of the dynamic index is used alongside the original dynamic index to estimate intraspecific interactions and interspecific interaction strengths in a three species food chain consisting of, the dwarf broad bean, *Vicia faba* (Linnaeus) as a basal species, the pea aphid, *Acyrthosiphon pisum* (Harris) as a herbivore species, and green lacewing larvae, *Chrysoperla carnea* as a carnivore species. The sign (positive or negative) of intraspecific interaction strength estimates for basal species varied with food chain structure. The estimated ratios of intra- to interspecific interaction strengths for basal and consumer species took values between -0.01 and -0.001. It was not possible to draw conclusions about the magnitude of the ratio of intraspecific to interspecific interaction strength estimates for consumer/predator species since the variation in the data was too large.

Chapters 3-5 are theoretical analyses focused on the effect of press perturbations to focal species on the equilibrium biomass densities of *all* species in the community; these perturbations allow for the quantification of a species *total net effect*. In Chapter 3 it is found that there is a strong and consistent positive relationship between a species body size and its total net effect for a set of 97 synthetic food webs and also for the Ythan Estuary and Tuesday Lake food webs (empirically described food webs). A negative relationship between the linkage density of a species and its total net effect was present for 38 of the 97 synthetic food webs analysed and also for the Ythan Estuary food web, indicating that a species total net effect may depend on the structure of the community in which it is embedded.

Chapter 4 represents an analysis of food chains where interaction strengths have been defined allometrically using predator-prey body size ratios. The chapter shows how ecological constraints (due to allometric scaling) on the magnitude of entries in the community matrix cause the patterns observed in the inverse community matrix and thus explain the relationship between a species body mass and its total net effect in a community. Finally, in Chapter 5, the relationship between a species linkage density and its total net effect is analysed using a range of food webs of size 12 or 16 with two alternative structures and varying complexity. The analyses show that, on a web level, any potential effect of linkage density is masked by the overwhelming positive relationship between body size and total net effect. Examining the relationship between a species linkage density and its total net effect within trophic levels found that a negative relationship occurred frequently within the basal and herbivore trophic levels but was rare within the carnivore trophic level. The mechanism by which highly connected species could potentially have weak total net effects was not clear, but it was possible to conclude that a negative relationship is not a consequence of parameterising the community matrix using predator-prey body size ratios and allometric constraints and is a consequence of the pattern of interaction strengths in the surrounding web.

CHAPTER 1

GENERAL INTRODUCTION

Introduction

The benefits that ecosystems provide to humanity are collectively referred to as *ecosystem services* and include the vital processes of provisioning (the production of renewable resources), supporting (processes that underpin all other services, for example nutrient recycling) and regulating (processes that help maintain the status quo, for example, pest-control) (Millenium Ecosystem Assessment 2005). At present, human activities are having an increasingly negative impact on the environment resulting in climate change, habitat transformation, changes to global biogeochemistry and rates of biodiversity loss (Vitousek et al. 1997, Barnosky et al. 2011, Estes et al. 2011). The impact of biodiversity loss on ecosystem services is still a topic of intense study; while increased knowledge and advances in technology may increase the benefits derived from some resources, it has been shown that the loss of biodiversity reduces the efficiency of ecosystem services resulting in lower rates of provisioning and an accelerated rate of environmental change (Hooper et al. 2005a, Schröter et al. 2005, Cardinale et al. 2012). In this context of human induced environmental change, understanding and predicting the behaviour of ecological communities is of great importance.

Mathematical models in food web ecology

An ecological community is a group of species that coexist in the same location at the same time; a food web is an example of an ecological community where the species are linked via trophic interactions. Mathematical models are a useful tool for understanding real world systems and predicting their behaviour, however, the complexity inherent in ecological communities makes the task of building useful models extremely difficult. Modelers face two main difficulties; first, ecological communities are so complex that at present we lack accurate community descriptions. For example, communities often consist of thousands of species and most published food webs contain at most hundreds of species (Pimm et al. 1991), which means that either many species are ignored or the food webs are aggregated by pooling certain species together into trophic species (Martinez 1991, 1993b, Solow and Beet 1998). The second difficulty faced by modelers is that even these inaccurate, simplified descriptions of food webs are extremely complex mathematically; creating a locally stable dynamic food web model in which hundreds of species coexist still remains a challenge today. In short, mathematical models are inaccurate representations of empirical descriptions of food webs which, in turn, are inaccurate representations of food webs found in nature. Despite these difficulties and despite the current lack of accurate predictive models, utilising the conceptual framework of mathematical models has greatly advanced our understanding of ecological communities.

Complexity and Stability

The most well-known example of using mathematical models to explore the properties of an ecological community is May's seminal result (May 1972), where he showed that for communities in which interaction strengths between species are randomly assigned, communities with many species are less stable than communities with few species. May's result contradicted the previously held theory that complexity in ecological communities confers stability (MacArthur 1955, Elton 1958). The models that May used in his analysis were not useful in the sense that they explained or predicted the behaviour of ecological communities, but they inspired researchers to question how complex ecological communities can be stable. What are the mechanisms by which complexity in ecological communities can be reconciled with stability? Current theories propose that food web structure and the prevalence of weak interaction strengths between species may affect the stability of a system (McCann et al. 1998, McCann 2000, Emmerson and Yearsley 2004, Neutel et al. 2007, Allesina and Pascual 2008, Allesina and Tang 2012). Studies have also shown that the application of predator-prey body mass ratios and allometric scaling to define interaction strengths between species promotes stability in food web models (Yodzis 1981, Jonsson and Ebenman 1998, Emmerson and Raffaelli 2004, Brose et al. 2006b, Otto et al. 2007).

Food web metrics

Definitions play a key role in Mathematics and the study of food webs has been enhanced by the use of clear, precise definitions of quantities and concepts associated with food webs. Table 1.1 gives a summary of some of the common definitions used in food web ecology and which will be used throughout this thesis.

Table 1.1 Summary of definitions used in food web ecology

Concept	Definition
Measured at the species level	
Body size (m)	The average biomass of a species
Trophic position	The number of species below a given species in a food chain +1
Trophic height	The mean trophic position
Numerical population density (N)	The number of individuals of a given species in a defined area
Population biomass density (B)	The biomass of a given species in a defined area
Total number of links (l)	The number of trophic links of an individual species
Linkage density (LD)	The number of trophic links of an individual species/ the number of species in the food web (l/S)
Generality (g)	The number of prey items a species has
Vulnerability (v)	The number of predators that a species has
Interaction strength	The effect of one species on another species[1]
Measured at the web level	
Web size (S)	The number of distinct species in a food web[2]
Total number of links (L)	The number of trophic links in a food web
Web connectance (C)	L/S^2
Linkage density/Complexity	The average number of links per species (L/S)
Proportion of basal species (B)	B/S
Proportion of intermediate species (I)	I/S
Proportion of top species (T)	T/S
Omnivory	The proportion of species that feed on more than one trophic level
Generality (G)	The mean number of prey items a species has
Vulnerability (V)	The mean number of predators that a species has
Weighted Generality (G’)	The mean number of prey items a species has where each species is weighted by its proportional biomass consumption
Weighted Vulnerability (V’)	The mean number of predators that a species has where each species is weighted by its proportional biomass contribution to available resources.
Maximum path length	The length of the longest food chain present in a food web
Average path length	The mean length of all food chains in a food web
Average shortest path length (D)	The mean of all shortest paths between all species
Mean clustering coefficient (Cl)	The number of links between species that have a direct link to a focal species divided by the number of links that could possibly exist between them. This ratio is averaged over all species in the web to give the mean clustering coefficient

The mean of all shortest paths between all species

The number of links between species that have a direct link to a focal species divided by the number of links that could possibly exist between them. This ratio is averaged over all species in the web to give the mean clustering coefficient

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[1] This is a general definition of interaction strength; interaction strengths have been defined in numerous ways (Berlow et al. 2004). In this thesis interaction strengths are defined precisely in terms of a Lotka-Volterra system as the coefficients of the community matrix see p.11

[2] Species can be defined as individual species or aggregated into functional species with implications for food web structure.

Food web structure and static food web models

The functioning and stability of ecological communities is dependent on their structure (Borrvall et al. 2000, McCann 2000, May 2001, Sole and Montoya 2001, Dunne et al. 2002b, Hooper et al. 2005b). Static food web models consider only the structure of a food web and do not consider the way that species population densities fluctuate over time (the dynamics of a food web). Models that recreate food web structures can provide insights into the mechanisms behind observed food web patterns as well as creating synthetic food webs on which to test theories. Early analysis of food web structure indicated that some food web properties were scale invariant. In particular, it was observed that linkage density (L/S) was constant with respect to species richness which would imply that web connectance (L/S^2) decreases with species richness (Cohen and Briand 1984, Cohen et al. 1986). This observation was used in the cascade model (Cohen and Newman 1985) to produce food web structures using two parameters: the number of species S and the linkage density L/S. The linkage density parameter L/S was held constant to reflect the scale invariance of linkage density but the value of S could vary to produce webs of different size. The model assigned links between species randomly using just two assumptions: (1) species are assigned a random number from the uniform interval [0, 1] and organised hierarchically according to their number; (2) each species can only feed on species that are lower than themselves in the hierarchy. Despite its simplicity the cascade model described the observed patterns in empirical food webs well in comparison to a model where the links are assigned completely at random. One notable limitation was that although, in general, species do feed on species below them in a food chain, loops (A eats B, B eats C, C eats A) including cannibalism do occur in empirical food webs; the cascade model does not account for this.

Improvement in the quality of empirical data cast doubt on the scale invariance of certain food web properties (Martinez 1993a, 1994, Dunne et al. 2002a, Schmid-Araya et al. 2002, Montoya and Solé 2003, Dunne et al. 2004, Riede et al. 2010) and later models sought to create the patterns observed in the improved data (see Table 1.2 for a summary of some of the recent patterns identified). The niche model (Williams and Martinez 2000) used two parameters, species richness S and connectance L/S^2. It is important to note that both S and L/S^2 were varied to create webs of different sizes and complexity; there was no assumption made about the scaling of linkage density or connectance with species richness.

Table 1.2 Patterns found in current empirical food web data

Pattern[1]	**Studies**
Linkage Density/Complexity increases with species richness	(Hall and Raffaelli 1991, Martinez 1994, Schmid-Araya et al. 2002, Montoya and Solé 2003, Riede et al. 2010)
Connectance decreases with species richness[2]	Hall and Raffaelli, 1991, Martinez, 1994, Schmid-Araya et al., 2002, Montoya and Solé, 2003, Riede et al., 2010)
There is variation in linkage density/complexity across ecosystem types[3]	(Chase 2000, Link 2002, Riede et al. 2010)
The proportion of basal species decreases with species richness	(Schoener 1989, Martinez 1993a, 1994, Riede et al. 2010)
The proportion of intermediate species increases with species richness	(Martinez 1993a, 1994, Riede et al. 2010)
The proportion of top species decreases with species richness	(Martinez 1993a, 1994, Riede et al. 2010)
The proportion of omnivorous species increases with species richness	(Riede et al. 2010)
The average shortest path length decreases with species richness	(Williams et al. 2002, Riede et al. 2010)
The mean clustering coefficient increases with species richness.[4]	(Riede et al. 2010)
Food webs are often organised into compartments of species that interact frequently among themselves	(Krause et al. 2003, Allesina and Pascual 2009, Rezende et al. 2009, Stouffer and Bascompte 2011)
Maximum food chain length is usually between four and five but can be longer e.g. a maximum food chain length of 9 was recorded for the Ythan Estuary food web	(Pimm 1982, Hall and Raffaelli 1991)
Species numerical abundance (*N*) scales negatively with body mass (*m*). The reported exponent is often near -3/4 or -1	(Peters 1983, Cohen et al. 2003, Brown et al. 2004, Jonsson et al. 2005, White et al. 2007, Blanchard et al. 2009, Reuman et al. 2009)
Species trophic height (*Th*) scales positively with body mass (*m*)	(Cohen et al. 2003, Jonsson et al. 2005, Riede et al. 2011)
Predator-prey body size ratios decrease with trophic height	(Riede et al. 2011)

[1] It is important to note that many of these patterns are sensitive to the methods used to gather the data. (Martinez 1991, 1999)

[2] (Riede et al. 2010) noted that the significance of this result was marginal and that further study is needed to confirm or refute this finding

[3] (Riede et al. 2010) found significant variation between river and terrestrial systems only. See (Dunne et al. 2004) for an alternative finding

[4] This contradicts earlier findings by (Dunne et al. 2002a) and (Camacho et al. 2002).

Interaction strengths and dynamic models

Static food web models account for the number of species present in a community and who eats whom. If we wish to examine stability, the effects of environmental perturbations, species extinctions and species invasions then we must also consider the way that species interact. Dynamic models define interaction strengths between species to capture the way that species population densities fluctuate over time. The general form of a consumer-resource system can be written as:

$$\frac{dR}{dt} = f_1(R) + g_1(R, C)$$

$$\frac{dC}{dt} = f_2(C) + g_2(R, C)$$

Where R represents the population density (numerical or biomass) of a resource or prey species and C represents the population density of a consumer or predator species. The function $f_1(R)$ represents the growth rate of the resource species in the absence of the consumer species and the function $f_2(C)$ represents the death rate of the consumer species in the absence of the resource species. The function $g_1(R, C)$ represents the units of resource species consumed per unit of the consumer species and is referred to as the *functional response*. The function $g_2(R, C)$ represents the effect a unit of the resource species has on the consumer species growth rate, i.e. the efficiency of the conversion from resource matter into consumer matter. The most widely used dynamic model is the Lotka-Volterra model where species growth rates and death rates are constant and the functional response is linear (Holling's type I functional response). Throughout this thesis population density is measured in units of biomass so the Lotka-Volterra model for a community with S species is of the form:

$$\frac{dB_i}{dt} = B_i\left(r_i + \sum_{j=1}^{S} a_{ij} B_j\right)$$

where B_i is the biomass of species i (measured in kg or g), for a resource species r_i is positive and represents the per unit mass growth rate of species i in the absence of a consumer species. For consumer species the r_i term is negative and represents the per unit mass death rate of species i in the absence of resource species. The per unit mass effect of consumer species *j* feeding on resource species *i* per unit of time is denoted by a_{ij}. Note that the intraspecific term a_{ii} incorporates species self-limitation into the model so that for resource species, a_{ii} may be thought to represent $\frac{r_i}{K_i}$ where K_i is the carrying capacity of species *i* and thus resource species exhibit logistic growth. The type I functional response used in the Lotka-Volterra model assumes that the consumer's consumption rate of a resource species is independent of the resource species density (Figure 1.1). This assumption implies that the handling time (the time it takes to consume a resource species) is negligible and is not a realistic assumption for many consumer-resource interactions.

Whilst not used in this thesis, Holling's type II and type III functional responses incorporate a handling time per unit of resource, reflecting the time it takes for a consumer to manipulate and eat a prey item. The incorporation of a handling time leads to a functional response that becomes a saturating function of resource density.

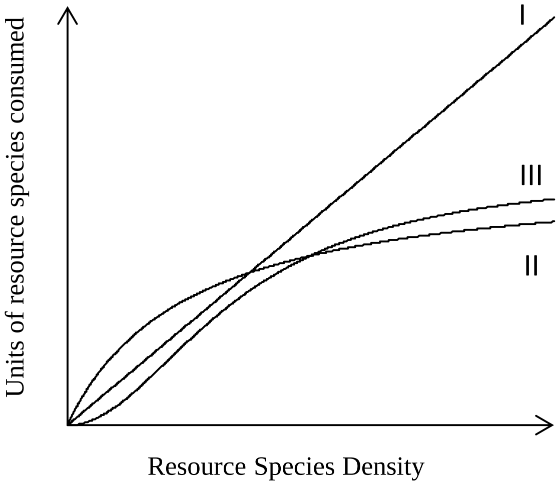


Figure 1.1 The variation in type I, II and III functional responses with respect to resource species density.

Some empirical data suggests that functional responses may also vary with consumer density (Arditi and Ginzburg 1989, Reeve 1997, Abrams and Ginzburg 2000). The Beddington DeAngelis functional response (Beddington 1975, DeAngelis et al. 1975) incorporates a *predator interference* term into the Holling type II functional response formula that reduces the attack rate when predator densities are high. Ratio dependent functional responses express the functional response as a function of the ratio of predator-prey densities $f\left(\frac{B_i}{B_j}\right)$ (Arditi and Ginzburg 1989). Empirical estimates of functional response have found evidence for all types of functional response depending on the nature of the consumer resource interaction (Arditi and Ginzburg 1989, Reeve 1997, Case 2000, Jeschke et al. 2004, Sarnelle and Wilson 2008, Begon et al. 2009). The form of the functional response has implications regarding the stability of a multi-species system. A type I functional response has a stabilising effect since resource species densities are kept in check by consumers. The saturation of type II and III functional responses at high resource species densities means that resource species can reach a point where they will increase unchecked which makes it difficult to use type II and III functional responses to model large complex systems (May 1973). In this thesis, type I functional responses were used for their simplicity but since the analyses presented in Chapters 3, 4 and 5 consider the effect of small perturbations away from equilibrium, we may assume that any non-linear functional responses are well described by a type I functional response (Case 2000).

Sequential assembly models incorporate dynamics into the assembly process so the resulting topology of a sequentially assembled web is a consequence of the dynamics underlying the component species (Drossel et al. 2001, Virgo et al. 2006). The topology of the webs used in Chapter 3 of this thesis were a result of a sequential assembly algorithm implemented by Säterberg et al. (2013).

The stability of Lotka-Volterra systems

In the context of food web ecology, the term stability has an intuitive meaning that the populations of species present in a community will persist through time with no extinctions. In order to persist, it is expected that when subject to a disturbance or perturbation, the community has the ability to return to its original state. Three commonly used stability concepts for a Lotka- Volterra system are: *local stability, global stability* and *permanence.*

In theoretical studies, the most frequently used criterion is *local stability*. For a Lotka-Volterra system, let **A** represent the community matrix that contains the interaction strengths between every pair of species in the community and let **r** represent a column vector that contains the growth rates of all species present in the community. An equilibrium point **B*** is a point at which the growth rate of all species is 0 so that:

$$\boldsymbol{r} + \boldsymbol{A}\boldsymbol{B}^* = 0$$

and therefore

$$\boldsymbol{B}^* = -\boldsymbol{A}^{-1}\boldsymbol{r}$$

The Jacobian matrix associated with the system contains the partial derivatives of the population growth equations with respect to each species, therefore the ij^{th} element of the Jacobian matrix represents the change in the growth rate of species i with respect to the population biomass of species j. For a system with a type I functional response, the ij^{th} element of the Jacobian matrix **C** is given by

$$c_{ij} = \frac{\partial}{\partial B_j}\left(\frac{dB_i}{dt}\right) = a_{ij}B_i^*$$

and **C** may be written as

$$\boldsymbol{C} = diag(\boldsymbol{B}^*)\boldsymbol{A}$$

The equilibrium point **B*** is said to be *feasible* if the equilibrium abundances of all species are positive and *locally stable* if the real parts of all the eigenvalues of **C** are negative. If an equilibrium point is locally stable then population densities subject to a small perturbation will return to equilibrium. A locally stable equilibrium point can be described as an *attractor*. The return trajectory that the populations follow after a perturbation depends on the imaginary parts of the eigenvalues. The imaginary parts of an eigenvalue produce a circular oscillation, so, for the case where the imaginary parts are non-zero, the trajectory will spiral into the equilibrium point. If the imaginary parts of the eigenvalues are zero then the population densities follow a monotonic trajectory back to the equilibrium point. It is possible for more than one locally stable equilibrium point to exist, in which case a system has alternative stable states. A large enough perturbation can shift the populations from one stable state to another (May 1977, Scheffer et al. 2001). A criticism of using local stability as a measure of community stability is that it only holds in the neighbourhood of the equilibrium point and gives no indication of how large this neighbourhood is, i.e. it gives no indication of how large a perturbation the system can withstand before the populations move away from equilibrium (Haydon 1994, Chen and Cohen 2001). A system that is globally stable can withstand any arbitrarily large perturbation within the feasible domain (for a system with S species, the feasible domain is $\mathbb{R}_+^S$). The global stability of a system is determined by showing that a *Lyapunov* function for the system exists which can be a challenge for complex systems.

Systems that are not locally stable may still persist within the feasible domain. Population densities may follow well defined stable limit cycles or chaotic orbits. In these circumstances, *permanence* may be a more suitable criterion for assessing the stability of a system. A system is said to be permanent if all population densities with nonzero starting densities remain in a fixed bounded domain of $\mathbb{R}_+^S$ that is a nonzero distance from the boundary (Anderson et al. 1992). Permanence can be shown by satisfying two conditions: (1) the population densities of all species are bounded above and (2) any orbit approaching the boundary will move away from it (Anderson et al. 1992). Since any predator-prey system that includes intraspecific interaction terms will be bounded above, condition 1 is satisfied for most Lotka-Volterra systems. Condition 2 can be checked by finding a function whose time average acts a Lyapunov function near the boundary of the feasible domain which can be expressed as a linear programming problem and solved numerically (Jansen 1987, Law and Blackford 1992). A recent study investigating the relationship between local stability and permanence in Lotka-Volterra systems found a positive correlation between local stability and permanence, indicating that local stability may be a good indicator of permanence (Townsend et al. 2010). Although improvements in computing power mean that permanence may be checked numerically, studies that have used permanence as a criterion for system stability have been restricted to webs with fewer than 20 species (Chen and Cohen 2001, Emmerson and Yearsley 2004, Christianou and Ebenman 2005, Townsend et al. 2010).

Interaction strengths and the community matrix

In a Lotka-Volterra system, the parameters determining the nature and the strength of an interaction between two species are referred to as interaction strengths and are often denoted by a_{ij}. The units of a_{ij} can be quantified either in terms of per capita effects or per unit biomass effects. In this thesis, a_{ij} represents the per unit mass effect of species j feeding on species i per unit of time. Units of biomass were chosen to facilitate comparisons with other studies (O'Gorman et al. 2010, Berg et al. 2011). The community matrix, denoted by A, is the matrix whose ij^{th} entry is a_{ij}, thus the community matrix contains the interaction strengths between every pair of species in the community. For a type I functional response, the a_{ij} terms are constant and do not vary with population densities. Some studies define interaction strengths in terms of the Jacobian matrix (often denoted by C) where the entries, c_{ij}, represent the per unit mass effect of species *j* on the *population* biomass of species *i* per unit of time at equilibrium (Neutel et al. 2002, Neutel et al. 2007, Montoya et al. 2009).

Parameterising Lotka-Volterra models in such a way that leads to feasible, persistent and/or stable communities has remained a challenge when modeling complex multispecies communities (Berlow et al. 2004, Neutel et al. 2007). Assigning interaction strengths at random often leads to communities that are unstable or not persistent (May 1972, Haydon 2000), and yet clearly complex ecological communities do persist in nature. Recent studies have found that by using ecological information to parameterise food web models, it is possible to create food web models that are both complex and stable (Yodzis 1981, Jonsson and Ebenman 1998, Emmerson and Raffaelli 2004, Andersen and Beyer 2006, Brose et al. 2006b, Otto et al. 2007, Zhang et al. 2013). In particular, the relation of allometric scaling and body mass based energy requirements to food webs has led to the development of mechanistic body-sized based parameterisations of the Lotka-Volterra model. The fundamental concept is that species energy requirements and growth rates are governed by their metabolic rate which has been shown to scale with body mass (*m*). Whole organism metabolic rate scales as $m^{3/4}$ so that the per unit mass metabolic rate scales as $m^{-1/4}$ (Brown et al. 2004). Defining interaction strengths between species using predator-prey body size ratios and allometric scaling has been shown to promote stability in food web models and explain community structure and dynamics (Yodzis 1981, Jonsson and Ebenman 1998, Emmerson and Raffaelli 2004, Andersen and Beyer 2006, Brose et al. 2006b, Otto et al. 2007, Berlow et al. 2009, O'Gorman et al. 2010, Zhang et al. 2013).

Interaction strengths have also been estimated empirically using a measure referred to as the *dynamic index* (Wootton 1997, Sala and Graham 2002, Navarrete and Castilla 2003, Emmerson and Raffaelli 2004). The measure is calculated using data from mesocosm experiments where the density of a prey species is measured in the presence and absence of a predator species. The dynamic index is derived from the discrete-time version of the generalised Lotka-Volterra multispecies equations (Laska and Wootton 1998). The derivation uses two equations: one describing the biomass density of the prey species (species *i*) in the presence of the predator species (species *j*) at time $t, B_{i,t}^{+j}$, and the other describing the biomass density of the prey species in the absence of the predator species at time $t, B_{i,t}^{-j}$:

$$B_{i,t}^{+j} = B_{i,0} \exp\left[\left(r_i + a_{i,j}B_{j,0} + \sum_{k \neq j} a_{i,k}B_{k,0}\right)t\right] \qquad \text{(1a)}$$

$$B_{i,t}^{-j} = B_{i,0} \exp\left[\left(r_i + \sum_{k \neq j} a_{i,k}B_{k,0}\right)t\right] \qquad \text{(1b)}$$

where $B_{i,0}$ is the initial biomass density of species i at time t=0, r_i is the intrinsic growth rate of species i, $a_{i,j}$ is the per unit mass effect of species j on species i per unit of time and the summations are over the n species in the community. Rearranging equations (1a) and (1b) gives the dynamic index for a_{ij}

$$a_{i,j} = \frac{\ln\left(B_{i,t}^{j+} \middle/ B_{i,t}^{j-} \right)}{B_{j,0}\ t}$$

If a study measures per capita interaction strengths then the biomass densities are replaced with numerical densities. Measuring interaction strengths empirically, using the dynamic index or otherwise, is extremely difficult (Laska and Wootton 1998, Abrams 2001, Berlow et al. 2004, Wootton and Emmerson 2005). In addition to the direct effect that the experiment is supposed to measure, changes in the density of the prey species may also be attributed to *indirect effects* where the effect of the predator species is mediated by one or more intermediate species. When we measure the impact of the predator species on the prey species empirically the choice of time scale for the experiment will influence the extent to which indirect effects are measured. Nonlinearities in the functional response of species will affect the efficacy of empirically estimated interaction strengths in Lotka-Volterra models (Abrams 2001). An index for empirically estimating the parameters for type II functional response has been proposed, but currently no estimates have been made using experimental data (Novak and Wootton 2010).

Intraspecific interaction strengths

The diagonal elements of the community matrix, $a_{ii,}$ represent intraspecific interaction strengths and the local stability of a Lotka-Volterra system is dependent on the scaling of intraspecific interactions strengths relative to interspecific interaction strengths. In general, the more negative a systems intraspecific interaction strengths are, the more likely it is that the system will be locally stable (Saunders 1978, Yodzis 1981, Haydon 1994). Despite the importance of the scaling of intraspecific with interspecific interaction strengths little is known about their relative strengths in natural communities resulting in a great deal of uncertainty over the parameterisation of the community matrix. There is a lack of empirical data that can be used to inform the scaling of intraspecific and interspecific interactions for Lotka-Volterra models, and whilst there are several methods used to estimate interspecific interaction strengths empirically (Berlow et al. 2004), there is no clear method for estimating intraspecific interaction strengths. Chapter 2 presents a study where a modification of the dynamic index (referred to as the intraspecific dynamic index) is used alongside the dynamic index to estimate intraspecific and interspecific interaction strengths in a three species food chain. The experiment used food chains of increasing length (1 to 3 species); a plant-only food chain (*Vicia faba*), a plant-herbivore food chain (*Vicia faba-Acyrthosiphon pisum*) and a plant-herbivore-predator (*Vicia faba-Acyrthosiphon pisum-Chrysoperla carnea*) food chain. Data regarding species biomass densities from each food chain was collected and the resulting intra and interspecific interaction strengths were then compared to examine how they scaled within and across trophic levels.

The inverse community matrix and net effects

In this thesis we define the *pairwise net effect* and the *total net effect* of a species within the Lotka-Volterra framework as first considered by Bender et al. (1984) (but see (Berlow et al. 2009) for an alternative definition). The *pairwise* net effect of species *j* on species *i* is the sum of both the direct effects and indirect effects of species *j* on species *i*, it represents the change in equilibrium biomass density of species *i* following a change in the growth rate of species *j*. The analysis presented by Bender et al. showed that the pairwise net effect of species *j* on species *i* can be calculated by applying a press perturbation to the equilibrium biomass density of species *j*, the effect of this press perturbation on the equilibrium biomass density of species *i* in a multispecies community is defined by the ij^{th} inverse element of the community matrix, A^{-1}. Such a press perturbation can occur through the sustained removal or addition of a constant biomass of a species to a community (e.g. fishing) or through a change in the intrinsic growth/mortality rate of a species (e.g. global warming induced changes to intrinsic rates or habitat loss). The *total* net effect of species *j* on the community represents the effect that a press perturbation to species *j* has on the equilibrium biomass densities of *all* species in the community and is given by the sum of the absolute values of elements of column *j* in the inverse community matrix. This measure was formally defined by Berg et al. (2011) where it was referred to as the sensitivity of equilibrium abundances to changes in growth rates. A similar measure, referred to as the *mean* net effect (the mean of the absolute values in column *j* of the inverse community matrix) has also been used to examine net effects within a community (Montoya et al. 2005 O'Gorman et al. 2010).

Analysis of the inverse community matrix has the potential to inform how a community will respond to press perturbations and identify keystone species (Berg et al. 2011), however, due to the uncertainty surrounding the parameterisation of the community matrix and the complex nature of the inversion process, understanding and predicting the nature of net effects in a community remains a challenge. When Yodzis considered the effect of press perturbations on a set of sixteen empirical food webs he found that the response of the communities was highly indeterminate (Yodzis 1988). Yodzis found that not only were the magnitudes of species responses to a press perturbation unpredictable, the direction (either an increase or a decrease in population density) of a species responses could also vary depending on the parameterisation of the food web. In an attempt to show whether the direction of species responses could be determined from community structure alone, Dambacher, Li et al. (2003) explored the effect of food web structure on the qualitative response of communities to press perturbations. The study examined the proportion of positive and negative feedback cycles that make up each element of the inverse community matrix and found that the direction of species response to a press perturbation is sometimes based solely on community structure, however, they found that in general, the elements of the inverse community matrix are a mixture of positive and negative feedback cycles and the direction of the response is dependent on the magnitude of the entries in the community matrix *A*.

Rather than relating the entries of the community matrix to the entries in its inverse, recent studies (Montoya et al. 2005, Montoya et al. 2009, O'Gorman et al. 2010, Berg et al. 2011) instead related patterns in the inverse matrix directly to species traits. These studies examined the mean net effects of species in the Ythan Estuary and Broadstone Stream food webs (Montoya et al. 2005) and in Lough Hyne (O'Gorman et al. 2010), it was found that species with high linkage density had weak mean net effects within the community. However no relationship between a species linkage density and its total net effect was found for the Baltic Sea and Lake Vättern food webs (Berg et al. 2011). In the same analyses, a positive relationship between a species body mass and its total net effect was found for the Ythan Estuary food web and the Baltic Sea and Lake Vättern food webs. In Chapter 3 these relationships are examined further on a set of 97 synthetic food webs generated by an assembly algorithm (Säterberg et al. 2013) and the Ythan Estuary, and Tuesday Lake empirical food webs. Specifically, we examine how species traits (body size and linkage density) and food web properties (species richness, connectance, mean clustering coefficient, average shortest path length and the proportion of basal, herbivore, intermediate and top carnivore species) affect the *total* net effect that a species has in a community. In Chapter 4 the relationship between a species body mass and its total net effect is examined analytically using simple food chains. The community matrices are parameterised using allometric scaling and predator-prey body size ratios and the relationship between body size and total net effect is examined. Since the entries in the inverse community matrix are determined by the entries in the community matrix, the parameterisation of the community matrix is key to understanding the mechanisms behind the observed relationship. In the final Chapter, the relationship between a species linkage density and its total net effect is examined analytically and graphically using a range of food webs of size 12 or 16 with two alternative structures and varying complexity. Since species linkage density effects the structure of the food web and the way that indirect effects travel through a food web web we may expect it to relate to the impact a species has on a community. The net effects analyses presented in this thesis hope to establish whether there are relationships between a species traits and its impact on the community in which it is embedded and if so, why these relationships are present.

CHAPTER 2

QUANTIFYING INTRASPECIFIC AND INTERSPECIFIC INTERACTION STRENGTHS IN A THREE SPECIES FOOD CHAIN

Abstract

When modeling ecological communities using Lotka-Volterra models, little is known about the values of intraspecific interaction strengths. They are often arbitrarily set to the value of -1 yet the relationship between intraspecific and interspecific interaction strengths is fundamental to the behaviour of the system. The Dynamic Index has been used to obtain empirical estimates of interspecific interaction strengths. In the following chapter, the Intraspecific Dynamic Index, which is a novel extension of the Dynamic Index that can be used to estimate intraspecific interaction strengths, is derived. The study also presents the results of a 3-trophic level mesocosm experiment. Data from the experiment was used to test the effectiveness of the Dynamic Index and its extension at estimating intra- and interspecific interaction strengths.

The sign (positive or negative) of intraspecific interaction strength estimates for basal species varied with food chain structure and estimated ratios of intra- to interspecific interaction strengths for basal/consumer species took values between -0.01 and -0.001. It was not possible to draw conclusions about the magnitude of the ratio of intraspecific to interspecific interaction strength estimates for consumer/predator species since the variation in the data was too large.

Estimates of interspecific interaction strengths were calculated for more than one density of basal and consumer species. These estimates indicate that interspecific interaction strengths are not constant with respect to species density and may follow a type II or type III functional response. The results indicate that the Dynamic Index and the Intraspecific Dynamic Index can be used to gain a more complete insight into species interaction strengths. Estimates from these indices reveal the potential of indirect effects and variation between individuals to greatly influence species interaction strengths.

Introduction

The Lotka- Volterra model has been used in numerous studies to gain insights into the structure and functioning of ecological communities (May 1972, Pimm and Lawton 1977, Pimm 1982, Arditi and Ginzburg 1989, Law and Blackford 1992, Emmerson and Raffaelli 2004, Eklöf and Ebenman 2006). A major issue within the Lotka- Volterra model framework arises over the choice of the parameter values that define the strength of interactions between and within species. Assigning interaction strengths at random often leads to communities that are unstable or not persistent (Haydon 2000) and increasing the complexity of communities with randomly assigned interaction strengths has a further destabilising effect (May 1973). Parameterising Lotka-Volterra models in such a way that leads to persistent and feasible communities has remained a challenge in predicting the dynamics of complex multispecies communities and food webs (Berlow et al. 2004, Neutel et al. 2007). The particular arrangement of interaction strengths across trophic levels, when determined by body size (Jonsson and Ebenman 1998, Emmerson and Raffaelli 2004, Brose et al. 2006b), has been shown to have important implications with regard to community stability, resilience, biodiversity, and the patterning of abundance or biomass densities across trophic levels (Yodzis 1981, de Ruiter et al. 1995, Jonsson and Ebenman 1998, Berlow 1999, Neutel et al. 2002, Jansen and Kokkoris 2003, Emmerson and Raffaelli 2004, Neutel et al. 2007). In particular, the use of ecological constraints and empirical information to inform the pattern of interaction strengths has helped to reconcile complexity with stability (Yodzis 1981, Moore and William Hunt 1988, de Ruiter et al. 1995, Jonsson and Ebenman 1998, McCann et al. 1998, Neutel et al. 2002, Emmerson and Raffaelli 2004, Neutel et al. 2007).

Intraspecific interaction strengths

The local stability of a community described by a Lotka-Volterra system is dependent on the intraspecific interactions. A necessary (but not sufficient) condition for local stability of a community is that the sum of the intraspecific interaction strengths is less than zero (May 1973) and in general, a system is more likely to be locally stable the more negative its intraspecific interaction strengths become (Saunders 1978, Yodzis 1981, Haydon 1994). Diagonal dominance occurs when the intraspecific interaction strength of *each* species in a system is greater than the sum of all its interspecific interaction strengths. When all intraspecific interaction strengths in a system are negative, then diagonal dominance of a system results in local stability. Consequently, when modelling a natural community using Lotka-Volterra dynamics, if intraspecific interaction strengths are not estimated from ecological data then local stability of the system can occur by choosing sufficiently negative intraspecific interaction strengths. Such parameterisations may not reflect the true nature of the community. The relationship between the values of intraspecific interaction strengths and the local stability of the system has been used to measure the stability of Lotka-Volterra models of soil communities (Neutel et al. 2002, Neutel et al. 2007), highlighting the important role that intraspecific interaction strengths play in community dynamics.

Intraspecific interactions have probably received less attention than interspecific interactions because it is often incorrectly assumed that the community matrix can be rescaled to a standard intraspecific interaction strength (commonly taken to be -1). This practice may have its roots in Levin's original definition of the community matrix where the interspecific interaction strengths were scaled to the intraspecific interaction strengths (Levins 1968), but may also arise from a misunderstanding of May's demonstration that a matrix can be rescaled by choosing a different timescale (May 1972). Rescaling the community matrix to a different timescale simply involves multiplying the community matrix by a constant, but if there is variation in the values of intraspecific interaction strengths then rescaling will not remove this variation. When interspecific interaction strengths are estimated carefully using ecological information, arbitrarily assigning a value of -1 to all the intraspecific interaction strengths will change the pattern of interaction strengths, which will alter important properties of the community matrix (Haydon, 1994).

Pimm and Lawton (1977) argued that negative density effects of predators and consumers can be achieved solely through interaction with their prey since if the predator/consumer density increases, the prey density will decrease and the food shortage will decrease the density of the predator (Pimm and Lawton 1977, Pimm 1982). However, for systems where non-basal intraspecific interaction strengths have been set to zero, it has been shown that increasing productivity in the system produces unrealistic responses in equilibrium abundance/biomass distributions across trophic levels (Ginzburg and Akçakaya 1992). Including non-zero intraspecific interaction strengths for all species avoids this problem (Abrams 1994, Gleeson 1994). Little is therefore known about the scaling of intraspecific and interspecific interactions for dynamical predator prey models. Some studies have defined intraspecific interaction strength to be stronger for basal species than for consumer and predator species since it has been argued that basal species are sedentary and have to compete for space and light (Emmerson and Raffaelli 2004, Christianou and Ebenman 2005, Eklöf and Ebenman 2006). While this assumption may be true in terrestrial systems, it may not apply to basal species in aquatic systems since phytoplankton are not sedentary but float with the current.

A few studies have assumed that intraspecific interaction strengths scale with body size with an exponent of -1/4 (Virgo et al. 2006, Lewis and Law 2007, Lewis et al. 2008). This scaling is derived by considering basal species equilibrium biomass densities in the absence of consumer species. At equilibrium, a basal species biomass density B_i^* can be related to its growth rate r_i and its intraspecific interaction coefficient a_{ii} by $B_i^* = \frac{r_i}{a_{ii}}$. It has been observed that the scaling of species population biomass across trophic levels is often invariant with body size (Peters 1983, Schmid et al. 2000) and that species growth rates scale with so body size (Blueweiss et al. 1978, Peters 1983) with an exponent of -1/4 which implies that intraspecific interaction strengths also scale with body size with an exponent of -1/4. This relationship may not hold in multispecies systems where equilibrium biomass densities are also affected by consumer species. There is a lack of system-specific ecological data that can be used to inform the scaling of intraspecific and interspecific interactions for dynamical predator prey models and whilst there are several methods used to estimate interspecific interaction strengths empirically (Berlow et al. 2004), there is no clear method for estimating intraspecific interaction strengths.

Measuring intraspecific and interspecific interaction strengths

The Dynamic Index (Wootton 1997, Laska and Wootton 1998) is a technique that has been used with some success to measure the strength of interspecific interaction strengths in communities (Wootton 1997, Sala and Graham 2002, Navarrete and Castilla 2003, Emmerson and Raffaelli 2004, O'Gorman et al. 2008, McCluney and Sabo 2009, O'Connor 2009). In this study we use the Dynamic Index (DI) to measure interspecific interaction strengths and present the Intraspecific Dynamic Index (IDI), which is an extension of the dynamic index that measures intraspecific interaction strengths (see Methods below). We also describe a mesocosm experiment to apply these measures to a three species food chain. The aim was to test the effectiveness of the DI and IDI at estimating interaction strengths and to quantify how intraspecific and interspecific interaction strengths vary across three trophic levels.

Materials and Methods

We developed an extension of the dynamic index that can be used to estimate intraspecific interaction strengths from experimental data. The same data set can be used to estimate interspecific interaction strengths using the original DI and thus enable us to gain insight into the scaling of intraspecific and interspecific interaction strengths in the same system. The method was applied to biomass time-series data from a mesocosm experiment. The experiment used three food chains of increasing length; a plant-only food chain (food chain A; strictly this is not a food chain, but we use the terminology for consistency), a plant-herbivore food chain (food chain B) and a plant-herbivore-predator food chain (food chain C). Each food chain was run for both high and low initial species biomass densities and the resulting intra and interspecific interaction strengths were then compared to examine how they scaled within and across trophic levels.

Estimating interspecific interactions using DI

The dynamic index can be derived from the discrete-time version of the generalised Lotka-Volterra multispecies equations (Laska and Wootton 1998). The derivation uses two equations: one describing the biomass density of the prey species (species *i*) in the presence of the predator species (species *j*) at time *t*, $B_{i,t}^{+j}$, and the other describing the biomass density of the prey species in the absence of the predator species at time *t*, $B_{i,t}^{-j}$:

$$B_{i,t}^{+j} = B_{i,0} \exp\left[\left(r_i + a_{i,j}B_{j,0} + \sum_{k \neq j} a_{i,k}B_{k,0}\right)t\right] \qquad \text{(1a)}$$

$$B_{i,t}^{-j} = B_{i,0} \exp\left[\left(r_i + \sum_{k \neq j} a_{i,k}B_{k,0}\right)t\right] \qquad \text{(1b)}$$

where $B_{i,0}$ is the initial biomass density of species *i* at time *t*=0, r_i is the intrinsic growth rate of species *i*, $a_{i,j}$ is the per unit mass effect of species *j* on species *i* per unit of time and the summations are over the *n* species in the community. We note that many of the previous studies used species abundance rather than biomass (Wootton 1997, Sala and Graham 2002, Navarrete and Castilla 2003, Emmerson and Raffaelli 2004). Here we use species biomass, as in Brose, Berlow and Martinez (2005a) and O’Gorman and Emmerson (2009) to facilitate the comparison of interaction strength estimates from different ecosystem types. Rearranging equations (1a) and (1b) gives the DI for $a_{i,j}$

$$a_{i,j} = \frac{\ln\left(B_{i,t}^{j+} \big/ B_{i,t}^{j-} \right)}{B_{j,0}\; t} \qquad (2)$$

Thus when we calculate interaction strength using the DI we are calculating the $a_{i,j}$ values in the discrete-time version of the generalised Lotka-Volterra multispecies equations. The $a_{i,j}$ value represents the rate of change in biomass of species *i* caused by a unit of biomass of species *j*. The DI for all pairs of species give all the off -diagonal elements of the un-scaled community matrix (the elements of the community matrix before they are scaled by the diagonal intraspecific terms). We state this explicitly since the term interaction strength has been used to describe many different quantities in community ecology, for a comprehensive review see (Berlow et al. 2004). Equation (2) assumes that the initial biomass of a species in equation (1a) is the same as in equation (1b), and that population growth rate is purely a linear function of the species biomasses. This second assumption in particular may not hold in real communities (Alberti et al. 2008, Otto et al. 2008).

Estimating intraspecific interactions using IDI

To estimate the intraspecific interaction strength of species *i* we adapt equation (1a) by considering different initial biomass densities of species *i*

$$B_{i,t}^{H} = B_{i,0}^{H} \exp\left[\left(r_i + a_{i,i} B_{i,0}^{H} + \sum_{k \neq i} a_{i,k} B_{k,0} \right) t \right] \qquad (3a)$$

$$B_{i,t}^{L} = B_{i,0}^{L} \exp\left[\left(r_i + a_{i,i} B_{i,0}^{L} + \sum_{k \neq i} a_{i,k} B_{k,0} \right) t \right] \qquad (3b)$$

where superscript ^{H} and ^{L} denote high and low initial biomass densities, respectively. Dividing equation (3a) by equation (3b) and rearranging to isolate the intraspecific interaction parameter $a_{i,i}$ we obtain:

$$a_{i,i} = \frac{\ln\left(\frac{B_{i,t}^{H} B_{i,0}^{L}}{B_{i,t}^{L} B_{i,0}^{H}}\right)}{\left(B_{i,0}^{H} - B_{i,0}^{L}\right)t} \qquad (4)$$

which we call the Intraspecific Dynamic Index (IDI) (see Appendix A for details). As for the DI, equation (4) assumes that the initial biomass of species *k*, $B_{k,0}$, is the same in equations (3a) and (3b) (except for species *i*) and that the *biomass density* of species *i* does not affect the way that species *i* interacts with other species in the community (including itself).

Experimental method

Species biomasses for three types of food chains (food chains A, B and C, Figure 2.1) were collected from mesocosms under laboratory conditions. All food chains had dwarf broad bean, *Vicia faba* (Linnaeus) as a basal species, food chains B and C had the pea aphid, *Acyrthosiphon pisum* (Harris) as a herbivore species, and food chain C had green lacewing larvae, *Chrysoperla carnea* (Stephens) as a predator species. Each mesocosm consisted of one plant pot (diameter 14.5cm) inside a 32.5 x 32.5 x 32.5cm Bugdorm® cage with polyester netting (96 x 26 mesh/square inch) and a transparent Ethylene Vinyl Acetate front and top panels over an Acrylonitrile Butadiene Styrene frame.

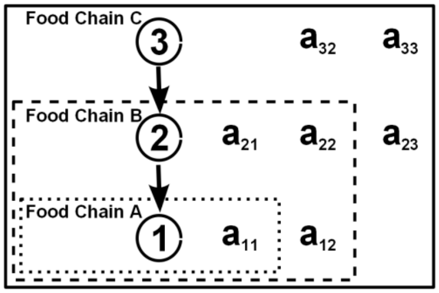


Figure 2.1 Schematic representation of the experiment showing which interaction strengths can be calculated from each food chain.

The initial biomass density of each species in a food chain was varied in a fully factorial design, with biomass density taking values of either high or low (Figure 2.2). This gave 2, 4 and 8 treatments for food chains A, B and C respectively. Low biomass density treatments corresponded to one broad bean plant, 100 pea aphids and 4 lacewing larvae per pot. High biomass density treatments corresponded to three broad bean plants, 200 pea aphids and 8 lacewing larvae per pot.

This gave 2, 4 and 8 treatments for food chains A, B and C respectively. The experiment was repeated in three separate time blocks with two replicates running in each block: 22nd - 29th February 2008 (replicates R1, R2), 7th – 14th March 2008 (replicates R3, R4) and 21st – 28th March 2008 (replicates R5, R6). Details of the mesocosm set up and the biomass collection are given in Appendix B. All biomasses were measured in grams and time, *t*, was measured in days which implies that the units of the interaction parameters $a_{i,i}$ and $a_{i,j}$ are $g^{-1}.d^{-1}$.

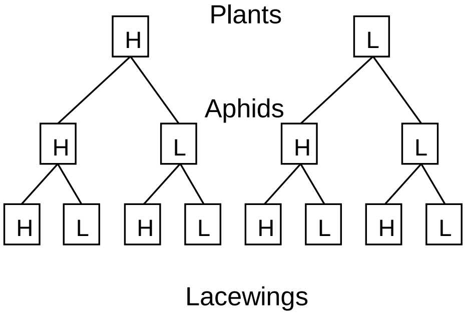


Figure 2.2 Design of food chain and density treatments. H represents high biomass density treatment and L represents low biomass density treatment

Data analysis

We used the DI and IDI to calculate interaction strength estimates from all possible combinations of food chain data. This resulted in multiple estimates for each interaction strength due to different food chains and different initial biomass densities (Table 2.1). For example, the plant intraspecific interaction strength a_{11} could be estimated from food chain A, B and C, but the lacewing intraspecific interaction strength a_{33} could only be estimated from food chain C (see Figure 2.1). Moreover, we obtained two estimates of a_{11} from food chain B (due to the low and high initial aphid biomass treatments) and four estimates of a_{11} from food chain C (due to the low and high initial aphid and lacewing biomass treatments). In the cases where there was an intraspecific interaction strength estimate for each food chain we quantified the effect of food web structure on interaction strength estimates. Interaction strength estimates from different biomass treatments and different food web structures could be compared because interaction strength estimates were measured in $g^{-1}.d^{-1}$ (i.e. on a per unit mass basis).

We performed two analyses that tested the influences of food web structure and initial species biomass upon our interaction strength estimates. The effect of food web structure on each interaction strength estimate was analysed using a mixed effect model with food web structure (food chains A, B or C) as a fixed effect and experimental replicates (R1-R6) as a random effect. Tukey's HSD post-hoc test was used to identify differences in the estimates of intraspecific interaction strength among food chain treatments. The effect of initial species biomass on each interaction strength estimate was also analysed using mixed effect models with starting biomass densities as fixed effects (represented as B_{10}, B_{20} and B_{30} for plants, aphids and lacewings with each being either Low or High) and experimental round as a random effect (R1-R6). Interspecific interaction strengths estimated from the DI method are not completely independent because the same biomass data from the treatment where the predator species is absent can contribute to two estimates of interaction strength. To account for this we included an additional random factor (absence) that indicated where two estimates shared data from the 'absence' treatment.

Models were selected using stepwise deletion with the likelihood ratio test (AIC gave identical results for all but one model) and we present the results from any fixed effects that were retained. Where effects are reported in the results we present the parameter estimate and its standard error (after Bates (2008)). The full set of parameter estimates and associated standard errors for the selected models are given in Tables 2.2 and 2.3. Homogeneity of variance and normality of the standardised residuals was satisfied for all models. All statistical analyses were undertaken using R version 2.12.0 (R Development Core Team 2013), mixed effect models used the 'lme4' package and Tukey's HSD test was carried out using the 'multcomp' package. The calculation of the intraspecific and interspecific parameters was performed using MATLAB version 7.7.0 (MATLAB 2008).

Results

Data from nine mesocosm replicates could not be used to calculate interaction strengths because their aphid populations crashed to zero (all when plant biomass was low, with three instances in the plant-aphid treatment and six instances in the plant-aphid-lacewing treatment). Data from these replicates were removed from the analysis. One plant in a low plant biomass treatment for food chain A was identified as an outlier (Grubb's test for outliers $p < 0.05$) because its growth rate per unit mass was over four times smaller than the other plants in the same treatment. The data for this plant gave unrealistic, positive plant-aphid interspecific interaction strength estimates and was therefore removed from the analysis.

Scaling of intraspecific and interspecific interaction strengths across and within trophic levels

The magnitude of the intraspecific interaction strength estimates and the variation within replicates for both intraspecific and interspecific interaction strength estimates increased with trophic level (Table 2.1). The variability between replicates in the same treatment was so large for a_{22}, a_{23} and a_{33} that no effects of species biomass densities could be detected and the true values of the interaction strengths could not be inferred (Table 2.1-2.4). The ratio of a_{11} / a_{12} lies between -0.01 and -0.001 (Table 2.2) but it is not possible to draw conclusions about the magnitude of ratio of a_{22} / a_{23} since estimates of a_{22} and a_{23} were highly variable.

Effect of food web structure on interaction strength estimates

Estimates of the basal intraspecific interaction strength, a_{11} could be both positive or negative depending on the particular food chain studied (food chain A estimate –0.009 ± 0.007 $g^{-1}d^{-1}$, food chain B estimate 0.023 ± 0.008 $g^{-1}d^{-1}$, food chain C estimate 0.017 ± 0.008 $g^{-1}d^{-1}$, Figure 2.3a). The a_{11} estimate for food chain A (plant only) was more negative than the estimate for food chain B but not significantly different from food chain C (Tukey's HSD $p < 0.05$). This indicates that intraspecific interaction strength need not be constant with respect to food web structure, contrary to the assumption made in equation (2) for the dynamic index. Food web structure did not have a significant effect on the a_{12} and a_{22} estimates (Figure. 2.3, Table 2.1). The effect of food web structure on the a_{23} and a_{33} estimates could not be tested since these estimates could only be obtained from food chain C (Figure 2.1).

Table 2.1 Interaction strength estimates made using the DI or IDI

Interaction	Food Chain	Estimate ($g^{-1}d^{-1}$) Mean ± SE	Mean of Absolute Values ± SE
a_{11}	A	-0.009 ± 0.003	0.009 ± 0.003
	B	0.014 ± 0.005	0.019 ± 0.004
	C	0.008 ± 0.003	0.014 ± 0.002
a_{12}	B	-2.5 ± 0.35	2.5 ± 0.34
	C	-2.1 ± 0.17	2.0 ± 0.17
a_{22}	B	-7.1 ± 3.5	9.6 ± 2.8
	C	-2.2 ± 2.4	6.1 ± 1.9
a_{23}	C	-0.56 ± 38.12	135 ± 31
a_{33}	C	-28 ± 24	96 ± 14

Effect of species biomasses on interaction strength estimates

Our estimates of intraspecific interaction strengths (a_{11}, a_{22}, a_{33}) were not affected by the initial species biomasses. Estimates of plant-aphid interspecific interaction strengths a_{12} showed evidence of being influenced by initial species biomasses while aphid-lacewing interaction strength estimates a_{23} did not (Tables 2.2, 2.3 and 2.4). The estimated value of a_{12} was influenced by both the initial plant and aphid densities (Figures 2.4 and 2.5). High initial biomasses of plants or aphids made a_{12} estimates less negative (e.g. for food chain B high plant biomass $a_{12}= -1.7 \pm 0.46$ $g^{-1}d^{-1}$, low plant biomass $a_{12}= -3.4 \pm 0.37$, high aphid biomass $a_{12}= -1.9 \pm 0.35$ $g^{-1}d^{-1}$, low aphid biomass $a_{12}= -3.0 \pm 0.58$ $g^{-1}d^{-1}$, Table 2.1). For food chain C there was some evidence that the combined effect of high plant and high aphid initial densities was not additive (Table 2.4). The estimates from food chain C were not influenced by the initial lacewing densities.

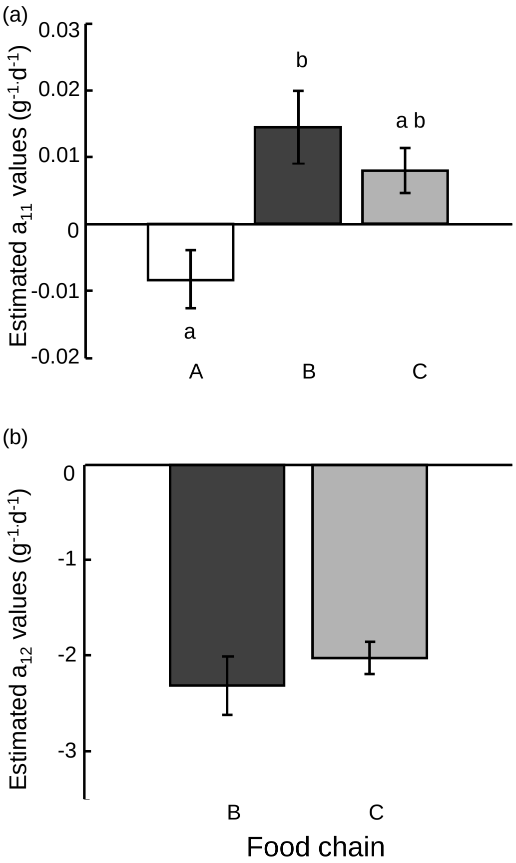


Figure 2.3 The effect of food web structure on (a) plant intraspecific interaction strength estimates and (b) plant-aphid interspecific interaction strength estimates. The plant only food chain (food chain A) is shown in white, the plant-aphid food chain (food chain B) is shown in black and the plant-aphid-lacewing food chain (food chain C) is shown in grey**.**

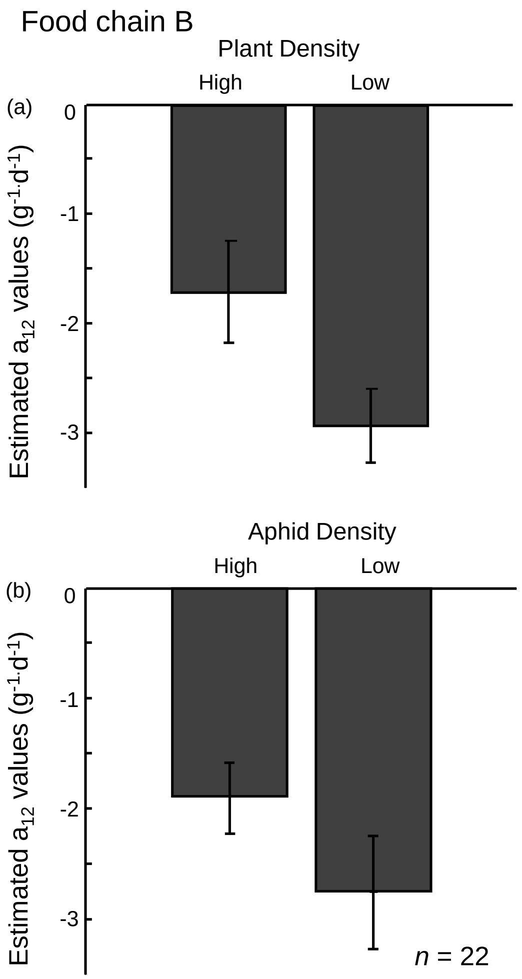


Figure 2.4 The effect of (a) plant biomass density and (b) aphid biomass density on plant- aphid interspecific interaction strength estimates for the plant-aphid food chain (food chain B).

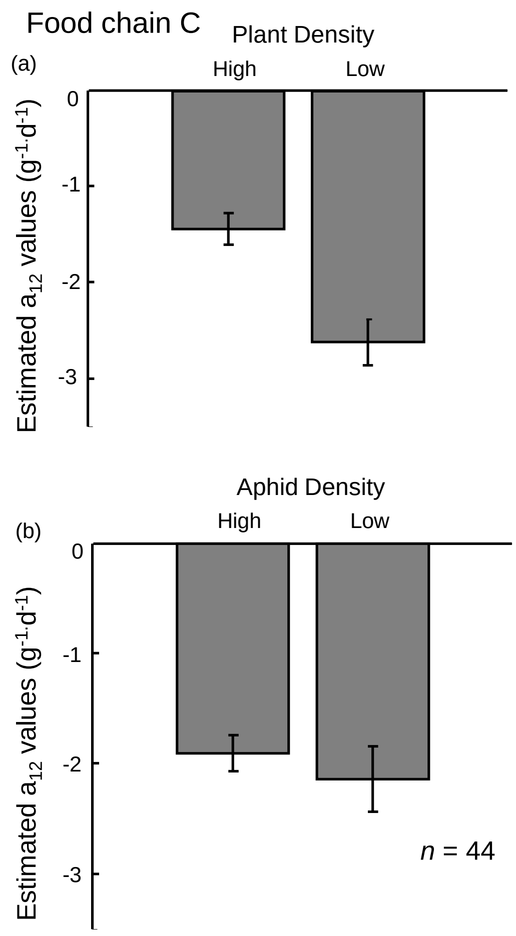


Figure 2.5 The effect of (a) plant biomass density and (b) aphid biomass density on plant-aphid interspecific interaction strength estimates for the plant-aphid-lacewing food chain (food chain C).

Table 2.2 The effect of initial species biomass density and food chain identity on interaction strength estimates made using the DI and IDI

Interaction Strength Estimate Mean ± SE (g^{-1}d^{-1})	**High Density Plant Treatment**	**Low Density Plant Treatment**	**High Density Aphid Treatment**	**Low Density Aphid Treatment**	**High Density Lacewing Treatment**	**Low Density Lacewing Treatment**
a_{11} Food Chain B	-	-	0.016 ± 0.009	0.013 ± 0.007	-	-
a_{11} Food Chain C	-	-	0.008 ± 0.005	0.008 ± 0.004	0.007 ± 0.005	0.009 ± 0.005
a_{12} Food Chain B	-1.7 ± 0.46*	-3.4 ± 0.37*	-1.9 ± 0.35 *	-3.0 ± 0.58 *	-	-
a_{12} Food Chain C	-1.4 ± 0.16*	-2.9 ± 0.25*	-1.9 ± 0.17*	-2.3 ± 0.32*	-2.1 ± 0.28	-2.1 ± 0.23
a_{22} Food Chain B	-5.1 ± 2.5	-10.1 ± 8.5	-	-	-	-
a_{22} Food Chain C	-0.54 ± 0.89	-7.1 ± 9.7	-	-	-2.8 ± 2.8	-1.5 ± 4.0
a_{23} Food Chain C	-0.51 ± 26.4	-0.66 ± 99.8	50.6 ± 61.8	-39.6 ± 47.5	-6.5 ± 25.9	5.1 ± 71.1
a_{33} Food Chain C	-2.6 ± 33.6	-53.6 ± 33.7	-23.3 ± 42.5	-32.9 ± 24.1	-	-

Table 2.3 Models used to investigate the effect of food web structure on interaction strength estimates.

Food Chain Datasets	**Full Model**	**Final Model (after model selection)**	**Parameter Estimate ± SE (from final model)**	
A, B, C	a_{11} ~ food chain + (1|round)	a_{11} ~ food chain + (1|round)	Food chain A	-0.009±0.007
			Food chain B	0.023±0.008
			Food chain C	0.017±0.008
B, C	a_{12} ~ food chain +(1| absence) + (1|round)	a_{12} ~ (1|absence) + (1|round)	NA	
B, C	a_{22} ~ food chain + (1|round)	a_{22} ~ + (1|round)	NA	

Table 2.4 Models used to investigate the effect of initial species biomass density on interaction strength estimates**.**

Dataset	Full Model	Final Model (after model selection)	Parameter Estimate ± SE (from final model)	
Food chain B	$a_{11} \sim B_{20} + (1 \mid \text{round})$	$a_{11} \sim (1 \mid \text{round})$	NA	
Food chain C	$a_{11} \sim B_{20} * B_{30} + (1 \mid \text{round})$	$a_{11} \sim (1 \mid \text{round})$	NA	
Food chain B	$a_{12} \sim B_{10} * B_{20} + (1 \mid \text{absence}) + (1 \mid \text{round})$	$a_{12} \sim B_{10} + B_{20} + (1 \mid \text{absence}) + (1 \mid \text{round})$	B_{10}	1.64±0.64
			B_{20}	1.02±0.41
Food chain C	$a_{12} \sim B_{10} * B_{20} * B_{30} + (1 \mid \text{absence}) + (1 \mid \text{round})$	$a_{12} \sim B_{10} * B_{20} + (1 \mid \text{absence}) + (1 \mid \text{round})$	B_{10}	1.74±0.43
			B_{20}	0.93±0.35
			$B_{10}: B_{20}$	-0.96±0.47
Food chain B	$a_{22} \sim B_{10} + (1 \mid \text{round})$	$a_{22} \sim + (1 \mid \text{round})$	NA	
Food chain C	$a_{22} \sim B_{10} * B_{30} + (1 \mid \text{round})$	$a_{22} \sim + (1 \mid \text{round})$	NA	
Food chain C	$a_{23} \sim B_{10} * B_{20} * B_{30} + (1 \mid \text{absence}) + (1 \mid \text{round})$	$a_{23} \sim (1 \mid \text{absence}) + (1 \mid \text{round})$	NA	
Food chain C	$a_{33} \sim B_{10} * B_{20} + (1 \mid \text{round})$	$a_{22} \sim (1 \mid \text{round})$	NA	

Discussion

This study is the first to use a standardized technique to simultaneously obtain empirical estimates for both intra- and interspecific interaction strengths at a whole food chain scale from the same set of data. Like the original dynamic index, the intraspecific dynamic index provides a simple way of estimating interaction strengths using variations in abundances or biomass densities. The simultaneous estimation of intra- and interspecific interaction strengths for our plant-aphid-lacewing food chain detects non-linearity in interspecific interactions that would not be possible to detect if the initial species biomass were not allowed to vary.

Four broad patterns emerge from this study. First, both the intra- and interspecific interaction strength estimates become larger and more variable with increasing trophic level (Table 1). Second, the ratio of intra- to interspecific interaction strengths for the basal species is very small, indicating that interspecific effects are much larger in magnitude than intraspecific effects. Third, the sign of intraspecific interaction strength (+ or -) for the basal species depends on the presence or absence of higher trophic level consumers (Figure 2.3). Fourth, the plant-aphid interspecific interaction strength estimates were dependent upon the initial plant and aphid biomass (Figures 2.4 and 2.5).

Estimating interaction strengths across trophic levels

The magnitude and variation of interaction strength estimates increased with trophic level. This is partly due to the behaviour of the DI calculation, which divides by the biomass of the predator species (equation 2), and the behaviour of the IDI calculation, which divides by the difference between initial biomasses of the focal species (equation 4). A positive correlation between the magnitude of interaction strengths and trophic level is expected from our data because lacewing biomass density was lower than aphid biomass density, which in turn was considerably lower than plant biomass density. The dependence of interaction strength estimates on the initial biomass density (or abundance) of the predator species is a feature of the dynamic index (Novak and Wootton 2010) and is highlighted in the present study where the top predator species was present at low biomass densities.

The increasing variation of interaction strength estimates with trophic level could also be due to the length of the food chain, because longer chains may allow more factors to affect the interaction strength estimates. Consider the aphid-lacewing interaction strength, a_{23}. Lotka-

Volterra dynamics assume that the final aphid biomass in paired plant-aphid-lacewing and plant-aphid treatments should only differ due to the presence of lacewings. However the individual plants and aphids also differ between these treatments and this variation may also have contributed to the differences in final aphid biomasses, distorting the effect of lacewing. In short, the variation in a_{23} values could reflect the effect of plants on aphids and aphids on aphids in addition to the effect of lacewings on aphids. Cannibalism by lacewing larvae could also increase the variability in estimates of a_{23} and a_{33}. Chance encounters between lacewing larvae resulted in one larvae consuming the other (personal observation) which would reduce the rate of predation on the aphids and directly affect the final biomass of lacewing larvae.

Ratio of plant intraspecific to interspecific interaction strengths

The estimated intraspecific interaction strength for plants is approximately 100-1000 times smaller in magnitude than the interspecific interaction strength between plants and aphids which may be smaller than the ratios in other systems. Aphids are a pest species, which reproduce quickly and, at high densities, cause considerable damage to plants. In the natural environment aphid population densities are often suppressed by a variety of natural enemies and only become a pest when populations exceed economically damaging thresholds (Hutchison and Hogg 1984, Aquilino et al. 2005). In the treatment for food chain B, there was no predation on aphids, so populations grew exponentially causing a large reduction in plant biomass. Similarly, in treatments for food chain C, the lacewing larvae failed to suppress the aphid populations so plant biomass was greatly reduced. Therefore, the ratios estimated for plants and aphids in this study may be smaller than ratios in the environments where aphid populations are kept in check by a variety of natural enemies and smaller than ratios for other pairs of species in different systems.

The intraspecific: interspecific ratios found in this study are smaller in magnitude than the ratios used in many previous theoretical studies (Table 2.5) which may reflect the fact that the food chains analysed in this study were unstable. If theoretical studies of community dynamics were to use similar values of intraspecific: interspecific ratios to those found in empirical studies, then, in order to ensure local stability, stricter conditions would need to be placed on the pattern of interspecific interaction strengths. However, we note that this study focuses on three species only and in order to inform the choice of interaction strengths in theoretical studies more information about the patterning of interaction strengths within and between a wide range of species is necessary. Further applications of this technique to estimate the patterning of intra- and interspecific interaction strengths in other systems could provide this information.

Table 2.5 Ratios of aii / aij reported in the literature, where aii is the intraspecific interaction strength of a basal species and aij is their interspecific interaction strength with a primary consumer.

Number of Basal Species (i)	Number of Primary Consumers (j)	Estimation[a]	Ratio a_{ii} / a_{ij}		Study
			Min	Max	
1	1	Empirical	-0.01	-0.001	This study (food chain B)
1	1	Empirical	-0.008	-0.0008	This study (food chain C)
2	3	Empirical	0.03	0.08	Neutel et al. (2007)[b]
2	4	Empirical	0	0.03	de Ruiter et al. (1995)[b]
4	1	Empirical	0.01	0.57	Schmitz (1997)
4-6	4	Theoretical	2	30	Petchey et al. (2008b)
Variable	Variable	Theoretical	2	70	Eklöf & Ebenman (2006)
3	3	Theoretical	1	Infinite	Christianou & Ebenman (2005)
4	57	Theoretical	0.0003	500000	Emmerson & Raffaelli (2004)[c]
1	1	Theoretical	0.01	0.01	Jonsson & Ebenman (1998)

[a] a_{ii} / a_{ij} ratios from empirical studies estimate a_{ij} directly from experimental data whilst a_{ii} are inferred from biological data rather than measured experimentally (with the exception of this study).

[b] Neutel *et al* (2007) and de Ruiter et al. (1995) define interaction strength to be elements of the Jacobian matrix, Φ_{ij}. We converted these elements into the community matrix by dividing the Jacobian by the equilibrium biomass of species *i*, i.e. $a_{ij} = \frac{\Phi_{ij}}{B_i^*}$.

[c] Interaction strengths in this study used predator-prey body sizes from the Ythan Estuary to estimate interaction strengths. We class these estimates as theoretical since they did not come from experimental data.

The effect of food web structure on interaction strengths

Plant intraspecific interaction strengths were found to vary with food web structure. It is not clear whether the differences in intraspecific interaction strength estimates are due to changes in plant conspecific interactions or non-linearity in the plant-aphid interspecific interaction strength. To estimate the plant intraspecific interaction strength (a_{11}) it was assumed that the plant-aphid interspecific interaction strength (a_{12}) is constant with respect to plant biomass density which implies that aphids have a linear functional response. If a_{12} is not constant then the differences between plant biomasses used to calculate the a_{11} term may be caused by biologically meaningful variation in the a_{12} term, reflecting a non-linear functional response.

Ecologically, it is entirely possible that intraspecific interactions are not constant with respect to food web structure. For example, plants in severe environments (severity here includes disturbances such as herbivory) can benefit from the proximity of neighbouring plants since under stressful conditions the benefits of a neighbour can outweigh the costs of competition (Brooker and Callaghan 1998, Brooker et al. 2008). In a field experiment where both plant (*Collinsia torreyi*) and herbivore (*Euphydryas editha*) densities were manipulated, it was found that the herbivores only reduced the fitness of the plants at low plant biomass density, but not at high plant biomass density (Parmesan 2000). It has also been observed that the crab *Chasmagnathus granulatus* regulates the balance of competitive and facilitative interactions between plant species *Spartina densiflora* and *Sarcocornia perennis* in Argentinean marshes (Alberti et al. 2008).

We found that plant-aphid interspecific interaction strength estimates did not vary between food web structures. This result is in contrast to Otto et al. (2008) who found that the presence of a second predator changed the interaction strength between a predator and herbivore. Plant- herbivore interaction strengths were not calculated for the Otto et al. (2008) study but it was identified that the assemblage of predators did have an impact on plant biomass.

In the present study it is clear that aphids were limited by absolute resource abundance rather than relative resource abundance which may explain why the lacewing larvae did not affect aphid biomass. In an insightful discussion of herbivory that considered the behaviour of the individual herbivore and the consequences of this behaviour in an ecosystem context Schmitz et al. (2008) proposed that if herbivores are limited by their rate of consumption rather than by resource availability, then predators (at a third trophic level) can have an impact on plant biomass since the remaining herbivores cannot increase their rate of consumption to compensate for the biomass that would have been consumed by the herbivores removed through predation. Alternatively, if herbivores are limited by the total amount of resources available for consumption then predators will not have an impact on plant biomass since the remaining herbivores will increase their consumption and the amount of biomass lost due to herbivory will not change.

The effect of species biomass density on interaction strengths

It is widely accepted that the interspecific interaction strength between a predator and prey species can vary with prey species density (Ruesink 1998, Case 2000, Sarnelle 2003, Vucic-Pestic et al. 2010). In this study, we found that aphids had a greater impact on plant biomass when plants were at low biomass density. This is consistent with a type II functional response where consumption rates (and therefore interaction strengths) decrease with increasing prey density. It is possible that part of the mechanism underlying the relationship between plant biomass density and plant- aphid interaction strength is attributable to the response of the plants to aphid damage, but since plant-aphid interactions are highly complex (Goggin 2007, Guerrieri and Digilio 2008), disentangling the effect of aphid functional response from plant response to aphid herbivory is difficult. This problem does not apply to predator- prey relationships where predators kill prey in discrete units and have a known functional response.

The DI is calculated using the same starting prey densities for the treatments where predators are present and absent which means that the DI makes no assumptions on the form of the interaction strength between predator and prey, it simply provides a figure to quantify the value of interaction strength for particular species densities. It is only when the DI is calculated at more than one prey density that one can inform the way interaction strength changes with prey density (Novak and Wootton 2010).

Conclusions

A limitation of many studies is the enumeration of just one measurable response (e.g. change in biomass or abundance) but numerous causes (e.g. prey species density, presence or absence of predator(s), predator(s) species density, species behaviour) may interact in a complicated way (Bender et al. 1984). This considerable problem applies to all previous studies using abundances and biomasses to estimate interaction strengths. The present experiment highlights the difficulty in extracting parameters from experimental data, e.g. the aphid-lacewing interspecific interaction estimate made using DI index assumes that any change in aphid biomass density is due to lacewing predation, but it is clear that plant biomass density had the greatest effect on aphid biomass density. So even if the model underlying the DI is a good approximation of species growth rates, it seems that small differences between individuals can have large effects on growth rates which can mask the interaction being estimated.

Given the complexities underlying measurable changes in species densities, we suggest that a great deal of uncertainty remains over the nature of species interaction strengths and empirical estimates of species interaction strengths should be used cautiously in making predictions about the real world consequences of future environmental change. Despite decades of research we still find that our ability to empirically measure simple interactions is limited, and that a gap still exists between the requirements of models and the availability of data with which to accurately parameterise them. Whilst the results of the present study only provide crude estimates of species interactions, they do provide qualitative insights into the presence of nonlinearities and indirect effects, which illustrates the importance of community structure on community dynamics.

We conclude that the IDI can be used to estimate intraspecific interaction strengths between species but these estimates can be affected by variation between individuals and, in the presence of other species, can be affected by non-linearities in interspecific interaction strengths and indirect effects. The results from this study found that both the magnitude of interaction strength estimates and the variation associated with the estimates increased with trophic level, that the ratio of intra- to interspecific interaction strength is small (a_{11} / a_{12} lies between -0.01 and -0.001), that intraspecific interaction strengths can vary with food web structure and that plant-herbivore interaction strengths can be nonlinear. To further understand how species interact within a community will require more experimental data that manipulates multiple species at multiple densities, that describes who interacts with whom, that quantifies species population dynamics through time (on more than just two occasions), and which ultimately provides a framework within which to validate model predictions regarding the future consequences of biodiversity loss.

APPENDIX A

Derivation of the Intraspecific Dynamic Index

Given the discrete-time version of the generalised Lotka-Volterra multispecies equations:

$$B^{H}_{i,t} = B^{H}_{i,0}\exp\left[\left(r_i + \sum_{j=1}^{n-1} a_{i,k}B_{k,0} + a_{ii}B^{H}_{i,0}\right)t\right] \quad \text{(1a)}$$

$$B^{L}_{i,t} = B^{L}_{i,0}\exp\left[\left(r_i + \sum_{j=1}^{n-1} a_{i,k}B_{k,0} + a_{ii}B^{L}_{i,0}\right)t\right] \quad \text{(1b)}$$

where :

$B^{H}{}_{i,t}$ is the biomass of species i at time t in the treatment where the initial density of species i was high

$B^{L}{}_{i,t}$ is the biomass of species i at time t in the treatment where the initial density of species i was low

$B^{H}{}_{i,0}$ is the initial biomass of species i in the high treatment

$B^{L}{}_{i,0}$ is the initial biomass of species i in the low treatment

r_i is the intrinsic growth rate of species i

a_{ik} is the per unit mass effect of species k on species i

$B_{k,0}$ is the initial biomass of species k

a_{ii} is the per unit mass effect of species i on itself

t is the length of time that the experiment runs for

Dividing equation (1a) by equation (1b) gives:

$$\frac{B^{H}_{i,t}}{B^{L}_{i,t}} = \frac{B^{H}_{i,0}}{B^{L}_{i,0}}\exp\left[\left(r_i + \sum_{j=1}^{n-1} a_{i,k}B_{k,0} + a_{ii}B^{H}_{i,0} - r_i - \sum_{j=1}^{n-1} a_{i,k}B_{k,0} - a_{ii}B^{H}_{i,0}\right)t\right]$$

$$= \frac{B^{H}_{i,0}}{B^{L}_{i,0}}\exp\left[\left(a_{ii}B^{H}_{i,0} - a_{ii}B^{H}_{i,0}\right)t\right]$$

Rearranging and taking the natural log of both sides of the equation, we obtain:

$$\ln\left(\frac{B^{H}_{i,t}B^{L}_{i,0}}{B^{L}_{i,t}B^{H}_{i,0}}\right) = \left(a_{ii}B^{H}_{i,0} - a_{ii}B^{H}_{i,0}\right)t$$

Thus

$$a_{ii} = \frac{\ln\left(\dfrac{B^{H}_{i,t}B^{L}_{i,0}}{B^{L}_{i,t}B^{H}_{i,0}}\right)}{\left(B^{H}_{i,0} - B^{L}_{i,0}\right)t}$$

APPENDIX B

Details of Experimental Method

Plants were grown under identical conditions for each time block. Approximately 150 broad bean seeds were soaked in water for 2 days, and then placed in trays of damp vermiculite for 8 days to germinate. After germination, 60 plants of similar size were selected and transplanted into pots filled with vermiculate and 100ml of Hoagland solution (concentration 1.6g of Hoagland per 1000ml of water). An additional 20 plants that varied in size were grown and used to calculate the relationship between a plant's fresh weight and dry weight. All the plants were placed under 30 watt Grolux fluorescent lights and after four days were given another 100ml of Hoagland solution. The lights had a day-night cycle of 16:8 hours. The plants remained under the lights for a further ten days where they were given 50ml of Hoagland solution every other day until the start of the experiment.

On the first day of the experiment 56 plants of a similar size were selected for the mesocosm experiment. Each whole plant was weighed after its roots were washed gently and dried, to remove any remaining vermiculite. Plants were then re-potted in vermiculite in their different density treatments, labelled and each pot was given 500ml of water followed by 200ml of Hoagland solution.

A stock culture of *Acyrthosiphon pisum* was reared under laboratory conditions on dwarf broad bean plants under 30 watt Grolux fluorescent lights with a day-night cycle of 16:8 hours. Fourth instar/adult aphids of length 2 – 3.5mm with an estimated mean length of 2.75mm were evenly distributed onto mesocosm plants with a dampened brush. Lacewing larvae were obtained commercially (Koppert Biological Systems in the Netherlands), and second instar lacewing larvae with a length of between 3 – 5mm were put onto plants using a damp brush.

All mesocosms were placed under 30 watt Grolux fluorescent lights with a day night cycle of 16:8 hours. On days three and five of the experiment each pot was given a further 200ml of Hoagland solution. At the end of the experiment the dry weight of the plants was estimated by removing the plants from the pots, washing the roots gently to remove all visible traces of vermiculite, and then dried in the oven at 60°C for 3 days. Living aphids and lacewing were carefully removed from each mesocosm and put into 70% alcohol before they were later dried at 60°C for 3 days.

To calculate interaction strengths, dry weights for each species at the start of the experiment were required. The initial dry weight of each plant was calculated from the relationship between fresh weight and the dry weight of the plants ($y = 0.27 + 0.06x$, $r^2 = 0.73$, $n = 71$). To estimate the initial dry weight of aphids and lacewing larvae, the initial abundances in each treatment were multiplied by the average dry weight of an adult aphid (0.000264g) and a second instar lacewing larva (0.000195g).

CHAPTER 3

PATTERNS OF TOTAL NET EFFECTS ACROSS FOOD WEBS OF VARYING SIZE AND COMPLEXITY

Abstract

The impact that a species has on the community in which it is embedded can be measured as a species' *total net effect*, which quantifies how a small sustained change in the equilibrium biomass density of an individual species affects the equilibrium biomass densities of *all* other species in the community. In this study, I examine how species traits (body size and linkage density) affect the total net effect that a species has in its community. The relationships were investigated over a range of food web properties (species richness, connectance, mean clustering coefficient, average shortest path length and the proportion of basal, herbivore, intermediate and top carnivore species) using a set of 100 synthetic webs and 2 real webs (Ythan Estuary and Tuesday Lake).

The results from this study show that there is a strong positive relationship between the body size of a species and the total net effect it has on a community, that is; species with a large body size have a large impact on their community. This relationship was found to be consistent whether trophic interaction strengths are measured on a per unit mass or per capita basis and the relationship holds for webs of varying size and complexity. The relationship between the linkage density of a species and the total net effect it has on a community seems to depend on the structure of the surrounding community. A negative relationship between the linkage density of a species and the total net effect it has on a community was found for a subset of 38 synthetic webs The webs where the negative relationship was present have low clustering coefficients and long average shortest path lengths compared to the subset of webs where the relationship was not present. The negative relationship between species linkage density and total net effects breaks was not present for smaller simpler webs.

Introduction

Ecosystems throughout the globe are changing due to human activities (Vitousek et al. 1997, Steffen et al. 2005), these changes can affect food webs through biodiversity loss (Pimm et al. 1995, Brooks et al. 2002, Butchart et al. 2010) and shifts in species traits (Root et al. 2003). Biodiversity loss reduces the size of food webs and simplifies their structure, while shifts in species traits can alter intrinsic rates and interactions between species. Additionally, interactions between species are affected by the size and structure of the surrounding community (Paine 1966, Koh et al. 2004, Otto et al. 2008) and changes to a single species can affect the entire community through the spread of direct and indirect effects (Schmitz et al. 2003, Ebenman and Jonsson 2005), thus the impacts of biodiversity loss, and changes to species traits, on ecological communities remain unclear.

The impact that a species has within communities of varying size and structure can be quantified by examining the *total net effect* of each species within the community. The *total* net effect of a species is a measure that quantifies how a small sustained change in the equilibrium biomass density of that individual species affects the equilibrium biomass densities of *all* other species in the community. This type of small sustained change in the equilibrium biomass (or population) density of a species was considered by Bender et al. (1984) where it was described as a *press perturbation*, and has since been studied in Yodzis 1988, Schmitz 1997, Laska and Wootton 1998, Montoya et al 2005, Montoya, Woodward et al. 2009, O'Gorman, Jacob et al. 2010, and in particular Berg et al. (2011) where it was used as a measure of community robustness.

The total net effect of a species has been largely defined within the Lotka-Volterra framework. In a Lotka-Volterra system, the parameters determining the nature and the strength of an interaction between two species are referred to as interaction strengths and are often denoted by a_{ij}. The units of a_{ij} can vary and can be quantified either in terms of *per capita* effects or *per unit biomass* effects. Here, we consider a_{ij} to represent the per unit mass effect of species j feeding on species i per unit of time. The community matrix is the matrix whose ij^{th} entry is a_{ij}, thus the community matrix contains the interaction strengths between every pair of species in the community, and it is often denoted by A. For clarity we note that the community matrix, A is different to the Jacobian matrix (often denoted by C) where the entries, c_{ij}, represent the per unit mass effect of species j on the *population* biomass of species i per unit of time. The analysis presented by Bender et al. (1984) shows that the net effect of species *j* on species *i* (the sum of both direct and indirect effects) can be calculated by applying a press perturbation to the equilibrium biomass density of species *j*, the effect of this press perturbation on the equilibrium biomass density of species *i* in a multispecies community is defined by the *ij*th element of the community matrix, A^{-1}. Such a press perturbation can occur through the sustained removal or addition of a constant biomass of a species to a community (e.g. fishing) or through a change in the intrinsic growth/mortality rate of a species (e.g. global warming induced changes to intrinsic rates or habitat loss). An alternative measure of net effects was used in a study by Berlow et al. (2009) where simulations were run to estimate the net effect of species in 600 different communities, ranging from 10-30 species. The net effect of species *j* on species *i* was defined to be the difference in the time averaged population biomass of species *i* in the presence and absence of species *j*.

When Yodzis considered the effect of press perturbations on a set of sixteen empirical food webs he found that the response of the communities was highly indeterminate (Yodzis 1988). Yodzis defined the elements of the community matrices randomly from within an ecologically plausible interval. For each of the 16 food webs he considered, 100 different feasible and locally stable parameterisations of the community matrix were examined. He found that not only were the magnitudes of species responses to a press perturbation unpredictable, the direction (either an increase or a decrease in population density) of a species responses could also vary depending on the parameterisation of the food web. He concluded that predicting the response of a community to a press perturbation would be *a daunting prospect indeed* (Yodzis 1988).

The elements of the inverse community matrix, A^{-1}, are determined by the structure and the magnitude of the entries in the community matrix *A*. Dambacher, Li et al. (2003) explored the effect of food web structure on the qualitative response of communities to press perturbations. The study examined the proportion of positive and negative feedback cycles that make up each element of the inverse community matrix and found that the direction of species response to a press perturbation is sometimes based solely on community structure, however, they found that in general, the elements of the inverse community matrix are a mixture of positive and negative feedback cycles and the direction of the response is dependent on the magnitude of the entries in the community matrix *A*.

The present study aims to further our understanding of the response of communities to press perturbations by investigating the factors that determine the magnitude of species net effects in communities. Specifically, by examining how species traits (body size and linkage density) and food web properties (species richness, connectance, mean clustering coefficient, average shortest path length and the proportion of basal, herbivore, intermediate and top carnivore species) affect the *total* net effect that a species has in a community. To understand the mechanisms driving these relationships we examine the relationship between species traits, food web properties and the community matrix and also between the community matrix and its inverse (Figure 3.1). Finally we checked the consistency of the relationships when trophic interactions were measured on a per capita basis rather than a per unit mass basis.

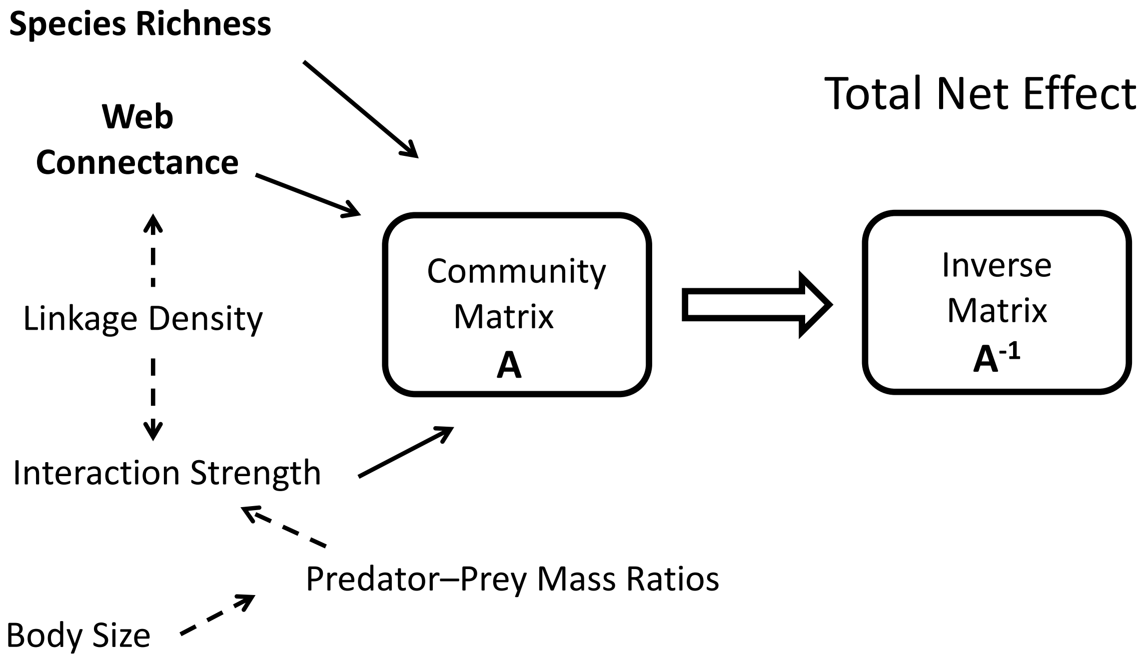


Figure 3.1 A schematic representation, showing how species total net effects can be influenced by species traits and food web properties via the community matrix. Note that food web properties are shown in bold type and species traits are shown in regular type.

Materials and Methods

Consider the following Lotka-Volterra system where dynamics of species *i* in a community consisting of *n* species is given by:

$$\frac{dB_i}{dt} = B_i\left(r_i + \sum_{j=1}^{n} a_{ij} B_j\right)$$

where B_i is the biomass of species *i*, r_i is the intrinsic growth rate of species *i* (kg.kg^{-1}t^{-1}) and a_{ij} is the per unit mass effect of species *j* feeding on species i per unit of time (kg^{-1}t^{-1}). We define the net effect of species *j* on species *i* to be the change in the equilibrium biomass density of species *i* due to the sum of both the direct and indirect effects caused by a small press perturbation to species *j*. The net effect of species *j* on species *i* is given by the ij^{th} element of the inverse community matrix, A^{-1}, denoted by γ_{ij} (Bender et al. 1984). The total net effect of species *j* is a measure of the change in equilibrium biomass densities of all species in the community following a small press perturbation to species *j*. We denote the total net effect of species *j* by S_j which is defined to be the sum of the absolute values of elements of column j in the inverse community matrix A^{-1}, i.e. $S_j = \sum_{i=1}^{n} |\gamma_{ij}|$ this measure was first used by (Berg et al. 2011) where it was referred to as the sensitivity of equilibrium abundances to changes in growth rates.

To examine the relationship between a species trait and the community matrix and between the community matrix and its inverse we calculate the following metrics: the *total direct effect of a species*, the *mean direct effect of a species* and the *variation in the direct effect of a species* (see Table 3.1 for definitions).

Table 3.1 Definitions of the community matrix metrics.

Description	**Formula**
The total direct effects of species *j*, D_j , is defined to be the sum of the absolute values of the j^{th} column of the community matrix A:	$D_j = \sum_{i=1}^{n} \lvert a_{ij} \rvert$
The average direct effect of species *j*, is given by:	$\overline{D}_j = \frac{\sum_{i=1}^{n} \lvert a_{ij} \rvert}{n}$
The variation in the direct effect of species *j*, is given by*:*	$Var(D_j) = \frac{\sum_{i=1}^{n} \left(\lvert a_{ij} \rvert - \overline{D}_j \right)^2}{n-1}$

Food Webs

Analyses were carried out on two sets of food webs; 100 synthetic webs and 2 real webs (Ythan Estuary and Tuesday Lake). Each of the 100 synthetic food webs was created sequentially using an assembly algorithm from a previous study (Säterberg et al. 2013). The algorithm was initiated with a feasible locally stable community consisting of 7 competing basal species whose body masses were drawn from a uniform distribution. At each step a new species was added to the community and the dynamics observed. Each new species, either basal, herbivore or carnivore was chosen at random and allocated a body mass drawn from a uniform distribution associated with the relevant trophic position. All feeding interactions were determined from this body mass (see Appendix C for a detailed description). After each addition, the new equilibrium was checked for feasibility and local stability. If the new equilibrium did not satisfy the criteria then the community was returned to the previous step and the process repeated. If these criteria were satisfied then the new community was retained and the process repeated until the community contained 50 species.

The Ythan Estuary is located near Aberdeen in Scotland where the Ythan River meets the North Sea. The Ythan Estuary food web is well resolved and has been studied extensively (Hall and Raffaelli 1991, Dunne et al. 2002a, Montoya and Solé 2002, Emmerson and Raffaelli 2004). The version used in this study has is a total of 87 species, consisting of 4 basal species (detritus, phytoplankton, algae and particulate organic matter), 31 herbivore species (including macroinvertebrates, birds and fish) and 52 carnivore species (including crustaceans, molluscs, polychaetes, fish and birds) (Emmerson and Raffaelli 2004). The body sizes range from 10^{-11} to 10^{2} kg. Tuesday Lake is a freshwater lake located in Michigan, United States. The Tuesday lake food web is one of the most widely studied food webs (Cohen et al. 2003, Reuman and Cohen 2004, Jonsson et al. 2005, Petchey et al. 2008a, Thierry et al. 2011, Eklöf et al. 2012). The version used in this study describes a pelagic community containing 51 species, consisting of 29 basal species (phytoplankton), 15 herbivore species (zooplankton) and 7 carnivore species (zooplankton and fish) (Cohen et al. 2003). The body sizes range from 10^{-13} to 10^{-1} kg.

Population Dynamics

All food webs were initially parameterised following the energetics based approach used in (Säterberg et al. 2013) (see Appendix C for details) with one difference; interspecific competition between basal species was not included in any of the food webs used in this study. Interspecific competition between basal species was removed for this study because we focus on the relationship between the linkage density, defined by trophic interactions, of a species and its total net effect in the community. The inclusion of non-trophic interactions in the community matrix would alter both the linkage density of a species and the inverse community matrix. The removal of interspecific competition between basal species in this study had a destabilising effect on the synthetic food webs used and, in addition, it was not possible to obtain feasible, stable parameterisations for the two real food webs using this parameterisation method alone. It was necessary to introduce an additional parameterisation algorithm (Pimenov, manuscript in preparation) that made small adjustments to the community matrix by allowing the parameter that determined the strength of trophic interactions to vary between ecological limits, this algorithm consistently produced food webs that were feasible, and locally stable (Appendix C).

Extinction sequences

To investigate the effect of biodiversity loss on the relationships between species body size, linkage density and total net effects, a series of extinction sequences were carried out on the synthetic and real webs to create subsets of food webs of varying size and complexity. For each pre-extinction food web, 100 different random extinction sequences were simulated. After setting initial biomass abundances to equilibrium values, a primary extinction removed a single (randomly chosen) species from the web and the dynamics of the new community were monitored. At this point the population biomasses could settle down to a new equilibrium, cycle, or secondary extinctions could occur. The simulation was stopped when all species biomass abundances were within 10% of the new equilibrium biomass abundances. Any species exhibiting a 99.9% decline in biomass density were removed, recorded as secondary extinctions and the simulation continued. If there were no further secondary extinctions and the new equilibrium was locally feasible and stable then the results were recorded and the next primary extinction took place. If species biomass abundances did not settle to within 10% of the new equilibrium biomass abundances within 10,000 time steps then the biomass abundances were checked and any species exhibiting a 99.9% decline in biomass density were removed, recorded as secondary extinctions and the simulation continued. This sequence of events was repeated until all species had been lost from the community. Secondary extinctions often occurred, so the size of the community after each primary extinction varied.

Data analysis

For each pre-extinction food web (containing all 50 species), the relationships between the total net effect of species j, and the body size and linkage density of species j were examined using multiple linear regression analysis, where the data for each explanatory variable was standardised before use. The effect of the measure used to estimate interaction strengths (per unit mass vs. per capita) on the relationship between species traits and total net effects was checked by performing the same multiple regression analysis on the set of synthetic food webs where interaction strengths were measured on a per-capita basis.

To further understand the relationships, a data set was created from all the pre-extinction synthetic webs that showed a negative relationship between species total net effects and linkage density (approximately 40% showed this negative relationship). The new data set was split containing the following four trophic groups: basal, herbivore, intermediate consumers and top carnivores. For each trophic group, the relationships between a species total net effect and its body size and linkage density were examined using a mixed effect model with species body size and linkage density as fixed effects and food web ID as a random effect on the intercept and on the slope of species linkage density.

To investigate why the total net effect of each species, in the community, was related to its body size and linkage density we calculated Pearson’s correlation coefficients between a species body size/linkage density and its total direct effect, D_j (the column sum of a species entries in the community matrix) and between a species total direct effect, D_j and its total net effect.

The effect of food web structure on the relationship between species linkage density and total net effects was examined further by splitting the synthetic webs into two data sets, one set where the statistical analysis detected a negative relationship between species linkage density and total net effects and one set where it did not. Differences in the following food web properties were checked using t-tests: food web connectance, mean clustering coefficient, average shortest path length and the proportion of basal, herbivore, intermediate and top carnivore species.

The effect of biodiversity loss on the relationship between species body size, linkage density and total net effect was explored using data from the extinction sequences. For each complete food web, the extinction sequences yielded a subset of webs of varying size and complexity and for each sub-web the Pearson's correlation coefficient between species body size and total net effect and species linkage density and total net effect was calculated.

Models were selected using stepwise deletion with the likelihood ratio test. Final parameter estimates, along with standard errors for all parameters retained in each model, are presented in Appendix D (Tables D1, D2 and D6). Homogeneity of variance and normality of the standardised residuals was satisfied for all models. All statistical analyses were undertaken using R version 2.14.2 (R Development Core Team 2013), mixed effect models used the 'lme4' package. The simulations and calculation of correlation coefficients were performed using MATLAB version 7.7.0 (MATLAB 2008).

Results

The relationships between species body size, linkage density and total net effect were initially analysed for each of the synthetic webs and for the Tuesday Lake food web before any extinctions sequences were run. Three of the synthetic webs had ill-conditioned community matrices (likely due to large differences in the order of magnitude of entries) so were excluded from the analysis, leaving a set of 97 synthetic webs of size 50 to be analysed. The community matrix for the Ythan estuary food web was also ill-conditioned but rather than exclude this data set entirely we analysed the largest well-conditioned sub-web (containing 53 species) obtained from the extinction sequences.

Out of the 97 synthetic food webs it was found that 8 had a significant negative correlation between species body size and linkage density (see Appendix D, Table D3). For these 8 webs species linkage density was excluded as an explanatory variable due to collinearity. Initially species trophic height was also considered as an explanatory variable but since it was strongly collinear with body size in all the webs examined it was also excluded (see Appendix D, Tables D3 and D4). The full linear model used for each of the remaining 89 synthetic webs and the two real webs included body size, linkage density and their two-way interaction as explanatory variables.

The relationship between a species body size and its total net effect

There was a positive relationship between the body size of a species and its total net effect for all the webs analysed (see Figure 3.2a for correlation coefficients and Appendix D, Tables D1 and D2 for linear models), indicating that larger bodied species have the greatest total net effect in a community. Further, over all 97 synthetic food webs, body size accounted for, on average, 87% of the variation in total net effects, thus we conclude that body size is the most influential factor in determining a species total net effect in the community. There was a negative relationship between the body size of a species and its total direct effect, D_j and a negative relationship between a species total direct effect, D_j and its total net effects for the synthetic webs (Figure 3.2b and c) and the real food webs (Appendix D, Table D5).

For the set of synthetic food webs where trophic interactions were measured on a per capita basis, the relationship between the body size of a species and its total net effect remained positive (Figure 3.2d for correlation coefficients and Appendix D Table D6 for linear models). However, there was a positive relationship between the body size of a species and its total direct effect, D_j, (Figure 3.2e) and a positive relationship between a species total direct effect, $\mathrm{D_j}$ and its total net effect (Figure 3.2f). Despite differences in the community matrices, perturbations to large bodied species have the greatest impact on equilibrium densities for both per capita and per unit mass measures.

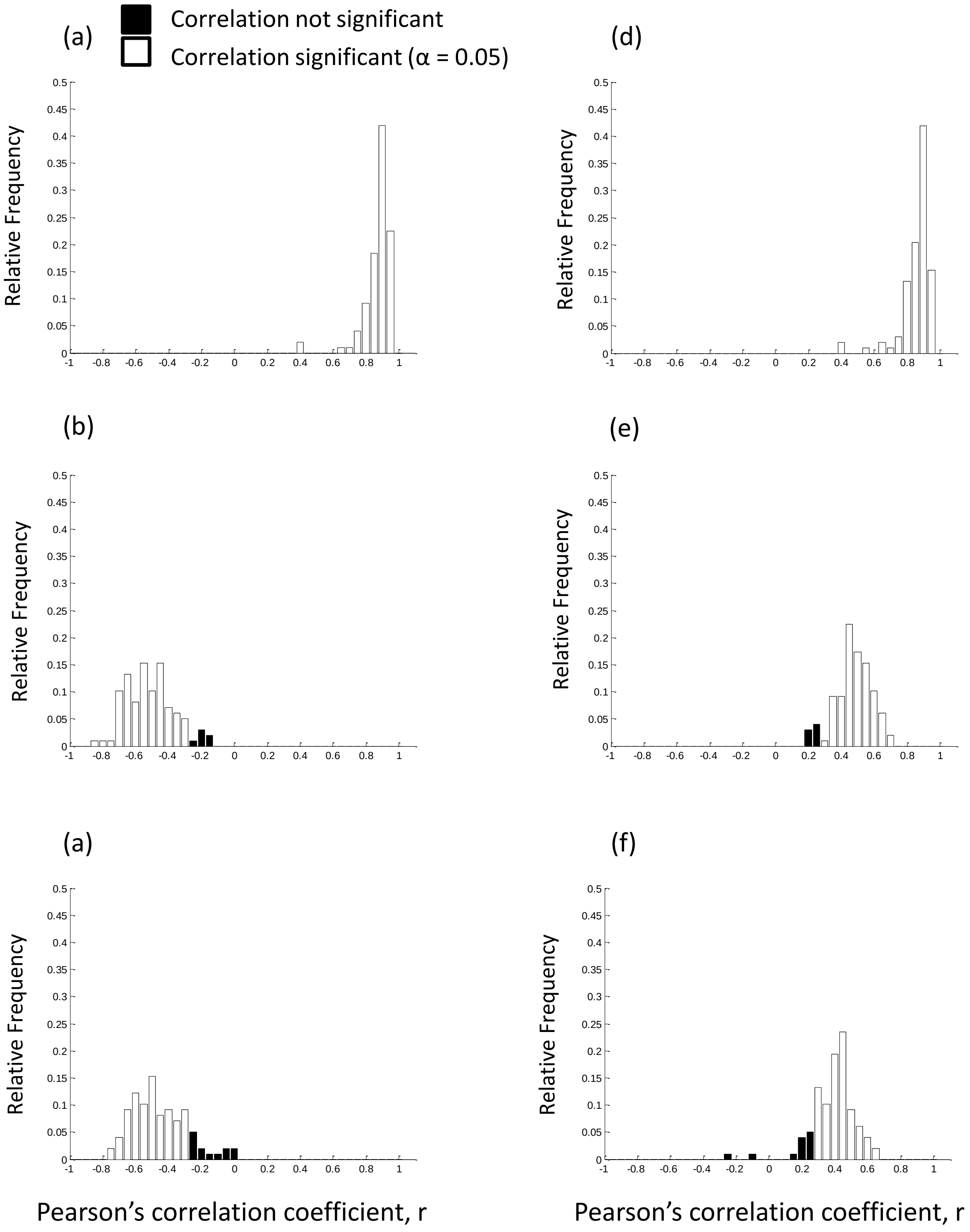


Figure 3.2 The distribution of Pearson's correlation coefficients (r) between (a) a species body size and its total net effects (per unit mass measure), (b) a species body size and its total direct effect D_j (per unit mass measure), (c) a species total direct effect D_j and its total net effect (per unit mass measure), (d) a species body size and its total net effects (per capita measure) (e) a species body size and its total direct effect, D_j (per capita measure) (f) a species total direct effect, D_j and its total net effect (per capita mass measure).

The relationship between a species linkage density and its total net effect

In the set of 89 synthetic webs where species linkage density was not collinear with body size, there was a negative relationship between the linkage density of a species and its total net effect for 38 webs, a weak positive relationship for 1 web and for the remaining 50 webs species linkage density was not retained in the model (see Figure 3.3 for a summary or Appendix D, Table D1 for details). Out of the subset of 38 webs that showed a negative relationship between species linkage density and total net effect there were 4 webs that also retained a two way interaction between species body size and linkage density, suggesting that, in those webs, the relationship between linkage density and total net effect may depend on the body size of a species. There was a negative correlation between species linkage density and total net effects for the Ythan Estuary sub-web but the Tuesday Lake food web showed a positive correlation (Appendix D, Table D2).

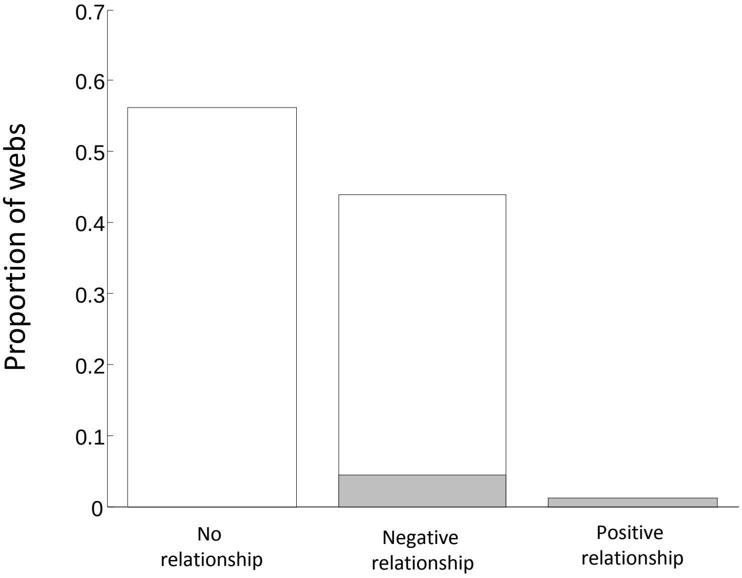


Figure 3.3 Bar chart showing the proportion of food webs that showed (i) no relationship, (ii) a negative relationship or (iii) a positive relationship between species linkage density and total net effect. The grey shading represents the proportion of food webs where there was an interaction term present between body size and linkage density**.**

Further analysis of the set of 38 webs that showed a negative relationship between species linkage density and total net effect indicates that this negative relationship only occurs in the basal and herbivore trophic levels (Table 3.2). The positive relationship between body size and total net effects is consistent within the basal, herbivore and intermediate consumer trophic levels but no relationship was detected between body size and net effects for the top carnivores (Table 3.2). The lack of relationship for top carnivores may be due to the small number of top carnivores present in the food webs.

Table 3.2 Results from the four mixed effects models analysing the relationship between species body size, linkage density and total net effect within each trophic level for the set of 38 webs that showed a negative relationship between linkage density and total net effect. Models were selected using stepwise deletion with the likelihood ratio test and therefore all terms retained in the model and Table 3.2 are of importance.

Trophic Level	**Intercept**		**Body Size**		**Linkage Density**	
	Estimated Coefficient	**Standard Error**	**Estimated Coefficient**	**Standard Error**	**Estimated Coefficient**	**Standard Error**
1	4.33	0.13	0.21	0.02	-0.16	0.05
2	9.02	0.14	0.38	0.03	-0.43	0.06
3	8.54	0.13	0.33	0.06		
4	9.51	0.15				

The full model analysed was given by: $\log(Y_{jk}) \sim \alpha + \beta_1(\log(m_{jk})) + \beta_2(L_{jk}) + \beta_3(\log(m_{jk})L_{jk}) + \gamma_k + \beta_{2k}(L_{jk}) + \varepsilon$ where Y_{jk} represents the total net effect of species j in food web k, m_{jk} represents the body mass of species j in food web k and L_{jk} represents the linkage density of species j in food web k.

The parameter γ_k represents the random effect of food web k on the intercept and β_{2k} represents the random effect of food web k on the slope for linkage density.

Final model for trophic level 1: $\log(Y_{jk}) \sim \alpha + \beta_1(\log(m_{jk})) + \beta_2(L_{jk}) + \gamma_k + \beta_{2k}(L_{jk}) + \varepsilon$

Final model for trophic level 2: $\log(Y_{jk}) \sim \alpha + \beta_1(\log(m_{jk})) + \beta_2(L_{jk}) + \gamma_k + \beta_{2k}(L_{jk}) + \varepsilon$

Final model for trophic level 3: $\log(Y_{jk}) \sim \alpha + \beta_1(\log(m_{jk})) + \gamma_k + \varepsilon$

Final model for trophic level 4: $\log(Y_{jk}) \sim \alpha + \gamma_k + \varepsilon$

Correlations between a species linkage density and its total direct effect, D_j, its mean net effect, $\overline{D}_j$ and the variance of the direct effects, $\mathrm{Var}(D_j)$ were checked for all 38 webs that showed a negative relationship between species linkage density and its total net effect but no relationships were found (Appendix D, Table D7).

To check the effect of food web structure on the relationship between linkage density and total net effect, the synthetic food webs were split into two groups; group A contained all 38 webs that showed a negative relationship between linkage density and total net effect and group B contained all 50 webs where no relationship was found. Differences in food web properties where checked using t-tests. The mean clustering coefficient for webs in group A (0.19) was significantly less than the mean clustering coefficient for webs in group B (0.22, p = 0.04, n = 88) and the average shortest path length for webs in group A was significantly longer (1.92) than the average shortest path length for webs in group B (1.86, p = 0.01, n = 88). No significant differences in food web connectance or the proportion of species at each trophic level were detected.

For the case where trophic interaction strengths were measured on a per capita basis, there were 83 synthetic webs where the community matrices were invertible and species linkage density was not collinear with body size. Out of this set of 83 webs, there was a negative relationship between the linkage density of a species and its total net effect for 27 webs and for the remaining 56 webs species linkage density was not retained in the model (Appendix D Table D6). Out of the 27 webs where a negative relationship was found for the per capita measure, 25 of these also showed a negative relationship for the per unit mass measure, giving a positive percentage agreement value of 93%. Out of the 56 webs where a negative relationship was not detected for the per capita measure, 45 of these did not show a negative relationship for the per unit mass measure, giving a negative percentage agreement value of 80%. Overall, out of the 83 webs, the detection of a negative relationship (or not) was consistent for both measures in approximately 84% of the webs (Table 3.3).

Table 3.3 The effect of the unit of measurement on the distribution of webs that had a negative relationship between species linkage density and total net effects.

Per unit mass measure	Per capita measure		
	Negative Relationship	**No Relationship**	**Total**
Negative Relationship	25	11	36
No Relationship	2	45	47
Total	27	56	83

The effect of biodiversity loss on total net effects

The mean net effect was calculated for each pre-extinction synthetic food web and for each food web generated by the extinction sequences. For each pre-extinction synthetic food web and its subset (97 data sets), Pearson's correlation coefficient between the mean net effect and web size was calculated. The correlations show that larger webs have larger mean net effects (Figure 3.4).

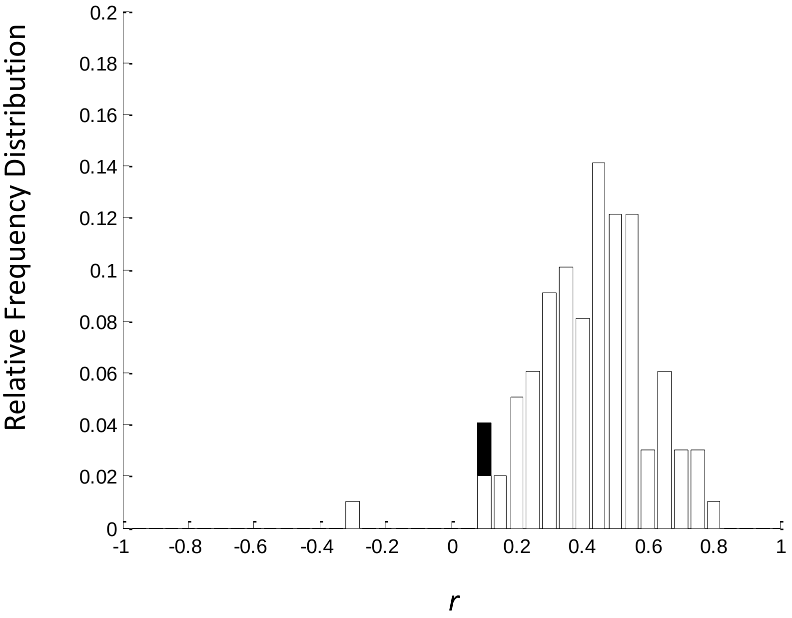


Figure 3.4 The distribution of Pearson's correlation coefficients (r) between webs size and the mean net effect calculated for each web for all 97 data sets generated from the synthetic webs. All data sets apart from one showed a positive relationship between web size and mean net effect. The mean net effect for each web was calculated by averaging over all the rows and columns of A^{-1}

The correlation coefficient between species body size and total net effect was calculated for all 97 pre-extinction synthetic webs and their subsets. The positive relationship between species body size and total net effect holds as webs get smaller (Figure 3.5a). To check whether the negative relationship between species linkage density and total net effects remains as webs get smaller, the correlation coefficient between species linkage density and total net effect was calculated for the set of 38 synthetic webs that showed a negative relationship and their subsets (Figure 3.5b). In general, the relationship seemed to break down as webs got smaller, although some strong negative correlations did remain for smaller webs. It is possible that the strong negative correlations found for small webs are due to an increase in collinearity between linkage density and body size as webs get smaller.

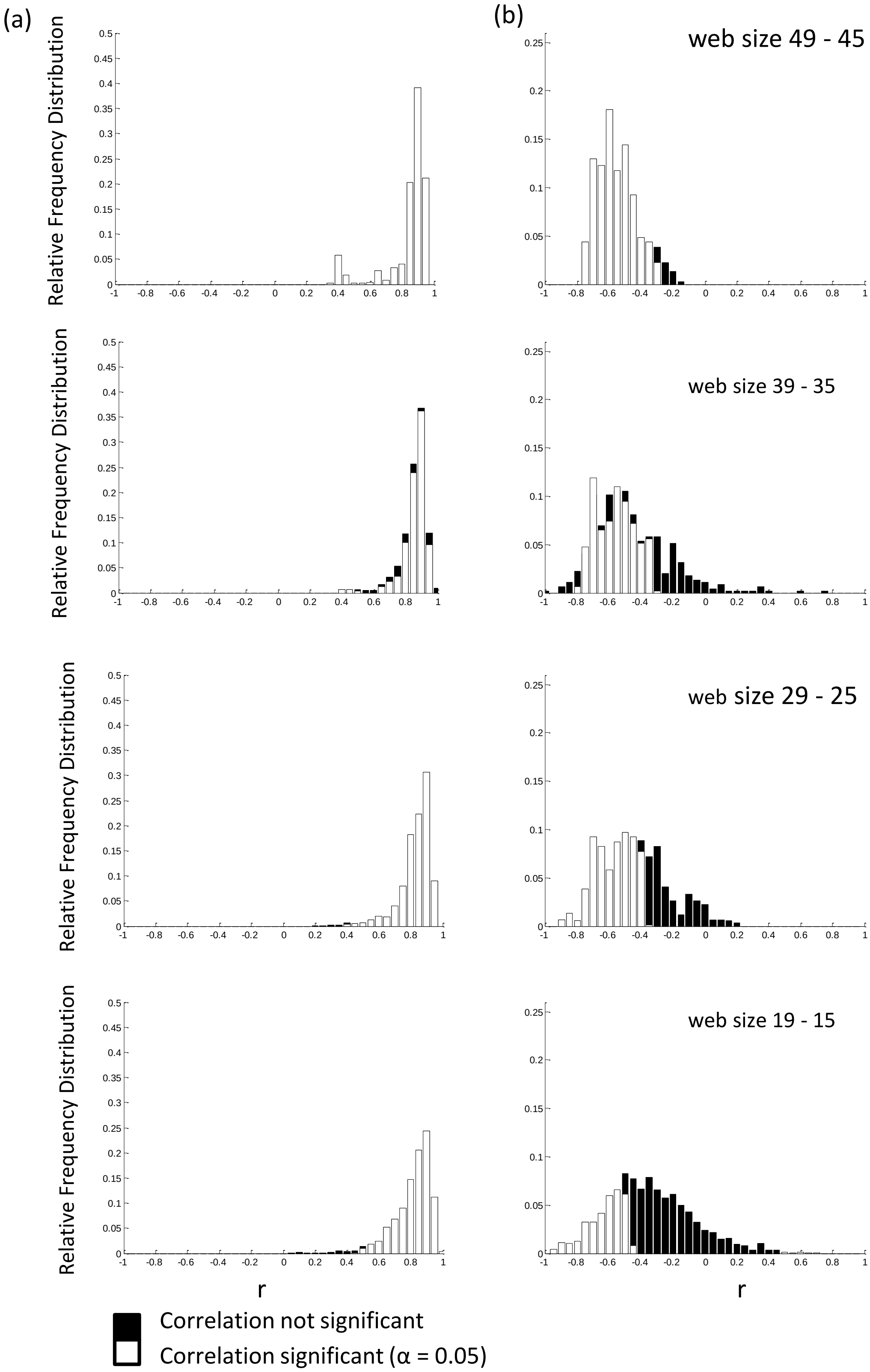


Figure 3.5 (a) The positive relationship between species body size and total net effects holds as webs get smaller. (b) The negative relationship between species linkage density and total net effects breaks down as webs get smaller.

Discussion

Five main results emerged from this study: first, there is a strong positive relationship between the body size of a species and the total net effect it has on a community (Figure, 3.2a, Appendix D, Tables D1 and D2 and Figure 3.5a). Second, the relationship between the linkage density of a species and the total net effect it has on a community seems to depend on the structure of the community: the subset of food webs where a negative relationship between a species linkage density and its total net effect was detected have low clustering coefficients and long average shortest path lengths compared to the subset of webs where the relationship was not detected. Third, the relationships between body size and species total net effects are consistent whether trophic interaction strengths are measured on a per unit mass or per capita basis. Fourth, on average, species have larger net effects in species rich communities (Figure 3.4). Fifth, the positive relationship between species body size and total net effects holds as webs get smaller, but the negative relationship between species linkage density and total net effects breaks down as webs get smaller.

Body Size

There was a strong positive relationship between the body size of a species and the total net effect it has on a community for all the webs examined, supporting the results from previous studies on the Ythan Estuary food web (Montoya 2005) and the Baltic Sea and Lake Vättern food webs (Berg et al. 2011), where, for each food web a positive relationship between species body size and total net effect was found. This result implies that perturbations to species with a large body size will have greatest impact on the equilibrium biomass distribution of a community. However we note the results from (Berg et al. 2011) where the relationship between body size and total net effect depended on the type of perturbation applied. If the perturbation considered was of the same order of magnitude to all species regardless of body size then a positive relationship was found. For the Baltic Sea and Lake Vättern food webs, if the perturbation applied was proportional to the growth rate of a species then the relationship was reversed and the smallest species tended to have the largest net effect in the community. For completeness we checked the relationship between body size and total net effect, when the perturbation was proportional to the growth rate and we found that the relationship remained positive but was weak and was only significant for 37 of the 97 synthetic food webs (Appendix D, Table D8). For our synthetic data set the positive relationship between body size and total net effects was strong enough that the scaling of the total net effects by the growth rate of a species did not affect the sign of the relationship, only the magnitude. This different result may be due to the fact that the synthetic webs used in this study are more strictly size structured than the real webs used in Berg et al. (2011). The study by Montoya (2005) did not detect a relationship between body size and the average net effect of a species for the Broadstone stream food web. One possible explanation put forward was that since there was a high level of redundancy in the top trophic level of the Broadstone stream, species of a similar size may compensate following perturbations to large bodied species thus reducing the impact of the perturbation. Alternatively, it was proposed that the Broadstone stream food web did not contain the large predators such as birds that were present in the Ythan Estuary food web so that the gradient of body size present in the Broadstone stream food web was not large enough for the relationship to emerge. It is interesting to note that in the study (Montoya 2005), the community matrix for the Ythan Estuary food web was parameterised using predator-prey body size ratios, similarly to the study presented here, whereas the Broadstone stream food web was parameterised empirically using information from gut analysis (Woodward and Hildrew 2002).

To identify the mechanism leading to a positive relationship between body size and total net effect, we examined the column sums of the community matrix (the total direct effect D_j) and found that they were negatively correlated with species body size, and that in turn the column sums of the community matrix were negatively correlated with the column sums of the inverse matrix (the total net effects) (Figure 3.2 and 3.6 for an overview). The negative relationship between species body size and its entries in the community matrix is a consequence of the metabolic based parameterisation of the food webs, one which has been widely implemented in a number of studies, e.g. (Yodzis and Innes 1992, Brose et al. 2005a, Otto et al. 2007, O'Gorman et al. 2010). Species with a large body size have a lower per unit mass consumption rate than species with a small body size, thus per unit mass interaction strengths (the entries in the community matrix) are smaller. In light of this, the positive relationship between species body size and its total net effect seems counterintuitive: species with small direct effects have large net impacts on equilibrium biomass abundances. This relationship is a result of the inversion process which, for a community of 50 species, is difficult to elucidate. We considered whether the negative relationship between the column sums of the community matrix (D_j) and the column sums of its inverse matrix (total net effect) was simply a result of the inversion process, but it is not true in general that if column j of a matrix has a small sum (relative to the other columns) then column j of the inverse matrix will have a large sum (relative to the other columns). This fact is highlighted when we consider the case where trophic interactions are measured on a per capita basis:

species with a large body size have strong trophic interactions and thus the column sums of the community matrix are large. When we checked the relationship between the column sums of the community matrix and its inverse (where trophic interactions are measured on a per capita basis) we found a positive relationship, i.e. species with a large total direct effect also have a large net effect. We conclude that the relationship between a species body size and its total net effect is not driven by the column sums of the community matrix but, encouragingly, the relationship is consistent for both per unit mass and per capita measures of interaction strength.

The results from the extinction sequences showed that species with a large body size have the greatest net effect in the community regardless of species richness. As food webs decreased in size, species with a large body size still had the greatest total net effect in the community. The strength and consistency of this positive relationship predicts that a wide range of ecological communities can be greatly affected by perturbations to large bodied species, which has been documented empirically (Wootton 1993, Estes and Duggins 1995, Shurin et al. 2002, Estes et al. 2011). To further add to the vulnerability of communities, it has also been documented that large bodied species are often the most at risk to human-induced perturbations (Petchey et al. 1999, Myers and Worm 2003, Estes et al. 2011).

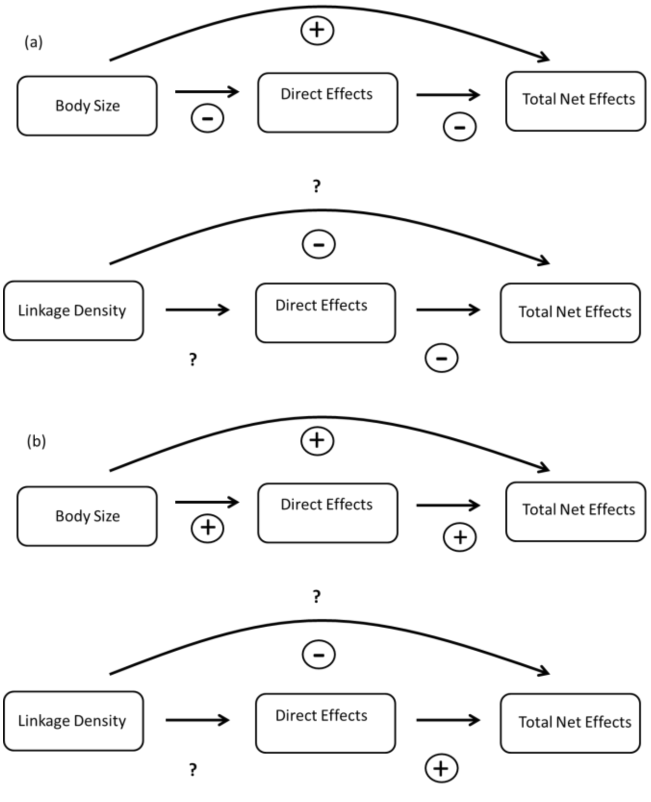


Figure 3.6 Diagram summarizing the relationships between a species body size, linkage density, total direct effects D_j, and its total net effects for case (a) where trophic interactions are measured on a per unit mass basis and for case (b) where trophic interactions are measured on a per capita basis. Species linkage density is not correlated with total direct effects $D_{j,}$ the mean direct effects or the variance of the direct effects Var(D_j).

Linkage Density

The negative relationship between the linkage density of a species and its total net effect was only present for 38 of the 97 food webs analysed, indicating that a species total net effect may depend on the structure of the community in which it is embedded. A negative relationship between species linkage density and its average net effect was found in the experimental marine communities of Lough Hyne studied by O'Gorman et al. (2010), where average species net effects were calculated empirically (using a modification of the dynamic index) and theoretically (using metabolic scaling similar to the present study). Both the theoretical and the empirical estimates of average net effects had a negative relationship with species linkage density. This negative relationship was also found for the Ythan Estuary and Broadstone Stream food webs (Montoya et al 2005), but was not present in the Baltic Sea and Lake Vättern food webs (Berg et al. 2011).

Further examination of the set of 38 webs where a negative relationship between linkage density and total net effect was detected, found that the negative relationship was only present in the basal and herbivore trophic levels. This could be due to the fact that the negative relationship between linkage density and total net effect is relatively weak and the lower numbers of consumer and top carnivore species make it less likely to be detected statistically.

For the 38 synthetic webs where the negative relationship between species linkage density and total net effect was present, there were no obvious relationships detected between the linkage density of a species and its entries in the community matrix. The lack of relationships is possibly due to the overwhelming effect of body size on a species direct effect; however, there were structural differences between the set of 38 synthetic food webs where the negative relationship was present and the set of 50 synthetic webs where it was not. The 38 synthetic webs where the negative relationship was present had significantly lower clustering coefficients and significantly longer average shortest path lengths than the 50 webs where the relationship was not present. To calculate the clustering coefficient, the number of feeding links between species that have a direct link to a focal species is divided by the number of links that could possibly exist between them and this ratio is averaged over all species in the web. Thus, for the set of food webs where a negative relationship was detected, a species neighbours are less likely to be connected to each other than in the set of webs where the relationship was not detected. It is possible that the effect of a species having many links to other species is reduced in webs with high clustering coefficients since the clusters of species may act in a similar way to a highly connected species.

The average shortest path length is calculated by averaging the most direct path between each species pair in the food web. The set of webs where the negative relationship between species linkage density and total net effects was present had significantly longer average shortest path lengths that the set of webs that did not; one possible explanation for this is that in webs with a long average shortest path length, there are no shortcuts (through omnivory) and therefore there are more links for a species effect to pass through, weakening interactions so that weak effects are weakened further in webs with a long average shortest path length. Although have possible biological reasons for the effect of food web structure on the relationship between species linkage density and total net effect have been outlined, it should be noted that while the results were statistically significant, it is possible that they may not be biologically significant and further investigation is needed.

The analysis of the relationship between linkage density and species total net effect for the synthetic webs where trophic interactions were measured on a per capita basis found a set of 27 webs where the negative relationship was present; 25 out of the set of 27 per capita webs were also present in the set of 38 per unit mass webs. The consistency of the results across different patterns of interaction strength in the community matrix (i.e. per capita or per unit mass measures of interaction strength) indicates that the negative relationship is a result of the topological structure of the community matrix.

The negative relationship between linkage density and total net effect broke down as biodiversity decreased. As biodiversity decreases, so too does the potential number of trophic links that a species can have, thus the gradient of linkage density is reduced and the relationship breaks down.

Mean net effect

The mean net effect for a community (the mean entry in the inverse community matrix) had a positive correlation with biodiversity; larger webs had larger mean net effects. If a community has a large mean net effect then small changes to a species equilibrium biomass densities cause large changes to the distribution of community biomass densities. The larger the changes in equilibrium biomass densities the more likely it is that a community is destabilised and extinctions will occur. This may imply that communities with high biodiversity are less stable than communities with few species, as shown for the community matrix (May 1973) where interaction strengths are randomly assigned. May's (1973) results have since been contradicted in many studies where ecological and empirical information was used to estimate trophic interaction strengths (Yodzis 1981, Moore and William Hunt 1988, de Ruiter et al. 1995, Jonsson and Ebenman 1998, McCann et al. 1998, Neutel et al. 2002, Emmerson and Raffaelli 2004, Neutel et al. 2007). In general, it is not true that the larger the dimensions of a matrix the larger the elements of its inverse so although we have found this pattern in our study, examination of species total net effects in other studies is needed.

In this study we examined the total net effect of a species by summing the absolute values of the entries of the inverse community matrix which gives a measure of the influence of a species in a community. Given the complex nature of the inversion process, it is difficult to predict entries in the inverse community based on entries in the community matrix (Yodzis 1988, Dambacher et al. 2003). The aggregation of species pairwise net effects into a measure of a species total net effect has revealed relationships between species traits and its net effects that were indeterminate when examined at a finer scale. We found that species body size is overwhelmingly important in determining the impact of a species; species with large body size had a large impact on the distribution of equilibrium biomass abundances. The impact of highly connected species on equilibrium biomass abundances was less clear and may depend on the structure of the community; for a subset of webs, highly connected species had a small impact on the distribution of equilibrium biomass abundances. The overwhelming effect of body size on a species net effect may have masked the effect of species linkage density and examination of communities with a less rigid size structure may be necessary. These results may be useful in identifying keystone species and eventually may have implications for conservation strategies for size-structured communities.

APPENDIX C

Here we describe the derivation of the metabolic scaling used to parameterise the community matrix for the food webs used in Chapters 3, 4 and 5 (Säterberg et al. 2013). Consider the following Lotka-Volterra system where the dynamics of species i in a community consisting of n species is given by:

$$\frac{dBi}{dt} = B_i\left(r_i + \sum_{j=1}^{n} a_{ij}B_j\right)$$

where B_i is the biomass density of species i, r_i is the intrinsic growth rate of species i and a_{ij} is the per unit mass effect of the consumer species j feeding on the resource species i per unit of time.

Growth rates

Let m_i represent the body mass of species i. The growth rate of species i is related to the body mass of species i by:

$r_i = C_r m_i^{-\frac{1}{4}}$ (Blueweiss et al. 1978, Peters 1983)

where C_r is positive (here set to 0.0041) if species i is a basal species and negative (set to -1.1935 $10^{\wedge-5)}$ if species i is a consumer species (McCoy and Gillooly 2008).

Trophic interaction strengths

The trophic interaction, strengths, a_{ij}, represent the per unit mass effect of the consumer species j on the growth rate of the resource species i. To estimate a_{ij}, we first consider the metabolic requirements of the consumer species j. The per unit mass feeding rate of species j with body mass m_j can be described by:

$F_j = C_F m_j^{-\frac{1}{4}}$ (Peters 1983) (1)

where the feeding rate is measured in units kg.kg^{-1}day^{-1}. A consumer species may feed on more than one resource species so multiplying the feeding rate of an individual consumer species j (1) by its prey preference, (z_{ij}), gives the biomass of species i consumed by an individual of species j:

$$F_{ij} = z_{ij} C m_j^{-\frac{1}{4}} \qquad (2)$$

Now F_{ij} represents the per unit mass effect of species j on the growth rate of the population biomass density of species i, (i.e. $F_{ij} = a_{ij} B_i$ where B_i is the biomass density of species i). To estimate the per unit mass effect of an individual of species j on the per unit mass growth rate of species i we divide the expression through by the biomass density of species i. The number of individuals in a population has been shown to scale with body mass as $N_i = C_i m_i^{-\frac{3}{4}}$ (Brown et al. 2004) so we can write:

$$B_i = N_i m_i = C_i m_i^{\frac{1}{4}} \qquad (3)$$

Dividing (3) by yields:

$$a_{ij} = z_{ij} C_{aij} \left(m_i m_j\right)^{-\frac{1}{4}}$$

where C_{aij} is a parameter that determines the strength of the consumer-resource interaction. The per unit mass effect of the resource species i on the consumer species j, a_{ji} is given by

$$a_{ji} = -e a_{ij}$$

where e is the conversion efficiency, set to 0.1.

Intraspecific competition

For basal species, the intraspecific term a_{ii} scaled with body mass as:

$$a_{ii} = C_{aii} m_i^{\frac{1}{2}}$$

following the scaling observed in a phytoplankton study (Cermeño et al. 2006). For consumer species the intraspecific term scaled with body mass as:

$$a_{ii} = C_{aii} m_i^{-\frac{1}{4}}$$

following the scaling used in (Virgo et al. 2006) and (Lewis and Law 2007).

The prey preference function

The prey preference function was defined to be a truncated Gaussian function:

$$z_{ij}{}^{*} = \frac{1}{\sigma\sqrt{2\pi}} exp\left[-\frac{1}{2}\left[\frac{\log(\beta m_i/m_j)}{\sigma}\right]^2\right]$$

for $m_i < m_j$ and $-\delta\sigma \leq \log\left(\sigma\frac{m_i}{m_j}\right) \leq \delta\sigma$

The value $z_{ij}{}^{*}$ is dependent on:

1. The resource and consumer body masses, m_i and m_j
2. The optimum consumer resource body mass ratio β (the mean of the preference function)
3. The standard deviation of the preference function, σ
4. The number of standard deviations away from the mean at which point the probability density curve is set to 0, δ. This represents the number of standard deviations away from the optimal consumer-resource body mass ratio at which the consumer stops feeding on the resource.

The value of $z_{ij}{}^{*}$ was standardised so that the sum of $z_{ij}{}^{*}$ over all resource species is one:

$$z_{ij} = z_{ij}^{*}\frac{1}{\sum_i z_{ij}^{*}}$$

Adjusting the parameterisation

The parameterisation of the original food webs used in Säterberg et al. (2013) included terms for basal interspecific competition but including non-trophic interactions in the community matrix for this study would alter both the linkage density of a species and the inverse community matrix. Interspecific competition terms were removed for this study which had a destabilising effect on the synthetic food webs used so it was necessary to introduce an additional parameterisation algorithm (Pimenov et al. manuscript in preparation) that made small adjustments to the community matrix by allowing the parameter that determined the strength of trophic interactions between individual consumer and resource pairs C_{aij} to vary within ecological limits:

$${C_{aij}}^{min} \leq C_{Caij} \leq {C_{aij}}^{max}$$

where ${C_{aij}}^{min}$ corresponds to the consumption rate at which species j has zero growth rate in the absence of predators (survival consumption rate), and ${C_{aij}}^{max}$ can be chosen arbitrarily between ${C_{aij}}^{min}$ and the maximal consumption rate to allow enough variation of C_{aij}.

APPENDIX D

Table D1 Results from the 97 linear models showing the relationship between species total net effect and species body size and linkage density.

Full model: $\log(Y_j) \sim \alpha + \beta_1(\log(m_{j})) + \beta_2(L_j) + \beta 2(m_j L_j) + \varepsilon$

Where Y_j is the total net effect of species *j*, m_j is the body mass of species *j* and L_j is the linkage density of species *j*.

No results for webs 41, 58 and 84 due to ill conditioned community matrices.

Webs shown in red were analysed using the Full model: Net Effects ~ Constant + Body Size since body size and linkage density were collinear.

Web	Intercept		Body Size		Linkage Density		Linkage Density: Body Size	
	Estimated Coefficient	Standard Error	Estimated Coefficient	Standard Error	Estimated Coefficient	Standard Error	Estimated Coefficient	Standard Error
1	8.16	0.13	1.63	0.13				
2	7.26	0.14	1.83	0.14				
3	6.84	0.08	1.82	0.08				
4	9.70	0.12	1.63	0.12				
5	7.16	0.09	1.83	0.09				
6	8.97	0.17	1.77	0.17	-1.00	0.17		
7	7.68	0.14	1.73	0.16	-0.35	0.16		
8	8.67	0.15	1.55	0.16	-0.33	0.16		
9	7.48	0.13	1.91	0.13				
10	7.73	0.15	1.58	0.16	-0.43	0.16		
11	7.48	0.15	1.76	0.15				
12	7.33	0.16	1.61	0.16				
13	6.30	0.12	1.34	0.12				
14	7.70	0.13	1.84	0.14				
15	7.34	0.12	1.23	0.13	-0.42	0.13		
16	7.60	0.12	1.84	0.12				
17	8.38	0.21	1.74	0.23	-1.56	0.23		
18	7.52	0.09	1.48	0.10	-0.48	0.10		
19	8.49	0.09	1.49	0.11	-0.25	0.11		
20	7.45	0.12	1.51	0.13	-0.36	0.13		
21	7.99	0.15	1.82	0.15				
22	8.62	0.13	1.69	0.16	-0.58	0.16		
23	7.28	0.12	2.06	0.12				
24	8.97	0.27	1.19	0.35	0.06	0.29	-0.89	0.34
25	6.45	0.15	1.37	0.15				
26	7.69	0.10	1.87	0.10				
27	8.18	0.11	1.72	0.11				
28	7.96	0.09	1.72	0.09				
29	7.53	0.09	1.93	0.09	-0.26	0.09		
30	7.09	0.14	1.78	0.14				

Table D1 continued

Web	Intercept		Body Size		Linkage Density		Linkage Density: Body Size	
	Estimated Coefficient	Standard Error	Estimated Coefficient	Standard Error	Estimated Coefficient	Standard Error	Estimated Coefficient	Standard Error
31	8.48	0.15	1.77	0.16	-0.32	0.16		
32	8.65	0.14	1.76	0.14	-0.33	0.14		
33	7.68	0.10	1.59	0.10				
34	7.56	0.11	1.61	0.15	-0.29	0.12	0.39	0.18
35	7.13	0.13	1.98	0.13				
36	7.62	0.09	1.70	0.09				
37	7.09	0.10	1.72	0.10				
38	6.94	0.14	1.57	0.14				
39	8.28	0.16	2.17	0.18	-0.39	0.18		
40	7.37	0.10	2.18	0.12	-0.44	0.10	-0.29	0.09
41								
42	9.74	0.21	0.80	0.26	-0.89	0.26		
43	7.67	0.09	1.68	0.09				
44	7.85	0.13	2.18	0.13				
45	8.64	0.15	1.91	0.15				
46	7.32	0.15	1.91	0.15				
47	8.45	0.23	1.52	0.27	-0.55	0.27		
48	8.91	0.15	1.93	0.15				
49	9.28	0.16	1.81	0.17				
50	8.92	0.22	1.04	0.41	-0.60	0.22	0.60	0.26
51	8.67	0.17	2.12	0.20	-0.54	0.20		
52	7.55	0.14	1.90	0.14				
53	9.52	0.16	1.55	0.16				
54	7.35	0.10	1.73	0.10				
55	7.76	0.12	2.00	0.12				
56	8.03	0.13	1.77	0.13				
57	6.61	0.10	1.90	0.11	-0.35	0.12	-0.19	0.09
58								
59	7.77	0.08	2.07	0.08				
60	7.63	0.12	1.59	0.12	-0.42	0.12		
61	7.40	0.11	1.73	0.15	-0.40	0.15		
62	9.30	0.23	2.22	0.23				
63	7.20	0.12	1.57	0.12				
64	6.70	0.08	1.78	0.08				
65	6.50	0.09	1.44	0.10	-0.32	0.10		

Table D1 continued

Web	Intercept		Body Size		Linkage Density		Linkage Density: Body Size	
	Estimated Coefficient	Standard Error	Estimated Coefficient	Standard Error	Estimated Coefficient	Standard Error	Estimated Coefficient	Standard Error
66	9.17	0.15	2.20	0.15	-0.56	0.15		
67	8.18	0.13	1.90	0.13				
68	7.70	0.11	2.03	0.11				
69	7.89	0.10	1.81	0.11				
70	8.49	0.17	2.14	0.17				
71	7.56	0.11	1.77	0.11				
72	7.88	0.17	1.75	0.17	-0.44	0.17		
73	6.51	0.15	1.60	0.16	-0.36	0.16		
74	6.68	0.20	1.52	0.24	-0.65	0.24		
75	10.32	0.31	0.98	0.32				
76	7.88	0.10	1.67	0.11				
77	7.43	0.11	1.64	0.13	-0.28	0.13		
78	7.95	0.15	2.18	0.16				
79	8.36	0.15	2.12	0.16				
80	7.81	0.14	1.83	0.15				
81	7.66	0.12	1.87	0.12				
82	8.68	0.20	2.11	0.20				
83	8.12	0.14	1.89	0.15				
84								
85	8.22	0.17	2.13	0.18	-0.77	0.18		
86	8.25	0.13	2.05	0.14	-0.29	0.14		
87	7.65	0.08	1.83	0.09	-0.17	0.09		
88	8.19	0.17	1.48	0.17	-0.53	0.17		
89	7.93	0.13	1.92	0.15	-0.40	0.15		
90	7.26	0.10	1.46	0.13	-0.43	0.13		
91	8.82	0.15	1.78	0.15				
92	6.65	0.09	1.71	0.09				
93	7.98	0.15	1.81	0.15				
94	7.54	0.10	1.68	0.10	-0.23	0.10		
95	8.90	0.18	1.61	0.23	-0.43	0.23		
96	9.69	0.15	1.89	0.15				
97	8.17	0.18	1.66	0.18				
98	8.13	0.11	2.03	0.11				
99	8.29	0.16	1.67	0.20	-0.43	0.20		
100	7.43	0.09	1.96	0.09				

Table D2 Results from the linear models showing the relationship between species total net effect and species body size and linkage density for the Ythan Estuary and Tuesday Lake food webs.

Full model: $\log(Y_j) \sim \alpha + \beta_1(\log(m_j)) + \beta_2(L_j) + \beta2(m_jL_j) + \varepsilon$

Y_j is the total net effect of species *j*, m_j is the body mass of species *j* and L_j is the linkage density of species *j*.

Web	Intercept		Body Size		Linkage Density	
	Estimated Coefficient	Standard Error	Estimated Coefficient	Standard Error	Estimated Coefficient	Standard Error
Ythan Estuary	3.38	0.23	0.69	0.24	-0.85	0.24
Tuesday Lake	-0.63	0.09	1.47	0.10	0.36	0.10

Table D3 Correlations between species traits for the synthetic food webs, correlations larger (in magnitude) than 0.7 are shown in red

Web	Body Size vs Trophic Height		Body Size vs Linkage Density		Body Size vs Predator Prey - Ratio		Body Size vs Biomass Abundance		Body Size vs Generality		Body Size vs Vulnerability	
	Correlation coefficient r	p - value	Correlation coefficient r	p - value	Correlation coefficient r	p - value	Correlation coefficient r	p - value	Correlation coefficient r	p - value	Correlation coefficient r	p - value
1	0.850	<0.001	-0.200	>0.05	-0.747	<0.001	-0.807	< 0.001	0.547	<0.001	-0.788	<0.001
2	0.851	<0.001	-0.321	<0.05	-0.751	<0.001	-0.729	< 0.001	0.435	<0.05	-0.711	<0.001
3	0.860	<0.001	-0.489	<0.001	-0.603	<0.001	-0.835	< 0.001	0.414	<0.05	-0.810	<0.001
4	0.794	<0.001	-0.803	<0.001	-0.881	<0.001	-0.686	< 0.001	0.428	<0.05	-0.282	<0.05
5	0.832	<0.001	-0.565	<0.001	-0.717	<0.001	-0.743	< 0.001	0.439	<0.05	-0.776	<0.001
6	0.827	<0.001	-0.244	>0.05	-0.851	<0.001	-0.808	< 0.001	0.760	<0.001	-0.480	<0.001
7	0.833	<0.001	-0.472	<0.001	-0.713	<0.001	-0.765	< 0.001	0.490	<0.001	-0.728	<0.001
8	0.792	<0.001	-0.369	<0.05	-0.720	<0.001	-0.773	< 0.001	0.622	<0.001	-0.715	<0.001
9	0.863	<0.001	-0.255	>0.05	-0.705	<0.001	-0.790	< 0.001	0.703	<0.001	-0.755	<0.001
10	0.839	<0.001	-0.263	>0.05	-0.669	<0.001	-0.792	< 0.001	0.506	<0.001	-0.629	<0.001
11	0.829	<0.001	-0.192	>0.05	-0.739	<0.001	-0.725	< 0.001	0.767	<0.001	-0.508	<0.001
12	0.825	<0.001	-0.455	<0.001	-0.656	<0.001	-0.659	< 0.001	0.546	<0.001	-0.588	<0.001
13	0.854	<0.001	-0.158	>0.05	-0.666	<0.001	-0.827	< 0.001	0.511	<0.001	-0.748	<0.001
14	0.875	<0.001	-0.715	<0.001	-0.583	<0.001	-0.631	< 0.001	0.357	<0.05	-0.701	<0.001
15	0.846	<0.001	-0.296	<0.05	-0.750	<0.001	-0.787	< 0.001	0.593	<0.001	-0.631	<0.001
16	0.842	<0.001	-0.515	<0.001	-0.626	<0.001	-0.750	< 0.001	0.453	<0.001	-0.540	<0.001
17	0.898	<0.001	-0.375	<0.001	-0.746	<0.001	-0.762	< 0.001	0.660	<0.001	-0.708	<0.001
18	0.824	<0.001	-0.379	<0.001	-0.726	<0.001	-0.742	< 0.001	0.654	<0.001	-0.590	<0.001
19	0.775	<0.001	-0.540	<0.001	-0.704	<0.001	-0.683	< 0.001	0.599	<0.001	-0.641	<0.001
20	0.855	<0.001	-0.259	>0.05	-0.750	<0.001	-0.784	< 0.001	0.601	<0.001	-0.640	<0.001
21	0.837	<0.001	-0.217	>0.05	-0.778	<0.001	-0.760	< 0.001	0.604	<0.001	-0.662	<0.001
22	0.858	<0.001	-0.579	<0.001	-0.828	<0.001	-0.795	< 0.001	0.592	<0.001	-0.574	<0.001
23	0.834	<0.001	-0.191	>0.05	-0.582	<0.001	-0.760	< 0.001	0.599	<0.001	-0.717	<0.001
24	0.845	<0.001	-0.503	<0.001	-0.581	<0.001	-0.387	< 0.05	0.450	<0.05	-0.717	<0.001
25	0.850	<0.001	0.047	>0.05	-0.575	<0.001	-0.819	< 0.001	0.584	<0.001	-0.783	<0.001
26	0.828	<0.001	-0.586	<0.001	-0.739	<0.001	-0.766	< 0.001	0.694	<0.001	-0.491	<0.001
27	0.833	<0.001	0.025	>0.05	-0.650	<0.001	-0.847	< 0.001	0.654	<0.001	-0.691	<0.001
28	0.821	<0.001	-0.562	<0.001	-0.753	<0.001	-0.827	< 0.001	0.644	<0.001	-0.713	<0.001
29	0.863	<0.001	-0.101	>0.05	-0.504	<0.001	-0.746	< 0.001	0.596	<0.001	-0.605	<0.001
30	0.841	<0.001	-0.435	<0.05	-0.679	<0.001	-0.861	< 0.001	0.442	<0.05	-0.728	<0.001
31	0.855	<0.001	-0.304	<0.05	-0.708	<0.001	-0.767	< 0.001	0.628	<0.001	-0.765	<0.001
32	0.825	<0.001	-0.176	>0.05	-0.552	<0.001	-0.790	< 0.001	0.553	<0.001	-0.708	<0.001
33	0.847	<0.001	-0.387	<0.05	-0.686	<0.001	-0.804	< 0.001	0.514	<0.001	-0.741	<0.001
34	0.843	<0.001	-0.434	<0.05	-0.700	<0.001	-0.762	< 0.001	0.643	<0.001	-0.586	<0.001
35	0.855	<0.001	-0.721	<0.001	-0.614	<0.001	-0.694	< 0.001	0.625	<0.001	-0.647	<0.001
36	0.844	<0.001	-0.592	<0.001	-0.755	<0.001	-0.823	< 0.001	0.465	<0.001	-0.758	<0.001
37	0.869	<0.001	-0.291	<0.05	-0.584	<0.001	-0.734	< 0.001	0.443	<0.05	-0.691	<0.001
38	0.849	<0.001	-0.125	>0.05	-0.719	<0.001	-0.866	< 0.001	0.648	<0.001	-0.786	<0.001
39	0.867	<0.001	-0.350	<0.05	-0.773	<0.001	-0.763	< 0.001	0.631	<0.001	-0.690	<0.001
40	0.911	<0.001	-0.553	<0.001	-0.729	<0.001	-0.627	< 0.001	0.619	<0.001	-0.741	<0.001
41							0	0				
42	0.818	<0.001	-0.580	<0.001	-0.690	<0.001	-0.427	< 0.05	0.482	<0.001	-0.717	<0.001
43	0.853	<0.001	-0.488	<0.001	-0.764	<0.001	-0.679	< 0.001	0.474	<0.001	-0.639	<0.001
44	0.838	<0.001	-0.259	>0.05	-0.748	<0.001	-0.863	< 0.001	0.720	<0.001	-0.703	<0.001
45	0.841	<0.001	-0.439	<0.05	-0.799	<0.001	-0.774	< 0.001	0.626	<0.001	-0.525	<0.001
46	0.842	<0.001	-0.579	<0.001	-0.653	<0.001	-0.619	< 0.001	0.553	<0.001	-0.566	<0.001
47	0.784	<0.001	-0.535	<0.001	-0.649	<0.001	-0.779	< 0.001	0.550	<0.001	-0.238	> 0.05
48	0.841	<0.001	-0.129	>0.05	-0.639	<0.001	-0.760	< 0.001	0.610	<0.001	-0.746	<0.001
49	0.805	<0.001	-0.781	<0.001	-0.730	<0.001	-0.614	< 0.001	0.431	<0.05	-0.454	<0.05
50	0.798	<0.001	-0.652	<0.001	-0.680	<0.001	-0.669	< 0.001	0.497	<0.001	-0.580	<0.001

Table D3 continued

Web	Body Size vs Trophic Height		Body Size vs Linkage Density		Body Size vs Predator Prey - Ratio		Body Size vs Biomass Abundance		Body Size vs Generality		Body Size vs Vulnerability	
	Correlation coefficient r	p - value	Correlation coefficient r	p - value	Correlation coefficient r	p - value	Correlation coefficient r	p - value	Correlation coefficient r	p - value	Correlation coefficient r	p - value
51	0.833	<0.001	-0.473	<0.05	-0.699	<0.001	-0.596	< 0.001	0.561	<0.001	-0.635	<0.001
52	0.807	<0.001	-0.145	>0.05	-0.767	<0.001	-0.772	< 0.001	0.626	<0.001	-0.734	<0.001
53	0.844	<0.001	-0.125	>0.05	-0.780	<0.001	-0.825	< 0.001	0.650	<0.001	-0.706	<0.001
54	0.848	<0.001	-0.233	>0.05	-0.593	<0.001	-0.825	< 0.001	0.602	<0.001	-0.685	<0.001
55	0.870	<0.001	-0.177	>0.05	-0.746	<0.001	-0.805	< 0.001	0.614	<0.001	-0.755	<0.001
56	0.786	<0.001	-0.293	<0.05	-0.593	<0.001	-0.719	< 0.001	0.705	<0.001	-0.622	<0.001
57	0.827	<0.001	-0.344	<0.05	-0.757	<0.001	-0.847	< 0.001	0.658	<0.001	-0.666	<0.001
58							0	0				
59	0.812	<0.001	-0.432	<0.001	-0.689	<0.001	-0.815	< 0.001	0.563	<0.001	-0.694	<0.001
60	0.865	<0.001	-0.198	>0.05	-0.875	<0.001	-0.842	< 0.001	0.648	<0.001	-0.592	<0.001
61	0.855	<0.001	-0.668	<0.001	-0.846	<0.001	-0.785	< 0.001	0.572	<0.001	-0.650	<0.001
62	0.833	<0.001	-0.781	<0.001	-0.790	<0.001	-0.617	< 0.001	0.394	<0.05	-0.399	<0.05
63	0.856	<0.001	-0.376	<0.05	-0.704	<0.001	-0.803	< 0.001	0.487	<0.001	-0.573	<0.001
64	0.825	<0.001	-0.573	<0.001	-0.712	<0.001	-0.768	< 0.001	0.450	<0.05	-0.562	<0.001
65	0.849	<0.001	-0.409	<0.001	-0.737	<0.001	-0.821	< 0.001	0.475	<0.001	-0.700	<0.001
66	0.810	<0.001	-0.262	>0.05	-0.642	<0.001	-0.694	< 0.001	0.694	<0.001	-0.600	<0.001
67	0.862	<0.001	0.097	>0.05	-0.739	<0.001	-0.752	< 0.001	0.742	<0.001	-0.770	<0.001
68	0.844	<0.001	-0.582	<0.001	-0.755	<0.001	-0.800	< 0.001	0.491	<0.001	-0.664	<0.001
69	0.877	<0.001	-0.278	>0.05	-0.736	<0.001	-0.822	< 0.001	0.644	<0.001	-0.779	<0.001
70	0.823	<0.001	-0.346	<0.05	-0.701	<0.001	-0.833	< 0.001	0.635	<0.001	-0.527	<0.001
71	0.831	<0.001	-0.244	>0.05	-0.587	<0.001	-0.601	< 0.001	0.590	<0.001	-0.660	<0.001
72	0.843	<0.001	-0.106	>0.05	-0.707	<0.001	-0.757	< 0.001	0.746	<0.001	-0.555	<0.001
73	0.820	<0.001	-0.342	<0.05	-0.677	<0.001	-0.780	< 0.001	0.547	<0.001	-0.591	<0.001
74	0.860	<0.001	-0.504	<0.001	-0.662	<0.001	-0.838	< 0.001	0.428	<0.05	-0.737	<0.001
75	0.845	<0.05	-0.814	<0.001	-0.778	<0.001	-0.379	< 0.05	0.343	<0.05	-0.592	<0.001
76	0.828	<0.001	-0.110	>0.05	-0.424	<0.05	-0.733	0.000	0.573	<0.001	-0.696	<0.001
77	0.847	<0.001	-0.476	<0.05	-0.656	<0.001	-0.747	< 0.001	0.414	<0.05	-0.764	<0.001
78	0.827	<0.001	-0.152	>0.05	-0.698	<0.001	-0.844	< 0.001	0.713	<0.001	-0.614	<0.001
79	0.848	<0.001	-0.722	<0.001	-0.719	<0.001	-0.782	< 0.001	0.645	<0.001	-0.719	<0.001
80	0.856	<0.001	-0.214	>0.05	-0.714	<0.001	-0.706	< 0.001	0.685	<0.001	-0.585	<0.001
81	0.848	<0.001	-0.332	<0.05	-0.766	<0.001	-0.823	< 0.001	0.592	<0.001	-0.743	<0.001
82	0.826	<0.001	-0.759	<0.001	-0.783	<0.001	-0.644	< 0.001	0.465	<0.001	-0.499	<0.001
83	0.835	<0.001	-0.297	<0.05	-0.771	<0.001	-0.772	< 0.001	0.666	<0.001	-0.717	<0.001
84							0	0				
85	0.857	<0.001	-0.334	<0.05	-0.762	<0.001	-0.821	< 0.001	0.509	<0.001	-0.679	<0.001
86	0.855	<0.001	-0.373	<0.05	-0.719	<0.001	-0.792	< 0.001	0.765	<0.001	-0.638	<0.001
87	0.810	<0.001	-0.468	<0.001	-0.601	<0.001	-0.849	< 0.001	0.503	<0.001	-0.644	<0.001
88	0.857	<0.001	0.002	>0.05	-0.744	<0.001	-0.801	< 0.001	0.777	<0.001	-0.736	<0.001
89	0.855	<0.001	-0.511	<0.001	-0.680	<0.001	-0.713	< 0.001	0.594	<0.001	-0.661	<0.001
90	0.843	<0.001	-0.613	<0.001	-0.746	<0.001	-0.743	< 0.001	0.543	<0.001	-0.521	<0.001
91	0.820	<0.001	-0.502	<0.001	-0.716	<0.001	-0.816	< 0.001	0.602	<0.001	-0.488	<0.001
92	0.837	<0.001	-0.574	<0.001	-0.643	<0.001	-0.795	< 0.001	0.437	<0.05	-0.674	<0.001
93	0.846	<0.001	-0.176	>0.05	-0.647	<0.001	-0.859	< 0.001	0.596	<0.001	-0.790	<0.001
94	0.816	<0.001	-0.209	>0.05	-0.474	<0.05	-0.803	< 0.001	0.580	<0.001	-0.686	<0.001
95	0.827	<0.001	-0.614	<0.001	-0.936	<0.001	-0.790	< 0.001	0.629	<0.001	-0.598	<0.001
96	0.847	<0.001	-0.476	<0.001	-0.772	<0.001	-0.829	< 0.001	0.625	<0.001	-0.555	<0.001
97	0.834	<0.001	-0.130	>0.05	-0.765	<0.001	-0.902	< 0.001	0.625	<0.001	-0.709	<0.001
98	0.848	<0.001	-0.094	>0.05	-0.668	<0.001	-0.734	< 0.001	0.673	<0.001	-0.772	<0.001
99	0.803	<0.001	-0.575	<0.001	-0.820	<0.001	-0.741	< 0.001	0.514	<0.001	-0.481	<0.001
100	0.851	<0.001	-0.529	<0.001	-0.827	<0.001	-0.776	< 0.001	0.519	<0.001	-0.687	<0.001

Table D4 Correlations between species traits for the real food webs, correlations larger (in magnitude) than 0.7 are shown in red

Web	**Body Size vs Trophic Height**		**Body Size vs Linkage Density**		**Body Size vs Predator Prey - Ratio**		**Body Size vs Generality**		**Body Size vs Vulnerability**	
	Correlation coefficient r	**p - value**	**Correlation coefficient r**	**p - value**	**Correlation coefficient r**	**p - value**	**Correlation coefficient r**	**p - value**	**Correlation coefficient r**	**p - value**
Ythan Estuary	0.767	< 0.001	-0.252	> 0.05	0.256	< 0.001	0.567	< 0.001	-0.524	< 0.001
Tuesday Lake	0.849	< 0.001	0.320	< 0.05	0.846	< 0.001	0.840	< 0.001	-0.428	< 0.05

Table D5 Real food webs: the second column shows the correlation between a species body size and its total direct effect. The third column shows the correlations between a species total direct effect and its total net effect.

Web	Body Size vs Direct Sum(D_j)		Direct Sum (D_j) vs Total Net Effect	
	Correlation coefficient r	p - value	Correlation coefficient r	p - value
Ythan Estuary	-0.838	< 0.001	-0.691	< 0.001
Tuesday Lake	-0.8273	< 0.001	-0.755	< 0.001

Table D6 Results from the 91 linear models showing the relationship between species total net effect and species body size and linkage density where trophic interaction strength is measured on a per capita basis.

Full model: log(Yj) ~ α + β1(log(mj)) + β2(Lj) + β2(mjLj) + ε

Yj is the total net effect of species j, mj is the body mass of species j and Lj is the linkage density of species j. No results for webs 24, 41, 42, 53, 75, 84, 98, 99 and 100 due to ill conditioned community matrices. Webs shown in red were analysed using Full model: Net Effects ~ Constant + Body Size since body size and linkage density were collinear

Web	**Intercept**		**Body Size**		**Linkage Density**		**Linkage Density: Body Size**	
	Estimated Coefficient	**Standard Error**	**Estimated Coefficient**	**Standard Error**	**Estimated Coefficient**	**Standard Error**	**Estimated Coefficient**	**Standard Error**
1	13.33	0.17	1.62	0.17				
2	12.88	0.13	1.35	0.14	-0.48	0.13	0.43	0.15
3	12.47	0.08	1.84	0.08				
4	14.02	0.12	1.63	0.12				
5	12.99	0.11	1.77	0.11				
6	12.03	0.15	1.75	0.16	-0.87	0.16		
7	12.50	0.14	1.67	0.16	-0.38	0.16		
8	13.25	0.16	0.96	0.32	-0.57	0.18	0.56	0.26
9	13.41	0.13	1.88	0.13				
10	12.35	0.16	1.65	0.17	-0.51	0.17		
11	12.90	0.15	1.21	0.15	-0.36	0.16	0.39	0.13
12	12.46	0.16	1.64	0.16				
13	12.96	0.27	1.17	0.27				
14	12.58	0.29	1.74	0.29				
15	13.67	0.13	1.23	0.14	-0.32	0.14		
16	13.21	0.14	1.77	0.14				
17	13.14	0.17	1.11	0.23	-0.30	0.18	0.94	0.28
18	13.30	0.09	1.51	0.09				
19	13.04	0.10	1.43	0.12	-0.35	0.12		
20	12.74	0.14	1.76	0.14				
21	13.33	0.16	1.77	0.16				
22	13.08	0.13	1.68	0.16	-0.51	0.16		
23	11.81	0.20	2.23	0.20				
24								
25	12.89	0.15	1.43	0.15				
26	13.04	0.09	1.88	0.09				
27	14.68	0.13	1.78	0.13				
28	13.39	0.10	1.69	0.11				
29	13.36	0.09	1.82	0.09				
30	12.54	0.12	1.87	0.12				

Table D6 continued

Web	Intercept		Body Size		Linkage Density		Linkage Density: Body Size	
	Estimated Coefficient	Standard Error	Estimated Coefficient	Standard Error	Estimated Coefficient	Standard Error	Estimated Coefficient	Standard Error
31	13.49	0.15	1.83	0.15				
32	13.50	0.13	1.76	0.13	-0.34	0.13		
33	13.67	0.10	1.59	0.11				
34	12.29	0.10	1.90	0.10				
35	12.24	0.13	1.92	0.13				
36	13.06	0.11	1.81	0.11				
37	13.62	0.10	1.64	0.10				
38	12.41	0.16	1.64	0.16				
39	12.63	0.22	2.10	0.22				
40	12.01	0.11	1.87	0.13	-0.43	0.13		
41								
42								
43	13.46	0.09	1.67	0.09				
44	12.36	0.14	2.17	0.14				
45	12.56	0.17	1.85	0.17				
46	12.47	0.13	1.81	0.13				
47	11.42	0.21	1.56	0.25	-0.47	0.25		
48	13.69	0.16	1.88	0.16				
49	12.42	0.17	1.82	0.17				
50	12.52	0.15	1.80	0.20	-0.40	0.20		
51	12.52	0.15	1.80	0.20	-0.40	0.20		
52	12.95	0.13	1.89	0.13				
53								
54	13.75	0.10	1.74	0.10				
55	13.53	0.13	1.89	0.13				
56	12.79	0.12	1.68	0.13				
57	11.84	0.10	1.83	0.11	-0.25	0.11		
58	13.37	0.21	1.82	0.21				
59	12.95	0.08	2.04	0.08				
60	13.93	0.13	1.52	0.14	-0.59	0.14		
61	12.22	0.12	1.97	0.12				
62	12.24	0.18	2.08	0.18				
63	13.15	0.15	1.74	0.15				
64	13.10	0.10	1.78	0.10				
65	12.46	0.10	1.55	0.11	-0.30	0.11		

Table D6 continued

Web	Intercept		Body Size		Linkage Density		Linkage Density: Body Size	
	Estimated Coefficient	Standard Error	Estimated Coefficient	Standard Error	Estimated Coefficient	Standard Error	Estimated Coefficient	Standard Error
66	12.13	0.16	2.16	0.17	-0.50	0.17		
67	13.60	0.15	1.88	0.15				
68	13.06	0.11	2.03	0.11				
69	13.76	0.12	1.73	0.12				
70	12.29	0.18	2.17	0.18				
71	13.76	0.11	1.76	0.11				
72	13.29	0.15	1.79	0.16	-0.39	0.16		
73	12.04	0.13	1.73	0.13				
74	12.76	0.10	1.51	0.12	-0.24	0.12		
75								
76	13.69	0.12	1.68	0.12				
77	12.52	0.18	1.58	0.18				
78	12.74	0.13	2.23	0.13				
79	12.68	0.13	2.10	0.14				
80	13.11	0.13	1.82	0.13				
81	12.52	0.12	1.86	0.12				
82	11.79	0.18	2.06	0.18				
83	13.08	0.14	1.85	0.14				
84								
85	12.46	0.17	2.14	0.18				
86	12.60	0.12	2.01	0.13	-0.33	0.13		
87	13.12	0.09	1.77	0.11	-0.24	0.11		
88	13.75	0.15	1.19	0.16	-0.69	0.16	0.47	0.16
89	12.17	0.13	1.92	0.15	-0.38	0.15		
90	12.80	0.10	1.53	0.13	-0.27	0.13		
91	13.54	0.16	1.89	0.16				
92	12.48	0.21	1.63	0.21				
93	12.84	0.17	1.86	0.17				
94	13.29	0.10	1.69	0.11	-0.26	0.11		
95	13.06	0.19	1.82	0.19				
96	14.02	0.15	1.87	0.15				
97	12.94	0.19	1.75	0.19				
98								
99								
100								

Table D7 Synthetic webs: the second column shows the correlation between a species linkage density and its total direct effect.

The third column shows the correlation between a species linkage density and the variance of its entries in the community matrix. The fourth column shows the correlations between a species linkage density and its average entry in the community matrix.

Web	Linkage Density vs Column Sum (Dj)		Linkage Density vs Var (D_j)		Linkage Density vs mean(D_j)	
	Correlation coefficient r	p - value	Correlation coefficient r	p - value	Correlation coefficient r	p - value
6	-0.235	> 0.05	-0.450	< 0.05	-0.319	< 0.05
7	-0.003	> 0.05	0.112	> 0.05	-0.019	> 0.05
8	-0.091	> 0.05	-0.176	> 0.05	-0.192	> 0.05
10	-0.085	> 0.05	-0.056	> 0.05	-0.191	> 0.05
15	0.193	> 0.05	0.090	> 0.05	0.025	> 0.05
17	0.047	> 0.05	-0.284	< 0.05	-0.222	> 0.05
18	0.274	> 0.05	-0.337	< 0.05	-0.096	> 0.05
19	0.024	> 0.05	0.071	> 0.05	-0.184	> 0.05
20	0.126	> 0.05	0.011	> 0.05	0.068	> 0.05
22	-0.038	> 0.05	0.182	> 0.05	-0.060	> 0.05
29	0.020	> 0.05	-0.034	> 0.05	-0.082	> 0.05
31	0.234	> 0.05	0.065	> 0.05	0.071	> 0.05
32	0.017	> 0.05	0.061	> 0.05	-0.018	> 0.05
34	-0.082	> 0.05	0.003	> 0.05	-0.198	> 0.05
39	-0.100	> 0.05	0.044	> 0.05	-0.196	> 0.05
40	0.064	> 0.05	-0.168	> 0.05	-0.071	> 0.05
42	-0.021	> 0.05	-0.018	> 0.05	-0.106	> 0.05
47	-0.269	> 0.05	-0.362	< 0.05	-0.357	< 0.05
50	-0.125	> 0.05	-0.034	> 0.05	-0.273	> 0.05
51	-0.069	> 0.05	0.185	> 0.05	-0.083	> 0.05
57	0.110	> 0.05	-0.179	> 0.05	-0.093	> 0.05
60	0.094	> 0.05	-0.073	> 0.05	-0.051	> 0.05
61	-0.021	> 0.05	0.003	> 0.05	-0.163	> 0.05
65	0.152	> 0.05	-0.022	> 0.05	-0.125	> 0.05
66	-0.084	> 0.05	-0.188	> 0.05	-0.154	> 0.05
72	-0.148	> 0.05	-0.361	< 0.05	-0.170	> 0.05
73	-0.053	> 0.05	-0.099	> 0.05	-0.160	> 0.05
74	0.134	> 0.05	0.048	> 0.05	-0.023	> 0.05
77	-0.110	> 0.05	0.063	> 0.05	-0.120	> 0.05
85	-0.084	> 0.05	-0.267	> 0.05	-0.346	< 0.05
86	0.034	> 0.05	0.187	> 0.05	-0.025	> 0.05
87	0.020	> 0.05	0.071	> 0.05	-0.021	> 0.05
88	0.111	> 0.05	-0.072	> 0.05	0.019	> 0.05
89	-0.061	> 0.05	0.002	> 0.05	-0.077	> 0.05
90	-0.139	> 0.05	-0.250	> 0.05	-0.319	< 0.05
94	-0.069	> 0.05	-0.229	> 0.05	-0.159	> 0.05
95	-0.071	> 0.05	0.097	> 0.05	-0.185	> 0.05
99	-0.278	> 0.05	-0.407	< 0.05	-0.339	< 0.05

Table D8 The correlation between species body size and the elasticity of equilibrium biomass densities

Web	Body Size vs Elasticity	
	Correlation coefficient r	p - value
1	0.237	> 0.05
2	0.3246	< 0.05
3	0.383	< 0.05
4	0.3071	< 0.05
5	0.2239	> 0.05
6	0.1202	> 0.05
7	0.2029	> 0.05
8	0.1484	> 0.05
9	0.2537	> 0.05
10	0.1737	> 0.05
11	0.1717	> 0.05
12	0.5483	> 0.05
13	0.2852	< 0.05
14	0.2126	> 0.05
15	0.266	> 0.05
16	0.3227	< 0.05
17	0.2349	> 0.05
18	0.334	< 0.05
19	0.2441	> 0.05
20	0.2571	> 0.05
21	0.2812	< 0.05
22	0.1482	> 0.05
23	0.2281	> 0.05
24	0.1892	> 0.05
25	0.2447	> 0.05
26	0.4193	< 0.05
27	0.3868	< 0.001
28	0.2185	> 0.05
29	0.3541	< 0.05
30	0.2892	< 0.05

Table D8 continued

Web	Body Size vs Elasticity	
	Correlation coefficient r	p - value
31	0.2876	< 0.05
32	0.2477	> 0.05
33	0.3171	< 0.05
34	0.2994	< 0.05
35	0.2234	> 0.05
36	0.2586	> 0.05
37	0.4204	< 0.05
38	0.2183	> 0.05
39	0.238	> 0.05
40	0.2157	> 0.05
41		
42	0.2307	> 0.05
43	0.5386	< 0.001
44	0.1917	> 0.05
45	0.1228	> 0.05
46	0.1968	> 0.05
47	0.1039	> 0.05
48	0.1961	> 0.05
49	0.1952	> 0.05
50	0.2872	< 0.05
51	0.1006	> 0.05
52	0.3836	< 0.05
53	0.3148	< 0.05
54	0.3195	< 0.05
55	0.3008	< 0.05
56	0.2535	> 0.05
57	0.2879	< 0.001
58		
59	0.4351	< 0.05
60	0.1686	> 0.05
61	0.1328	> 0.05
62	0.0781	> 0.05
63	0.2486	> 0.05
64	0.3137	< 0.05
65	0.426	< 0.05

Table D8 continued

Web	Body Size vs Elasticity	
	Correlation coefficient r	p - value
66	0.2043	> 0.05
67	0.3223	< 0.05
68	0.3219	< 0.05
69	0.314	< 0.05
70	0.2684	> 0.05
71	0.3023	< 0.05
72	0.2535	> 0.05
73	0.2339	> 0.05
74	0.173	> 0.05
75	0.1971	> 0.05
76	0.1885	> 0.05
77	0.2977	< 0.05
78	0.3168	< 0.05
79	0.2515	> 0.05
80	0.2753	> 0.05
81	0.206	> 0.05
82	0.1487	> 0.05
83	0.3152	< 0.05
84		
85	0.1761	> 0.05
86	0.2085	> 0.05
87	0.4479	< 0.05
88	0.163	> 0.05
89	0.3022	< 0.05
90	0.2213	> 0.05
91	0.1538	> 0.05
92	0.4506	< 0.001
93	0.266	> 0.05
94	0.2564	> 0.05
95	0.142	> 0.05
96	0.2572	> 0.05
97	0.1378	> 0.05
98	0.3813	< 0.05
99	0.1627	> 0.05
100	0.3597	< 0.05

CHAPTER 4

WHY DO LARGE BODIED SPECIES HAVE A STRONG TOTAL NET EFFECT ON THEIR COMMUNITY?

Abstract

In Chapter 3, it was observed that species with a large body size have a large impact on their surrounding community, as measured through a species *total net effect*. The total net effect that a species has on a community is calculated by summing the absolute values of the entries for each column of the inverse community matrix. The matrix inversion process is extremely complex and while it is possible to observe the relationship between a species body size and its total net effect, the mechanism causing this relationship is unclear. The study presented in the following chapter, examines the column sums of the inverse community matrices for food chains consisting of 3-6 species. The simplicity of the community matrices associated with these food chains enables direct examination of the column sums of the inverse community matrices.

The community matrix for each food chain was parameterised under the assumptions that a predator preys upon species with a smaller body size and that a predator's rate of consumption is proportional to its own body size. To keep the analysis as general as possible, the parameters that determine the strength of interactions between species (predator-prey body mass ratio, ecological efficiency and intraspecific competition) were allowed to vary within ecologically defined limits and the effect of these parameters on the relationship between body mass and total net effects was examined. The analysis showed that the relationship between a species body size and its total net effect is a consequence of the body size based parameterisation of the community matrix. It also highlighted that the strength of intraspecific interactions in relation to interspecific interactions and ecological efficiency affect the impact that a species has on its community.

Introduction

Conservation of the natural world is dependent on an ecosystem approach: all life is part of a complex set of interactions between and within the biotic and abiotic environments. However, the limited resources available to conservationists means that conservation efforts must be prioritised and therefore it is of interest to identify which species have a large effect on their community (Paine 1969, 1995, Power et al. 1996, Christianou and Ebenman 2005, Sutherland et al. 2009). One method of identifying species that have large impacts on the communities in which they are embedded is to examine the *total net effect* of each species in the community. The *total* net effect of species j is a measure of the sensitivity of the equilibrium biomass densities of *all* species in the community following a *press perturbation* of species j. A press perturbation is a small sustained change in the growth rate of a species which can be achieved through the sustained removal or addition of a constant biomass of a species to a community or through a change in the intrinsic growth/mortality rate of a species. In a Lotka-Volterra system, the parameter describing the per unit mass effect of species j feeding on species i per unit of time is denoted by a_{ij}. The community matrix (denoted by A) contains every pairwise interaction in the community and therefore describes the structure and dynamics of the entire community. Bender et al. (1984) showed that the net effect of species j on species i (the sum of both direct and indirect effects) following a press perturbation is the ij^{th} element of the inverse community matrix, A^{-1}. The *total* net effect of species j on the community represents the effect that a press perturbation to species j has on the equilibrium biomass densities of *all* species in the community and is given by the sum of the absolute values of elements of column j in the inverse community matrix.

Previous studies (Yodzis 1988, Schmitz 1997, Dambacher et al. 2003, Montoya et al. 2009) have focused on understanding the distribution of pairwise net effects between species. Initially, it was concluded that the net effect of one species on another was indeterminate due to food web complexity (Yodzis 1988), however approaches using empirical and/or allometric information to estimate the elements of the community matrix improved the determinacy of net effects (Schmitz 1997), and it was found that in general, highly connected species had weak net effects (Montoya et al. 2009). In Chapter 3 and in three previous studies, pairwise net effects were aggregated into a measure of a species *total* net effect (Chapter 3 and Berg et al. 2011) or *mean* net effect (Montoya et al. 2005 O'Gorman et al. 2010). The data presented in Chapter 3 showed that species with a large body mass and high trophic position had a large total net effect in a community, supporting the findings from the Ythan Estuary food web (Montoya et al. 2005), and the Baltic Sea and Lake Vättern food webs (Berg et al. 2011). This result implies that perturbations to species with a large body mass will have the greatest impact on the equilibrium biomass distribution of a community; this effect is compounded further by the possibility that species with a large body mass are often the species facing the greatest threat from environmental change (Petchey et al. 1999, Purvis et al. 2000, Denney et al. 2002, Myers and Worm 2003, Sutherland et al. 2009, Estes et al. 2011).

The community matrices for the food webs analysed in Chapter 3 were parameterised similarly to the Ythan Estuary Food web (Montoya 2005) and the Baltic Sea and Lake Vättern food webs (Berg et al. 2011) using predator-prey body mass ratios. In particular, the parameterisation of the community matrix in Chapter 3 and the Berg et al (2011) study used allometric scaling where the consumption rate of an individual predator is defined to be proportional to its body mass raised to the power of 3/4. The application of predator-prey body mass ratios and allometric scaling to define interaction strengths between species has been shown to promote stability in food web models and explain community structure and dynamics (Yodzis 1981, Jonsson and Ebenman 1998, Emmerson and Raffaelli 2004, Andersen and Beyer 2006, Brose et al. 2006b, Otto et al. 2007, Berlow et al. 2009, O'Gorman et al. 2010, Zhang et al. 2013). Analysis of the community matrix and its inverse in Chapter 3 found: (1) a negative relationship between a species body mass and its total direct effect (the sum of the absolute values of its entries in the community matrix), and (2) a negative relationship between a species total direct effect and its total net effect. Due to the complexity of the inversion process, an outstanding question concerns the mechanisms causing the positive relationship between a species body mass and its total net effect. The present study aims to show how ecological constraints (due to allometric scaling) on the magnitude of entries in the community matrix cause the patterns we have observed in the inverse community matrix and thus explain the relationship between a species body mass and its total net effect in a community.

To show that the positive relationship between a species body mass and its total net effect is a consequence of allometric scaling we start with a simple three species food chain where the inverse community matrix is simple enough to consider analytically. Trophic interactions between the species are defined using predator-prey body mass ratios and allometric scaling. To keep the analysis as general as possible, assumptions regarding the parameters that determine the strength of interactions between species (predator-prey body mass ratio, ecological efficiency and intraspecific competition) are kept to a minimum and then the relationship between body mass and total net effects for the food chain is examined in the context of these parameters. The analysis is then extended to four, five and six species food chains and the range of values of the parameters that ensure a positive relationship between species body mass and net effect are compared to the distribution of parameters found in the synthetic and real food webs examined in Chapter 3. Finally, we repeat the analyses for the case where predator-prey body mass ratios decrease with body mass/trophic height which has been observed in marine, lake and terrestrial food webs (Riede et al. 2011) and occurs in the food webs analysed in Chapter 3.

Materials and Methods

Consider a food web, consisting of S species whose dynamics are described by the following Lotka-Volterra equations:

$$\frac{dB_i}{dt} = B_i\left(r_i + \sum_{j=1}^{S} a_{ij} B_j\right) \qquad (1)$$

where B_i is the biomass of species i (measured in kg), for basal species r_i is positive and represents the per unit mass growth rate of species i, for consumer species the r_i term is negative and represents the per unit mass death rate of species i and a_{ij} is the per unit mass effect of consumer species j feeding on resource species i per unit of time.

Following the metabolic scaling used in Chapter 3 to parameterise (1) we define the per unit mass growth/mortality rates and consumer-resource interaction strengths in terms of body mass. The per unit mass growth rate of species i is defined to be:

$r_i = C_r m_i^{-1/4}$ (kg.kg^{-1}t^{-1})

where m_i is the body mass of species i and C_r is a positive constant for basal species and a negative constant for consumer species. The per unit mass effect of consumer species j feeding on resource species i per unit of time, a_{ij} is defined to be:

$$a_{ij} = C_{aij} p_{ij} (m_i m_j)^{-\frac{1}{4}} \qquad (\text{kg}^{-1}\text{t}^{-1})$$

where C_{aij} is a constant, p_{ij} represents the proportion of resource species i present in consumer species j's diet and m_i and m_j represent the resource and consumer species body masses respectively. The per unit mass effect of the resource species i on the consumer species j, a_{ji} is given by

$$a_{ji} = -e a_{ij}$$

where e is the conversion efficiency.

The scaling of intraspecific and interspecific interactions has important implications for the behavior of the system. In general, a dynamic system is more likely to be locally stable when intraspecific interaction strengths become more negative (Saunders 1978, Yodzis 1981, Haydon 1994). If the intraspecific interaction strength of *each* species in a system is greater than the sum of all its interspecific interaction strengths then diagonal dominance occurs and the system is guaranteed to be stable. (Ginzburg and Akçakaya 1992, Abrams 1994, Gleeson 1994, Haydon 1994). Analysis by McPeek (2014) showed that the response of a community to the removal of a top predator is dependent on the relative values of consumer species intraspecific and interspecific interaction strengths. Despite this evidence that the relative scaling of intraspecific and interspecific interaction strengths is of fundamental importance for community dynamics, there is little empirical information available. The experimental data in Chapter 2 found intraspecific interaction strengths for the basal species to be between 100 and 1000 times weaker than interspecific interaction strengths but it was not possible to estimate the scaling of intraspecific interaction strengths for consumer species from the data. To maintain generality we allow the intraspecific interaction terms to vary and consider the following two cases: first where intraspecific interaction strengths scale with interspecific interactions for *each* species (see Appendix E), and second where intraspecific competition is the same for all basal species and intraspecific competition is the same for all consumer species. We define:

$a_{ii} = C_b a_{ij}$ for basal species and $a_{ii} = C_c a_{ik}$ for consumer species where C_b and C_c are parameters that we can vary to investigate how the magnitude of a_{ii} values affect the pattern of total net effects. Here, species j is a herbivore species (body mass m_2 in Figure. 4.1) and species k is a carnivore species (body masses m_3, m_4, m_5 or m_6 in Figure 4.1).

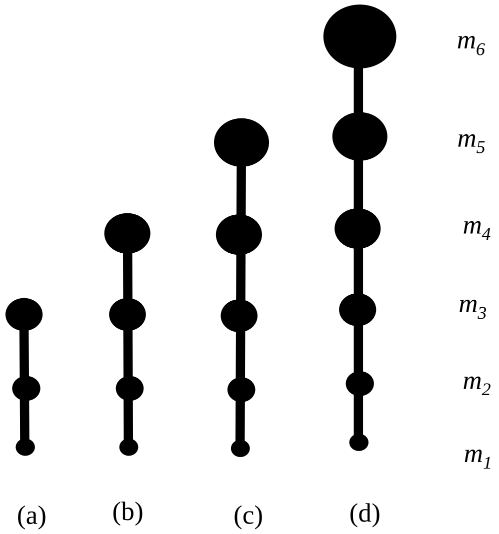


Figure 4.1 Food web motifs of the 3, 4, 5 and 6 species food chains examined.

Three Species Food Chain

For the simple food chain shown in Figure 4.1(a), let m_1, m_2 and m_3 denote the body masses of the basal, herbivore and carnivore species respectively. Let q^* represent the predator-prey body mass ratios so that $q^* = \frac{m_2}{m_1} = \frac{m_3}{m_2}$ then we can write:

$$m_2 = q^* m_1$$
$$m_3 = (q^*)^2 m_1$$

and,

$$a_{12} = C_{a12}(m_1 m_2)^{-\frac{1}{4}} = C_{a12}(q^* m_1^2)^{-\frac{1}{4}} = C_{a12}(m_1^{-\frac{1}{2}})(q^*)^{-\frac{1}{4}}$$

$$a_{23} = C_{a23}(m_2 m_3)^{-\frac{1}{4}} = C_{a23}((q^*)^3 m_1^2)^{-\frac{1}{4}} = C_{a23}(m_1^{-\frac{1}{2}})(q^*)^{-\frac{3}{4}}$$

To simplify the form of the a_{ij} entries we replace $(q^*)^{\frac{1}{4}}$ with the variable q and since C_{aij} is a constant that scales the magnitude of *all* the a_{ij} entries we replace $C_{aij} m_1^{-\frac{1}{2}}$ with the value

-1. This gives $a_{12} = -\frac{1}{q}$ and $a_{23} = -\frac{1}{q^3}$ so that the community matrix A for the simple food chain shown in Figure 4.1(a) is of the form:

$$\begin{pmatrix} \frac{-C_b}{q} & -\frac{1}{q} & 0 \\ \frac{e}{q} & \frac{-C_c}{q^3} & -\frac{1}{q^3} \\ 0 & \frac{e}{q^3} & \frac{-C_c}{q^3} \end{pmatrix}$$

Note that the intraspecific interaction terms are defined to be same for all basal species, $\frac{-C_b}{q}$, and the same for all consumer species, $\frac{-C_c}{q^3}$. This is consistent with many previous studies (Emmerson and Raffaelli 2004, Christianou and Ebenman 2005, Eklöf and Ebenman 2006, Petchey et al. 2008b, Berg et al. 2011) where basal intraspecific interaction strengths are constant (often set to -1) and consumer intraspecific interaction strengths are constant, but smaller in magnitude (often set to -0.1 or -0.01), however, since there is so little known about the scaling of intraspecific interaction strengths we also consider the case where intraspecific interaction strengths scale with interspecific interactions for *each* species (Appendix E). Note that for the case where intraspecific interaction terms are defined to be same for all consumer species, C_c represents the intraspecific: interspecific strength ratio for the herbivore species only. For the case where intraspecific interaction terms scale with interspecific interactions, C_c represents the intraspecific: interspecific strength ratio for *each* species.

The total net effect of a species in the community is represented by the column sums of the absolute values of the inverse matrix, A^{-1}. To investigate the ordering of the column sums we examine the column sums of the simpler but identically scaled matrix,

$B = det(A)A^{-1}$,

where $\det(A)$ is the determinant of the community matrix A. Inverting A, multiplying by the determinant, $det(A)$ and taking the absolute value of the resulting entries gives:

$$B_+ = \begin{pmatrix} \frac{C_c^2 + e}{q^6} & \frac{C_c}{q^4} & \frac{1}{q^4} \\ \frac{C_c e}{q^4} & \frac{C_b C_c}{q^4} & \frac{C_b}{q^4} \\ \frac{e^2}{q^4} & \frac{C_b e}{q^4} & \frac{e q^2 + C_b C_c}{q^4} \end{pmatrix}$$

where B_+ represents the matrix of the absolute values of the entries of B. The column sums are:

$$S_1 = \frac{C_c^2 + e}{q^6} + \frac{C_c e + e^2}{q^4}$$

$$S_2 = \frac{C_b C_c + C_b e + C_c}{q^4}$$

$$S_3 = \frac{1 + C_b + C_b C_c}{q^4} + \frac{e}{q^2}$$

The ordering of the column sums from largest to smallest represents the species in the community in order of their total net effect, from largest to smallest. It is clear that the ordering of the sums is dependent on the relative values of the parameters q, C_b, C_c and e. We aim to evaluate the ordering of the column sums with minimum constraints placed on the parameters, however, ecological constraints allow us to make the following assumptions:

1. If we exclude the possibility of positive intraspecific interaction coefficients (mutualism between individuals of the same species) we may assume that q, C_b, C_c and e are all positive.
2. Since energy is always lost between trophic levels, we may assume $0 < e < 1$.
3. For size based parameterisations such as the one used in Chapter 3 it is often assumed that a consumer species will always feed on smaller species, so that $q > 1$.

Given the complex nature of the column sums we make one or both of the following further assumptions:

4. The value of q is large enough to ensure that the column sum is dominated by the term with the smallest power of q in the denominator.
5. Consumer intraspecific competition, C_c, is small compared to the other parameters.

Since it is given that q is greater than 1, the assumption that q is large enough to ensure that the column sum is dominated by the term with the smallest power of q in the denominator does not require q to be very large due to the nature of power functions, this is illustrated in Figure 4.2. This technique is common practice in asymptotic analysis where a function that cannot be expressed explicitly is approximated by the leading terms of its power series. We examine two situations: first where the assumption that C_c is small compared to the other parameters holds and second where C_c is unconstrained. In the first situation, the ratio of intra- interspecific interaction strength for consumers, C_c, is set to zero, then for fixed C_b and e the body mass ratio parameter q is allowed to become large. In ecological terms, this would equate to a situation where consumer intraspecific competition is weak compared to intraspecific competition amongst basal species. The assumption that consumer intraspecific competition is small compared to the other parameters is based on the biological argument that basal species are sedentary and have to compete for space and light, thus consumer intraspecific interaction strengths can be considered to be small compared to basal intraspecific interaction strength (Emmerson and Raffaelli 2004, Christianou and Ebenman 2005, Eklöf and Ebenman 2006). In the second situation, C_c, C_b and e are fixed and the body mass ratio parameter q is allowed to become large.

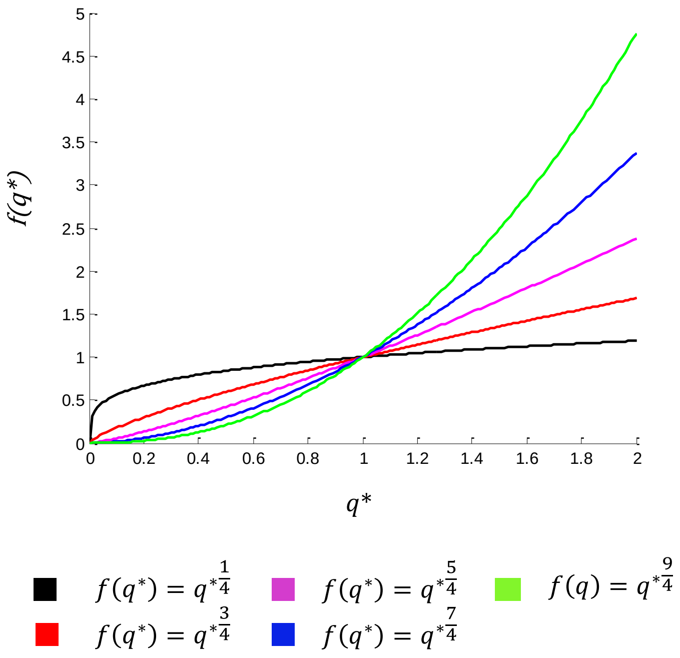


Figure 4.2 Graph showing how functions of increasing powers of the predator-prey ratio $q*$ increase rapidly for $q*$ greater than 1.

Food Chain Analysis

To evaluate the ordering of the columns sums S_1, S_2 and S_3 for the three species food chain we first investigate the case where consumer intraspecific competition is small compared to the other parameters by setting $C_c = 0$ and then allowing q to become large so that the column sums are:

$$\mathrm{S_1} = \frac{\mathrm{e}}{\mathrm{q}^6} + \frac{\mathrm{e}^2}{\mathrm{q}^4}$$

$$S_2 = \frac{C_b e}{q^4}$$

$$S_3 = \frac{e}{q^2}$$

Comparing the terms of S_2 and S_3 it is clear that $S_2 < S_3$ since q^2 is much smaller than q^4. The ordering of S_1 and S_2 is dependent on the values of the parameters e and C_b. Now,

$$S_2 - S_1 = \frac{C_b e}{q^4} - \left(\frac{e}{q^6} + \frac{e^2}{q^4}\right)$$

So we have $S_2 > S_1$ when

$$C_b e q^2 - e - e^2 q^2 > 0$$

i.e. when

$$C_b - e > \frac{1}{q^2}$$

If $C_b > e$ then this will hold provided q is large enough.

If consumer intraspecific competition is not set to 0 then the relationships are more complex. For fixed C_b, C_c, and e, if q is sufficiently large then the column sums are dominated by the terms:

$$S_1 = \frac{C_c e + e^2}{q^4}$$

$$S_2 = \frac{C_b C_c + C_b e + C_c}{q^4}$$

$$S_3 = \frac{1 + C_b + C_b C_c}{q^4} + \frac{e}{q^2}$$

Again, $S_2 < S_3$, because q^2 is much smaller than q^4 but the ordering of S_2 and S_1 depends on the relative magnitude of the parameters C_b, C_c and e. Here,

$$S_2 - S_1 = (C_bC_c + C_be + C_c) - (C_ce \ + e^2)$$

therefore $S_2 > S_1$ when

$$C_c + (C_b - e)(C_c \ + e) > 0 \qquad \text{Inequality (1)}$$

which holds for $C_b > e$. For $C_b < e$ the inequality depends on the relative values of C_b, e and C_c as illustrated in Figure 4.3.

The analysis for food chains of lengths 4, 5 and 6 with constant predator prey-body mass ratios is shown in Appendix F and the analysis for the case where predator-prey body mass ratios decrease with body mass/trophic position for food chains of lengths 3, 4, 5 and 6 is shown in Appendix G.

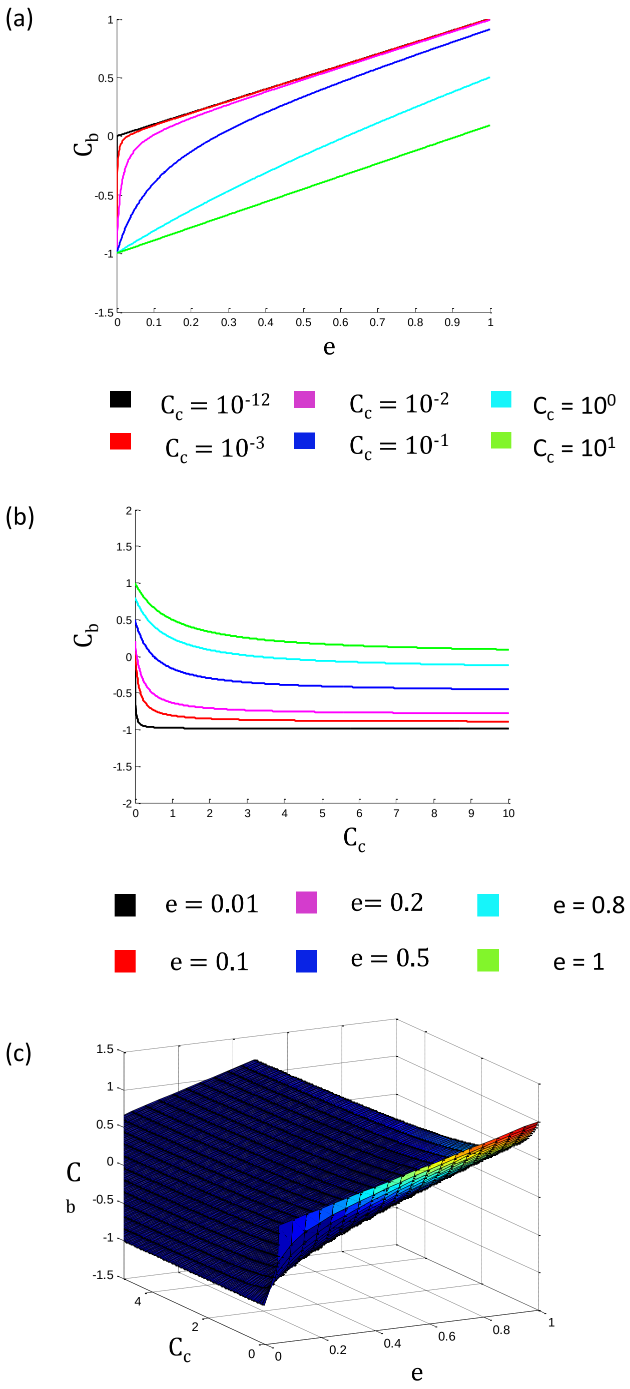


Figure 4.3(a) The ordering of the column sums S_1 and S_2 for the three species chain is shown by the plot of the function $\boldsymbol{C_b} = \mathbf{e} - \frac{\boldsymbol{C_c}}{\boldsymbol{e}+\boldsymbol{C_c}}$ for a range of values of C_c. The ordering $S_2 > S_1$ holds for the areas above the curves. As $C_c \rightarrow 0$ the graph becomes $C_b = e$ and as C_c becomes large the graph becomes $\boldsymbol{C_b} = \boldsymbol{e} - \mathbf{1}$ thus inequality (3) always holds for C_c large. (b) The ordering of the column sums S1 and S2 for the three species chain is shown by the plot of the function $\boldsymbol{C_b} = \mathbf{e} - \frac{\boldsymbol{C_c}}{\boldsymbol{e}+\boldsymbol{C_c}}$ for a range of values of e. The ordering S2 > S1 holds for the areas above the curves. (c) The ordering of the column sums S1 and S2 for the three species chain is shown by the three dimensional surface plot showing of the function $\boldsymbol{C_b} = \mathbf{e} - \frac{\boldsymbol{C_c}}{\boldsymbol{e}+\boldsymbol{C_c}}$. The ordering S2 > S1 holds for the volume above the surface.

Comparison with Synthetic and Real Webs

The analytical food chain analysis produced ranges of values of the parameters $C_{b,}$ C_c, and e that ensure a positive relationship between species body mass and total net effect. The range of values of $C_{b,}$ C_c, and e were then compared to the distribution of parameters found in a set of 97 synthetic webs and 2 real webs (Tuesday Lake and a reduced version of the Ythan Estuary). Each of the 97 synthetic food webs was created sequentially using an assembly algorithm from a previous study (Säterberg et al. 2013). The algorithm was initiated with a feasible locally stable community consisting of 7 competing basal species whose body masses were drawn from a uniform distribution. At each step a new species was added to the community and the dynamics observed. Each new species, either basal, herbivore or carnivore was chosen at random and allocated a body mass drawn from a uniform distribution associated with the relevant trophic position. All feeding interactions were determined from this body mass (see Appendix C for a detailed description). After each addition, the new equilibrium was checked for feasibility and local stability. If the new equilibrium did not satisfy the criteria then the community was returned to the previous step and the process repeated. If these criteria were satisfied then the new community was retained and the process repeated until the community contained 50 species. Previously, we have shown (Chapter 3 of this thesis) that there is a positive relationship between a species body mass and its total net effect for all of the food webs analysed. The parameters that determine the strength of interactions between species (predator-prey body mass ratio, ecological efficiency and intraspecific competition) for the synthetic and real food webs were calculated for each of the synthetic and real food webs and the distributions of the parameters compared to the values that emerged from the analytical food chain analysis. The analyses were performed using MATLAB version 7.7.0 (MATLAB 2008).

Results

Constant predator-prey body mass ratio

If C_c represents the intraspecific: interspecific strength ratio for *each* species so that intraspecific competition varies amongst consumer species, then for $C_b > e$ the ordering of species from largest body mass to smallest body mass corresponds precisely with the ordering of influence from largest total net effect to smallest total net effect for all food chains (see Table 4.1 for a summary of the orderings and Appendix E for analysis). For the case where consumer intraspecific competition, C_c is set to 0 then there is an emerging pattern where the ordering from largest body mass to smallest body mass corresponds precisely with the ordering of influence from largest total net effect to smallest total net effect for $C_b > e$ (see Table 4.1 for a summary of the orderings and Appendix F for analysis). For $C_b < e$ the ordering is not precise, however, powers of q ensure that there is a general pattern that largest body sizes are the most important.

If consumer intraspecific competition is not set to 0 and can vary among consumer species then the ordering of the species from largest body mass to smallest body mass does not always correspond with the ordering of influence from largest total net effect to smallest total net effect (Table 1), but is dependent on the relative magnitude of the parameters C_b, C_c and e governed by inequalities (1), (2) and (3) (shown in Table 4.2 and Figures 4.3, 4.4(a) and 4.4(b) respectively). The derivation of inequality (1) is shown above in the materials and methods section and the derivation of inequalities (2) and (3) is shown in Appendix F.

Table 4.1 Summary of the order of species total net effects for food chains of lengths, 3, 4 5 and 6 for the case where the predator-prey body size ratio, *q*, is constant.

Food Chain Length	**Constant predator-prey body size ratio (q)**			
	$C_c = 0$	**Condition**	$C_c \neq 0$	**Condition**
3	$S_1 < S_2 < S_3$	$C_b > e$	$S_1 < S_2 < S_3$	Inequality (3)
4	$S_1 < S_2 < S_3 < S_4$	$C_b > e$	$S_1 < S_2 < S_3 < S_4$	Inequality (3)
				Inequality (4)
5	$S_1 < S_2 < S_3 < S_4 < S_5$	$C_b > e$	$S_1 < S_2 < S_3 < S_5 < S_4$	Inequality (3)
				Inequality (4)
				Inequality (5)
6	$S_1 < S_2 < S_3 < S_4 < S_5 < S_6$	$C_b > e$	$S_1 < S_2 < S_3 < S_6 < S_5 < S_4$	Inequality (3)
				Inequality (4)
				Inequality (5)

Table 4.2 The inequalities governing the order of species total net effects for food chains of lengths 3, 4, 5 and 6.

Inequality (1)	$C_c + (C_b - e)(C_c + e) > 0$
Inequality (2)	$C_b e - C_b C_c - C_c + e - e^2 > 0$
Inequality (3)	$C_b e - C_b C_c - C_c - e^2 > 0$

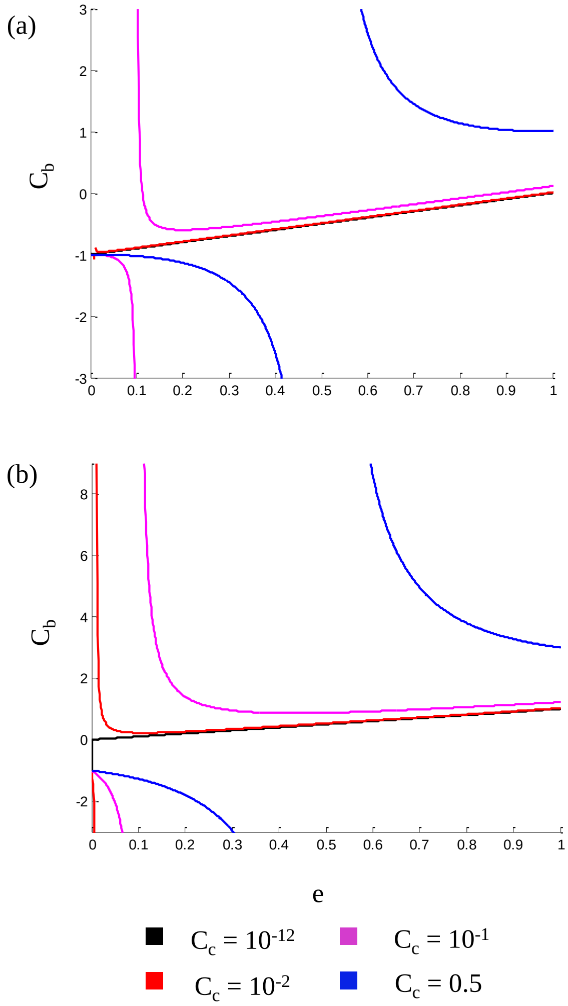


Figure 4.4 (a) the ordering of the column sums S3 and S4 for the four species chain is shown by the plot of the function $C_b = \frac{e^2}{e-C_c} - 1$ for a range of values of Cc. The ordering S4 > S3 is true for the area shown above and to the right of the upper set of curves. Figure 4.4 (b) the ordering of the column sums S3 and S5 for the five species food chain is shown by the plot of the function $C_b = \frac{e^2+C_c}{e-C_c}$ for a range of values of Cc. The ordering S5 > S3 is true for the area shown above and to the right of the upper set of curves.

For all of the food chains examined here, the column sums for the basal and herbivore species are always smaller than those for the carnivore species. If consumer intraspecific competition varies amongst consumer species or is set to 0 then the condition, $C_b > e$ is sufficient to ensure that the herbivore species have a larger total net effect than the basal species. For the case where consumer intraspecific competition is not set to 0 and is the same for all consumer species, the ordering of the basal and herbivore species is governed by the same inequality (3), (see Figure 4.3) for all the food chains examined. We note that for $C_b > e$, inequality (3) holds and the herbivore species has a larger total net effect than the basal species, i.e. the condition $C_b > e$ ensures that the herbivore species has a larger total net effect than the basal species for all cases considered here.

If consumer intraspecific competition varies among consumer species then the ordering of carnivore species from largest body mass to smallest body mass corresponds precisely with the order of influence from largest total net effect to smallest total net effect for all food chains for all possible values of the parameters. If consumer intraspecific competition, C_c is set to 0 then the ordering of the carnivore species is governed by inequalities (1), (2) and (3) (see Table 2.2); if the inequalities are satisfied then the ordering of carnivore species from largest body mass to smallest body mass corresponds precisely with the ordering of influence from largest total net effect to smallest total net effect for all food chains. If consumer intraspecific competition is not set to 0 then amongst the carnivore species, it seems that smaller carnivores have greater influence than larger carnivores with the exception of the smallest carnivore (body mass m_3), whose position in the order is dependent on the relative magnitude of the parameters C_b, C_c and e (see Table 2.1). The smallest carnivore has a smaller total net effect than the next largest carnivore (body mass m_4) when inequality (2) is satisfied (see Table 2.2 and Figure 4.4a) and has a smaller net effect than the largest bodied carnivores (body masses m_5 and m_6) when inequalities (2) and (3) are satisfied. We note that for the smallest carnivore to have a smaller total net effect than the next largest carnivore it is necessary, but not sufficient, that $C_c < e$ and to ensure that the smallest carnivore species has a smaller total net effect than the largest bodied carnivores (body masses m_5 and m_6) it is necessary, but not sufficient that $C_c < e < C_b$.

The distribution of the parameters q^*, C_b, C_c *and* e *in the synthetic food webs*

Next, consider the frequency distribution of the predator-prey ratios, q^*, that occurred in the 97 synthetic food webs analysed in Chapter 3 (see Figure 4.5a). The predator-prey ratios form three distinct distributions: the ratio between basal species and herbivore species, the ratio between herbivore and carnivore species and the ratio between carnivore and top carnivore species. The histogram shows that all of the basal-herbivore predator prey-ratios are greater than 1, with an average value of 10^9 (the power represents the mean of the base 10 logarithms of the predator-prey ratios) and that all of the herbivore-carnivore predator-prey body mass ratios are greater than 1, with an average value of $10^{2.1}$. These ratios satisfy the assumption that 'q is large enough' made in the analysis above. However there are a significant number of carnivore-top carnivore predator-prey ratios less than 1, which means that for many of the top carnivore species the assumption 'q large enough' is not met and the column sums representing the total net effects of the top carnivore species may not be dominated by the leading terms.

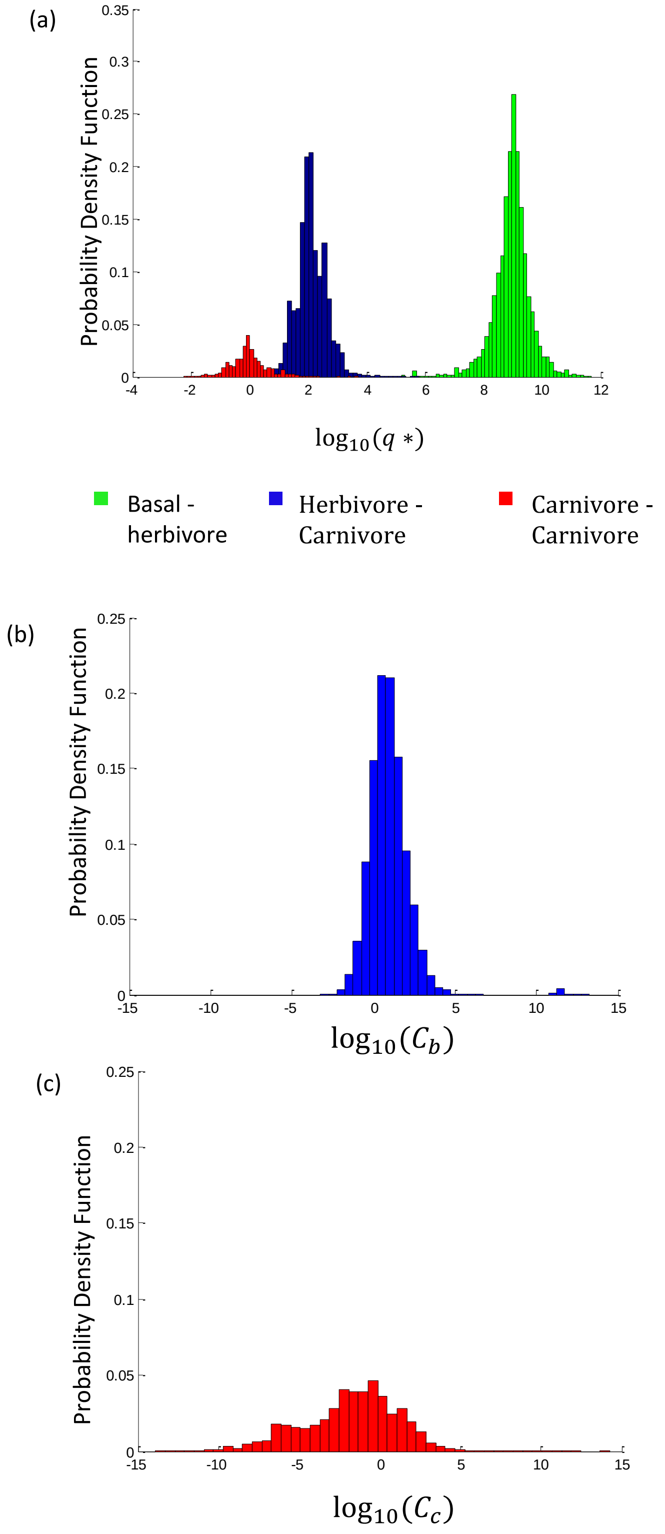


Figure 4.5 (a) Plot of the probability density function for predator-prey body size ratios for all of the predator-prey interactions present in the 50 synthetic webs analysed in Chapter 3. The predator-prey body size ratio decreases with trophic height and body size. Figures 4.5 (b) and (c) Plots of the probability density functions for the intra – interspecific interaction strength ratios for all interactions present in the 50 synthetic webs analysed in Chapter 3. The distributions show that basal intra-interspecific interaction ratios (Cb) were usually greater than 1 and, in general, were larger than consumer intra-interspecific interaction ratios (Cc) which were frequently less than 1

The ecological efficiency parameter, *e*, used in Chapter 3 was assumed to be 0.1. The frequency distributions of the parameters C_b and C_c for all 97 synthetic webs are shown in Figures 4.5(b) and (c). Examining the distributions of parameters for all 97 webs showed that over 97% of the values of C_b were greater than 0.1 and 26% of the values of C_c were less than 10^{-4}. These values of C_b and C_c correspond approximately to the first case we examined where C_b is greater than *e*, C_c is set to 0 and there is a perfect correlation between body mass and total net effect. However, on a per web basis, just one web had values of C_b and C_c where *all* values in the individual web satisfied C_b is greater than *e* and C_c is less than 10^{-4}.

Examining the distributions of parameters for all 97 synthetic webs showed that 58% of the values of C_c were less than 0.1 and on a per web basis, 46 webs had values of C_c where *all* values in the individual web satisfied C_c less than 0.1. Therefore, for over half of the synthetic webs examined the values of C_c were not less than *e* and we do not expect a correlation between body mass and total net effects within the carnivore species. Examination of the correlations between carnivore species body mass and total net effects found that just 4 webs had a significant (at the 5% level) positive correlation and 2 webs had a significant negative correlation. The average correlation over all 97 webs was 0.135. However, predator-prey body mass ratios still guarantee that basal and herbivore species have a weaker total net effect than carnivore species thus ensuring correlation between species body mass and total net effects for the whole food web. The correlations between species body mass and total net effect for each of the 97 food webs were not perfect; they ranged between 0.41- 0.97 with an average correlation of 0.87. This deviation from a perfect correlation may be due to smaller carnivore-top carnivore predator-prey mass ratios, the relatively large values of C_c or the more complex structure of the webs.

The distribution of the parameters q^*, C_b, C_c and e in the real food webs

The distributions of the predator-prey ratios, q^*, that occurred in the Tuesday Lake and Ythan Estuary food webs analysed in Chapter 3 are shown in Figures 4.6(a) and 4.7(a). The distribution of predator-prey body mass ratios show that the predator-prey ratios, q^* are nearly all greater than 1. Figures 4.6(b) and 4.7(b) show that basal intra-interspecific interaction ratios (C_b) were all greater than the efficiency *e* (set to 0.1). For the Tuesday Lake food web (Figure 4.6b) 28% of consumer intra-interspecific interaction ratios (C_c) were less than 0.1 and no ratios were less than 10^{-4}. For the Ythan Estuary food web, 81% of consumer intra-interspecific interaction ratios (C_c) were less than 0.1 and 18% were less than 10^{-4}. The smaller values of C_c found in the Ythan Estuary food web may lead us to believe that the correlation between species body mass and total net effects should be stronger for the Ythan Estuary food web than for the Tuesday Lake food web but this was not the case. The correlation between species body mass and total net effect was 0.91 for the Tuesday Lake food web but just 0.44 for the Ythan Estuary food web. The stronger correlation in the Tuesday Lake food web may be explained by the different compositions of the food webs; the Tuesday Lake food web consisted of 29 basal species, 15 herbivore species and just 7 carnivore species whereas the Ythan Estuary food web consisted of just 4 basal species, 24 herbivore species and 25 carnivore species, thus the overall size structuring in the Tuesday Lake food web is more distinct than the Ythan Estuary food web, contributing to a stronger correlation.

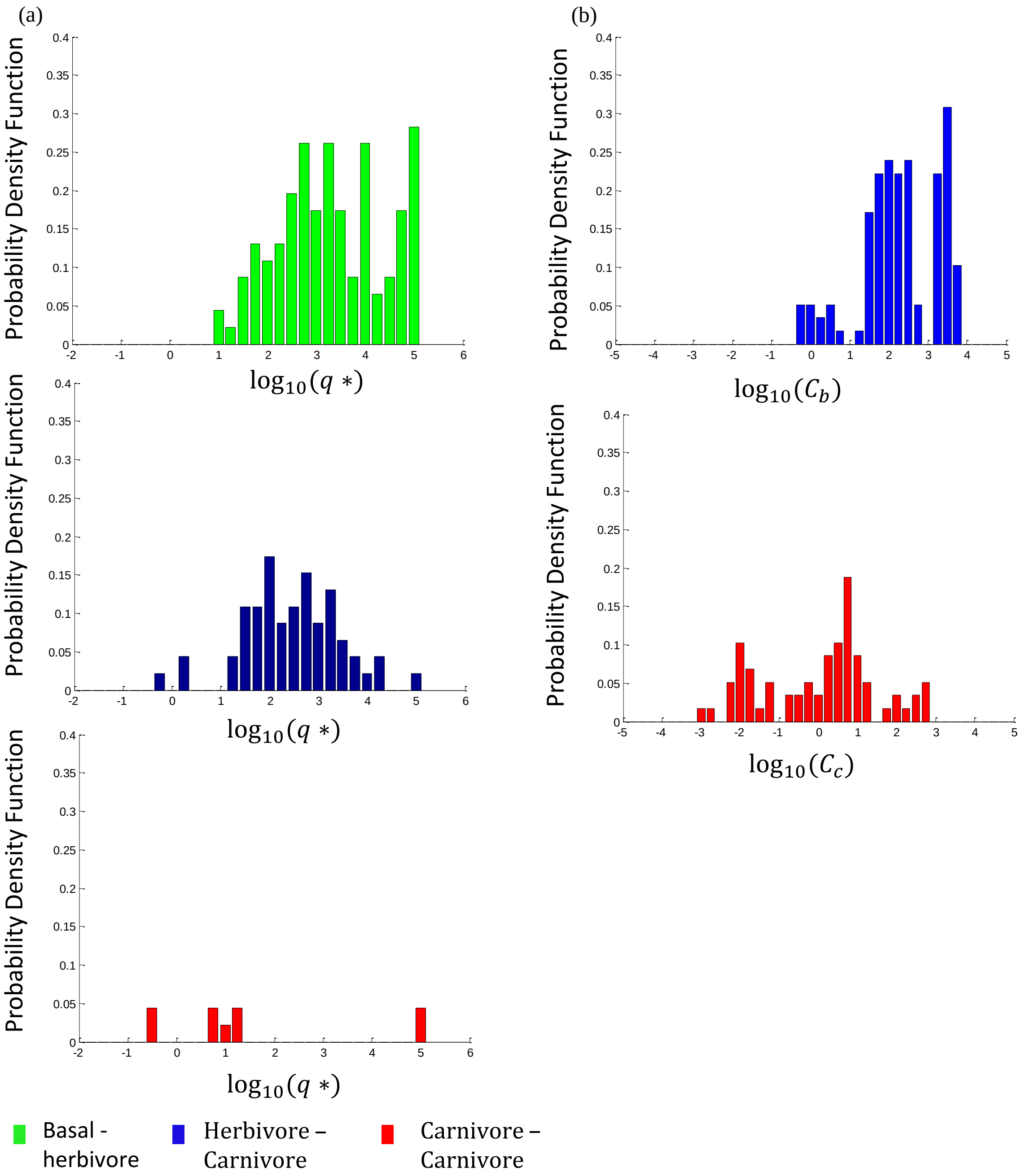


Figure. 4.6 (a) Plot of the probability density function for predator-prey body size ratios for all predator-prey interactions present in the Tuesday Lake food web analysed in Chapter 3. Figure 4.6 (b) Plot of the probability density functions for the intra–interspecific interaction strength ratios for all interactions present in the Tuesday lake food web analysed in Chapter 3. The distributions show that basal intra-interspecific interaction ratios (C_b)were usually greater than 1 and, in general, were larger than consumer intra-interspecific interaction ratios (C_c).

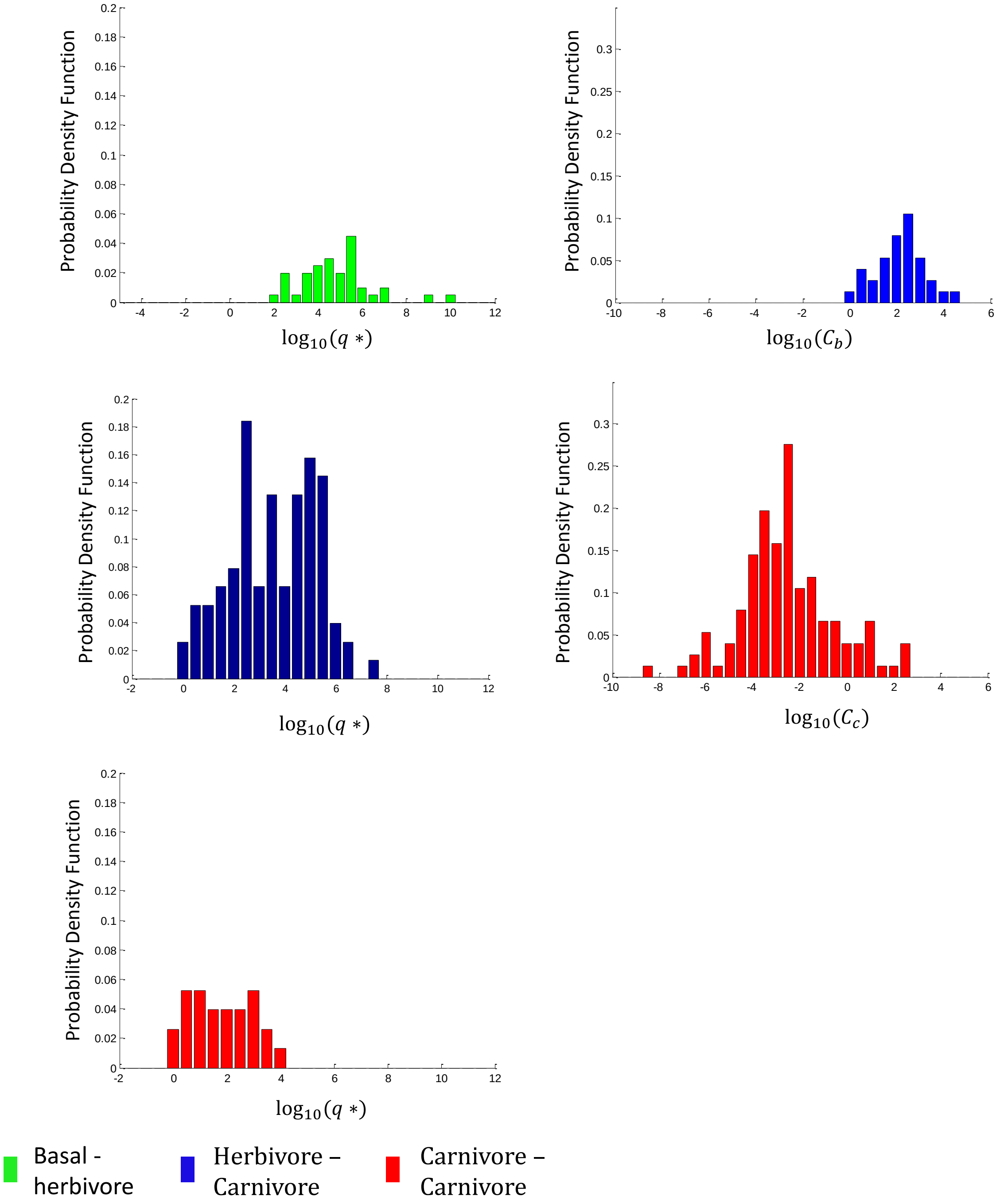


Figure 4.7 (a) Plot of the probability density function for predator-prey body size ratios for all predator-prey interactions present in the largest invertible sub-web of the Ythan Estuary food web analysed in Chapter 3 (contains 53 species). Figure 4.7 (b) Plot of the probability density functions for the intra–interspecific interaction strength ratios for all interactions present in the largest invertible sub-web of the Ythan Estuary food web analysed in Chapter 3. The distributions show that basal intra-interspecific interaction ratios (C_b) were usually greater than 1 and consumer intra-interspecific interaction ratios (C_c) were usually less than 1.

Predator-prey ratios decrease with trophic position and body-mass

The ranking of species in order of their total net effects for each food chain is shown in Table 4.3.

Table 4.3 summary of the order of species total net effects for food chains of lengths, 3, 4 5 and 6 for the case where the predator-prey body size ratio, q, decreases with trophic position and body-mass.

Food Chain Length	Decreasing predator-prey body size ratio (q)			
	$C_c = 0$	Condition	$C_c \neq 0$	Condition
3	$S_1 < S_2 < S_3$	$C_b > e$	$S_1 < S_2 < S_3$	
4	$S_1 < S_2 < S_3 < S_4$	$C_b > e$	$S_1 < S_2 < S_4 < S_3$	Inequality (3)
5	$S_1 < S_2 < S_4 < S_3 < S_5$	$C_b > e$	$S_1 < S_2 < S_5 < S_3 < S_4$	Inequality (3)
6	$S_1 < S_2 < S_4 < S_3 < S_5 < S_6$	$C_b > e$	$S_1 < S_2 < S_6 < S_5 < S_3 < S_4$	Inequality (3)

For food chains of length three and four, in the case where consumer intraspecific competition is set to 0, allowing predator-prey body mass ratios to decrease with trophic height has no effect on the relationship between species body mass and the magnitude of its total net effects, i.e. if consumer intraspecific competition is set to 0 then there is a precise ordering of increasing species total net effects with increasing body mass for $C_b > e$. For food chains of length five and six, in the case where consumer intraspecific competition is not set to 0, allowing predator-prey body mass ratios to decrease with trophic height caused a small change in the ordering of species; the two smallest carnivore species, (body masses m_3 and m_4) switched places in the ordering so that the carnivore with the smallest body mass (m_3) had a greater total net effect than its predator species (body mass m_4).

If consumer intraspecific competition is not set to 0 then the ordering of the carnivore species from largest body size to smallest body size does not correspond with the ordering of influence from largest total net effect to smallest total net effect. As in the case for constant predator-prey body mass ratios we find that for each of the food chains examined here, the column sums for the basal and herbivore species are always smaller than those for the carnivore species and the ordering of the basal and herbivore species is given by inequality (3) (Figure 4.3) for all food chains.

For the three species food chain this means that the orderings are no different to the case where the predator-prey body mass ratio, q, is constant. However, it seems that for food chains of length four, five and six, decreasing predator-prey body mass ratios changes the ordering of carnivore species. Recall, that for the case where q was constant and C_c was not set to 0, we found that smaller carnivores have greater influence than larger carnivores with the exception of the smallest carnivore (body mass m_3), whose position in the order is dependent on the relative magnitude of the parameters C_b, C_c and e (see Table 4.1 and Figures 4.4a and 4.4b) whereas for decreasing q there is no obvious ordering of total net effects with body mass (see Table 4.3).

Discussion

The food chains analysed here are much simplified representations of the synthetic and real webs that were examined in Chapter 3. For large webs, the relationship between the community matrix and its inverse can become lost in the complexity of the inverse operation. The simplicity of these food chains enables us to determine the mechanisms driving the relationship between body mass and total net effects. Analyses of these simple food chains showed that in an energetics based framework, where food webs are parameterised according to energetic constraints under the assumption that large bodied species eat small bodied species, in general, large species have greater total net effects than small species (subject to conditions on parameters). This finding explains the relationship observed in Chapter 3 where it was demonstrated that the total net effect of a species was highly correlated with its body mass.

We found that basal and herbivore species were always less influential than carnivore species and that the condition $C_b > e$ guaranteed that basal species were less influential than herbivore species for all food chains. Recall, the parameter e represents the ecological efficiency of the consumer species i.e. the fraction of prey biomass ingested by the consumer that is turned into new consumer biomass and the parameter C_b represents the ratio of intraspecific: interspecific interaction strengths for basal species. If C_b has a value that is less than one, then the effect of herbivory on the basal species is greater than the self-limiting effect of intraspecific competition amongst the herbivore species. How often the condition $C_b > e$ is satisfied in real food webs is unclear since intraspecific and interspecific interactions are notoriously difficult to measure empirically (Laska and Wootton 1998, Abrams 2001, Berlow et al. 2004, Wootton and Emmerson 2005).

Ecological efficiency is clearly bounded above by 1, it is estimated to lie between 0.02 and 0.32 (Begon et al. 2009) and has been shown to decrease with body mass in marine systems (Barnes et al. 2010). For the synthetic food webs parameterised using predator-prey body mass ratios and allometric scaling, C_b was greater than 1 (the upper bound of e) for 80% of the ratios calculated and greater than 0.1 for over 97% of the ratios calculated, thus the condition $C_b > e$ was satisfied for most species, and herbivores had a greater total net effect than basal species. However, the empirical measures of intraspecific and interspecific interaction strengths measured from the plant-aphid mesocosm experiment presented in Chapter 2 indicate that C_b lies between 0.01 and 0.001. Since the ecological efficiency estimate for the pea aphid is approximately 0.2 (Auclair 1965), the condition $C_b > e$ is not satisfied and we expect the basal species to have a larger total net effect than the herbivore species for that system. This example is somewhat counterintuitive; the reason the intraspecific: interspecific interaction strength ratio was so low was because the aphids had a large impact on the plants and yet we expect that the total net effect of the plants is greater than the total net effect of the aphids. It is important to note that since aphids are pest species, the intraspecific: interspecific interaction strength ratio estimated for plants and aphids in the study presented in Chapter 2 might be smaller than ratios in the environments where aphid populations are kept in check by a variety of natural enemies and smaller than ratios for other pairs of species in different systems.

The impact of both intraspecific competition and predation can vary with population density (through functional responses and carrying capacities), it can vary with the structure of the community and also with environmental conditions (Menge and Sutherland 1987, Goldberg et al. 1999, Case 2000, Sarnelle 2003, Otto et al. 2008, Schmitz et al. 2008, Alvarez et al. 2013). In light of this, it is likely that the relative importance of basal species and herbivore species will vary between communities and, over time, within a community; more empirical information is needed to estimate the extent of this variation.

For food chains of length four or greater, it was found that the ordering of carnivore species from largest body mass to smallest body mass corresponds precisely with the ordering of influence from largest total net effect to smallest total net effect for the case where consumer intraspecific interaction strength varies among consumer species (for all values of the parameters) and for the case where consumer intraspecific interaction strength is set to 0 (for $C_b > e$). If consumer intraspecific interaction strength is not set to 0 and is the same for all consumer species then, for the case where the predator-prey body mass ratio is constant, it seems that smaller carnivores have greater influence than larger carnivores with the exception of the smallest carnivore (body mass m_3), whose position in the order is dependent on the relative magnitude of the parameters C_b, C_c and e (Table 4.2 and Figures 4.4a and 4.4b). For the case where predator-prey body mass ratios decrease with body mass, and consequently trophic height, there is no obvious ordering of total net effects with body mass.

If intraspecific competition is the same for all consumer species, as trophic level increases intraspecific interaction strengths remain constant while interspecific interaction strengths decrease, thus intraspecific interaction strengths became relatively stronger for species at higher trophic levels. The fact that larger bodied carnivore species experience relatively stronger self-limitation may explain the pattern we see where smaller bodied carnivore species have greater net effects than larger bodied carnivore species. If intraspecific interaction strengths vary among consumer species then there is a precise ordering of increasing total net effects with increasing body mass and trophic level. Again, since we do not know how intraspecific interaction strengths scale with interspecific interaction strengths in real systems it is not possible to draw definite conclusions regarding the ordering of carnivore species.

The fact that the ordering of species net effects amongst carnivore species in longer food chains was not always clear may not have a large effect on the correlation of species body mass with total net effects in large complex food webs, since top carnivore species are rarer than species at lower trophic levels. For the synthetic webs analysed in Chapter 3, just 5% of species were top-carnivore species. For the Tuesday Lake food web there were just 2 top-carnivore species (representing less than 4% of all species) and for the Ythan Estuary web there were just 4 top carnivore species (representing less than 8% of all species). Therefore, the ordering amongst the carnivore species will not have a large effect on the overall relationship between body mass and net effect; the most important factor is that basal species have smaller net effects than herbivore species which have smaller net effects than carnivore species. This result alone is enough to ensure a strong correlation between body mass and net effect in complex webs.

In the synthetic webs and real webs analysed in Chapter 3 we note that the trophic levels are not clearly defined the way they are for a food chain since most species have more than one prey, thus species trophic heights are averaged. This, along with the fact that in food webs there are multiple species of similar size eating similar sized prey means that entries in the community matrix may be similar for multiple species and the precise ordering of these species will depend on the values assigned to intraspecific competition as well as the structure of the web.

For size structured communities where large species feed on smaller species, the results of this analysis indicate that, in general, large bodied species have the greatest net effect in a community (on a per unit mass basis). At a population level, the relationship between species body mass and total net effects is dependent on how population biomass density scales with body mass across trophic levels. The population biomass of species i, B_i, can be written as $B_i = N_i \times m_i$ where N_i is the numerical population density of species i and m_i is the average body mass of species i. If the previously reported scaling between numerical population density and body size ($N_i = m_i^{-1}$) (Peters 1983, Schmid et al. 2000) holds then $B_i = N_i \times m_i = m_i^{-1} \times m_i = m_i^0$ and population biomass density is invariant with body size across trophic levels thus the relationship between body mass and total net effect at the population level is unchanged. If the scaling exponent between population biomass density and body mass is greater than 0 then the positive relationship between body mass and total net effect at the population level is strengthened but if the scaling exponent is less than 0 then the positive relationship between body mass and total net effect at the population level is weakened. For a scaling exponent less than 0, whether the relationship holds at the population level or not will depend on the value of the scaling exponent and how strongly size structured the community is. Within the size structured North Sea community, exponents less than 0 have been reported for fish and epifaunal predator species and exponents greater than 0 have been reported for infaunal detritivore species (Blanchard et al. 2009), these values have the potential to alter the relationship between species body mass and total net effects at the population level.

Several conclusions can be drawn from the present study. First, in an energetics based framework, where food webs are parameterised according to energetic constraints under the assumption that large bodied species eat small bodied species, in general, large species have greater total net effects than small species. Second, the precise ordering of species is terms of their total net effect is dependent on the relative values of efficiency, e, and intraspecific: interspecific interaction strength ratios. Finally, the relationship between species body size and total net effect at the population level will also depend on how population biomass density scales with body mass and how strongly the community is size structured. Much information is known about the ecological efficiency parameter *e* (Begon et al. 2009, Barnes et al. 2010), and there is a growing body of empirical studies informing the size structuring of communities (Jennings and Warr 2003, Brose et al. 2005b, Brose et al. 2006a, Riede et al. 2011), and the scaling of population biomass density with body size (Peters 1983, Schmid et al. 2000, Blanchard et al. 2009, Wilson et al. 2010), but further empirical information regarding the scaling of intraspecific and interspecific interaction strengths is necessary before we can predict the total net effect of a species within a community.

APPENDIX E

Here we present the analysis for the food chains shown in Figures 4.1(a)-(d) under the assumption that consumer intraspecific interaction strength scales with consumer interspecific interaction strength so that:

$a_{ii} = C_b a_{i,i+1}$ for basal species and $a_{ii} = C_c a_{i,i+1}$ for consumer species

where C_b and C_c are parameters that we can vary to investigate how the magnitude of a_{ii} values affect the pattern of total net effects. Note that this definition cannot apply to the top predator so for the top predator we define intraspecific competition to be the same as for its prey species so that:

$a_{ii} = C_c a_{i-1,i}$ where *i* is a top predator.

For the simple three species food chain shown in Figure 4.1 (a) this does not change the community matrix *A* so the orderings of column sums will be unchanged.

Four Species Food Chain

For the simple food chain shown in Figure 4.1 (b), let m_1, m_2, m_3 and m_4 denote the body masses of the basal, herbivore, carnivore and top carnivore species respectively. Following the assumptions made for the case where consumer intraspecific competition is the same for all consumer species, the community matrix A for the four species food chain is of the form:

$$A = \begin{pmatrix} \frac{-C_b}{q} & -\frac{1}{q} & 0 & 0 \\ \frac{e}{q} & \frac{-C_c}{q^3} & -\frac{1}{q^3} & 0 \\ 0 & \frac{e}{q^3} & \frac{-C_c}{q^5} & -\frac{1}{q^5} \\ 0 & 0 & \frac{e}{q^5} & \frac{-C_c}{q^5} \end{pmatrix}$$

We examine the column sums of the absolute values of the entries of the matrix *B*, where, $B = det(A)A^{-1}$.

$$B_+ = \begin{pmatrix} \frac{C_c(C_c{}^2 + eq^2 + e)}{q^{13}} & \frac{C_c{}^2 + e}{q^{11}} & \frac{C_c}{q^9} & \frac{1}{q^9} \\ \frac{C_c{}^2 e + e^2}{q^{11}} & \frac{C_b C_c^2 + C_b e}{q^{11}} & \frac{C_b C_c}{q^9} & \frac{C_b}{q^9} \\ \frac{C_c e^2}{q^9} & \frac{C_b C_c e}{q^9} & \frac{C_c e q^2 + C_b C_c^2}{q^9} & \frac{eq^2 + C_b C_c}{q^9} \\ \frac{e^3}{q^9} & \frac{C_b e^2}{q^9} & \frac{e^2 q^2 + C_b C_c e}{q^9} & \frac{C_b C_c^2 + C_c e q^2 + C_b e q^2}{q^9} \end{pmatrix}$$

The matrix B_+ is the matrix whose entries are the absolute values of the entries of matrix B. The column sums are:

$$S_1 = \frac{C_c^3 + e}{q^{13}} + \frac{C_c{}^2 e + C_c e + e + e^2}{q^{11}} + \frac{C_c e^2 + e^3}{q^9}$$

$$S_2 = \frac{C_b e + C_b C_c^2 + C_c^2 + e}{q^{11}} + \frac{C_b C_c e + C_b e^2}{q^9}$$

$$S_3 = \frac{C_b C_c + C_b C_c^2 + C_b C_c e + C_c}{q^9} + \frac{C_c e + e^2}{q^7}$$

$$S_4 = \frac{1 + C_b + C_b C_c + C_b C_c^2}{q^9} + \frac{C_b e + C_c e + e}{q^7}$$

For sufficiently large q, the column sums are approximated by:

$$S_1 \approx \frac{C_c e^2 + e^3}{q^9}$$

$$S_2 \approx \frac{C_b C_c e + C_b e^2}{q^9}$$

$$S_3 \approx \frac{C_c e + e^2}{q^7}$$

$$S_4 \approx \frac{C_b e + C_c e + e}{q^7}$$

It is clear that $\max\{S_1, S_2\} < S_3 < S_4$ since q^7 is much smaller than q^9. The ordering of S_1 and S_2 depends on the relative magnitude of the parameters C_b, C_c and e.

The ordering $S_2 > S_1$ holds when

$$S_2 - S_1 = \frac{C_b C_c e + C_b e^2}{q^9} - \frac{C_c e^2 + e^3}{q^9} > 0$$

i.e. when

$$C_b(C_c + e) - e(C_c + e) > 0$$

which holds for $C_b > e$.

Five Species Food Chain

For the five species food chain shown in Figure 4.1 (c), let m_1, m_2, m_3, m_4 and m_5 denote the body masses of the species in order of increasing size and trophic height. Following the assumptions made for the four species food chain, the community matrix A for a five species food chain is of the form:

$$A = \begin{pmatrix} \frac{-C_b}{q} & -\frac{1}{q} & 0 & 0 & 0 \\ \frac{e}{q} & \frac{-C_c}{q^3} & -\frac{1}{q^3} & 0 & 0 \\ 0 & \frac{e}{q^3} & \frac{-C_c}{q^5} & -\frac{1}{q^5} & 0 \\ 0 & 0 & \frac{e}{q^5} & \frac{-C_c}{q^7} & -\frac{1}{q^7} \\ 0 & 0 & 0 & \frac{e}{q^7} & \frac{-C_c}{q^7} \end{pmatrix}$$

The column sums of the matrix B_+ which is the matrix containing the absolute values of the matrix entries of $det(A)A^{-1}$ are:

$$S_1 = \frac{C_c^4 + C_c^2 e}{q^{22}} + \frac{2C_c e^2 + C_c^3 e + e + e^2}{q^{20}} + \frac{C_c^2 e^2 + C_c e^2 + e^3}{q^{18}} + \frac{C_c e^3 + e^4}{q^{16}}$$

$$S_2 = \frac{C_b C_c^3 + C_b C_c e + C_c^3 + e}{q^{20}} + \frac{C_b C_c e + C_b C_c^2 e + C_c e + e}{q^{18}} + \frac{C_b C_c e^2 + C_b e^3}{q^{16}}$$

$$S_3 = \frac{C_b C_c^2 + C_b C_c^3 + C_b e + C_b C_c e + C_c^2 + e}{q^{18}} + \frac{C_b C_c^2 e + C_b C_c e^2 + C_c^2 e + e^2}{q^{16}} + \frac{C_c e^2 + e^3}{q^{14}}$$

$$S_4 = \frac{C_bC_c + C_bC_c^2 + C_bC_c^3 + C_bC_c^2e + C_c}{q^{16}} + \frac{C_bC_ce + C_be^2 + C_ce + C_c^2e + C_ce^2}{q^{14}}$$

$$S_5 = \frac{1+C_b + C_bC_c + C_bC_c^2 + C_bC_c^3}{q^{16}} + \frac{C_be + 2C_bC_ce + C_ce + C_c^2e + e}{q^{14}} + \frac{e^2}{q^{12}}$$

For non-zero consumer intraspecific competition and for sufficiently large q, the column sums are dominated by the terms:

$$S_1 \approx \frac{C_ce^3 + e^4}{q^{16}}$$

$$S_2 \approx \frac{C_bC_ce^2 + C_be^3}{q^{16}}$$

$$S_3 = \frac{C_ce^2 + e^3}{q^{14}}$$

$$S_4 \approx \frac{C_bC_ce + C_be^2 + C_ce + C_c^2e + C_ce^2}{q^{14}}$$

$$S_5 \approx \frac{e^2}{q^{12}}$$

It is clear that $\{S_1, S_2\} < S_3 < S_4 < S_5$. The ordering $S_2 > S_1$ holds when

$$S_2 - S_1 = \frac{C_bC_ce^2 + C_be^3}{q^{16}} - \frac{C_ce^3 + e^4}{q^{16}} > 0$$

i.e. when

$$C_b(C_c + e) - e(C_c + e) > 0$$

which holds for $C_b > e$.

Six Species Food Chain

For the six species food chain shown in Figure 4.1 (d), let m_1, m_2, m_3, m_4, m_5 and m_6 denote the body masses of the species in order of increasing size and trophic height. Following the assumptions made for the shorter food chains the community matrix A for the six species food chain is of the form:

$$A = \begin{pmatrix} \frac{-C_b}{q} & -\frac{1}{q} & 0 & 0 & 0 & 0 \\ \frac{e}{q} & \frac{-C_c}{q^3} & -\frac{1}{q^3} & 0 & 0 & 0 \\ 0 & -\frac{e}{q^3} & \frac{-C_c}{q^5} & -\frac{1}{q^5} & 0 & 0 \\ 0 & 0 & \frac{e}{q^5} & \frac{-C_c}{q^7} & -\frac{1}{q^7} & 0 \\ 0 & 0 & 0 & \frac{e}{q^7} & \frac{-C_c}{q^9} & -\frac{1}{q^9} \\ 0 & 0 & 0 & 0 & \frac{e}{q^9} & \frac{-C_c}{q^9} \end{pmatrix}$$

In the case where consumer intraspecific competition is not small compared to the other parameters and q is sufficiently large, the column sums are dominated by the terms:

$$S_1 \approx \frac{C_c e^4 + e^5}{q^{25}}$$

$$S_2 \approx \frac{C_b C_c e^3 + C_b e^4}{q^{25}}$$

$$S_3 \approx \frac{C_b C_c^2 e^2 + C_b C_c e^3 + C_c^2 e^2 + e^3}{q^{25}} + \frac{C_c e^3 + e^4}{q^{23}}$$

$$S_4 \approx \frac{C_b C_c^2 e^2 + C_b C_c^3 e}{q^{25}} + \frac{C_b C_c e^2 + C_b e^3 + C_c^2 e^2 + C_c e^3}{q^{23}}$$

$$S_5 = \frac{C_c e^2 + e^3}{q^{21}}$$

$$S_6 \approx \frac{C_b e^2 + 2C_c e^2 + e^2}{q^{21}}$$

It is clear that $\max\{S_1, S_2\} < S_3 < S_4 < S_5 < S_6$. The ordering of S_1 and S_2 depends on the relative magnitudes of the parameters. We have:

$$S_2 - S_1 = \frac{C_b C_c e^3 + C_b e^4}{q^{25}} - \frac{C_c e^4 + e^5}{q^{25}}$$

so that $S_2 > S_1$ when

$$C_b(C_c + e) - e(C_c + e) > 0$$

which, once again, holds for $C_b > e$.

APPENDIX F

Here we present the analysis for the food chains of length 4, 5 and 6 shown in Figure 4.1(b)-(d) where consumer intraspecific competition is the same for all consumers.

Four Species Food Chain

For the simple food chain shown in Figure 4.1 (b), let m_1, m_2, m_3 and m_4 denote the body masses of the basal, herbivore, carnivore and top carnivore species respectively. Following the assumptions made for the three species food chain, the community matrix *A* for the four species food chain is of the form:

$$A = \begin{pmatrix} \frac{-C_b}{q} & -\frac{1}{q} & 0 & 0 \\ \frac{e}{q} & \frac{-C_c}{q^3} & -\frac{1}{q^3} & 0 \\ 0 & \frac{e}{q^3} & \frac{-C_c}{q^3} & -\frac{1}{q^5} \\ 0 & 0 & \frac{e}{q^5} & \frac{-C_c}{q^3} \end{pmatrix}$$

We examine the column sums of the absolute values of the entries of the matrix *B,* where, $B = det(A)A^{-1}$.

$$B_+ = \begin{pmatrix} \frac{C_c({C_c}^2q^4 + eq^4 + e)}{q^{13}} & \frac{{C_c}^2q^4 + e}{q^{11}} & \frac{C_c}{q^7} & \frac{1}{q^9} \\ \frac{{C_c}^2eq^4 + e^2}{q^{11}} & \frac{C_bC_c^2q^4 + C_be}{q^{11}} & \frac{C_bC_c}{q^7} & \frac{C_b}{q^9} \\ \frac{C_ce^2}{q^7} & \frac{C_bC_ce}{q^7} & \frac{C_ceq^2 + C_bC_c^2}{q^7} & \frac{eq^2 + C_bC_c}{q^9} \\ \frac{e^3}{q^9} & \frac{C_be^2}{q^9} & \frac{e^2q^2 + C_bC_ce}{q^9} & \frac{C_bC_c^2 + C_ceq^2 + C_be}{q^7} \end{pmatrix}$$

The matrix B_+ is the matrix whose entries are the absolute values of the entries of matrix *B*.

The column sums are:

$$S_1 = \frac{C_c e}{q^{13}} + \frac{e^2}{q^{11}} + \frac{C_c^3 + C_c e + e^3}{q^9} + \frac{C_c^2 e + C_c e^2}{q^7}$$

$$S_2 = \frac{C_b e + e}{q^{11}} + \frac{C_b e^2}{q^9} + \frac{C_b C_c^2 + C_b C_c e + C_c{}^2}{q^7}$$

$$S_3 = \frac{C_b C_c e}{q^9} + \frac{C_b C_c + C_b C_c^2 + C_c + e^2}{q^7} + \frac{C_c e}{q^5}$$

$$S_4 = \frac{1 + C_b + C_b C_c}{q^9} + \frac{C_b C_c^2 + C_b e + e}{q^7} + \frac{C_c e}{q^5}$$

If we set consumer intraspecific competition to 0 and allow q to become large then the column sums are:

$$S_1 = \frac{e^2}{q^{11}} + \frac{e^3}{q^9}$$

$$S_2 = \frac{C_b e + e}{q^{11}} + \frac{C_b e^2}{q^9}$$

$$S_3 = \frac{e^2}{q^7}$$

$$S_4 = \frac{C_b e + e}{q^7}$$

Comparing the terms of S_4 and S_3 it is clear that $S_3 < S_4$. For q large enough, the powers of q ensure that $S_2 < S_3$ but again, the ordering of S_1 and S_2 is dependent on the values of the parameters e and C_b.

Assuming q is large enough, we have

$$S_2 - S_1 = \frac{C_b e^2}{q^9} - \frac{e^3}{q^9}$$

thus $S_2 > S_1$ when

$$C_b e^2 - e^3 > 0$$

i.e. when $C_b > e$ which is consistent with the result for the three species food chain.

If consumer intraspecific competition is not set to 0 then, for sufficiently large q, the column sums are approximated by:

$$S_1 \approx \frac{C_c^2 e + C_c e^2}{q^7}$$

$$S_2 \approx \frac{C_b C_c^2 + C_b C_c e + C_c{}^2}{q^7}$$

$$S_3 \approx \frac{C_b C_c + \ C_b C_c^2 + C_c + e^2}{q^7} + \frac{C_c e}{q^5}$$

$$S_4 \approx \frac{C_b C_c^2 + C_b e + e}{q^7} + \frac{C_c e}{q^5}$$

It is clear that $max\{S_1, S_2\} < min\{S_3, S_4\}$ since q^5 is much smaller than q^7. The ordering of S_3 and S_4 and the ordering of S_1 and S_2 depends on the relative magnitude of the parameters C_b, C_c and e.

Examining the difference between the column sums yields:

$$S_4 - S_3 = \frac{C_b C_c^2 + C_b e + e}{q^7} - \frac{C_b C_c + \ C_b C_c^2 + C_c + e^2}{q^7}$$

hence $S_4 > S_3$ when

$$C_b e - C_b C_c - C_c + e - e^2 > 0 \qquad \text{Inequality (2)}$$

Whether this inequality holds depends on the relative values of C_b, e and C_c as illustrated in Figure 4.4. Note that $C_c < e$ is a necessary condition for inequality (2) to hold.

The ordering $S_2 > S_1$ holds when

$$S_2 - S_1 = \frac{C_b C_c^2 + C_b C_c e + C_c^2}{q^7} - \frac{C_c^2 e + C_c e^2}{q^7} > 0$$

i.e. when

$$C_c + (C_b - e)(C_c \ + e) > 0$$

which is same as inequality (1) for the three species chain, thus the ordering $S_2 > S_1$ holds for $C_b > e$. For $C_b < e$ the inequality depends on the relative values of C_b, e and C_c as again illustrated in Figure 4.3.

Five Species Food Chain

For the five species food chain shown in Figure 4.1 (c), let m_1, m_2, m_3, m_4 and m_5 denote the body masses of the species in order of increasing size and trophic height. Following the assumptions made for the three and four species food chains the community matrix A for a five species food chain is of the form:

$$A = \begin{pmatrix} \frac{-C_b}{q} & -\frac{1}{q} & 0 & 0 & 0 \\ \frac{e}{q} & \frac{-C_c}{q^3} & -\frac{1}{q^3} & 0 & 0 \\ 0 & \frac{e}{q^3} & \frac{-C_c}{q^3} & -\frac{1}{q^5} & 0 \\ 0 & 0 & \frac{e}{q^5} & \frac{-C_c}{q^3} & -\frac{1}{q^7} \\ 0 & 0 & 0 & \frac{e}{q^7} & \frac{-C_c}{q^3} \end{pmatrix}$$

The column sums of the matrix B_+ which is the matrix containing the absolute values of the matrix enties of $det(A)A^{-1}$ are:

$$S_1 = \frac{C_c^2 e + e^2}{q^{20}} + \frac{C_c e^2 + e^3}{q^{18}} + \frac{C_c^2 e + e^4}{q^{16}} + \frac{C_c e^2}{q^{14}} + \frac{C_c^4 + C_c^2 e + C_c e^3}{q^{12}} + \frac{C_c^3 e + C_c^2 e^2}{q^{10}}$$

$$S_2 = \frac{C_b C_c e + C_b e^2 + C_c e}{q^{18}} + \frac{C_b e^3}{q^{16}} + \frac{C_b C_c e + C_c e}{q^{14}} + \frac{C_b C_c e^2}{q^{12}} + \frac{C_b C_c^3 + C_c^3 C_b C_c^2 e + C_c^3}{q^{10}}$$

$$S_3 = \frac{C_b e + C_b C_c e + e}{q^{18}} + \frac{C_b C_c e^2 + e^2}{q^{16}} + \frac{e^3}{q^{14}} + \frac{C_b C_c^2 e}{q^{12}} + \frac{C_b C_c^2 + C_b C_c^3 + C_c^2 + C_c e^2}{q^{10}} + \frac{C_c^2 e}{q^8}$$

$$S_4 = \frac{C_b C_c^2 e + C_b e^2}{q^{14}} + \frac{C_b C_c + C_b C_c^2 + C_c}{q^{12}} + \frac{C_b C_c^3 + C_b C_c e + C_c e}{q^{10}} + \frac{C_c^2 e}{q^8}$$

$$S_5 = \frac{1 + C_b + C_b C_c}{q^{16}} + \frac{e + C_b C_c^2 + C_b C_c e + C_b e}{q^{14}} + \frac{C_c e + e^2}{q^{12}} + \frac{C_b C_c^3 + C_b C_c e}{q^{10}} + \frac{C_c^2 e}{q^8}$$

Setting $C_c = 0$ the column sums are:

$$S_1 = \frac{e^2}{q^{20}} + \frac{e^3}{q^{18}} + \frac{e^4}{q^{16}}$$

$$S_2 = \frac{C_b e^2}{q^{18}} + \frac{C_b e^3}{q^{16}}$$

$$S_3 = \frac{C_b e + e}{q^{18}} + \frac{e^2}{q^{16}} + \frac{e^3}{q^{14}}$$

$$S_4 = \frac{C_b e^2}{q^{14}}$$

$$S_5 = \frac{1 + C_b}{q^{16}} + \frac{C_b e + e}{q^{14}} + \frac{e^2}{q^{12}}$$

Comparing the sums term by term yields the following orderings, max$\{S_1, S_2\}$ < min $\{S_3, S_4, S_5\}$and max$\{S_3, S_4\} < S_5$. The ordering of the pairs S_3, S_4 and S_1, S_2 are dependent on the values of the parameters e and C_b.

Assuming q is large enough, we have:

$$S_4 - S_3 = \frac{C_b e^2}{q^{14}} - \frac{e^3}{q^{14}}$$

whence $S_4 > S_3$ for

$$C_b e^2 - e^3 > 0$$

i.e. when $C_b > e$. The ordering of S_1 and S_2 is given by considering the equality

$$S_2 - S_1 = \frac{C_b e^3}{q^{16}} - \frac{e^4}{q^{16}}$$

so we have $S_2 > S_1$ when

$$C_b e^3 - e^4 > 0$$

which is, once again, when $C_b > e$.

For non-zero consumer intraspecific competition and for sufficiently large q, the column sums are dominated by the terms:

$$S_1 \approx \frac{C_c^3 e + C_c^2 e^2}{q^{10}}$$

$$S_2 \approx \frac{C_b C_c^3 + C_b C_c^2 e + C_c^3}{q^{10}}$$

$$S_3 \approx \frac{C_b C_c^2 + C_b C_c^3 + C_c^2 + C_c e^2}{q^{10}} + \frac{C_c^2 e}{q^8}$$

$$S_4 \approx \frac{C_b C_c^3 + C_b C_c e + C_c e}{q^{10}} + \frac{C_c^2 e}{q^8}$$

$$S_5 \approx \frac{C_b C_c^3 + C_b C_c e}{q^{10}} + \frac{C_c^2 e}{q^8}$$

Powers of q ensure that $\max\{S_1, S_2\} < \min\{S_3, S_4, S_5\}$. Within the carnivore species 3, 4, and 5 it is clear that $S_5 < S_4$ but the relationships between S_3 and S_5 and S_3 and S_4 are more complex.

We have :

$$S_5 - S_3 = \frac{C_b C_c^3 + C_b C_c e}{q^{10}} - \frac{C_b C_c^2 + C_b C_c^3 + C_c^2 + C_c e^2}{q^{10}}$$

thus $S_5 > S_3$ when

$$C_b e - C_b C_c - C_c - e^2 > 0 \qquad \text{Inequality (3)}$$

Whether this inequality holds depends on the relative values of C_b, e and C_c as illustrated in Figure 4.3. Note that the condition $C_c < e < C_b$ is necessary for inequality (3) to hold.

Similarly,

$$S_4 - S_3 = \frac{C_b C_c^3 + C_b C_c e + C_c e}{q^{10}} - \frac{C_b C_c^2 + C_b C_c^3 + C_c^2 + C_c e^2}{q^{10}}$$

so we have $S_4 > S_3$ when:

$$C_b e + e - C_b C_c - C_c - e^2 > 0$$

which is the same as inequality (2) which governs the ordering of S_3 and S_4 for the four species food chain, see Figure 4.4.

The ordering $S_2 > S_1$ holds when

$$S_2 - S_1 = \frac{C_b C_c^3 + C_b C_c^2 e + C_c^3}{q^{10}} - \frac{C_c^3 e + C_c^2 e^2}{q^{10}} > 0$$

i.e. when

$$C_c + (C_b - e)(C_c + e) > 0$$

which is the same inequality (1) which governs the ordering of S_1 and S_2 for the three and four species food chains, see Figure 4.3.

Six Species Food Chain

For the six species food chain shown in Figure 4.1 (d), let m_1, m_2, m_3, m_4, m_5 and m_6 denote the body masses of the species in order of increasing size and trophic height. Following the assumptions made for the shorter food chains the community matrix A for a six species food chain is of the form:

$$A = \begin{pmatrix} \frac{-C_b}{q} & -\frac{1}{q} & 0 & 0 & 0 & 0 \\ \frac{e}{q} & \frac{-C_c}{q^3} & -\frac{1}{q^3} & 0 & 0 & 0 \\ 0 & -\frac{e}{q^3} & \frac{-C_c}{q^3} & -\frac{1}{q^5} & 0 & 0 \\ 0 & 0 & \frac{e}{q^5} & \frac{-C_c}{q^3} & -\frac{1}{q^7} & 0 \\ 0 & 0 & 0 & \frac{e}{q^7} & \frac{-C_c}{q^3} & -\frac{1}{q^9} \\ 0 & 0 & 0 & 0 & \frac{e}{q^9} & \frac{-C_c}{q^3} \end{pmatrix}$$

Due to the increasing complexity of the matrix B_+, which is the matrix containing the absolute values of the matrix entries of $det(A)A^{-1}$, we first examine column sums where consumer intraspecific interaction strength is set to 0:

$$S_1 = \frac{e^3}{q^{29}} + \frac{e^4}{q^{27}} + \frac{e^5}{q^{25}}$$

$$S_2 = \frac{+C_b e^2 + e^3}{q^{29}} + \frac{C_b e^3}{q^{27}} + \frac{C_b e^4}{q^{25}}$$

$$S_3 = \frac{e^3}{q^{25}} + \frac{e^4}{q^{23}}$$

$$S_4 = \frac{C_b e + e}{q^{27}} + \frac{C_b e^2 + e^2}{q^{25}} + \frac{C_b e^3}{q^{23}}$$

$$S_5 = \frac{e^3}{q^{21}}$$

$$S_6 = \frac{1 + C_b}{q^{25}} + \frac{C_b e + e}{q^{23}} + \frac{C_b e^2 + e^2}{q^{21}}$$

For q sufficiently large, comparing the sums term by term yields the following orderings, $\max\{S_3, S_4\} < S_5 < S_6$ and $\max\{S_1, S_2\} < S_3$. The ordering of the pairs S_3, S_4 and S_1, S_2 are dependent on the values of the parameters e and C_b. For q large enough,

$$S_4 - S_3 = \frac{C_b e^3}{q^{23}} - \frac{e^4}{q^{23}}$$

therefore $S_4 > S_3$ when

$$C_b e^3 - e^4 > 0$$

i.e. when $C_b > e$. The ordering of S_1 and S_2 is given by considering the equality

$$S_2 - S_1 = \frac{C_b e^4}{q^{25}} - \frac{e^5}{q^{25}}$$

and $S_2 > S_1$ when

$$C_b e^4 - e^5 > 0$$

which is, once again, when $C_b > e$.

In the case where consumer intraspecific competition is not 0 and q is sufficiently large, the column sums are dominated by the terms:

$$S_1 \approx \frac{C_c^5 + C_c^3 e + C_c^2 e^3}{q^{15}} + \frac{C_c^4 e + C_c^3 e^2}{q^{13}}$$

$$S_2 \approx \frac{C_b C_c^2 e^2}{q^{15}} + \frac{C_b C_c^4 + C_b C_c^3 e + C_c^4}{q^{13}}$$

$$S_3 \approx \frac{C_b C_c^3 e}{q^{15}} + \frac{C_b C_c^3 + C_b C_c^4 + C_c^3 + C_c^2 e^2}{q^{13}} + \frac{C_c^3 e}{q^{11}}$$

$$S_4 \approx \frac{C_b C_c^2 + C_b C_c^3 + C_c^2 + C_c^2 e^2}{q^{15}} + \frac{C_b C_c^4 + C_b C_c^2 e + C_c^2 e}{q^{13}} + \frac{C_c^3 e}{q^{11}}$$

$$S_5 \approx \frac{C_c^2 e + C_c e^2}{q^{15}} + \frac{C_b C_c^4 + C_b C_c^2 e}{q^{13}} + \frac{C_c^3 e}{q^{11}}$$

$$S_6 \approx \frac{C_c e^2}{q^{15}} + \frac{C_b C_c^4 + C_b C_c^2 e}{q^{13}} + \frac{C_c^3 e}{q^{11}}$$

It is clear that $\max\{S_1, S_2\} < \min\{S_3, S_4, S_5, S_6\}$. Within the carnivore species 3, 4, 5 and 6 the ordering is $S_6 < S_5 < S_4$ but the ordering of S_3 with S_4, S_5 and S_6 depends on the relative magnitudes of the parameters. We have:

$$S_6 - S_3 = \frac{C_b C_c^4 + C_b C_c^2 e}{q^{13}} - \frac{C_b C_c^3 + C_b C_c^4 + C_c^3 + C_c^2 e^2}{q^{13}}$$

so that $S_6 > S_3$ when

$$C_b e - C_b C_c - C_c - e^2 > 0$$

This inequality is the same as inequality (3) derived for the ordering of S_5 and S_3 for the five species food chain, see Figure 4.3. To compare the ordering of S_3 with S_5 note that the coefficients for the term containing q^{13} are identical for S_5 and S_6 therefore the ordering of S_3 with S_5 is also governed by inequality (3). Similarly,

$$S_4 - S_3 = \frac{C_b C_c^4 + C_b C_c^2 e + C_c^2 e}{q^{13}} - \frac{C_b C_c^3 + C_b C_c^4 + C_c^3 + C_c^2 e^2}{q^{13}}$$

hence $S_4 > S_3$ when:

$$C_b e - C_b C_c - C_c + e - e^2 > 0$$

which is the same as inequality (2) which governs the ordering of S_3 and S_4 for the four species food chain, see Figure 4.4. Note that if inequality (3) holds then inequality (2) will also hold so that $S_3 < S_6 < S_5 < S_4$ but if inequality (2) does not hold then inequality (3) will not hold and $S_6 < S_5 < S_4 < S_3$.

The ordering $S_2 > S_1$ holds when

$$S_2 - S_1 = \frac{C_b C_c^4 + C_b C_c^3 e + C_c^4}{q^{13}} - \frac{C_c^4 e + C_c^3 e^2}{q^{13}}$$

i.e. when

$$C_c + (C_b - e)(C_c + e) > 0$$

which is the same as inequality (1) which governs the ordering of S_1 and S_2 for the three, four and five species food chains, see Figure 4.3.

APPENDIX G

The ordering of species net effects when predator-prey ratios decrease with trophic position and body-mass.

For the 97 synthetic food webs analysed it was found that predator-prey body mass ratios decreased with trophic height (see Figure 4.5), this pattern has also been observed in real food webs (Riede et al. 2011). To examine how decreasing predator-prey ratios with body mass affects the ordering of total net effects we examine the column sums of the inverse community matrix where the entries in the community matrix depend on varying predator-prey body mass ratios. We assume that the predator-prey body mass ratios are strongly ordered so that predator-prey body mass ratios between species at the bottom of the food chain are much larger than predator-prey body mass ratios between species at the top of the food chain. Note that we maintain the assumption that a consumer species will always feed on smaller species so that predator-prey body mass ratios are always greater than 1.

Parameterisation of Food Chains

We begin by defining the interaction strengths present in the community matrix for the longest food chain, containing six species (Figure. 4.1(d)). Since all the food webs analysed in this section are subsets of this six species food chain all the interaction strengths required to parameterise the food chains shown in Figures 4.1(a)-4.1(d) are defined by parameterising the six species food chain. For the simple six species food chain shown in Figure 4.1 (d), let m_1, m_2, m_3, m_4, m_5 and m_6 denote the body mass of species in order of increasing mass and trophic height. Let q_1^* represent the predator-prey body mass ratio $\frac{m2}{m1}$, let q_2^* represent predator-prey body mass ratio $\frac{m3}{m2}$, let q_3^* represent predator-prey body mass ratio $\frac{m4}{m3}$, let q_4^* represent the predator-prey body mass ratio $\frac{m5}{m4}$ and let q_5^* represent the predator-prey body mass ratio $\frac{m6}{m5}$.

Then we can write:

$$m_2 = q_1^* m_1$$

$$m_3 = q_2^* q_1^* m_1$$

$$m_4 = q_3^* q_2^* q_1^* m_1$$

$$m_5 = q_4^* q_3^* q_2^* q_1^* m_1$$

$$m_6 = q_5^* q_4^* q_3^* q_2^* q_1^* m_1$$

and,

$$a_{12} = C_{a12}(m_1 m_2)^{-\frac{1}{4}} = C_{a12}(q_1^* m_1^2)^{-\frac{1}{4}} = C_{a12}(m_1^{-\frac{1}{2}})(q_1^{*-\frac{1}{4}})$$

$$a_{23} = C_{a23}(m_2 m_3)^{-\frac{1}{4}} = C_{a23}(q_1^{*2} q_2{}^* m_1^2)^{-\frac{1}{4}} = C_{a23}(m_1^{-\frac{1}{2}})(q_1^{*-\frac{1}{2}})(q_2^{*-\frac{1}{4}})$$

$$a_{34} = C_{a34}(m_3 m_4)^{-\frac{1}{4}} = C_{a34}(q_1^{*2} q_2^{*2} q_3{}^* m_1^2)^{-\frac{1}{4}} = C_{a34}(m_1^{-\frac{1}{2}})(q_1^{*-\frac{1}{2}})(q_2^{*-\frac{1}{2}})(q_3^{*-\frac{1}{4}})$$

$$a_{45} = C_{a45}(m_4 m_5)^{-\frac{1}{4}} = C_{a45}(q_1^{*2} q_2^{*2} q_3^{*2} q_4{}^* m_1^2)^{-\frac{1}{4}}$$

$$= C_{a45}(m_1^{-\frac{1}{2}})(q_1^{*-\frac{1}{2}})(q_2^{*-\frac{1}{2}})(q_3^{*-\frac{1}{2}})(q_4^{*-\frac{1}{4}})$$

$$a_{56} = C_{a56}(m_4 m_5)^{-\frac{1}{4}} = C_{a56}(q_1^{*2} q_2^{*2} q_3^{*2} q_4{}^* m_1^2)^{-\frac{1}{4}}$$

$$= C_{a56}(m_1^{-\frac{1}{2}})(q_1^{*-\frac{1}{2}})(q_2^{*-\frac{1}{2}})(q_3^{*-\frac{1}{2}})(q_4^{*-\frac{1}{4}})$$

To simplify the form of the a_{ij} entries we replace $(q_i{}^*)^{\frac{1}{4}}$ with the variable q_i and since C_{aij} is a constant that scales the magnitude of *all* the a_{ij} entries we replace $C_{aij} m_1^{-\frac{1}{2}}$ with the value -1. This gives $a_{12} = -\frac{1}{q_1}, a_{23} = -\frac{1}{q_1^2 q_2}, a_{34} = -\frac{1}{q_1^2 q_2^2 q_3},\ a_{45} = -\frac{1}{q_1^2 q_2^2 q_3^2 q_4},$

$$a_{56} = -\frac{1}{q_1^2 q_2^2 q_3^2 q_4^2 q_5}$$

As for the case where q is considered constant, the intraspecific interaction strengths are defined to scale with the interspecific interactions so that $a_{ii} = C_b a_{12} = -\frac{C_b}{q_1}$ for basal species (i = 1) and

$a_{ii} = C_c a_{23} = -\frac{C_c}{q_1^2 q_2}$ for consumer species (i = 2,3,4,5,6).

Using this notation, the community matrix A for the six species food chain is of the form:

$$A = \begin{pmatrix} \frac{-C_b}{q_1} & -\frac{1}{q_1} & 0 & 0 & 0 & 0 \\ \frac{e}{q_1} & \frac{-C_c}{q_1^2 q_2} & -\frac{1}{q_1^2 q_2} & 0 & 0 & 0 \\ 0 & -\frac{e}{q_1^2 q_2} & \frac{-C_c}{q_1^2 q_2} & -\frac{1}{q_1^2 q_2^2 q_3} & 0 & 0 \\ 0 & 0 & \frac{e}{q_1^2 q_2^2 q_3} & \frac{-C_c}{q_1^2 q_2} & -\frac{1}{q_1^2 q_2^2 q_3^2 q_4} & 0 \\ 0 & 0 & 0 & \frac{e}{q_1^2 q_2^2 q_3^2 q_4} & \frac{-C_c}{q_1^2 q_2} & -\frac{1}{q_1^2 q_2^2 q_3^2 q_4^2 q_5} \\ 0 & 0 & 0 & 0 & \frac{e}{q_1^2 q_2^2 q_3^2 q_4^2 q_5} & \frac{-C_c}{q_1^2 q_2} \end{pmatrix}$$

The community matrices for the smaller food chains are defined as subsets of this matrix.

Three Species Food Chain

The community matrix A for the simple three species food chain shown in Figure 4.1 (a) is of the form:

$$A = \begin{pmatrix} \frac{-C_b}{q_1} & -\frac{1}{q_1} & 0 \\ \frac{e}{q_1} & -\frac{C_c}{q_1^2 q_2} & -\frac{1}{q_1^2 q_2} \\ 0 & \frac{e}{q_1^2 q_2} & -\frac{C_c}{q_1^2 q_2} \end{pmatrix}$$

Once again, to investigate the ordering of the column sums we examine the column sums of the simpler but identically scaled matrix $B = det(A)A^{-1}$ where:

$$B_+ = \begin{pmatrix} \frac{C_c^2 + e}{q_1^4 q_2^2} & \frac{C_c}{q_1^3 q_2} & \frac{1}{q_1^3 q_2} \\ \frac{C_c e}{q_1^3 q_2} & \frac{C_b C_c}{q_1^3 q_2} & \frac{C_b}{q_1^3 q_2} \\ \frac{e^2}{q_1^3 q_2} & \frac{C_b e}{q_1^3 q_2} & \frac{e q_1 q_2 + C_b C_c}{q_1^3 q_2} \end{pmatrix}$$

The matrix B_+ is the matrix whose entries are the absolute values of the entries of matrix *B*.

The column sums are:

$$\begin{aligned} S_1 &= \frac{C_c^2 + e}{q_1^4 q_2^2} + \frac{C_c e + e^2}{q_1^3 q_2} \\ S_2 &= \frac{C_c C_b + C_b e + C_c}{q_1^3 q_2} \\ S_3 &= \frac{1 + C_b + C_b C_c}{q_1^3 q_2} + \frac{e}{q_1^2} \end{aligned} \tag{6}$$

Comparing the column sums in (6) to the column sums in (2) for the case where the predator-prey body mass ratio q is constant we see that the numerators of the terms in the column sums are identical and that the relative scaling of terms in the denominator is the same ($q^6 < q^4 < q^2$ in (2) and $q_1^4 q_2^2 < q_1^3 q_2 < q_1^2$ in (6). So the ordering of column sums is identical to the case where q is constant.

Four Species Food Chain

The community matrix *A* for the four species food chain is of the form:

$$A = \begin{pmatrix} \frac{-C_b}{q_1} & -\frac{1}{q_1} & 0 & 0 \\ \frac{e}{q_1} & \frac{-C_c}{q_1^2 q_2} & -\frac{1}{q_1^2 q_2} & 0 \\ 0 & \frac{e}{q_1^2 q_2} & \frac{-C_c}{q_1^2 q_2} & -\frac{1}{q_1^2 q_2^2 q_3} \\ 0 & 0 & \frac{e}{q_1^2 q_2^2 q_3} & \frac{-C_c}{q_1^2 q_2} \end{pmatrix}$$

We examine the column sums of the absolute values of the entries of the matrix *B*, which equals

$$\begin{pmatrix} \frac{C_c^3 q_2^2 q_3^2 + C_c e q_2^2 q_3^2 + C_c e}{q_1^6 q_2^5 q_3^2} & \frac{C_c^2 q_2^2 q_3^2 + e}{q_1^5 q_2^4 q_3^2} & \frac{C_c}{q_1^5 q_2^2} & \frac{1}{q_1^5 q_2^3 q_3} \\ \frac{C_c^2 e q_2^2 q_3^2 + e^2}{q_1^5 q_2^4 q_3^2} & \frac{C_b C_c^2 q_2^2 q_3^2 + C_b e}{q_1^5 q_2^4 q_3^2} & \frac{C_b C_c}{q_1^5 q_2^2} & \frac{C_b}{q_1^5 q_2^3 q_3} \\ \frac{C_c e^2}{q_1^5 q_2^2} & \frac{C_b C_c e}{q_1^5 q_2^2} & \frac{C_b C_c^2 + C_c e q_1 q_2}{q_1^5 q_2^2} & \frac{C_b C_c + e q_1 q_2}{q_1^5 q_2^3 q_3} \\ \frac{e^3}{q_1^5 q_2^3 q_3} & \frac{C_b e^2}{q_1^5 q_2^3 q_3} & \frac{C_b C_c e + e^2 q_1 q_2}{q_1^5 q_2^3 q_3} & \frac{C_b e + C_b C_c^2 + C_c e q_1 q_2}{q_1^5 q_2^4} \end{pmatrix}$$

The column sums are:

$$S_1 = \frac{C_c e}{q_1^6 q_2^5 q_3^2} + \frac{C_c^3 + C_c e}{q_1^6 q_2^3} + \frac{e^2}{q_1^5 q_2^4 q_3^2} + \frac{e^3}{q_1^5 q_2^3 q_3} + \frac{C_c^2 e + C_c e^2}{q_1^5 q_2^2}$$

$$S_2 = \frac{C_b e + e}{q_1^5 q_2^4 q_3^2} + \frac{C_b e^2}{q_1^5 q_2^3 q_3} + \frac{C_b C_c^2 + C_b C_c e + C_c^2}{q_1^5 q_2^2}$$

$$S_3 = \frac{C_b C_c e}{q_1^5 q_2^3 q_3} + \frac{C_b C_c + C_b C_c^2 + C_c}{q_1^5 q_2^2} + \frac{e^2}{q_1^4 q_2^2 q_3} + \frac{C_c e}{q_1^4 q_2}$$

$$S_4 = \frac{C_b C_c^2 + C_b e}{q_1^5 q_2^4} + \frac{1 + C_b + C_b C_c}{q_1^5 q_2^3 q_3} + \frac{C_c e}{q_1^4 q_2^3} + \frac{e}{q_1^4 q_2^2 q_3}$$

Assuming that consumer intraspecific competition is small compared to the other parameters, we set $C_c = 0$, then the column sums are:

$$S_1 = \frac{e^2}{q_1^5 q_2^4 q_3^2} + \frac{e^3}{q_1^5 q_2^3 q_3}$$

$$S_2 = \frac{C_b e + e}{q_1^5 q_2^4 q_3^2} + \frac{C_b e^2}{q_1^5 q_2^3 q_3}$$

$$S_3 = \frac{e^2}{q_1^4 q_2^2 q_3}$$

$$S_4 = \frac{C_b e}{q_1^5 q_2^4} + \frac{1 + C_b}{q_1^5 q_2^3 q_3} + \frac{e}{q_1^4 q_2^2 q_3}$$

Comparing the terms of S_4 and S_3 it is clear that $S_3 < S_4$. The assumption that predator-prey ratios decrease with body mass means that we assume q_1 is much larger than q_2 which is in turn much larger than q_3 and all ratios are greater than 1. Comparing powers of q_1 yields $S_2 < S_3$. Since the powers of q_1 are equivalent for the terms in the column sums S_1 and S_2 we determine the order of S_1 and S_2 by assuming that the column sums are dominated by the terms containing the lowest power of q_2. This assumption gives us the ordering $S_1 < S_2$ when$C_b > e$, which is consistent with the case for constant q.

For the case when consumer intraspecific competition is not set to 0, the column sums are approximated by:

$$S_1 \approx \frac{e^3}{q_1^5 q_2^3 q_3} + \frac{C_c^2 e + C_c e^2}{q_1^5 q_2^2}$$

$$S_2 \approx \frac{C_b e^2}{q_1^5 q_2^3 q_3} + \frac{C_b C_c^2 + C_b C_c e + C_c^2}{q_1^5 q_2^2}$$

$$S_3 \approx \frac{e^2}{q_1^4 q_2^2 q_3} + \frac{C_c e}{q_1^4 q_2}$$

$$S_4 \approx \frac{C_c e}{q_1^4 q_2^3} + \frac{e}{q_1^4 q_2^2 q_3}$$

Comparing powers of q_1 yields $\max\{S_1, S_2\} < \min\{S_3, S_4\}$ and comparing powers of q_2 gives the ordering $S_4 < S_3$. Again, the powers of q_1 are equivalent for the terms in the sums S_1 and S_2 so the column sums are approximated by the terms containing the lowest powers of q_2, therefore, the ordering $S_2 > S_1$ holds when

$$S_2 - S_1 = \frac{C_b C_c^2 + C_b C_c e + C_c^2}{q_1^5 q_2^2} - \frac{e C_c^2 + C_c e^2}{q_1^5 q_2^2} > 0$$

i.e. when

$$C_c + (C_b - e)(C_c + e) > 0$$

which is same inequality (3) which governs the ordering of S_1 and S_2 for the food chains where q is constant (Figure 4.3)

Five Species Food Chain

The community matrix A for the five species food chain is of the form:

$$A = \begin{pmatrix} \frac{-C_b}{q_1} & -\frac{1}{q_1} & 0 & 0 & 0 \\ \frac{e}{q_1} & \frac{-C_c}{q_1^2 q_2} & -\frac{1}{q_1^2 q_2} & 0 & 0 \\ 0 & \frac{e}{q_1^2 q_2} & \frac{-C_c}{q_1^2 q_2} & -\frac{1}{q_1^2 q_2^2 q_3} & 0 \\ 0 & 0 & \frac{e}{q_1^2 q_2^2 q_3} & \frac{-C_c}{q_1^2 q_2} & -\frac{1}{q_1^2 q_2^2 q_3^2 q_4} \\ 0 & 0 & 0 & \frac{e}{q_1^2 q_2^2 q_3^2 q_4} & \frac{-C_c}{q_1^2 q_2} \end{pmatrix}$$

The column sums of matrix B_+, which is the matrix containing the absolute values of the matrix entries of $det(A)A^{-1}$, are:

$$S_1 = \frac{C_c^2 e + e^2}{q_1^8 q_2^6 q_3^4 q_4^2} + \frac{C_c^2 e}{q_1^8 q_2^6 q_3^2} + \frac{C_c^4 + C_c^2 e}{q_1^8 q_2^4} + \frac{C_c e^2 + e^3}{q_1^7 q_2^5 q_3^4 q_4^2} + \frac{e^4}{q_1^7 q_2^5 q_3^3 q_4} + \frac{C_c e^2}{q_1^7 q_2^5 q_3^2} + \frac{C_c e^3}{q_1^7 q_2^4 q_3}$$

$$+ \frac{C_c^3 e + C_c^2 e^2}{q_1^7 q_2^3}$$

$$S_2 = \frac{C_b C_c e + C_b e^2 + C_c e}{q_1^7 q_2^5 q_3^4 q_4^2} + \frac{C_b e^3}{q_1^7 q_2^5 q_3^3 q_4} + \frac{C_b C_c e + C_c e}{q_1^7 q_2^5 q_3^2} + \frac{C_b C_c e^2}{q_1^7 q_2^4 q_3} + \frac{C_b C_c^3 + C_b C_c^2 e + C_c^3}{q_1^7 q_2^3}$$

$$S_3 = \frac{C_b e + C_b C_c e + e}{q_1^7 q_2^5 q_3^4 q_4^2} + \frac{C_b C_c e^2}{q_1^7 q_2^5 q_3^3 q_4} + \frac{C_b C_c^2 e}{q_1^7 q_2^4 q_3} + \frac{C_b C_c^2 + C_b C_c^3 + C_c^2}{q_1^7 q_2^3} + \frac{e^2}{q_1^6 q_2^4 q_3^4 q_4^2}$$

$$+ \frac{e^3}{q_1^6 q_2^4 q_3^3 q_4} + \frac{C_c e^2}{q_1^6 q_2^3 q_3} + \frac{C_c^2 e}{q_1^6 q_2^2}$$

$$S_4 = \frac{C_b C_c^2 e + C_b e^2}{q_1^7 q_2^4 q_3^2 q_4} + \frac{C_b C_c + C_b C_c^2 + C_c}{q_1^7 q_2^4 q_3} + \frac{C_b C_c^3 + C_b C_c e}{q_1^7 q_2^3} + \frac{C_c e^2}{q_1^6 q_2^3 q_3^2 q_4} + \frac{C_c e}{q_1^6 q_2^3 q_3} + \frac{C_c^2 e}{q_1^6 q_2^2}$$

$$S_5 = \frac{1 + C_b + C_b C_c}{q_1^7 q_2^5 q_3^3 q_4} + \frac{C_b C_c e}{q_1^7 q_2^5 q_3^2} + \frac{C_b C_c^2 + C_b e}{q_1^7 q_2^4 q_3^2 q_4} + \frac{C_b C_c^3 + C_b C_c e}{q_1^7 q_2^3} + \frac{C_c e}{q_1^6 q_2^3 q_3^2 q_4} + \frac{e}{q_1^6 q_2^4 q_3^3 q_4}$$

$$+ \frac{e^2}{q_1^6 q_2^4 q_3^2} + \frac{C_c^2 e}{q_1^6 q_2^2}$$

If consumer intraspecific competition is set to 0, the column sums are:

$$S_1 = \frac{e^2}{q_1^8 q_2^6 q_3^4 q_4^2} + \frac{e^3}{q_1^7 q_2^5 q_3^4 q_4^2} + \frac{e^4}{q_1^7 q_2^5 q_3^3 q_4}$$

$$S_2 = \frac{C_b e^2}{q_1^7 q_2^5 q_3^4 q_4^2} + \frac{C_b e^3}{q_1^7 q_2^5 q_3^3 q_4}$$

$$S_3 = \frac{C_b e + e}{q_1^7 q_2^5 q_3^4 q_4^2} + \frac{e^2}{q_1^6 q_2^4 q_3^4 q_4^2} + \frac{e^3}{q_1^6 q_2^4 q_3^3 q_4}$$

$$S_4 = \frac{C_b e^2}{q_1^7 q_2^4 q_3^2 q_4}$$

$$S_5 = \frac{1 + C_b}{q_1^7 q_2^5 q_3^3 q_4} + \frac{C_b e}{q_1^7 q_2^4 q_3^2 q_4} + \frac{e}{q_1^6 q_2^4 q_3^3 q_4} + \frac{e^2}{q_1^6 q_2^4 q_3^2}$$

Comparing the terms of sums it is clear that max{S_1, S_2} < S_4 < S_3 < S_5 which is a different ordering than the one obtained for the case where q is constant. Since we assume that q_3 is much larger than q_4, to compare the column sums S_1 and S_2 we compare terms containing the lowest power of q_3 so that $S_1 < S_2$ when $C_b > e$ which is consistent with the case for q constant.

If consumer intraspecific competition is not set to 0 then, the column sums are dominated by the terms:

$$S_1 \approx \frac{C_c^3 e + C_c^2 e^2}{q_1^7 q_2^3}$$

$$S_2 \approx \frac{C_c^4 + C_b C_c^3 + C_b C_c^2 e}{q_1^7 q_2^3}$$

$$S_3 \approx \frac{C_c^2 + C_b C_c^2 + C_b C_c^3}{q_1^7 q_2^3} + \frac{e^2}{q_1^6 q_2^4 q_3^4 q_4^2} + \frac{e^3}{q_1^6 q_2^4 q_3^3 q_4} + \frac{C_c e^2}{q_1^6 q_2^3 q_3} + \frac{C_c^2 e}{q_1^6 q_2^2}$$

$$S_4 \approx \frac{C_b C_c^3 + C_b C_c e}{q_1^7 q_2^3} + \frac{C_c e^2}{q_1^6 q_2^3 q_3^2 q_4} + \frac{C_c e}{q_1^6 q_2^3 q_3} + \frac{C_c^2 e}{q_1^6 q_2^2}$$

$$S_5 \approx \frac{C_b C_c^3 + C_b C_c e}{q_1^7 q_2^3} + \frac{C_c e}{q_1^6 q_2^3 q_3^2 q_4} + \frac{e}{q_1^6 q_2^4 q_3^3 q_4} + \frac{e^2}{q_1^6 q_2^4 q_3^2} + \frac{C_c^2 e}{q_1^6 q_2^2}$$

It is clear that max{S_1 , S_2} < min{S_3, S_4, S_5}. Within the carnivore species 3, 4, and 5, if differences in the ordering $q_3 < q_2 < q_1$ are large enough then $S_5 < S_3 < S_4$.

The ordering $S_2 > S_1$ holds when

$$S_2 - S_1 = \frac{C_b C_c^3 + C_b C_c^2 e + C_c^3}{q_1^7 q_2^3} - \frac{C_c^3 e + C_c^2 e^2}{q_1^7 q_2^3} > 0$$

So that $S_2 > S_1$ when

$$C_c + (C_b - e)(C_c \ + e) > 0$$

which is same as inequality (2) governing the ordering of S_1 and S_2 for the three and four species food chains.

Six Species Food Chain

The community matrix A for the six species food chain is of the form:

$$A = \begin{pmatrix} \frac{-C_b}{q_1} & -\frac{1}{q_1} & 0 & 0 & 0 & 0 \\ \frac{e}{q_1} & \frac{-C_c}{q_1^2 q_2} & -\frac{1}{q_1^2 q_2} & 0 & 0 & 0 \\ 0 & -\frac{e}{q_1^2 q_2} & \frac{-C_c}{q_1^2 q_2} & -\frac{1}{q_1^2 q_2^2 q_3} & 0 & 0 \\ 0 & 0 & \frac{e}{q_1^2 q_2^2 q_3} & \frac{-C_c}{q_1^2 q_2} & -\frac{1}{q_1^2 q_2^2 q_3^2 q_4} & 0 \\ 0 & 0 & 0 & \frac{e}{q_1^2 q_2^2 q_3^2 q_4} & \frac{-C_c}{q_1^2 q_2} & -\frac{1}{q_1^2 q_2^2 q_3^2 q_4^2 q_5} \\ 0 & 0 & 0 & 0 & \frac{e}{q_1^2 q_2^2 q_3^2 q_4^2 q_5} & \frac{-C_c}{q_1^2 q_2} \end{pmatrix}$$

For $C_c = 0$, the column sums of the matrix B_+, which is the matrix containing the absolute values of the matrix entries of $det(A)A^{-1}$, are:

$$S_1 = \frac{e^3}{q_1^9 q_2^8 q_3^6 q_4^4 q_5^2} + \frac{e^4}{q_1^9 q_2^7 q_3^5 q_4^4 q_5^2} + \frac{e^5}{q_1^9 q_2^7 q_3^5 q_4^3 q_5}$$

$$S_2 = \frac{C_b e^2 + e^2}{q_1^9 q_2^8 q_3^6 q_4^4 q_5^2} + \frac{C_b e^3}{q_1^9 q_2^7 q_3^5 q_4^4 q_5^2} + \frac{e^5}{q_1^9 q_2^7 q_3^5 q_4^3 q_5}$$

$$S_3 = \frac{e^3}{q_1^8 q_2^6 q_3^5 q_4^4 q_5^2} + \frac{e^4}{q_1^8 q_2^6 q_3^5 q_4^3 q_5}$$

$$S_4 = \frac{C_b e + e}{q_1^9 q_2^7 q_3^5 q_4^4 q_5^2} + \frac{C_b e^2}{q_1^9 q_2^6 q_3^4 q_4^4 q_5^2} + \frac{C_b e^3}{q_1^9 q_2^6 q_3^4 q_4^3 q_5} + \frac{e^2}{q_1^8 q_2^6 q_3^5 q_4^4 q_5^2}$$

$$S_5 = \frac{e^3}{q_1^8 q_2^6 q_3^4 q_4^2 q_5}$$

$$S_6 = \frac{1+C_b}{q_1^9 q_2^7 q_3^5 q_4^3 q_5} + \frac{C_b e}{q_1^9 q_2^6 q_3^4 q_4^3 q_5} + \frac{C_b e^2}{q_1^9 q_2^6 q_3^4 q_4^2} + \frac{e}{q_1^8 q_2^6 q_3^5 q_4^3 q_5} + \frac{e^2}{q_1^8 q_2^6 q_3^4 q_4^2 q_5}$$

Assuming differences in the ordering $q_3 < q_2 < q_1$ are large enough and comparing the terms of sums yields $\max\{S_1, S_2\} < S_4 < S_3 < S_5 < S_6$ and as in the case for constant q, we have $S_1 < S_2$ when $C_b > e$.

If consumer intraspecific competition is not set to 0 then, for sufficiently large q_1, the column sums are approximated by:

$$S_1 \approx \frac{C_c^4 e}{q_1^9 q_2^4} + \frac{C_c^3 e^2}{q_1^9 q_2^4}$$

$$S_2 \approx \frac{C_c^4}{q_1^9 q_2^4} + \frac{C_b C_c^4}{q_1^9 q_2^4} + \frac{C_b C_c^3 e}{q_1^9 q_2^4}$$

$$S_3 \approx \frac{C_c^3}{q_1^9 q_2^4} + \frac{C_b C_c^3}{q_1^9 q_2^4} + \frac{C_b C_c^4}{q_1^9 q_2^4} + \frac{C_c e^2}{q_1^8 q_2^7 q_3^4 q_4^4 q_5^2} + \frac{e^3}{q_1^8 q_2^6 q_3^5 q_4^4 q_5^2} + \frac{e^4}{q_1^8 q_2^6 q_3^5 q_4^3 q_5} + \frac{C_c e^2}{q_1^8 q_2^5 q_3^4 q_4^2}$$
$$+ \frac{C_c e^3}{q_1^8 q_2^5 q_3^3 q_4} + \frac{C_c^2 e}{q_1^8 q_2^4 q_3} + \frac{C_c^3 e}{q_1^8 q_2^3}$$

$$S_4 \approx \frac{C_b C_c^2}{q_1^9 q_2^4} + \frac{C_b C_c^2 e}{q_1^9 q_2^4} + \frac{e^2}{q_1^8 q_2^6 q_3^5 q_4^4 q_5^2} + \frac{C_c e^2}{q_1^8 q_2^5 q_3^4 q_4^4 q_5^2} + \frac{e^3}{q_1^8 q_2^5 q_3^4 q_4^3 q_5} + \frac{C_c^2 e^2}{q_1^8 q_2^4 q_3^2 q_4} + \frac{C_c^2}{q_1^8 q_2^4 q_3}$$
$$+ \frac{C_c^3 e}{q_1^8 q_2^3}$$

$$S_5 \approx \frac{C_b C_c^4}{q_1^9 q_2^4} + \frac{C_b C_c^2 e}{q_1^9 q_2^4} + \frac{e^2}{q_1^8 q_2^6 q_3^4 q_4^4 q_5^2} + \frac{C_c e}{q_1^8 q_2^5 q_3^3 q_4} + \frac{C_c e^2}{q_1^8 q_2^5 q_3^2} + \frac{C_c^2 e^2}{q_1^8 q_2^4 q_3^2 q_4^2 q_5} + \frac{C_c^2 e}{q_1^8 q_2^4 q_3^2 q_4}$$
$$+ \frac{C_c^3 e}{q_1^8 q_2^3}$$

$$S_6 \approx \frac{C_b C_c^4}{q_1^9 q_2^4} + \frac{C_b C_c^2 e}{q_1^9 q_2^4} + \frac{e}{q_1^8 q_2^6 q_3^5 q_4^3 q_5} + \frac{e^2}{q_1^8 q_2^6 q_3^4 q_4^2 q_5} + \frac{C_c e}{q_1^8 q_2^5 q_3^4 q_4^3 q_5} + \frac{C_c e^2}{q_1^8 q_2^5 q_3^4 q_4^2} + \frac{C_c e^2}{q_1^8 q_2^5 q_3^2}$$
$$+ \frac{C_c^2 e}{q_1^8 q_2^4 q_3^2 q_4^2 q_5} + \frac{C_c^3 e}{q_1^8 q_2^3}$$

It is clear that $\max\{S_1, S_2\} < \min\{S_3, S_4, S_5, S_6\}$. Within the carnivore species 3, 4, 5 and 6 if differences in the ordering $q_4 < q_3 < q_2 < q_1$ are large enough then $S_6 < S_5 < S_3 < S_4$.

The ordering $S_2 > S_1$ holds when

$$S_2 - S_1 = \frac{C_b C_c^4 + C_b C_c^3 e C_c^4}{q_1^9 q_2^4} - \frac{C_c^4 e + C_c^3 e^2}{q_1^9 q_2^4} > 0$$

So that $S_2 > S_1$ when

$$C_c + (C_b - e)(C_c + e) > 0$$

which is same as inequality (3) governing the ordering of S_1 and S_2 for the three and four species food chains.

CHAPTER 5

FACTORS THAT DETERMINE WHETHER SPECIES WITH HIGH LINKAGE DENSITY HAVE WEAK TOTAL NET EFFECTS ON THEIR COMMUNITY

Abstract

It has been observed that weak interaction strengths between species in food webs can have a stabilising effect on the system. Most studies have focused on the role of species with weak *direct* effects, i.e. species whose entries in the community matrix are small in magnitude compared to other species in the community but a few recent studies have focused on species *net* effects and it has been observed that species with a high linkage density have weak net effects.

The study presented in Chapter 3 of this thesis analysed the relationship between a species linkage density and its total net effect for 97 synthetic food webs. A subset of 38 webs showed a negative relationship between linkage density and species total net effect indicating that the relationship between species linkage density and its total net effect may depend on the structure of the community in which it is embedded. In this study we examine the relationship between a species linkage density and its total net effect using a range of food webs of size 12 or 16 species with two alternative structures and varying complexity. The analyses show that, on a web level, any potential effect of linkage density is masked by the overwhelming positive relationship between body size and total net effect.

To remove the dominating effect of body size, the relationship between a species linkage density and its total net effect was examined within trophic levels. The analysis found that a negative relationship occurred frequently within the basal and herbivore trophic levels but was rare within the carnivore trophic level. For the webs examined, the negative relationship was not affected by web size or the ratio of basal: herbivore and carnivore species but was affected by the arrangement of links, indicating that the negative relationship between linkage density and total net effect is a consequence of the pattern of interaction strengths in the surrounding web.

Introduction

May’s seminal result from 1972 showed that, in general, complexity in food webs leads to instability (May 1972). This result contradicts evidence seen every day in the natural world around us, where throughout the globe large complex communities do persist in nature. Since May’s counter-intuitive result, numerous studies have shown that by using ecological information to inform food web models, complexity can be reconciled with stability (Yodzis 1981, Moore and William Hunt 1988, de Ruiter et al. 1995, Jonsson and Ebenman 1998, McCann et al. 1998, Neutel et al. 2002, Emmerson and Raffaelli 2004, Neutel et al. 2007). In particular, it has been observed that interaction strengths between species in a community are skewed so that weak interactions between species occur more frequently than strong interactions (Paine 1992, Fagan and Hurd 1994, Wootton 1997, Kokkoris et al. 1999, Bascompte et al. 2005, O'Gorman et al. 2010, Alvarez et al. 2013). This distribution of interaction strengths has been shown to have a stabilising effect on systems by coupling strong interaction strengths with negatively covarying weak interaction strengths (McCann 2000, O'Gorman and Emmerson 2009). Additionally, weak interaction strengths can dampen the knock on effect of strong consumer-resource interactions which in turn reduces fluctuations in population densities for the whole system (McCann et al. 1998, Neutel et al. 2002).

Interaction strengths can be defined loosely as a measure of the effect of one species on another species. In a Lotka-Volterra system we can define an interaction strength more precisely as a_{ij}, where a_{ij} represents the per unit mass effect of species j feeding on species i per unit of time. The community matrix is the matrix whose ij^{th} entry is a_{ij}, thus the community matrix contains the interaction strengths between every pair of species in the community, and it is often denoted by A. The *net* effect of species j on species i (the sum of both direct and indirect effects) is defined to be the ij^{th} element of the inverse community matrix, A^{-1} and can be calculated by applying a press perturbation to the equilibrium biomass density of species j (Bender et al. 1984). The *total* net effect of a species is a measure that quantifies how a small sustained change in the equilibrium biomass density of that individual species affects the equilibrium biomass densities of *all* other species in the community and is defined to be the sum of the absolute values of elements of column j in the inverse community matrix (Berg et al. 2011).

When measuring interactions strengths empirically it can be difficult to distinguish between direct effects and indirect effects (Wootton and Emmerson 2005, O'Connor et al. 2013) and the role of species with weak interaction strengths has mainly been investigated by considering species with weak direct effects, i.e. species whose a_{ij} entries in the community matrix are small in magnitude compared to other species in the community (McCann et al. 1998, McCann 2000, Neutel et al. 2002, Christianou and Ebenman 2005, O'Gorman and Emmerson 2009). A few studies have focused on species *net* effects (Montoya et al. 2005 Montoya et al. 2009, O'Gorman et al. 2010, Berg et al. 2011). For example, studies by Montoya et al. on the Ythan Estuary and Broadstone Stream food webs and by O’Gorman et al. on mesocosms in Lough Hyne found that species with high linkage density had weak *pairwise net effects* (Montoya et al. 2009) and weak *mean net effects* (Montoya et al. 2005 O'Gorman et al. 2010) on their community (the measures of a species mean net effect and total net effect are proportional and perfectly correlated). In contrast, Berg et al. (2011) examined the Baltic Sea and Lake Vättern food webs and found no relationship between a species linkage density and its total net effect. The study presented in Chapter 3 of this thesis analysed the relationship between a species linkage density and its total net effect for 97 synthetic food webs generated by an assembly algorithm (Säterberg et al. 2013). A subset of 38 webs showed a negative relationship between linkage density and species total net effect indicating that the relationship between species linkage density and its total net effect may depend on the structure of the community in which it is embedded. It is important to note that the analyses presented in Chapters 3 and 4 of this thesis highlight the fact that the body size of a species has an overwhelming influence on its total net effect in the community, thus, the effect of species linkage density may be difficult to detect when there is large range of body sizes and when body size covaries with linkage density. In this study we aim to establish whether species with high linkage density do have weak total net effects and if so what conditions lead to this relationship.

Materials and Methods

To determine whether there is a negative relationship between a species linkage density and its total net effect, we depart from the simple food chain used in Chapter 4 and consider more complex food webs that allow for a gradient of species linkage density. We considered three food web properties that might contribute to the relationship between species linkage density and total net effect: web size (species richness), web composition (the proportion of basal, herbivore and carnivore species) and web complexity (connectance). A step-wise approach was employed, considering webs of different size, composition and complexity, starting with a twelve species web consisting of four basal species, four herbivore species and four carnivore species (Figure 5.1). Ecologically, this web is not realistic, but it has a structure that allows for a gradient of species linkage density to be established, whilst being relatively simple. Five different cases were examined (see Figure. 5.1): case (a) where the basal species (species 1) is highly connected because it is fed upon by all four herbivore species; case (b) where the herbivore species (species 5) is highly connected because it preys on all four basal species; case (c) where the herbivore species (species 5) is highly connected as it is preyed upon by all four carnivore species; case (d) where the carnivore species (species 9) is highly connected preying on all four herbivore species; and case (e) where species 5 is highly connected preying on all four basal species *and* itself being preyed upon by all four carnivore species. It was important to examine all five cases since we expect species with large body sizes to be the most influential (Berg et al. 2011, Chapter 3 of this thesis). The different scenarios also vary the body size of the highly connected species, allowing us to disentangle the relative effects of body size and linkage density on the net effects. To check whether omnivorous links contribute to the relationship between species linkage density and total net effect we also examined the webs shown in Figures. 5.1(f) and 5.1(g) containing omnivorous links. In Figure 5.1(f) the basal species (species 1) is highly connected because it is preyed upon by all four herbivore species and all four carnivore species and in Figure 5.1(g) the carnivore species (species 9) is highly connected preying on all herbivore and all basal species.

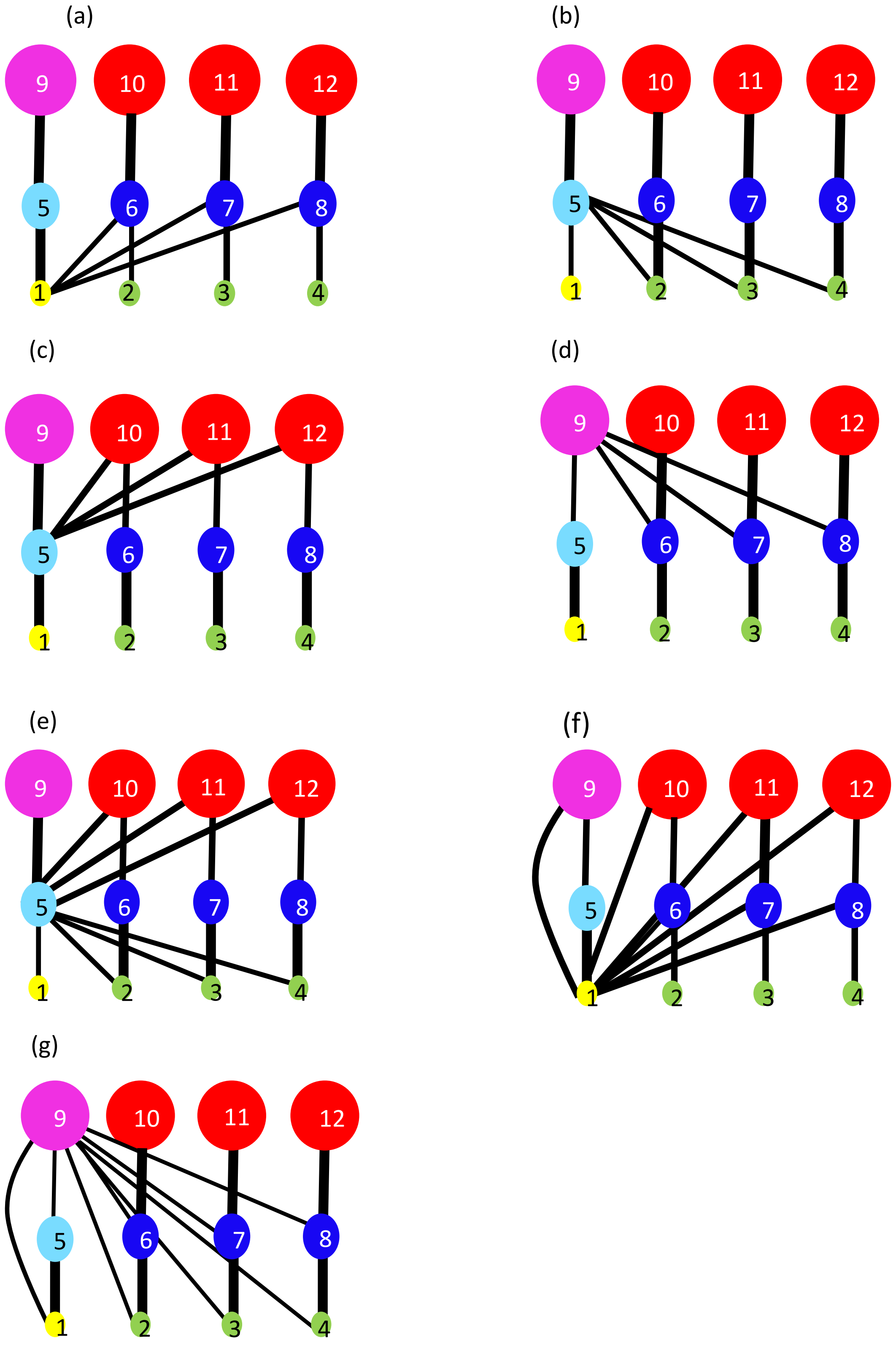


Figure.5.1 Food web motifs of the first set of food webs to be examined. We examine cases:

(a) basal species 1 is preyed on by all herbivore species
(b) herbivore species 5 preys on all basal species
(c) herbivore species 5 is preyed upon by all carnivore species
(d) carnivore species 9 preys upon all herbivore species
(e) herbivore species 5 preys upon all basal species and is preyed upon by all carnivore species.
(f) basal species 1 is preyed upon by all species
(g) carnivore species 9 preys upon all species

Next a set of food webs were examined where size, composition and complexity were varied systematically (see Figures 5.2-5.8 for web diagrams and Table 5.1 for an overview). For the set of webs where size was increased, web size was increased from 12 species to 16 species. For the set of webs where the composition was altered, the ratio of basal, herbivore and carnivore species was changed from 1:1:1 to 1:2:1 and for the set of webs where complexity was increased, the pattern of feeding links was changed from having one highly connected species and all other species minimally connected (with just one or where necessary two prey items) to varying patterns where the maximum gradient of linkage density was maintained (one species with the maximum number of links and one species with the minimum number of links), but more links were assigned between the remaining species. Note that for 16 species it was not possible to split the number of species evenly between trophic levels to maintain a ratio of exactly 1:1:1, the remaining species was assigned to the basal trophic level giving a ratio of 6:5:5, which we refer to as 1:1:1 for simplicity. The ratio of basal, herbivore and carnivore species (1:2:1) was chosen to approximate ratios found for the subset of the synthetic food webs analysed in Chapter 3 that showed a negative relationship between species linkage density and total net effect.

For the webs shown in Figures 5.2(a)-(e), web size was increased to 16 species but the original web composition was maintained as closely as possible (1:1:1) and apart from one highly connected species, web connectance was minimal. For the webs shown in Figures 5.3(a)-(e) web size was maintained at 12 species but the ratio of basal, herbivore and carnivore species was changed from 1:1:1 to 1:2:1 and apart from one highly connected species, web connectance was minimal. For the webs shown in Figures 5.4(a)-(f), web size was maintained at 12 species and the ratio of basal, herbivore and carnivore species was maintained as closely as possible (1:1:1), but web connectance was varied. For the webs shown in Figures 5.5(a)-(e) web size and web composition were changed but the complexity was unaltered. For the webs shown in Figures 5.6(a)–(f) we changed web size and complexity but web composition was kept as similar as possible (1:1:1). For the webs shown in Figures 5.7(a)-(f) we changed web composition and complexity but web size was unchanged. Finally, all three properties were changed (Figures. 5.8a-f).

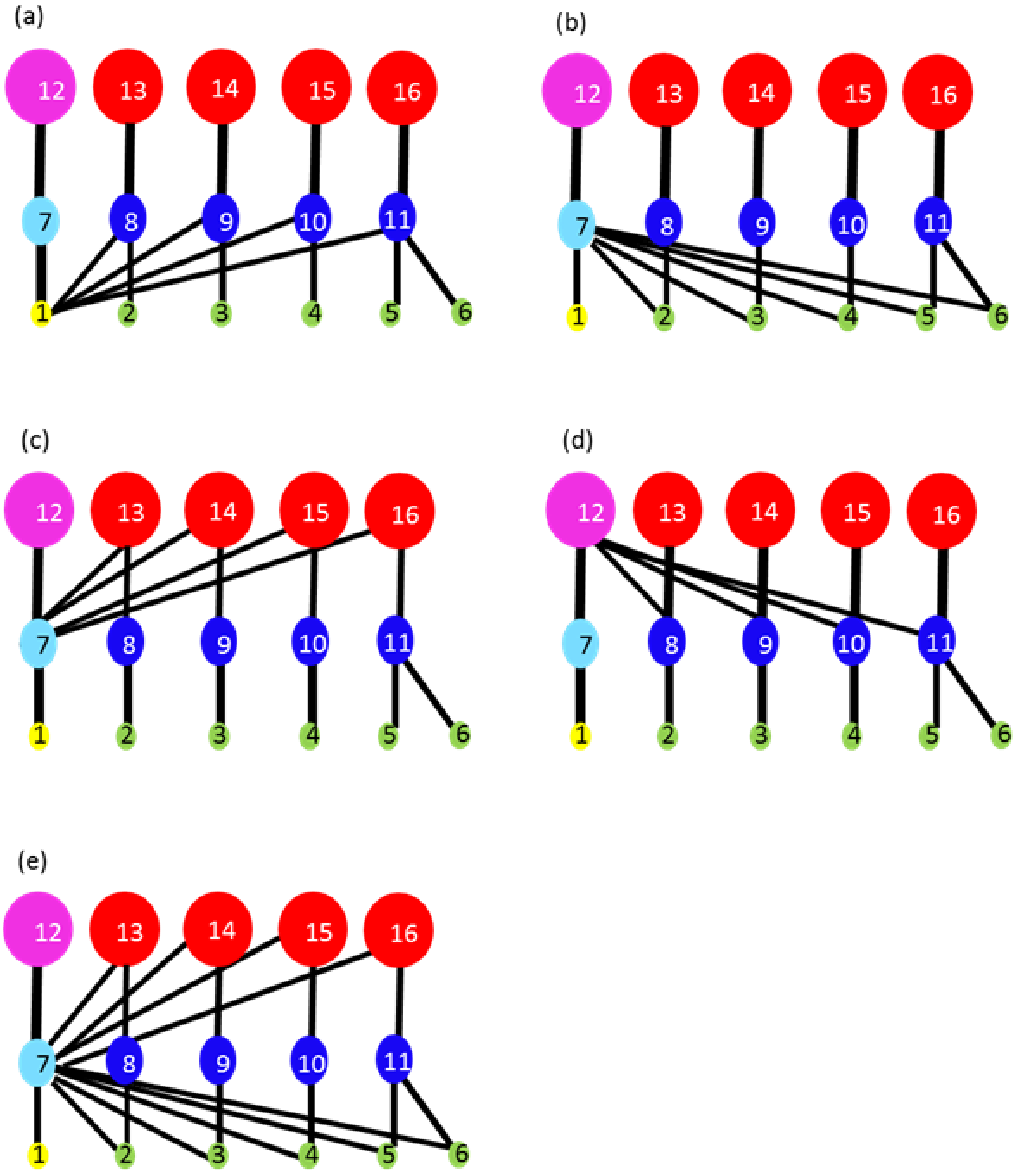


Figure. 5.2 Food web motifs of the set of 16 species food webs with a basal, herbivore and carnivore species ratio of (1:1:1) and minimal complexity (whilst allowing for one species to have the maximum number of links). We examine cases:

(a) basal species 1 is preyed on by all herbivore species
(b) herbivore species 7 preys on all basal species
(c) herbivore species 7 is preyed upon by all carnivore species
(d) carnivore species 12 preys upon all herbivore species
(e) herbivore species 7 preys upon all basal species and is preyed upon by all carnivore species.

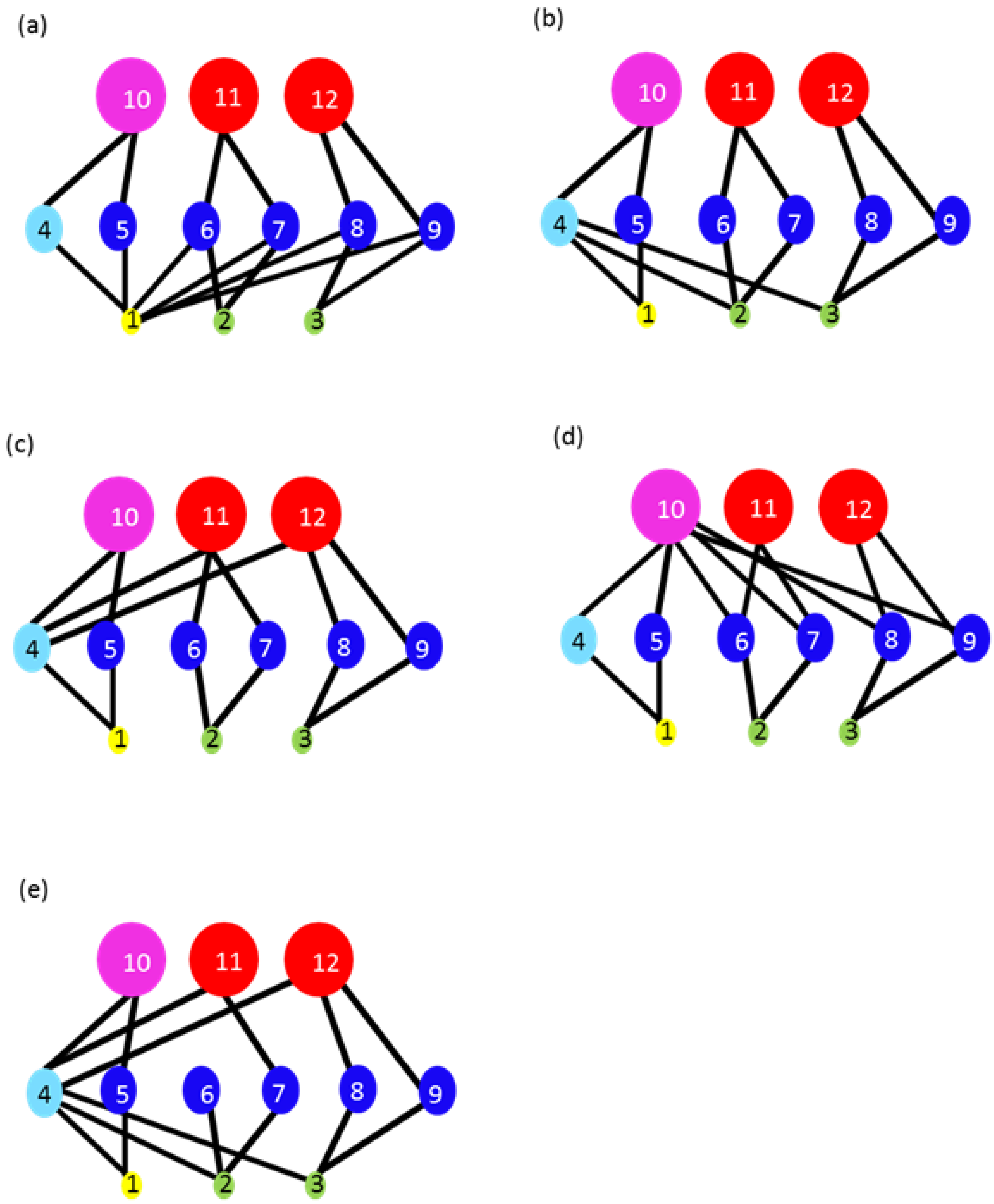


Figure. 5.3 Food web motifs of the set of 12 species food webs with a basal, herbivore and carnivore species ratio of (1:2:1) and minimal complexity (whilst allowing for one species to have the maximum number of links). We examine cases:

(a) basal species 1 is preyed on by all herbivore species
(b) herbivore species 7 preys on all basal species
(c) herbivore species 7 is preyed upon by all carnivore species
(d) carnivore species 12 preys upon all herbivore species
(e) herbivore species 7 preys upon all basal species and is preyed upon by all carnivore species.

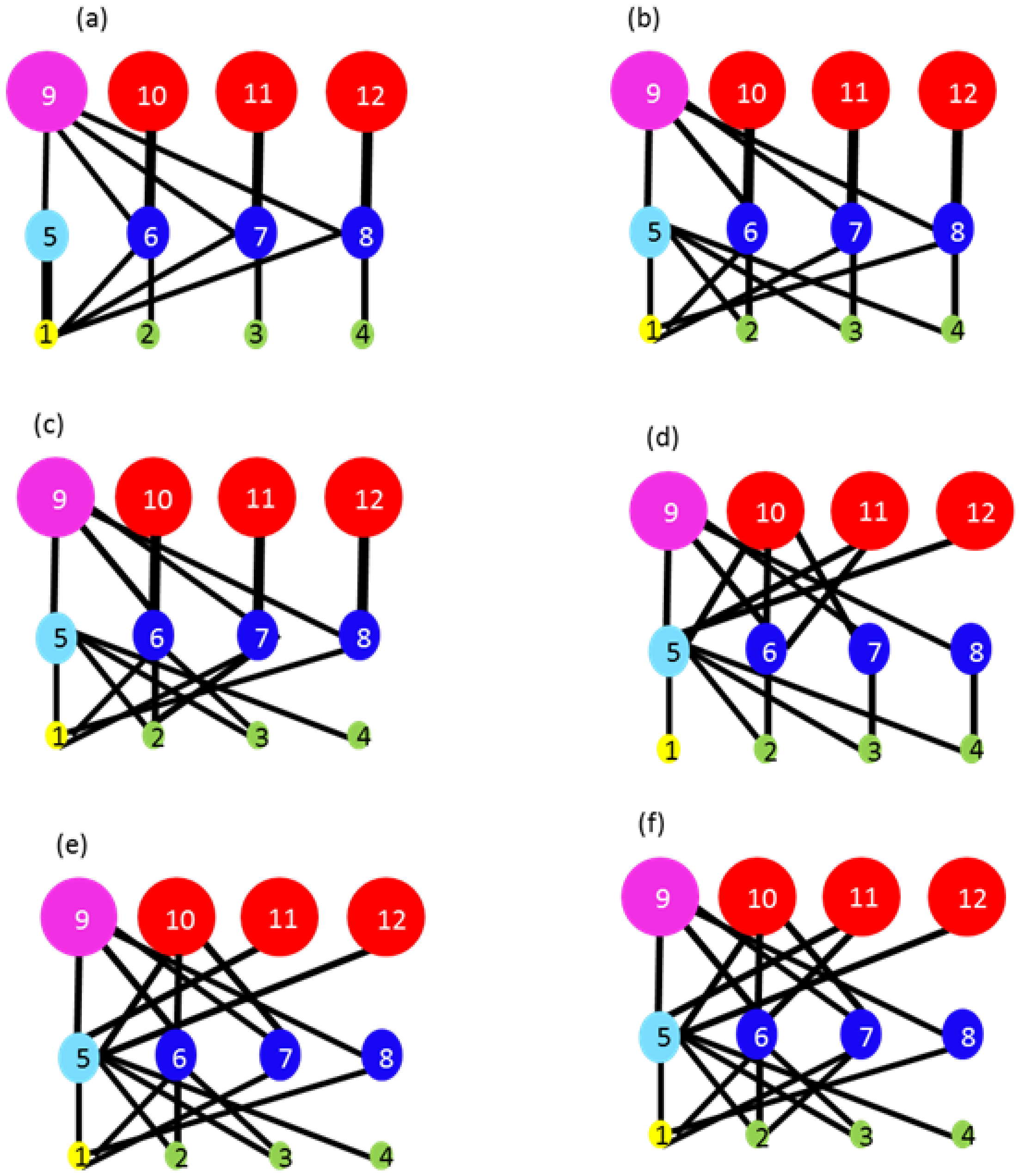


Figure 5.4 Food web motifs of the set of 12 species food webs with a basal, herbivore and carnivore species ratio of (1:1:1) and varying complexity.

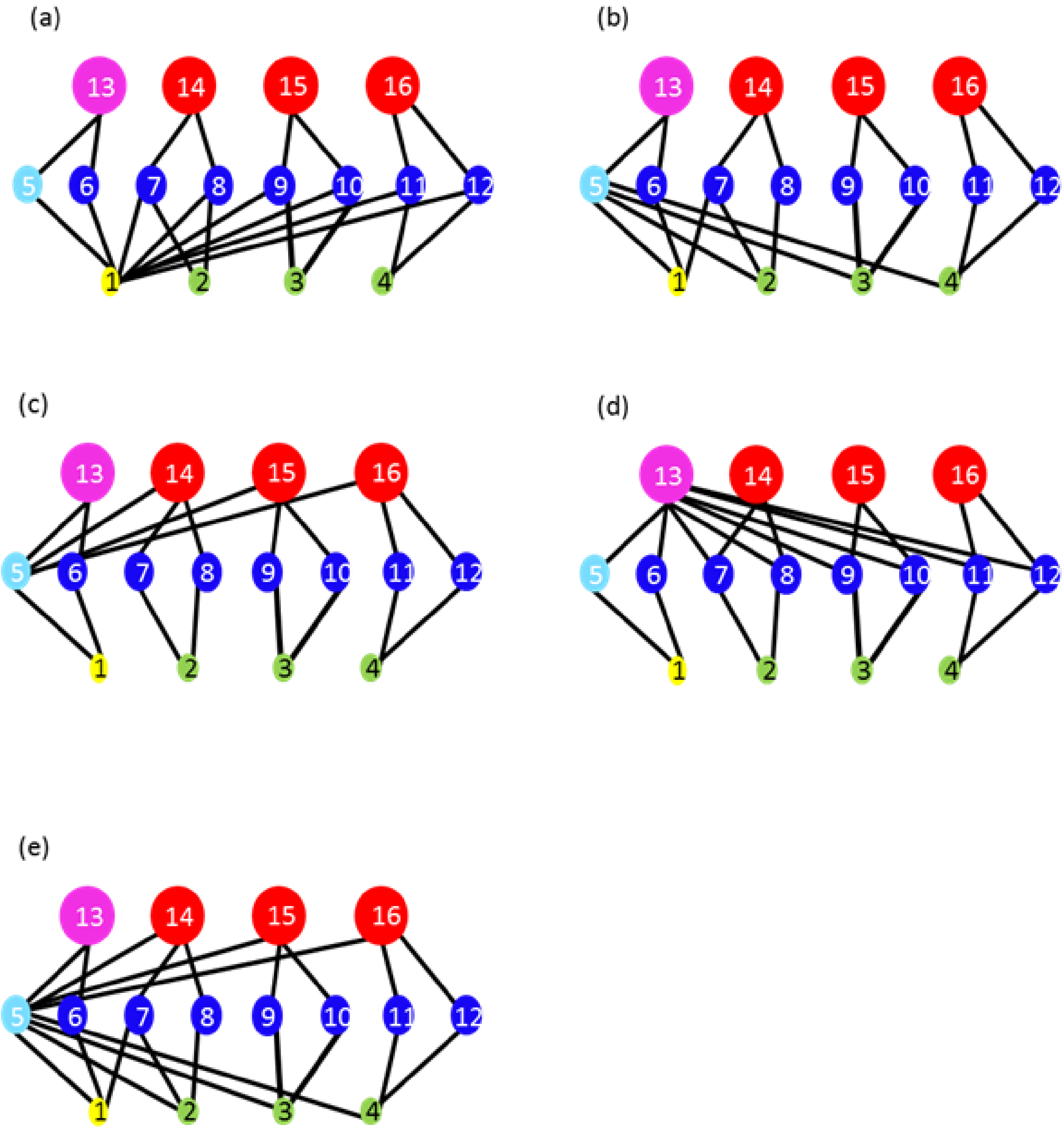


Figure. 5.5 Food web motifs of the set of 16 species food webs with a basal, herbivore and carnivore species ratio of (1:2:1) and minimal complexity (whilst allowing for one species to have the maximum number of links). We examine cases:

(a) basal species one is preyed on by all herbivore species
(b) herbivore species seven preys on all basal species
(c) herbivore species seven is preyed upon by all carnivore species
(d) carnivore species twelve preys upon all herbivore species
(e) herbivore species seven preys upon all basal species and is preyed upon by all carnivore species.

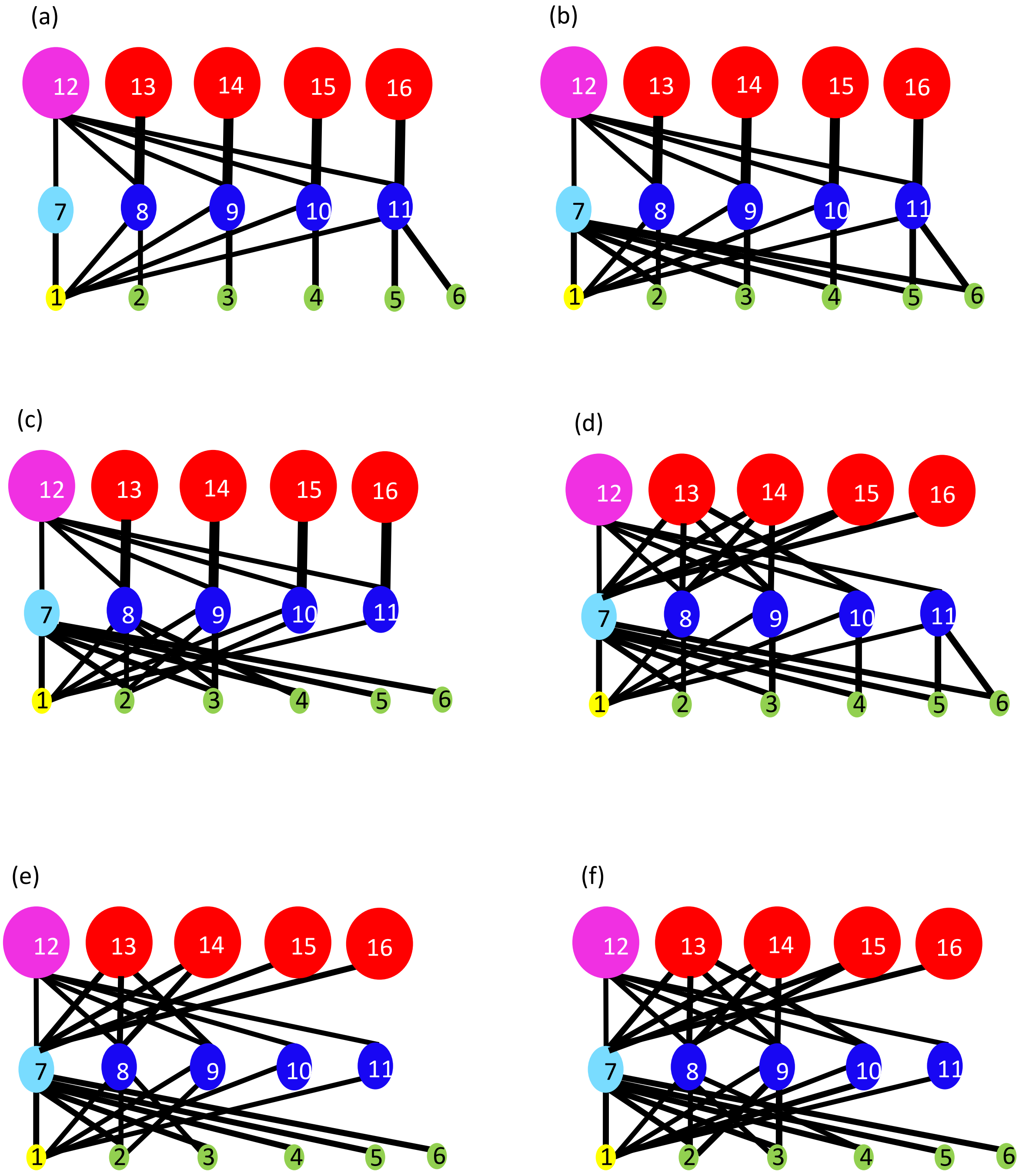


Figure 5.6 Food web motifs of the set of 16 species food webs with a basal, herbivore and carnivore species ratio of (6:5:5) and varying complexity.

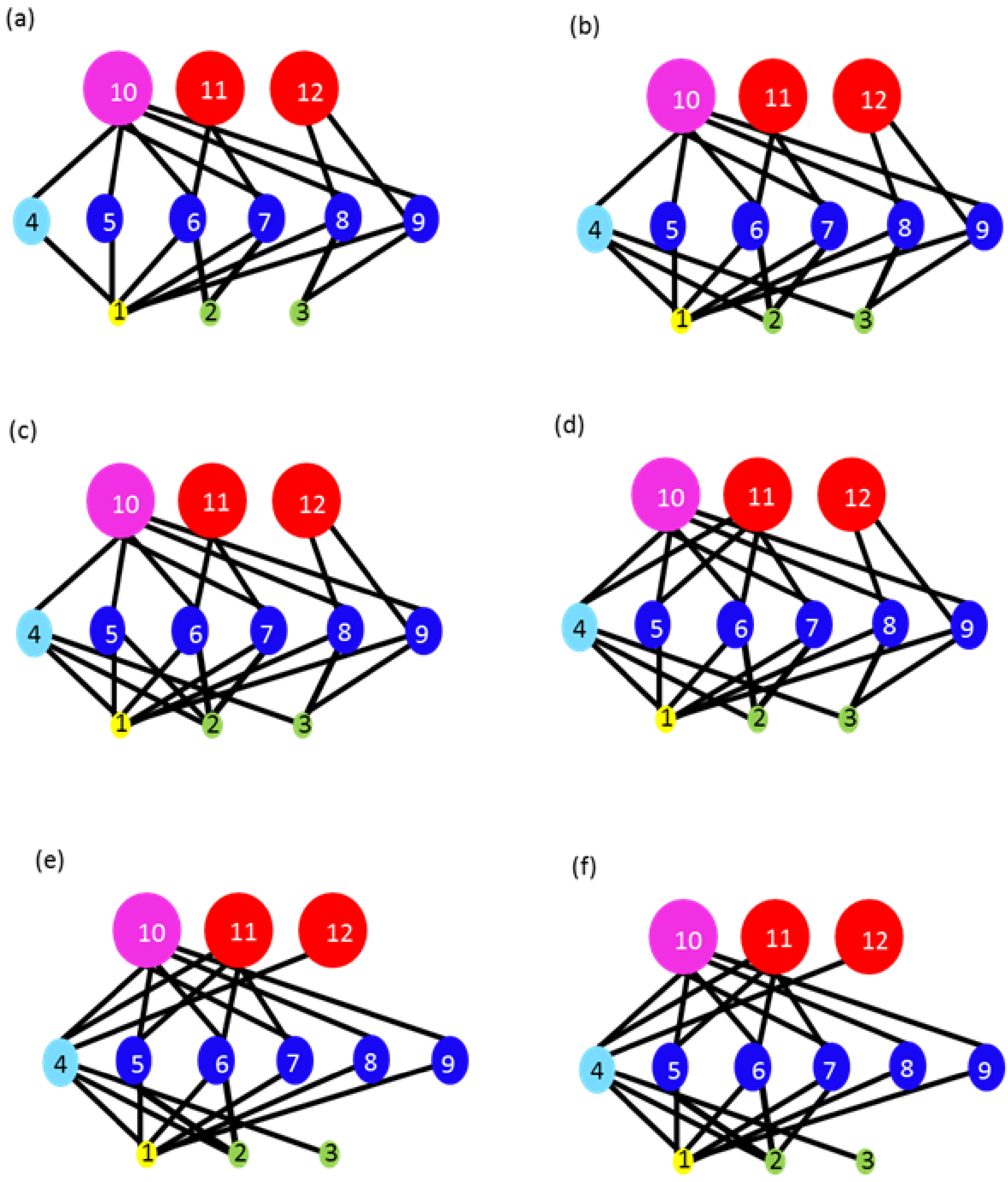


Figure. 5.7 Food web motifs of the set of 12 species food webs with a basal, herbivore and carnivore species ratio of (1:2:1) and varying complexity.

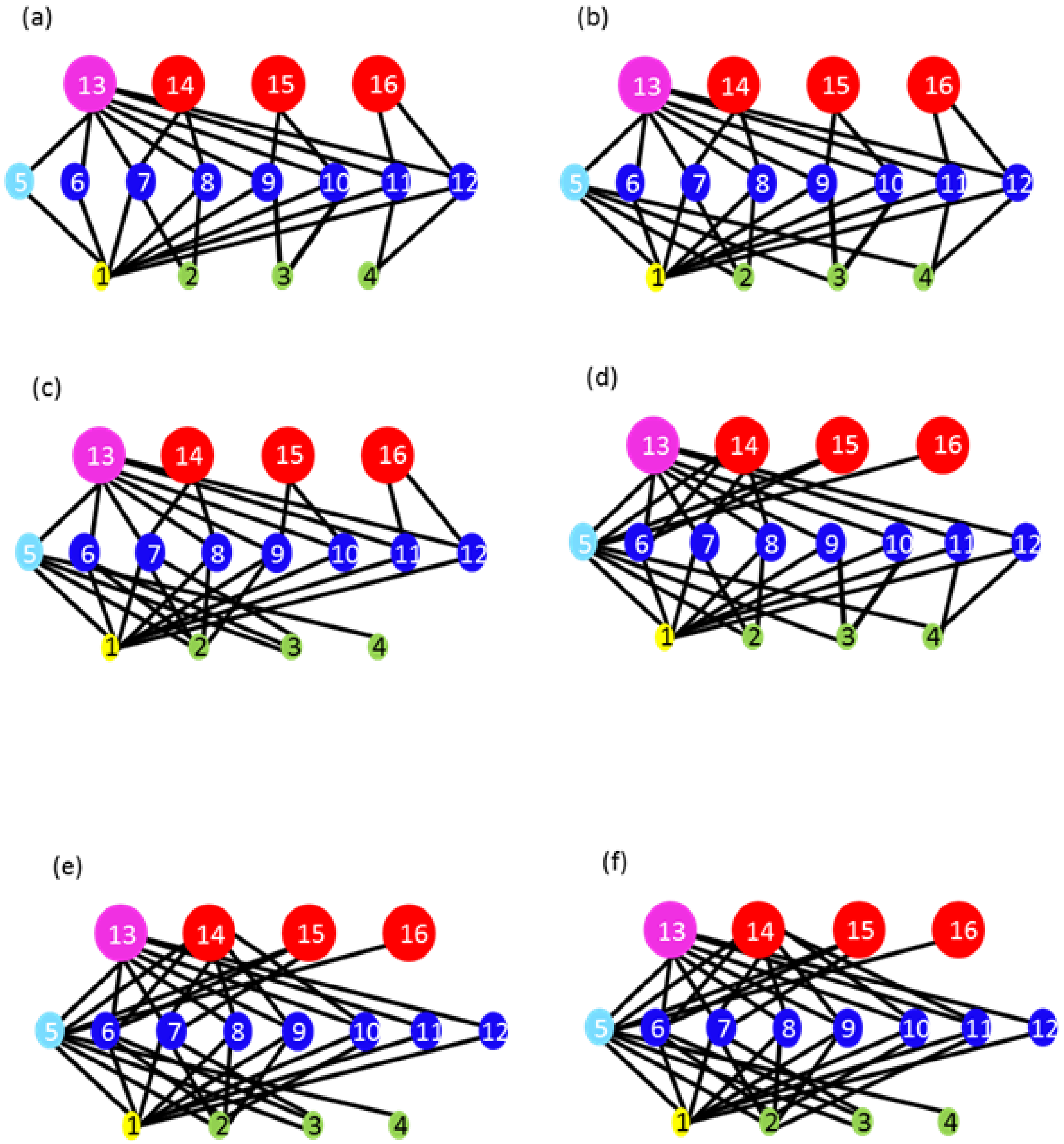


Figure. 5.8 Food web motifs of the set of 16 species food webs with a basal, herbivore and carnivore species ratio of (1:2:1) and varying complexity

Table 5.1 Summary of the systematic variation in species richness, composition (basal: herbivore: carnivore ratios) and complexity (connectance) for the food webs shown in Figures. 5.2-5.8.

Web Number	Species Richness	Basal: Herb: Carnivore Ratios	Complexity
1	12	1:1:1	Minimal
2	16	1:1:1	Minimal
3	12	1:2:1	Minimal
4	12	1:1:1	Varied
5	16	1:2:1	Minimal
6	16	1:1:1	Varied
7	12	1:2:1	Varied
8	16	1:2:1	Varied

A negative relationship between species linkage density and total net effect was present for some of the webs shown in Figures 5.2-5.8 but it was not consistent and there was no obvious explanation for this in relation to the structure of the webs examined. To further understand how food web structure may determine whether species with high linkage density have a weak total net effect we examined the 16 species food web with a ratio of basal, herbivore and carnivore species of 1:2:1 (shown in Figures 5.8a –f) in more detail. Excluding omnivorous links, examining all possible combinations of feeding links would have meant analysing 2^{64} food webs which was not feasible so, to reduce the number of webs examined, the following simplifying assumptions were made:

- all webs contained one basal species (chosen to be species one) that was preyed upon by all herbivore species.
- all webs contained one basal species (chosen to be species two) that was preyed upon by just one herbivore (chosen to be species five).
- all webs contained one carnivore species (chosen to be species thirteen) that preyed upon all herbivore species.
- all webs contained one carnivore species (chosen to be species fourteen) that preyed upon just one herbivore species (chosen to be species five).

These simplifying assumptions ensured that the maximum gradient of linkage density was maintained and reduced the number of permutations in the arrangement of feeding links. To reduce the number of webs further, the arrangement of links for basal species three and carnivore species fifteen was restricted. The number of links for basal species three was varied from 1-8 but just two alternative configurations were used: one where it was connected to the same herbivore as species fourteen and one where it was not (a total of 15 permutations). More specifically, links were assigned to the herbivore species with the lowest number. For example, when species three had just one link there were two alternative configurations: for the case where species three was connected to the *same* herbivore as species two then both species were connected to herbivore species five, but for the case where species three was *not* connected to the same herbivore as species two, then species three was connected to herbivore species six. Similarly, the number of links for carnivore species fifteen was varied from 1-8 but just two alternative configurations were used: one where it was connected to the same herbivore as species fourteen and one where it was not (a total of 15 permutations). Again, links were assigned to the herbivore species with the lowest number. Now, for the basal species, the feeding links for species one and two were fixed (just 1 permutation), species three had a total of 15 permutations, then all possible permutations of feeding links for species four were assigned (2^8 -1 permutations, we subtract the 1 since species four must be preyed upon by at least one herbivore species). For the carnivore species, the feeding links for species thirteen and fourteen were fixed (just 1 permutation), species fifteen had a total of fifteen permutations, then all possible permutations of feeding links for species sixteen were assigned (2^8-1 permutations). This gave a total of 1x1x15x255x1x1x15x255= 14,630,625 permutations. For each food web generated, Spearman's rank correlation coefficient was calculated between a species linkage density and its total net effect within each trophic level and for the overall web. The correlation coefficient was recorded along with web connectance, the number of links of each species and whether or not species two and three were connected to the same herbivore, or whether species fifteen and sixteen were connected to the same herbivore.

Parameterisation of the webs

The parameterisation of the more complex food webs was identical to the parameterisation used to investigate the relationship between species body size and its total net effect in Chapter 4. To recap, consider a food web, consisting of *S* species whose dynamics are described by the following Lotka-Volterra equations:

$$\frac{dB_i}{dt} = B_i\left(r_i + \sum_{j=1}^{S} a_{ij} B_j \right) \qquad (1)$$

where B_i is the biomass of species i (measured in g), for basal species r_i is positive and represents the per unit mass growth rate of species i, for consumer species r_i is negative and represents the per unit mass death rate of species i and a_{ij} is the per unit mass effect of consumer species j feeding on resource species i per unit of time.

The per unit mass growth rate of species i is defined to be:

$$r_i = C_r m_i^{-1/4} \text{ (kg.kg}^{-1}\text{t}^{-1}\text{)}$$

where m_i is the body mass of species i and C_r is a positive constant for basal species and a negative constant for consumer species. The per unit mass effect of consumer species j feeding on resource species i per unit of time, a_{ij} is defined to be:

$$a_{ij} = C_{aij} p_{ij} (m_i m_j)^{-\frac{1}{4}} \qquad \text{(kg}^{-1}\text{t}^{-1}\text{)}$$

where C_{aij} is a constant, p_{ij} represents the proportion of resource species i present in consumer species j's diet and m_i and m_j represent the resource and consumer species body masses respectively. Note that to simplify the case where a consumer species has multiple resource species we replaced the biomass based preference term z_{ij} used in Chapter 3 with the simpler term p_{ij} defined to be $\frac{1}{n_j}$ where n_j is the total number of resource species consumed by species j (O'Gorman et al. 2010). The per unit mass effect of the resource species i on the consumer species j, a_{ji} is given by

$$a_{ji} = -e a_{ij}$$

where e is the conversion efficiency.

For the *food chains* analysed in Chapter 4 of this thesis we defined intraspecific interaction strengths to scale with interspecific interaction strengths as:

$$a_{ii} = C_b a_{ij} \text{ for basal species and } a_{ii} = C_c a_{ik} \text{ for consumer species}$$

where C_b represents the ratio of intra-interspecific interaction strength for basal species and C_c represents the ratio of intra-interspecific interaction strength for consumer species. Species j is a herbivore species (body mass m_2 in Figure. 4.1) and species k is the smallest carnivore species (body mass m_3 in Figure 4.1). In an ecological context, large values of C_b occur when basal intraspecific competition is large compared to the effects of herbivory and large values of C_c occur when consumer intraspecific competition is large compared to the effects of predation. For the food webs analysed in this chapter, prey species can have multiple predator species so we define intraspecific interaction strengths to scale with the sum of interspecific interaction strengths as:

$a_{ii} = C_b \sum_{j \in \Omega_i} a_{ij}$ for basal species and $a_{ii} = C_c \sum_{j \in \Omega_i} a_{ij}$ for consumer species

where Ω_i represents the set of species that feed on species i.

For the food webs shown in Figures 5.1-5.8, let m_1, m_2 and m_3 denote the body masses of the basal, herbivore and carnivore species respectively (note that we have made the simplifying assumption that body mass is constant within each trophic level). Let q^* represent the predator-prey body size ratios so that $q^* = \frac{m2}{m1} = \frac{m3}{m2}$, then we can write:

$$m_2 = q^* m_1$$
$$m_3 = q^{*2} m_1$$

and,

$$a_{ij} = C_{aij} \frac{1}{n_j} (m_1 m_2)^{-\frac{1}{4}} = C_{aij} \frac{1}{n_j} (q^* m_1^2)^{-\frac{1}{4}} = C_{aij} \frac{1}{n_j} (m_1^{-\frac{1}{2}})(q^*)^{-\frac{1}{4}}$$

$$a_{jk} = C_{ajk} \frac{1}{n_k} (m_2 m_3)^{-\frac{1}{4}} = C_{ajk} \frac{1}{n_k} (q^{*3} m_1^2)^{-\frac{1}{4}} = C_{ajk} \frac{1}{n_k} (m_1^{-\frac{1}{2}})(q^*)^{-\frac{3}{4}}$$

where species i is a basal species, species j is a herbivore species and species k is a carnivore species. To simplify the form of the a_{ij} and a_{jk} entries we replace $(q^*)^{\frac{1}{4}}$ with the variable q and since $C_{aij} = C_{ajk}$ is a constant that scales the magnitude of *all* the a_{ij} and a_{jk} entries we replace $C_{aij} m_1^{-\frac{1}{2}}$ and $C_{ajk} m_1^{-\frac{1}{2}}$ with the value -1. This gives $a_{ij} = -\frac{1}{n_j q}$ and $a_{jk} = -\frac{1}{n_k q^3}$. The total net effect of a species in the community is represented by the column sums of the absolute values of the elements of the inverse matrix, A^{-1}.

For the food webs shown in Figures 5.1(a)-(g), we examine two situations: first where the ratio of consumer intra-interspecific interaction strength, C_c, is set to 0 and second where C_c is unconstrained. In ecological terms, setting C_c to 0 equates to a situation where consumer intraspecific competition is very weak compared to intraspecific competition amongst basal species. The assumption that consumer intraspecific competition is small compared to the other parameters is based on the biological argument that basal species are sedentary and have to compete for space and light, thus consumer intraspecific interaction strengths can be considered to be small compared to basal intraspecific interaction strength (Emmerson and Raffaelli 2004, Christianou and Ebenman 2005, Eklöf and Ebenman 2006). For the food webs shown in Figures 5.1(a)-(e), the column sums for each inverse community matrix were simple enough to be analysed directly, but for the omnivorous food webs shown in Figures 5.1(f) and 5.1(g) the column sums were too complex. To simplify the analysis, the ecological efficiency parameter, e, was set to 0.1 and the ordering of column sums was examined graphically for the cases $C_b = 100e$, $C_b = 10e$, $C_b = e$ and $C_b = 0.1e$. For the case where consumer intraspecific competition is not small compared to the other parameters, again the column sums were extremely complex so we examined the ordering of column sums graphically for fixed values of C_b, C_c and e. Although this is not a rigorous examination of the ordering of the column sums, all six possible orderings of the parameters C_b, C_c and e are considered (Table 5.2).

Table 5.2 Values used for the parameters Cb, Cc and e when examining the column sums of food webs 1(a)-(g) for the case where Cc is not set to 0. Case (i) represents the situation where the ratio of basal intra-interspecific interaction strength is 1 i.e. intraspecific interaction strengths are equal to interspecific interaction strengths, the ecological efficiency is 0.1 and the ratio of consumer intra-interspecific interaction strength is 0.01, i.e. intraspecific interaction strengths are one hundred times smaller than interspecific interaction strengths. It is not known which case occurs most frequently in empirical food webs and therefore it is of interest to see how the ordering of species is affected by the parameter values.

Case	Order of Parameters	Values of Parameters		
(i)	$C_c < e < C_b$	$C_b = 1$	$C_c = 0.01$	$e = 0.1$
(ii)	$C_c < C_b < e$	$C_b = 0.01$	$C_c = 0.001$	$e = 0.1$
(iii)	$e < C_c < C_b$	$C_b = 10$	$C_c = 1$	$e = 0.1$
(iv)	$e < C_b < C_c$	$C_b = 1$	$C_c = 10$	$e = 0.1$
(v)	$C_b < e < C_c$	$C_b = 0.01$	$C_c = 1$	$e = 0.1$
(vi)	$C_b < C_c < e$	$C_b = 0.001$	$C_c = 0.01$	$e = 0.1$

When we expanded the analysis over a range of food webs of varying size, composition and complexity it was not possible to consider all six possible orderings of the parameters C_b, C_c and e, so we focused on the ordering that corresponded most closely to the ordering found in the webs examined in Chapter 3, thus C_b was set to 1, C_c was set to 0.01 and e was set to 0.1. It was also necessary to fix the predator-prey body size ratio q which was set to 100. The analyses undertaken in the present study aim to investigate patterns in the inverse community matrix caused by variation in species linkage density and so webs were not checked for stability.

Statistical Analysis

Four data sets were generated by the permutations of the 16 species food web. For each web, four correlation coefficients between species linkage density and total net effect were calculated: one for the whole web and one for each of the basal, herbivore and carnivore trophic levels. The data sets were examined graphically and due to the large size of the data set, classification trees were initially used to examine the relationship between the correlation coefficients (the response variables) and food web properties (the explanatory variables). The correlation coefficients for each web were placed in one of two classes: webs with correlation coefficients less than -0.4 were classified as ‘negative relationship between linkage density and total net effects present’ and webs with correlation coefficients greater than -0.4 were classified as ‘no relationship between linkage density and total net effects present’. The value of -0.4 rather than 0 was chosen as an appropriate threshold, because coefficients between -0.4 and 0 indicate a weak negative correlation. We also repeated the analyses using -0.7 as the threshold for determining whether a negative relationship was present or not and the results were qualitatively consistent with those using a threshold value of -0.4.

The variables used to partition the data in the classification trees (i.e. the explanatory variables) were web connectance, the number of links of each species, whether or not the basal species with just one link (species two) and the basal species with a varying number of links (species three) were connected to the same herbivore and whether or not the carnivore species with just one link (species fourteen) and the carnivore species with a varying number of links (species fifteen) were connected to the same herbivore. Classification trees were run on each data set to detect patterns in web structure associated with a negative relationship between linkage density and total net effect. Web connectance was identified as a possible indicator as to whether a negative relationship between linkage density and net effect was present in a web, and therefore a logistic regression model was used to explore the relationship between the correlation coefficient classes and web connectance. Additionally, *t*-tests were used to determine whether differences in web connectance were significant between the two groups of correlation coefficients. The graphical analyses, food web permutations and calculation of correlation coefficients were performed using MATLAB version 7.7.0 (MATLAB 2008). The statistical analyses were undertaken using R version

3.0.2 (R Development Core Team 2013) , classification trees were calculated using the ‘rpart’, package and drawn using ‘rattle’(Williams 2011).

Results

Food webs 5.1(a)-(g) intraspecific interaction strength set to 0

For the twelve species food webs shown in Figures. 5.1(a)-(e), where consumer intraspecific competition is set to 0, the column sums are analysed in Appendix H and a summary of the results is presented in Table 5.3. The ordering of species was determined by species body size, where species with a large body size have the largest total net effect. When the ordering of species net effects within each trophic level (where species have the same body size) was examined, we did not find a consistent pattern. For the web shown in Figure 5.1(a) where basal species one had the maximum linkage density we found that the highly connected species had a smaller net effect than the other species within the same trophic level. For the web shown in Figure 5.1(b) where herbivore species five had the maximum linkage density (because it preyed upon all four basal species) it was found that the highly connected species had the same net effect as the other herbivore species. For the web shown in Figure 5.1(c) where the herbivore species five had the maximum linkage density (due to being preyed upon by all four carnivore species) and for the web shown in Figure 5.1(e) where species five again had the maximum linkage density (because it preyed on all four basal species *and* was preyed upon by all four carnivore species) it was found that the highly connected herbivore species had a smaller net effect than the other herbivore species. When the carnivore species had the maximum linkage density (Figure 5.1d) it was found that the highly connected carnivore species had a larger net effect than the other carnivore species. For the web shown in Figure 5.1(f) where the basal species was highly connected (preyed upon by all herbivore species and all carnivore species) and for the web shown in Figure 5.1(g) where the carnivore species was highly connected (preys upon all herbivore species and all basal species) it was found that for the cases where $C_b > e$, the highly connected species had a larger net effect than the other species within the same trophic level and for the case where $C_b \leq e$ the highly connected species had a smaller net effect than the other species within the same trophic level (see Appendix H Figures. H1a and H1b).

Food webs 1(a) – (g) intraspecific interaction strength is not set to 0

For the case where consumer intraspecific competition C_c is not set to 0, the species with the highest linkage density is not the species with the smallest net effect with the exception of the webs shown in Figures 5.1(a) and 5.1(f) where the basal species has the highest linkage density (see Table 5.3 for a summary and Appendix H Figures. H2a-g) for the orderings. For the web shown in Figure 5.1(g) where the carnivore species was highly connected it was found that the highly connected carnivore species had a smaller net effect than the other carnivore species for cases (ii), (iii) and (vi) (see Table 5.3 and Appendix H Figure H2g).

Table 5.3 Summary of the column sum analyses indicating whether the highly connected species has weak total net effects. For the case consumer intraspecific interaction strength is set to 0 ($C_c = 0$) and where it is positive ($C_c > 0$). For the webs shown in Figures 5.1(a)-(e) the position of the highly connected species relative to other species within the same trophic level was not affected by the values of the parameters Cb, Cc and e. For the web shown in Figure 5.(g) for Cc > 0 the highly connected carnivore has the weakest net effect when one of the three conditions is satisfied.

Food web	Cc	Highly connected species has weak total net effects?	Condition
5.1(a) basal fed on by all herbivores	0	Yes	None
	> 0	Yes	None
5.1(b) herbivore feeds on all basal species	0	No	None
	> 0	No	None
5.1(c) herbivore species fed on by all carnivores	0	Yes	None
	> 0	No	None
5.1(d) carnivore species feeds on all herbivores	0	No	None
	> 0	No	None
5.1(e) herbivore species feeds on all carnivores and is fed on by all basal species	0	Yes	None
	> 0	No	None
5.1(f) basal species fed on by all herbivores and carnivores	0	Yes	$C_b \leq e$
	> 0	Yes	None
5.1(g) carnivore species feeds on all herbivores and basal species	0	Yes	$C_b < e$
	> 0	Yes	$C_c < C_b < e$
			$e < C_c < C_b$
			$C_b < C_c < e$

Food webs 2 – 10: a range of web size, composition and complexity

As expected, body size was the most influential factor determining a species total net effect (Appendix I Figures. I1-I7), therefore we examined the relationship between linkage density and total net effect within each trophic level, where body mass was constant. For the food webs where complexity was not varied (Figures. 5.2, 5.3 and 5.5), the highly connected basal species was consistently the species with the smallest total net effect (see Table 5.4 for a summary and Appendix I Figures. I1a, I2a and I4a). For the webs where complexity was varied (see Figures. 5.4, 5.6, 5.7 and 5.8) the highly connected basal species was often the species with the smallest total net effect (see Table 4 for a summary and Appendix I Figures.

I3(a)(c)(e), I5(a)(c)(f), I6(a)(b)(e)(f) and I7(a)(b)(e)(f)). However for some of the arrangements of links the highly connected basal species had similar total net effects to the other basal species present (Appendix I Figures. I3(b)(d)(f), I5(b)(d)(e), I6(c)(d) and I7(c)(d)). For the food webs where complexity was not varied (Figures. 5.2, 5.3 and 5.5) the highly connected herbivore species was never the herbivore species with the smallest total net effect (see Appendix I Figures. I1(b)(c)(e), I2(b)(c)(e) and I4(b)(c)(e)). For the webs where complexity was varied (shown in Figures. 5.4, 5.6, 5.7 and 5.8), the highly connected herbivore species was sometimes the species with the smallest total net effect (see Appendix I Figures. I3(b)(d)(e), I5(c)(e), I6(e) and I7(c)(e)). The highly connected carnivore species was never the species with the smallest total net effect (see Appendix I Figures. I1-I7).

Table 5.4: summary of the column sum analyses indicating whether the highly connected species has weak total net effects for webs of varying size, composition and complexity (Figures 5.1-5.8).

Highly connected species	Food web	Species Richness	Composition	Complexity	Highly connected species has weak total net effects?
Basal	1	12	1:1:1	Minimal	Yes
	2	16	1:1:1	Minimal	Yes
	3	12	1:2:1	Minimal	Yes
	4	12	1:1:1	Varied	Dependent on links
	5	16	1:2:1	Minimal	Yes
	6	16	1:1:1	Varied	Dependent on links
	7	12	1:2:1	Varied	Dependent on links
	8	16	1:2:1	Varied	Dependent on links
Herbivore	1	12	1:1:1	Minimal	No
	2	16	1:1:1	Minimal	No
	3	12	1:2:1	Minimal	No
	4	12	1:1:1	Varied	Dependent on links
	5	16	1:2:1	Minimal	No
	6	16	1:1:1	Varied	Dependent on links
	7	12	1:2:1	Varied	Dependent on links
	8	16	1:2:1	Varied	Dependent on links

Permutations of the 16 species web with a trophic level ratio of (1:2:1)

For each web, four correlation coefficients between linkage density and total net effect were calculated: one for the whole web and one for each of the basal, herbivore and carnivore trophic levels. The correlation between linkage density and total net effect for the whole webs and for each trophic level varied and could be positive or negative (Figure 5.9). For the whole webs, most correlations between total net effect and linkage density were weak (positive or negative), with a mean value of 0.046, just 0.2% of correlations had a value of -

0.4 or less and just 1.2%of correlations had a value of 0.4 or more, Figure 5.9(a). For the basal trophic level, correlations between total net effect and linkage density varied between -1 and 1, with a mean value of -0.201, 31.2% of correlations had a value of -0.4 or less and 15.6% of correlations had a value of 0.4 or more, Figure 5.9(b). For the herbivore trophic level, correlations between total net effect and linkage density varied between -1 and 1, but were more frequently negative. The mean correlation coefficient was -0.227, 36.6% of correlations had a value of -0.4 or less and 7.5% of correlations had a value of 0.4 or more, Figure 5.9(c). The correlation coefficients for the carnivore trophic level were mostly strong and positive with a mean value of 0.6753, just 5.5% of correlation coefficients had a value of -0.4 or less and 79.2% of correlations had a value of 0.4 or more (Figure 5.9d).

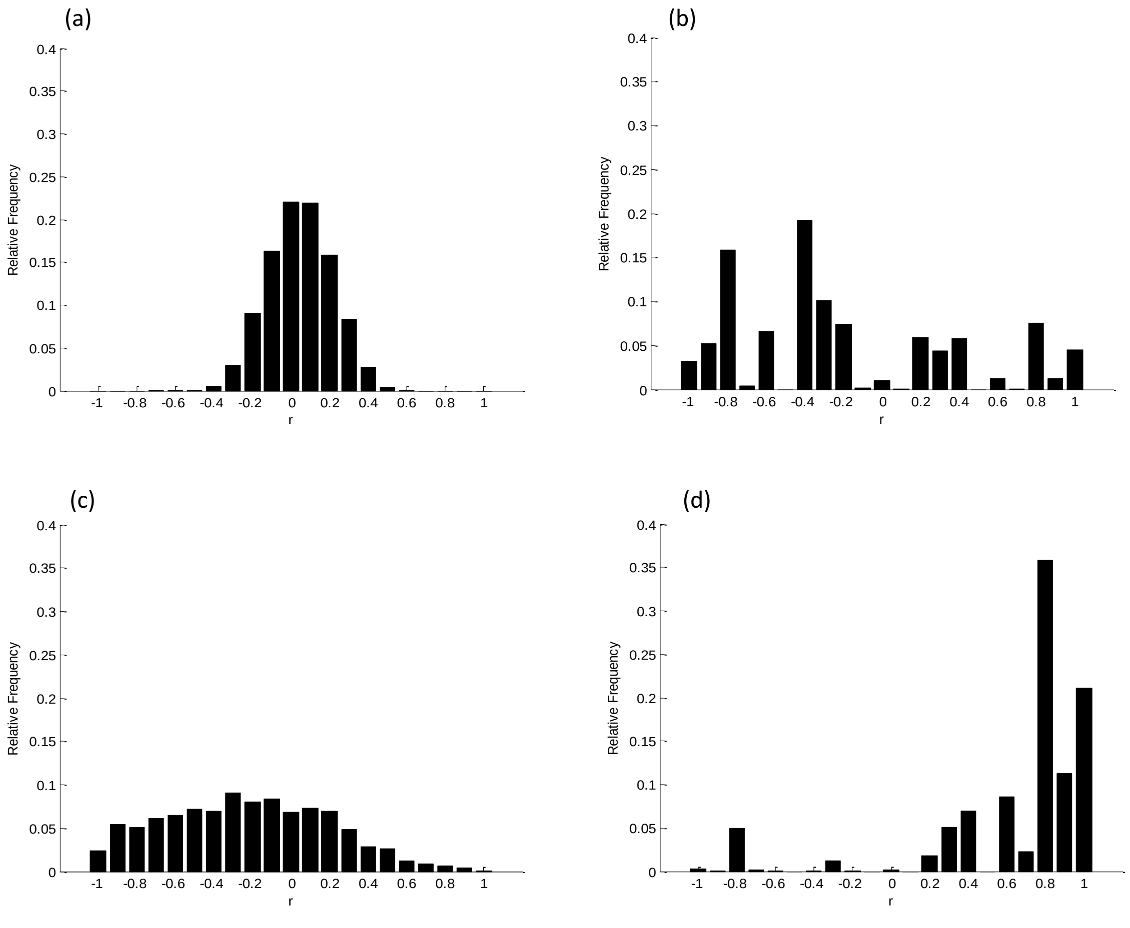


Figure 5.9 The distribution of the correlation coefficients between total net effect and linkage density for (a) the whole web (b) within the basal trophic level (c) within the herbivore trophic level and (d) within the carnivore trophic level.

The classification tree run on the correlation coefficients for the whole webs detected no web level patterns underlying the relationship between total net effect and linkage density. The tree did not progress beyond the root node which, for the complexity parameter chosen

(0.01), which indicated that splitting the data using the variables in the data set did not improve the missclasification error rate of the tree by 1% or more.

For the basal trophic level, a negative relationship occurred more frequently when three different conditions were met: (1) when the basal species with a varying number of links (species three) had just one link and was not connected to the same herbivore as the basal species with just one link (species two); (2) the basal species with a varying number of links (species three) had two or three links, was not connected to the same herbivore as the basal species with just one link (species two) and the linkage density of the carnivore species with a varying number of links (species fifteen) was less than five; and (3) the basal species with a varying number of links (species three) had eight links, and was (inevitably) connected to the same herbivore as the basal species with just one link (species two) and the linkage density of the carnivore species with a varying number of links (species fifteen) was less than 6 (see Figure 10(a) for the classification tree and Appendix J Figures J1(a) and (b) for bar charts showing how the proportion of negative correlations varied with the number of links for each species).

The missclassification rate for a classification tree gives the proportion of observations that were assigned to the incorrect class, i.e.the number of observations being assigned to the incorrect class divided by the total number of observations. In this study, an observation can be missclasified by assigning it to the class representing a correlation coefficient less than -0.4 when it has a correlation coefficient greater than -0.4 or by assigning it to the class representing a correlation coefficient greater than -0.4 when it has a correlation coefficient less than -0.4. The classification tree for the data obtained from the basal trophic level had a missclasification rate of 0.23.

For the herbivore trophic level, a negative relationship occurred more frequently for two different conditions: (1) when the web connectance was less than 0.29; and (2) when the web connectance was between 0.29 and 0.32 and the basal species with a varying number of links (species three) had one, two, three, seven or eight links (see Figure 10(b) for the classification tree and Appendix J Figures J2(a) and (b) for bar charts showing how the proportion of negative correlations varied with the number of links for each species). The classification tree for the herbivore trophic level has a missclasification rate of 0.30.

For the carnivore trophic level, a negative relationship occurred when the carnivore species with a varying number of links (species fifteen) had one link connected to the same herbivore as the carnivore species with just one link (species fourteen) and the carnivore species with links of varying number and position (species sixteen) had two, three, four, five or eight links (see Figure 11(c) for the classification tree and Appendix J Figures J3(a) and (b) for bar charts showing how the proportion of negative correlations varied with the number of links for each species). The classification tree for the carnivore trophic level has a missclasification rate of 0.005.

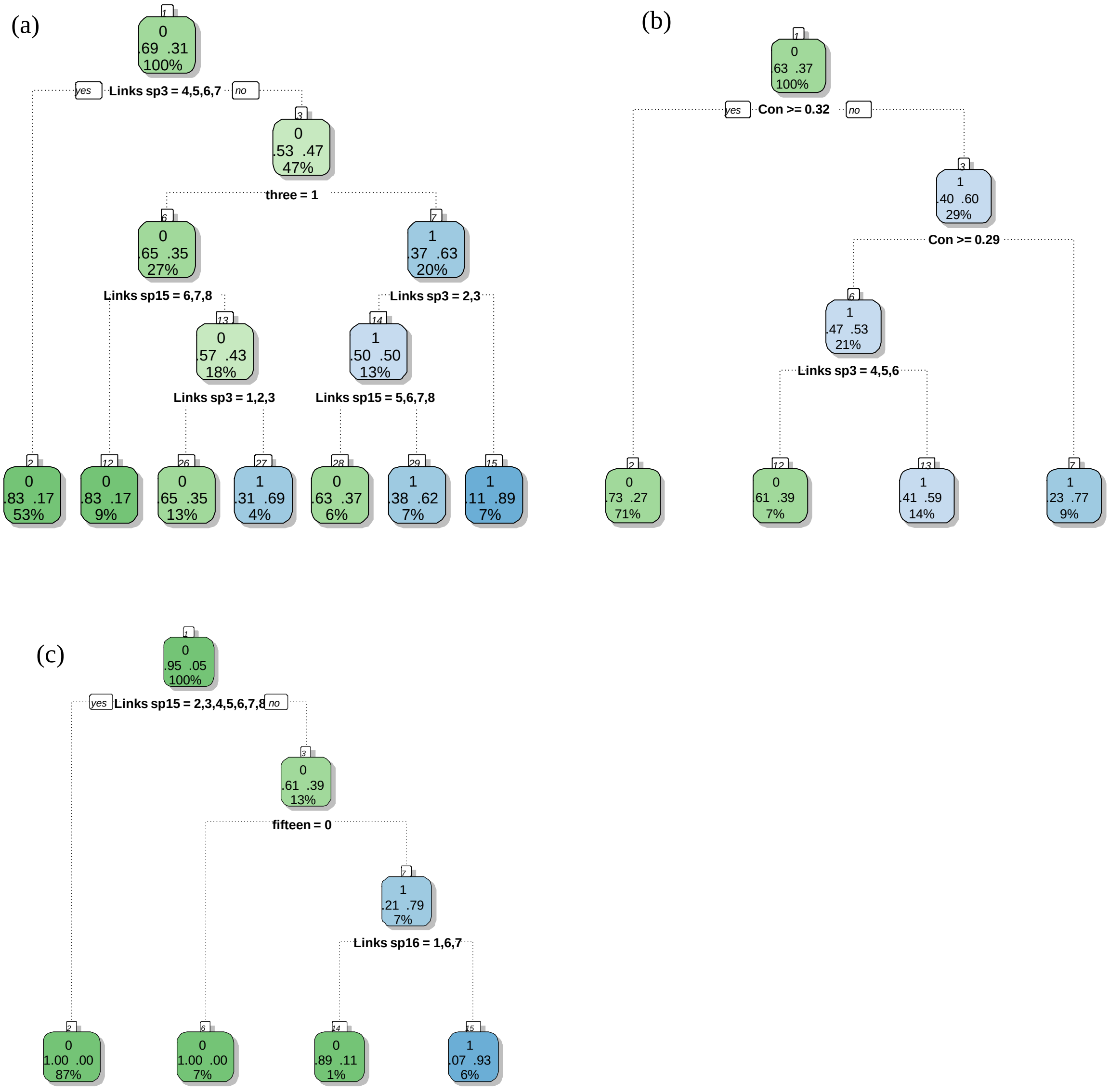


Figure 5.10 Classification trees for partitioning webs with a correlation coefficient less than -0.4 (1) from webs with a correlation coefficient greater than -0.4 (0) for (a) the basal trophic level (b) the herbivore trophic level and (c) the carnivore trophic level. The variable three indicates whether the basal species with a varying number of links (species three) was connected to the same herbivore as the basal species with just one link (species two) (1) or connected to a different herbivore (0). Similarly, the variable fifteen indicates whether the carnivore species with a varying number of links (species fifteen) was connected to the same herbivore as the carnivore species with just one link (species fourteen) (1) or connected to a different herbivore (0).

The negative correlation between total net effect and linkage density occurred more frequently in webs with low connectance for all trophic levels (Figure 5.11). The mean connectance for webs with a correlation coefficient less than -0.4 for the basal trophic level (mean connectance = 0.318) was significantly less than the mean connectance for webs with a correlation coefficient greater than -0.4 (mean connectance = 0.339), (*t*-test, $p < 0.001$, n = 14,630,623). The mean connectance for webs with a correlation coefficient less than -0.4 for the herbivore trophic level (mean connectance = 0.319) was significantly less than the mean connectance for webs with a correlation coefficient greater than -0.4 (mean connectance = 0.340), (*t*-test, $p < 0.001$, n = 14,630,623) and the mean connectance for webs with a correlation coefficient less than -0.4 for the carnivore trophic level (mean connectance = 0.306) was significantly less than the mean connectance for webs with a correlation coefficient greater than -0.4 (mean connectance = 0.334), (*t*-test, $p < 0.001$, n = 14,630,623).

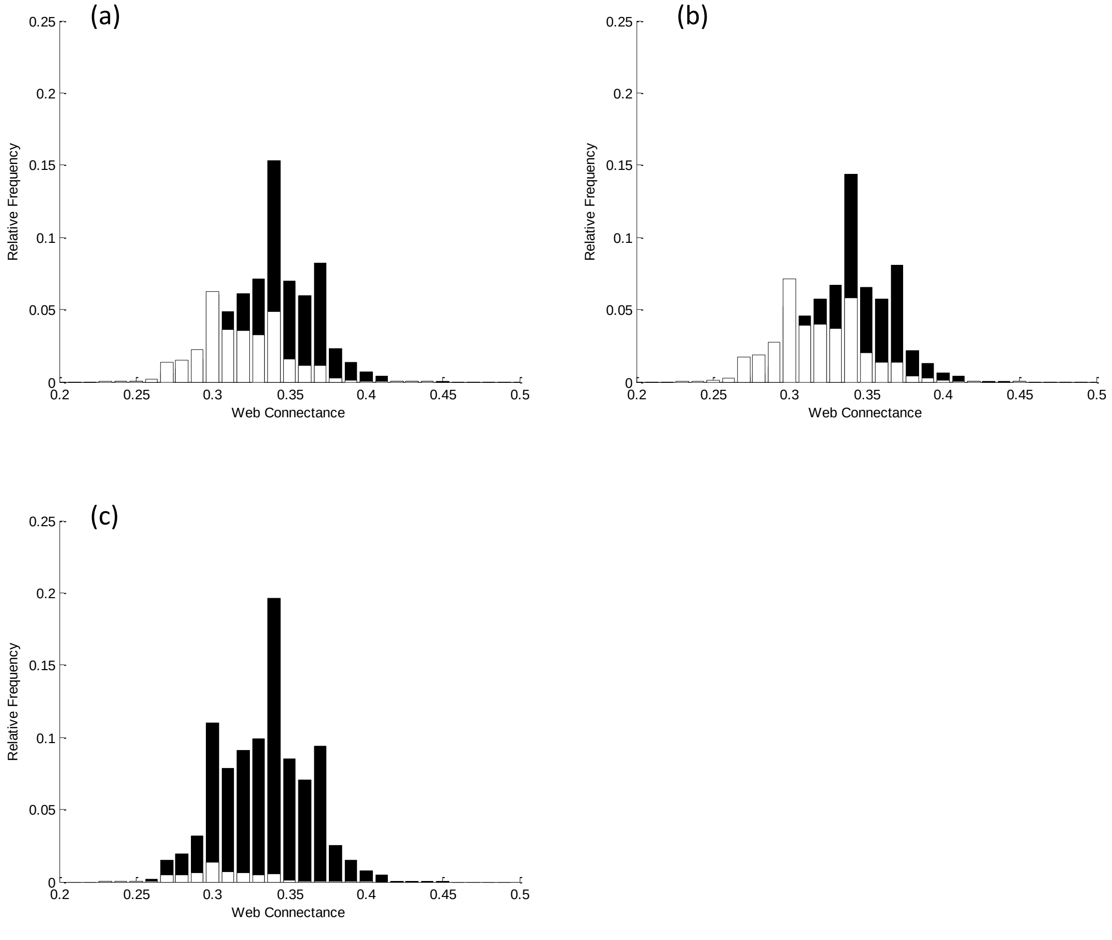


Figure 5.11 Distribution of web connectance for webs with a correlation coefficient more negative than -0.4 (white) and greater than -0.4 (black) for (a) the basal trophic level (b) the herbivore trophic level and (c) the carnivore trophic level.

Discussion

This study did not find a consistent relationship between a species linkage density and its total net effect. Direct and graphical examination of species total net effects showed that in a framework where interaction strengths are parameterised using predator-prey body size ratios and allometric constraints, species with a large body size have large total net effects and species with a small body size have weak total net effects, regardless of linkage density. For each of the 14,630,625 permutations of the 16 species food webs a correlation coefficient between species linkage density and total net effect was calculated at the web level (using all species), just 0.02% of those webs had a strong correlation coefficient less than -0.4. The relationship between species linkage density and total/mean net effect has only been investigated in three studies to date (Montoya et al. 2005, O'Gorman et al. 2010, Berg et al. 2011), a negative relationship was present for the study by Montoya et al. (2005) on the Ythan Estuary and Broadstone stream food webs and for the study by O’Gorman et al. (2010) on mescocosms in Lough Hyne but no relationship was present for the Baltic Sea and Lake Vättern food webs examined by Berg et al. (2011).

The lack of consistency that was found in the relationship between species linkage density and total net effect in this study indicates that the relationship is not a consequence of parameterising the community matrix using predator-prey body size ratios and allometric constraints. Since the positive relationship between body size and total net effects is so strong, it is worth considering that the negative relationship between linkage density and total net effect observed by Montoya et al. (2005) and O’Gorman et al. (2010) was a consequence of a negative relationship between species body size and linkage density, i.e. species with a small body size have a high linkage density. This relationship was not investigated for the Ythan Estuary and Broadstone stream webs, but for the Lough Hyne mesocosm webs, a positive relationship between linkage density and mean net effect was reported, so it is possible to conclude that the negative relationship was not a consequence of body size. O’Gorman et al. (2010) confirmed the lack of a body mass effect by maintaining web structure, but allowing interaction strengths to take on values that were no longer constrained by naturally occurring predator–prey body size ratios. Instead, interaction strengths were calculated from randomly chosen predator-prey body size ratios (for 1000 different permutations) and then the relationships between linkage density and mean net effects for those webs were subsequently examined when interaction strengths were no longer size structured. In these instances, the negative relationship remained, implying that it was not a consequence of the body size based parameterisations, which supports the finding from the present study.

The study by O'Gorman et al.(2010) also reported a negative relationship between species linkage density and an empirical measure of species mean net effect. An empirical measure of a species mean net effect was calculated using an adaptation of the dynamic index formula, so that, the denominator no longer included the time scale of the experiment. It was argued that since this measure estimates the long-term change in abundance, and is not a growth rate, it provides a measure of the net effect of one species on another. However, it should be noted that the original dynamic index was derived to estimate the direct effects of one species on another (the a_{ij} terms of the community matrix) using the discrete-time version of the generalised Lotka-Volterra multispecies equations. To estimate the a_{ij} terms using the dynamic index, the population density of prey species *i* is measured in the presence and absence of consumer species *j*, and its application does not require species to be at a local equilibrium. Net effects are defined to be the inverse elements of the community matrix and the net effect of species *j* on species *i* represents the effect that a small sustained change in the growth rate of species *j* has on the equilibrium biomass abundances of species *i*. To measure the net effect of species *j* on species *i*, the equilibrium biomass abundance of species *i* must be measured before and after a press perturbation is applied to species *j* (as per Schmitz 1997), altering the formula of the dynamic index does not give an empirical measure of this. This can be seen when we consider the dimensions of the two quantities: the dimensions of the inverse elements of the inverse community matrix are (*Mass.Time*), whereas the dimensions of the amended dynamic index formula are ($Mass^{-1}$).

Examination of the relationship between species linkage density and total net effect within trophic levels found that highly connected species can have a weak total net effect in comparison to species with the same body size (Tables 5.3 and 5.4 and Figure 5.10), but the relationship is not consistent and the conditions under which it occurs are not clear (Figure 5.10). Despite the unpredictable nature of the relationship some general observations can be made: within the basal and herbivore trophic levels, a strong negative relationship between linkage density and total net effects occurred more frequently than a strong positive relationship (Figure 5.9), for the food webs shown in Figures 5.1(a)-(e), when a negative relationship was present it held for all values of the parameters C_b (which represents the intra-interspecific interaction strength ratio for basal species) and *e* (the ecological efficiency) (Table 5.3). The size of the web and the ratio of basal: herbivore: carnivore species did not affect the relationship between species linkage density and total net effect for the food webs shown in Figures 5.2-5.8 (for C_b, C_c and e fixed), but the arrangement of links did have an effect (Table 5.4). Finally, the permutations of the 16 species food webs showed that a negative relationship between species linkage density and total net effect was more likely to occur in webs with low connectance (Figure 5.11).

The construction of the food webs in this study ensured that, within a specified set of food webs, the only differences between a highly connected species and a poorly connected species in the same trophic level were the interaction strengths and the arrangement of links. The fact that for some webs a highly connected species had a weak net effect but for other webs, that were identical in all respects apart from the arrangement of links of the surrounding species, the same highly connected species did not have a weak effect implies that the negative relationship between linkage density and total net effect is a consequence of the pattern of interaction strengths in the surrounding web and not solely the weaker interaction strengths of the highly connected species. The importance of web structure in determining the response of a community to a press perturbation was highlighted by Dambacher et al. (2003) who found that the direction of species response (an increase or decrease) to a press perturbation is sometimes based on community structure alone.

Within the basal trophic level a highly connected species had a weak total net effect for all the webs examined that had minimal complexity. Permutations of the 16 species food web showed that correlations between species linkage density and total net effects for the basal trophic level could vary from strongly negative to strongly positive (Figure 5.9b), but there were no distinct patterns in the arrangement of links that could distinguish, precisely, the webs that had strong negative correlations from those that did not. In general, there was a higher proportion of negative correlations between species linkage density and total net effects at the basal trophic level for webs where species had few links (Figure 5.11(a) and Appendix J Figures J1(a) and (b), but note that statistical significance of the difference between the mean connectance of webs with a correlation coefficient less than -0.4 and those with a correlation coefficient greater than -0.4 was likely considering the large sample size. Whether the difference is of ecological significance is unclear since there is a large amount of overlap between the two sets). It is possible that in webs where many species have a high linkage density the correlation between linkage density and total net effect is less likely to be strongly negative since the many highly connected species (within the same trophic level) are likely to have similar total net effects and thus the ordering of species (for

Spearman's rank correlation) may not lead to a strong negative correlation. This effect could be investigated by calculating Pearson's correlation coefficients between species linkage density and total net effects for larger webs. Alternatively, the presence of other highly connected species might alter the effect a highly connected species has in a community. In contrast to the general result that a negative correlation was more likely to occur for webs where species had few links, a strong negative correlation between species linkage density and total net effects at the basal trophic level is also more likely to occur in webs where basal species three or four had eight links (maximum linkage density) which supports the observation that the response of a species to a press perturbation is dependent on community structure (Dambacher et al. 2003).

The relationship between species linkage density and total net effect within the herbivore trophic level was affected by the value of consumer intraspecific interaction strength C_c.
For food web 1 where consumer intraspecific competition was set to zero, the highly connected herbivore species (five) was never the species with the smallest total net effect (Table 5.3), but when consumer intraspecific interaction strength was positive, species five had the smallest total net effect in food webs 1(c) and (e). Herbivore species five had high linkage density in webs 1(b),(c) and (e); in web (b) species five had high generality (it fed on all basal species), in web (c) species five had high vulnerability (it was preyed on by all carnivore species) and in web (e) it had high generality and vulnerability. The contrast in the results from web (b) with webs (c) and (e) might indicate that a herbivore species has a small total net effect if it has high vulnerability. Examination of the correlation coefficients for the permutations of the 16 species webs found that 32.1% of webs had a negative correlation between species generality and total net effect and 38.6% of webs had a negative correlation between species vulnerability and total net effect. A difference is present, but it is not large so further investigation is needed to determine whether a herbivore species total net effect is associated with its vulnerability.

Web size and the ratio of basal: herbivore: carnivore species did not affect the relationship for the food webs shown in Figures 5.2-5.8 (for C_b, C_c and e fixed). The arrangement of links did have an effect so that for the more complex webs examined (Figures. 5.4, 5.6, 5.7 and 5.8) the highly connected herbivore species had a weaker total net effect than other herbivore species for 8 out of 24 webs. This result together with the result from the basal trophic level implies that the total net effect of a species depends not just on individual species traits but on the structure of the web in which it is embedded. For the webs shown in

Figures 5.2, 5.3, and 5.5 with minimal complexity, there were contrasting results for the basal trophic level and the herbivore trophic level: the highly connected basal species had a weak total net effect relative to other basal species, but the highly connected herbivore species did not have a weak total net effect relative to other herbivore species (Table 5.4). However, in agreement with the result for the basal trophic level, permutations of the 16 species food web showed that the correlation coefficient between species linkage density and total net effects was more likely to be negative (less than -0.4), when web connectance was low (Figures. 5.10(b), and 5.11(b), but again note the large sample size). Webs where the basal species with varying links (species three or four) had eight links did not agree with this result (Appendix J Figures J2a and b) and there were no distinct patterns in the arrangement of links that could be used to distinguish the webs that had strong negative correlations from those that did not (Figure 10).

Regardless of parameter values, web size or web composition, the highly connected carnivore species was never the species with the smallest total net effect for the webs shown in Figures 5.1-5.8 (Tables 5.3 and 5.4). Permutations of the 16 species food web showed that the correlation coefficient between linkage density and total net effect for the carnivore trophic level was negative (less than -0.4) for just 5.5% of all webs.

Food webs 1(f) and (g) contained omnivorous links: in web (f) a basal species was fed on by all herbivore species and all carnivore species and in web (g) a carnivore species fed on all basal species and all herbivore species. In both omnivorous webs the highly connected species had weak total net effects at their respective trophic levels. For the basal trophic level this result is the same as for food web 1(a) where omnivorous links were not present but for the carnivore trophic level, this result is in contrast to the result for food web 1(d) where omnivorous webs were not present. Indeed, this result for the carnivore trophic level is in contrast to all the webs analysed with the exception of 5.5% of the webs from the permutations. It is not possible to draw conclusions about the effect of omnivory on a species total net effect based on the results from the two webs considered in this study. Moreover, this result is in contrast to the result from Chapter 3 of this thesis where the set of synthetic webs for which a negative relationship between species linkage density and total net effects was present had significantly longer average shortest path lengths that the set of webs that did not. Omnivory reduces the average shortest path length in a web so it is possible that webs with long average shortest path lengths contain fewer omnivorous links. Omnivory is known to alter stability properties of food webs, in particular, weak omnivorous links (weak direct effects) can increase the likelihood of local stability (Emmerson and Yearsley 2004, Gellner and McCann 2012). It creates shortcuts in energy flow around food webs, and in size structured communities omnivory will increase the predator-prey body size ratios used to determine interaction strengths, therefore omnivory has great potential to impact the way a perturbation affects a community. The effect of omnivory on a species total net effect is of interest for future studies.

In conclusion, there was not a consistent negative relationship between species linkage density and total net effect for the set of webs analysed in the present study. Body size determined the impact a species had in the community, so that, in strictly size-structured communities linkage density is not expected to determine a species total net effect. However, the webs used in this study were small and unrealistic in comparison to the Ythan Estuary, Broadstone Stream and Lough Hyne food webs where such a relationship was detected. It is possible that the particular arrangement of links found in some empirical food webs do generate a negative relationship between linkage density and total net effect. The distributions of correlation coefficents from the permutations of the 16 species food web (Figure 5.9) show that although the size, composition and parameterisation of all 14,630,625 food webs was the same, the relationship between linkage density and total net effects could vary considerably as a consequence of the arrangement of links alone.

The webs analysed in this study were not checked for stability and it has been shown that the arrangement of links in empirical food webs and in stable theoretical food webs is skewed so that weak interactions between species occur more frequently than strong interactions (Paine 1992, McCann et al. 1998, Kokkoris et al. 1999, O'Gorman and Emmerson 2009). It is also possible that the conditions imposed on the patterns of interaction strengths in food webs by the criterion of stability may have an impact on the relationship between a species linkage density and the its total net effect. This idea could be investigated further by running stability checks on the food webs generated by the permutations of the 16 species food web. Analysis of the relationship between linkage density and total net effect for the set of stable webs would reveal any possible effect of the stability criterion.

The mechanism by which highly connected species could potentially have weak total net effects is still not clear and without further knowledge of the conditons under which the relationship is present, uncovering this mechanism is unlikely, due to the complexity of the mathematical inversion process. It might be possible to find patterns common to webs where a negative relationship between linkage density and total net effects is present through further analysis of simple webs that include omivory and more realistic, stable, webs with varying properties, such as connectance, the gradient of linkage density, clustering coefficient and average shortest path length.

APPENDIX H

The community matrices for the five food webs shown in Figures. 5.1(a)-(e) are presented below along with analysis of the column sums for the case where consumer intraspecific interaction strength, C_c is set to 0.

Case (a): the basal species (species 1) is highly connected due to being preyed on by all four herbivore species. The community matrix A is:

$$A = \begin{bmatrix} \frac{-C_b}{q} & 0 & 0 & 0 & \frac{-1}{q} & \frac{-1}{2q} & \frac{-1}{2q} & \frac{-1}{2q} & 0 & 0 & 0 & 0 \\ 0 & \frac{-C_b}{q} & 0 & 0 & 0 & \frac{-1}{2q} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \frac{-C_b}{q} & 0 & 0 & 0 & \frac{-1}{2q} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \frac{-C_b}{q} & 0 & 0 & 0 & \frac{-1}{2q} & 0 & 0 & 0 & 0 \\ \frac{e}{q} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 & 0 & 0 & \frac{-1}{q^3} & 0 & 0 & 0 \\ \frac{e}{2q} & \frac{e}{2q} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 & 0 & 0 & \frac{-1}{q^3} & 0 & 0 \\ \frac{e}{2q} & 0 & \frac{e}{2q} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 & 0 & 0 & \frac{-1}{q^3} & 0 \\ \frac{e}{2q} & 0 & 0 & \frac{e}{2q} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 & 0 & 0 & \frac{-1}{q^3} \\ 0 & 0 & 0 & 0 & \frac{e}{q^3} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \frac{e}{q^3} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \frac{e}{q^3} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{e}{q^3} & 0 & 0 & 0 & \frac{-C_c}{q^3} \end{bmatrix}$$

The column sums of the absolute values of the entries of the inverse matrix A^{-1} are:

$$S_1 = \frac{q}{C_b} + \frac{eq^3}{4C_b}$$

$$S_2 = S_3 = S_4 = \frac{q}{C_b} + \frac{5eq^3}{4C_b}$$

$$S_5 = S_6 = S_7 = S_8 = q^3$$

$$S_9 = \frac{q^3}{C_b e} + \frac{q^3}{e} + \frac{q^5}{C_b}$$

$$S_{10} = S_{11} = S_{12} = \frac{q^3}{C_b e} + \frac{q^3}{e} + \frac{5q^5}{4C_b}$$

The highly connected basal species is the species with the smallest total net effect within the basal species level.

Case (b): the herbivore species (species 5) is highly connected due to feeding on all four basal species. The community matrix A is:

$$A=\begin{bmatrix}
\frac{-C_b}{q} & 0 & 0 & 0 & \frac{-1}{4q} & 0 & 0 & 0 & 0 & 0 & 0 & 0\\
0 & \frac{-C_b}{q} & 0 & 0 & \frac{-1}{4q} & \frac{-1}{q} & 0 & 0 & 0 & 0 & 0 & 0\\
0 & 0 & \frac{-C_b}{q} & 0 & \frac{-1}{4q} & 0 & \frac{-1}{q} & 0 & 0 & 0 & 0 & 0\\
0 & 0 & 0 & \frac{-C_b}{q} & \frac{-1}{4q} & 0 & 0 & \frac{-1}{q} & 0 & 0 & 0 & 0\\
\frac{e}{4q} & \frac{e}{4q} & \frac{e}{4q} & \frac{e}{4q} & \frac{-C_c}{q^3} & 0 & 0 & 0 & \frac{-1}{q^3} & 0 & 0 & 0\\
0 & \frac{e}{q} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 & 0 & 0 & \frac{-1}{q^3} & 0 & 0\\
0 & 0 & \frac{e}{q} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 & 0 & 0 & \frac{-1}{q^3} & 0\\
0 & 0 & 0 & \frac{e}{q} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 & 0 & 0 & \frac{-1}{q^3}\\
0 & 0 & 0 & 0 & \frac{e}{q^3} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 & 0 & 0\\
0 & 0 & 0 & 0 & 0 & \frac{e}{q^3} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 & 0\\
0 & 0 & 0 & 0 & 0 & 0 & \frac{e}{q^3} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0\\
0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{e}{q^3} & 0 & 0 & 0 & \frac{-C_c}{q^3}
\end{bmatrix}$$

The column sums of the absolute values of the entries of the inverse matrix A⁻¹ are:

$$S_1=\frac{q}{C_b}+\frac{eq^3}{4C_b}$$

$$S_2=S_3=S_4=\frac{q}{C_b}+\frac{5eq^3}{4C_b}$$

$$S_5=S_6=S_7=S_8=q^3$$

$$S_9=\frac{q^3}{C_be}+\frac{q^3}{e}+\frac{q^5}{C_b}$$

$$S_{10}=S_{11}=S_{12}=\frac{q^3}{C_be}+\frac{q^3}{e}+\frac{5q^5}{4C_b}$$

The highly connected herbivore species is not the species with the smallest total net effect within the herbivore trophic level.

Case (c): the herbivore species (species 5) is highly connected due to being preyed on by all four carnivore species. The community matrix A is:

$$A=\begin{bmatrix}
\frac{-C_b}{q} & 0 & 0 & 0 & \frac{-1}{q} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & \frac{-C_b}{q} & 0 & 0 & 0 & \frac{-1}{q} & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & \frac{-C_b}{q} & 0 & 0 & 0 & \frac{-1}{q} & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & \frac{-C_b}{q} & 0 & 0 & 0 & \frac{-1}{q} & 0 & 0 & 0 & 0 \\
\frac{e}{q} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 & 0 & 0 & \frac{-1}{q^3} & \frac{-1}{2q^3} & \frac{-1}{2q^3} & \frac{-1}{2q^3} \\
0 & \frac{e}{q} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 & 0 & 0 & \frac{-1}{2q^3} & 0 & 0 \\
0 & 0 & \frac{e}{q} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 & 0 & 0 & \frac{-1}{2q^3} & 0 \\
0 & 0 & 0 & \frac{e}{q} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 & 0 & 0 & \frac{-1}{2q^3} \\
0 & 0 & 0 & 0 & \frac{e}{q^3} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & \frac{e}{2q^3} & \frac{e}{2q^3} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 & 0 \\
0 & 0 & 0 & 0 & \frac{e}{2q^3} & 0 & \frac{e}{2q^3} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 \\
0 & 0 & 0 & 0 & \frac{e}{2q^3} & 0 & 0 & \frac{e}{2q^3} & 0 & 0 & 0 & \frac{-C_c}{q^3}
\end{bmatrix}$$

The column sums of the absolute values of the entries of the inverse matrix A^{-1} are:

$$S_1=\frac{q}{C_b}+\frac{eq^3}{C_b}$$

$$S_2=S_3=S_4=\frac{q}{C_b}+\frac{3eq^3}{C_b}$$

$$S_5=q^3$$

$$S_6=S_7=S_8=3q^3$$

$$S_9=\frac{4q^3}{C_be}+\frac{4q^3}{e}+\frac{10q^5}{C_b}$$

$$S_{10}=S_{11}=S_{12}=\frac{2q^3}{C_be}+\frac{2q^3}{e}+\frac{6q^5}{C_b}$$

The highly connected herbivore species is the species with the smallest total net effect within the herbivore trophic level.

Case (d): the carnivore species (species 9) is highly connected due to feeding on all four herbivore species. The community matrix A is:

$$A = \begin{bmatrix}
\frac{-C_b}{q} & 0 & 0 & 0 & \frac{-1}{q} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & \frac{-C_b}{q} & 0 & 0 & 0 & \frac{-1}{q} & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & \frac{-C_b}{q} & 0 & 0 & 0 & \frac{-1}{q} & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & \frac{-C_b}{q} & 0 & 0 & 0 & \frac{-1}{q} & 0 & 0 & 0 & 0 \\
\frac{e}{q} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 & 0 & 0 & \frac{-1}{4q^3} & 0 & 0 & 0 \\
0 & \frac{e}{q} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 & 0 & \frac{-1}{4q^3} & \frac{-1}{q^3} & 0 & 0 \\
0 & 0 & \frac{e}{q} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 & \frac{-1}{4q^3} & 0 & \frac{-1}{q^3} & 0 \\
0 & 0 & 0 & \frac{e}{q} & 0 & 0 & 0 & \frac{-C_c}{q^3} & \frac{-1}{4q^3} & 0 & 0 & \frac{-1}{q^3} \\
0 & 0 & 0 & 0 & \frac{e}{4q^3} & \frac{e}{4q^3} & \frac{e}{4q^3} & \frac{e}{4q^3} & \frac{-C_c}{q^3} & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & \frac{e}{q^3} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & \frac{e}{q^3} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & \frac{e}{q^3} & 0 & 0 & 0 & \frac{-C_c}{q^3}
\end{bmatrix}$$

The column sums of the absolute values of the entries of the inverse matrix A^{-1} are:

$$S_1 = \frac{q}{C_b} + \frac{7eq^3}{C_b}$$

$$S_2 = S_3 = S_4 = \frac{q}{C_b} + \frac{eq^3}{C_b}$$

$$S_5 = 7q^3$$

$$S_6 = S_7 = S_8 = q^3$$

$$S_9 = \frac{4q^3}{C_b e} + \frac{4q^3}{e} + \frac{28q^5}{C_b}$$

$$S_{10} = S_{11} = S_{12} = \frac{2q^3}{C_b e} + \frac{2q^3}{e} + \frac{8q^5}{C_b}$$

The highly connected carnivore species is not the species with the smallest total net effect within the carnivore trophic level.

Case (e): species 5 is highly connected due to preying on all four basal species and being predated on by all four carnivore species. The community matrix A is:

$$A = \begin{bmatrix} \frac{-C_b}{q} & 0 & 0 & 0 & \frac{-1}{4q} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \frac{-C_b}{q} & 0 & 0 & \frac{-1}{4q} & \frac{-1}{q} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \frac{-C_b}{q} & 0 & \frac{-1}{4q} & 0 & \frac{-1}{q} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \frac{-C_b}{q} & \frac{-1}{4q} & 0 & 0 & \frac{-1}{q} & 0 & 0 & 0 & 0 \\ \frac{e}{4q} & \frac{e}{4q} & \frac{e}{4q} & \frac{e}{4q} & \frac{-C_c}{q^3} & 0 & 0 & 0 & \frac{-1}{q^3} & \frac{-1}{2q^3} & \frac{-1}{2q^3} & \frac{-1}{2q^3} \\ 0 & \frac{e}{q} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 & 0 & 0 & \frac{-1}{2q^3} & 0 & 0 \\ 0 & 0 & \frac{e}{q} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 & 0 & 0 & \frac{-1}{2q^3} & 0 \\ 0 & 0 & 0 & \frac{e}{q} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 & 0 & 0 & \frac{-1}{2q^3} \\ 0 & 0 & 0 & 0 & \frac{e}{q^3} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \frac{e}{2q^3} & \frac{e}{2q^3} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 & 0 \\ 0 & 0 & 0 & 0 & \frac{e}{2q^3} & 0 & \frac{e}{2q^3} & 0 & 0 & 0 & \frac{-C_c}{q^3} & 0 \\ 0 & 0 & 0 & 0 & \frac{e}{2q^3} & 0 & 0 & \frac{e}{2q^3} & 0 & 0 & 0 & \frac{-C_c}{q^3} \end{bmatrix}$$

The column sums of the absolute values of the entries of the inverse matrix A^{-1} are:

$$S_1 = \frac{q}{C_b} + \frac{eq^3}{4C_b}$$

$$S_2 = S_3 = S_4 = \frac{q}{C_b} + \frac{11eq^3}{4C_b}$$

$$S_5 = q^3$$

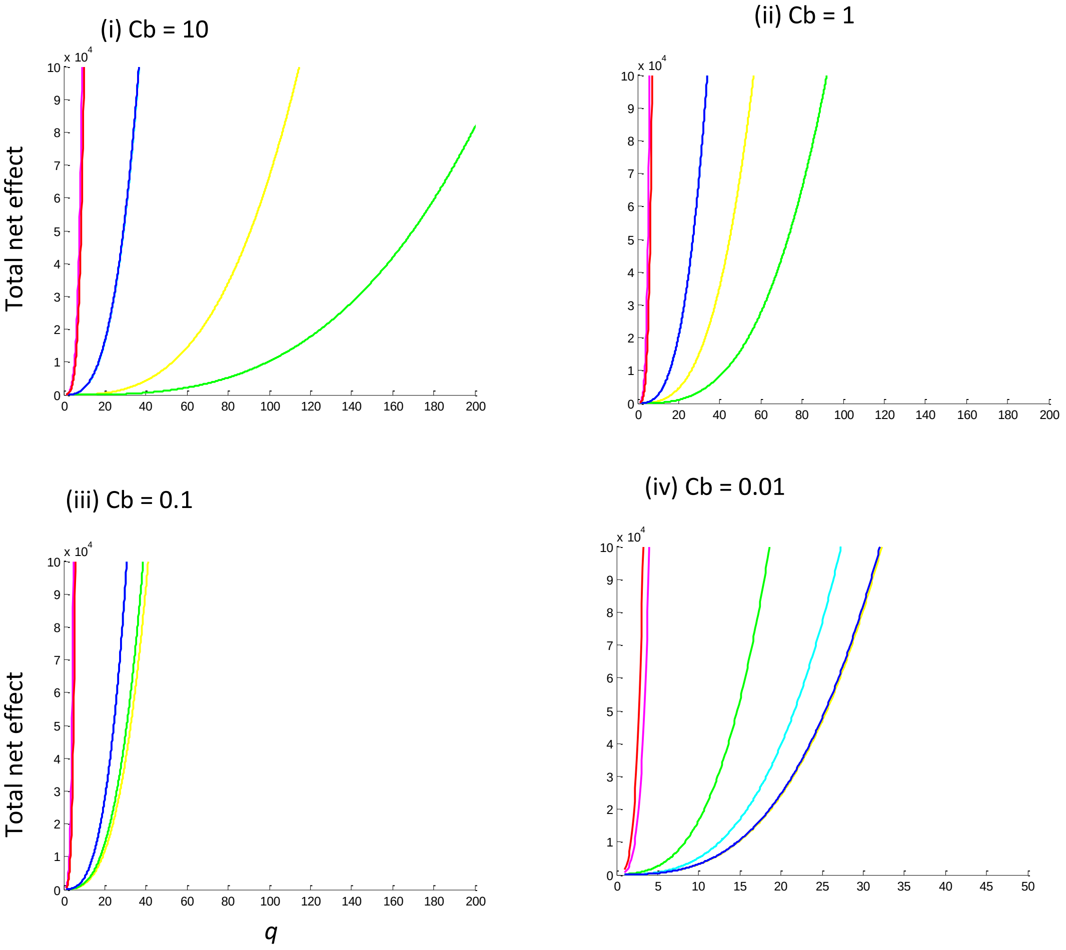
$$S_6 = S_7 = S_8 = 3q^3$$

$$S_9 = \frac{5q^3}{2C_b e} + \frac{4q^3}{e} + \frac{25q^5}{4C_b}$$

$$S_{10} = S_{11} = S_{12} = \frac{2q^3}{C_b e} + \frac{2q^3}{e} + \frac{11q^5}{2C_b}$$

The highly connected herbivore species is the species with the smallest total net effect within the herbivore trophic level.

The column sums of the omnivorous food webs 5.1(f) and 5.1(g) were too complex to examine directly so were examined graphically for the cases C_b = 100*e*, C_b = 10*e*, C_b = *e* and C_b = 0.1*e*.



🟨 Species 1 (basal)

🟩 Species 2, 3 and 4 (basal)

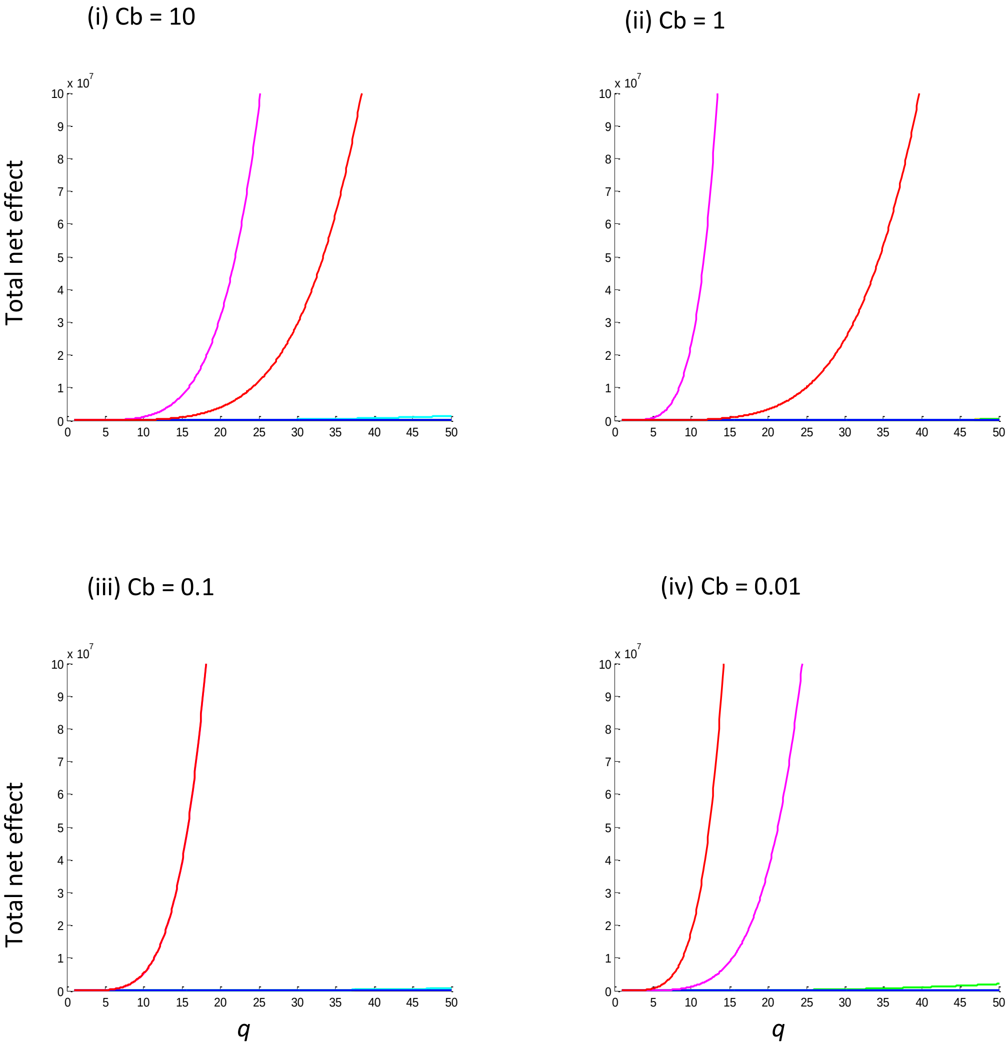
🟦 Species 5 (herbivore)

🟦 Species 6, 7 and 8 (herbivore)

🟪 Species 9 (carnivore)

🟥 Species 10, 11 and 12 (carnivore)

Figure H1(a) The ordering of the column sums for the omnivorous food web (f) for Cc = 0, Cb = 10, 1, 0.1, 0.01, and e = 0.1 Note that in Fig. (iv) the column sum for the highly connected basal species (is preyed upon by all herbivore species and all carnivore species and shown in yellow) is indistinguishable from the other basal species (shown in green).



🟨 Species 1 (basal)

🟩 Species 2, 3 and 4 (basal)

🟦 Species 5 (herbivore)

🟦 Species 6, 7 and 8 (herbivore)

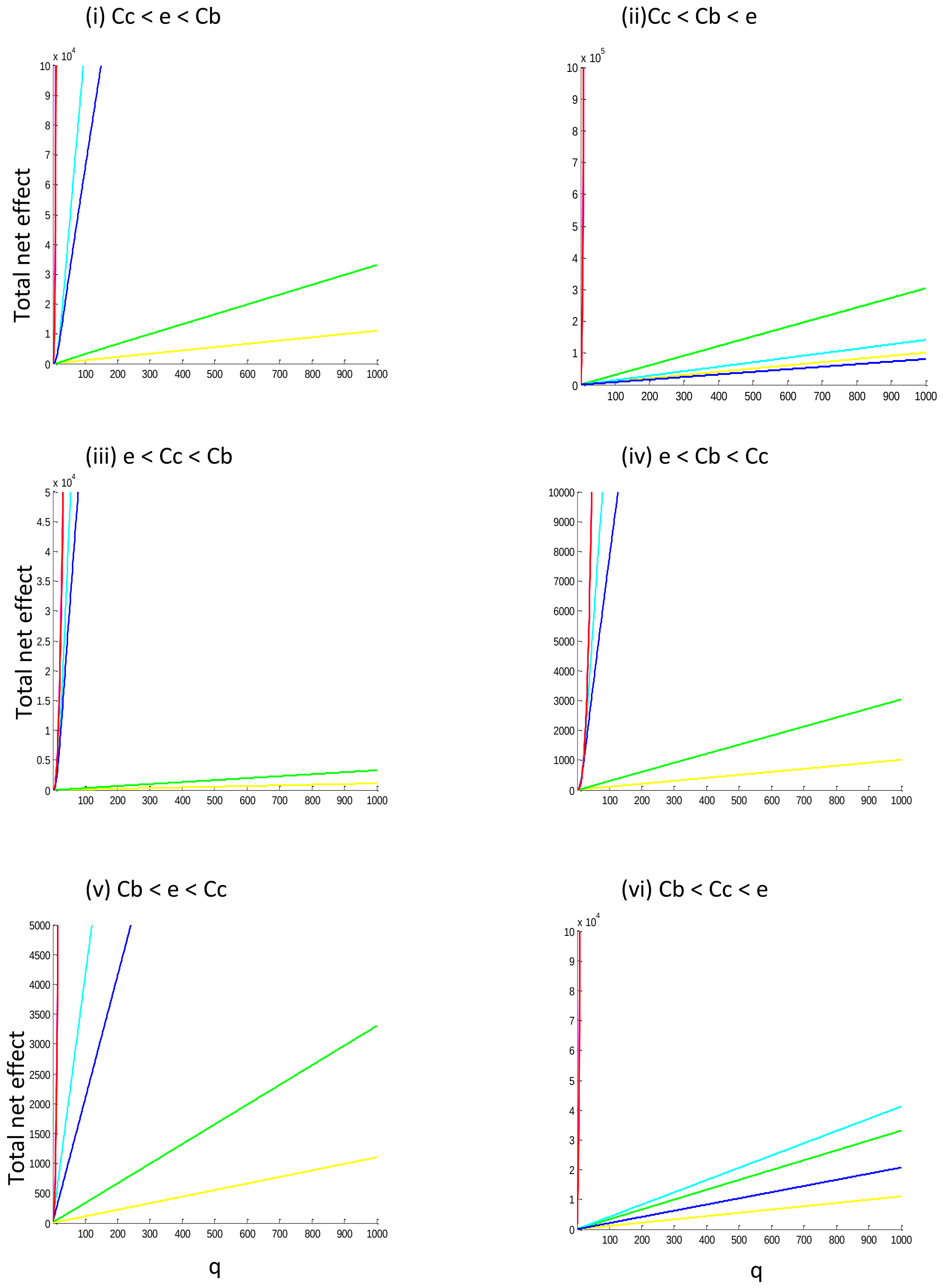
🟪 Species 9 (carnivore)

🟥 Species 10, 11 and 12 (carnivore)

Figure. H1(b) The ordering of the column sums for the omnivorous food web (g) for Cc = 0, Cb = 10, 1, 0.1, 0.01, and e = 0.1 The highly connected carnivore species (is preys upon all herbivore and basal species) is shown in pink. For graph (iii) the column sum for the highly connected carnivore species (preys upon by all herbivore and basal species and shown in pink) is indistinguishable from the other carnivore species (shown in red).

Consumer intraspecific interaction strength is not set to 0

For the case where consumer intraspecific interaction strength is not set to 0, the column sums of the inverse community matrix for the five food webs shown in Figures. 5.1(a)-(e) are examined graphically for fixed values of C_b, C_c and e.



🟨 Species 1 (basal)

🟩 Species 2, 3 and 4 (basal)

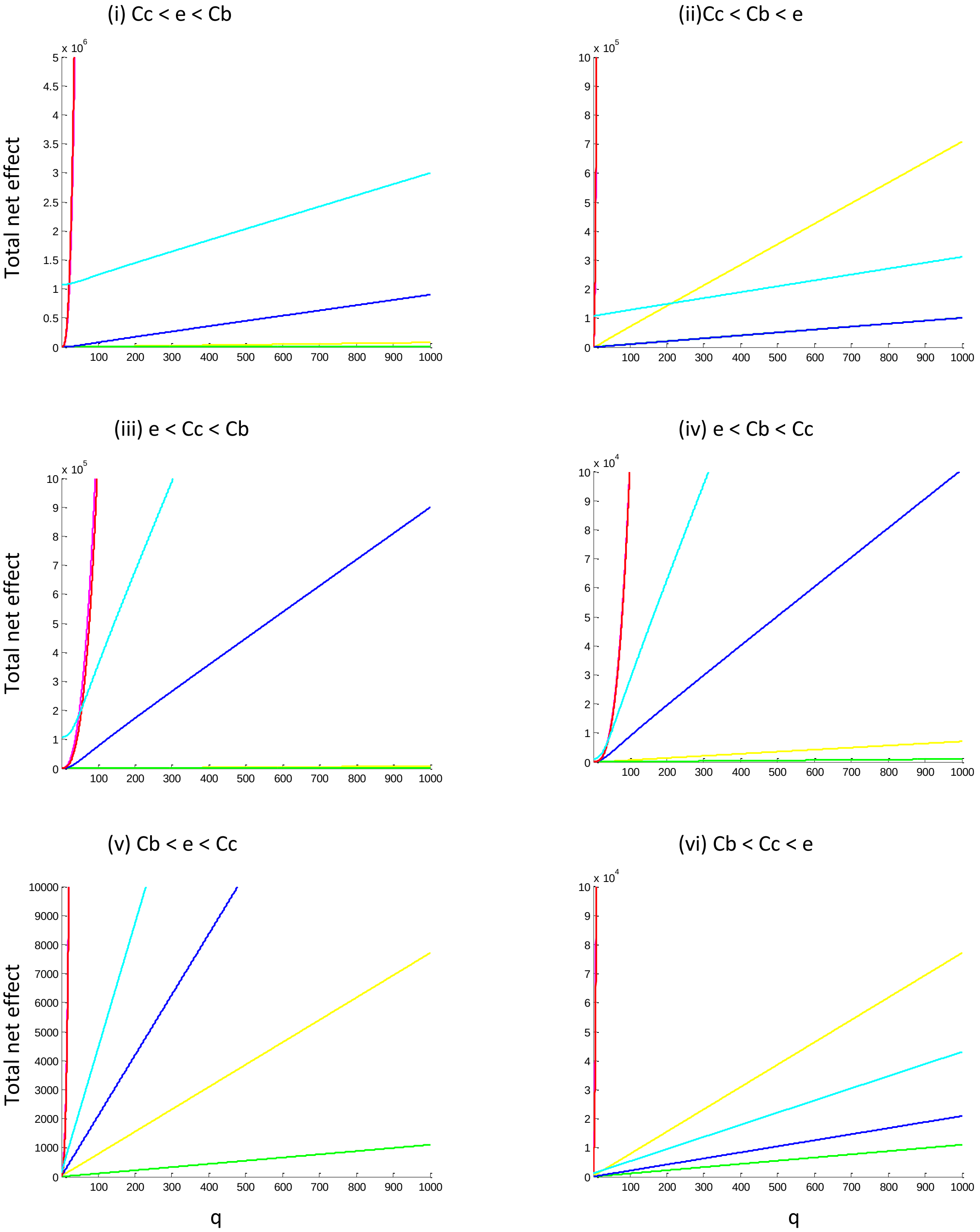
🟦 Species 5 (herbivore)

🟦 Species 6, 7 and 8 (herbivore)

🟪 Species 9 (carnivore)

🟥 Species 10, 11 and 12

Figure. H2(a) The ordering of the column sums for food web (a) with 6 different parameterisations. The highly connected basal species (preyed upon by all herbivore species) is shown in yellow.



🟨 Species 1 (basal)

🟩 Species 2, 3 and 4 (basal)

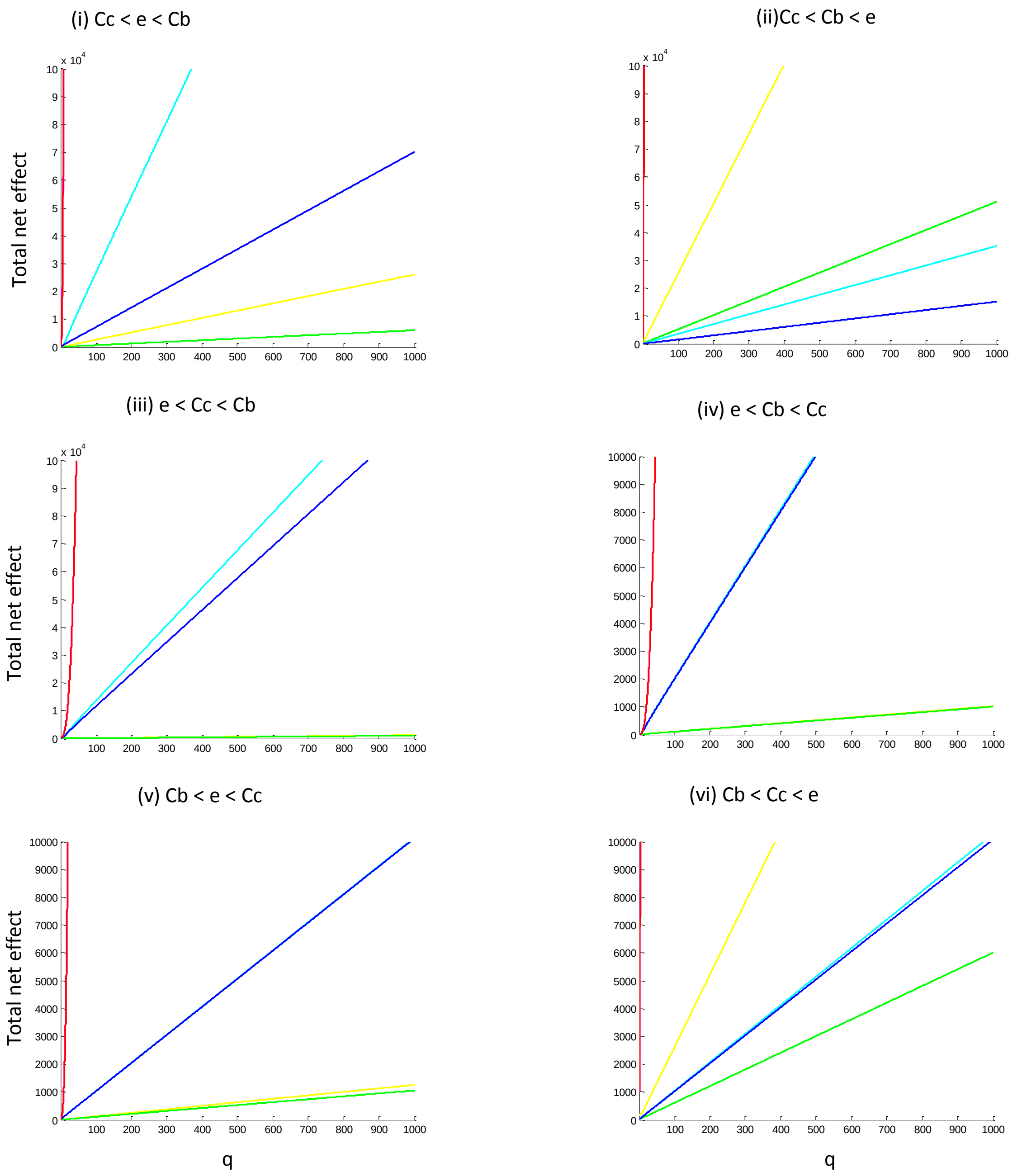
🟦 Species 5 (herbivore)

🟦 Species 6, 7 and 8 (herbivore)

🟪 Species 9 (carnivore)

🟥 Species 10, 11 and 12 (carnivore)

Figure. H2(b) The ordering of the column sums for food web (b) with 6 different parameterisations. The highly connected herbivore species (preys upon all basal species) is shown in light blue.



🟨 Species 1 (basal)

🟩 Species 2, 3 and 4 (basal)

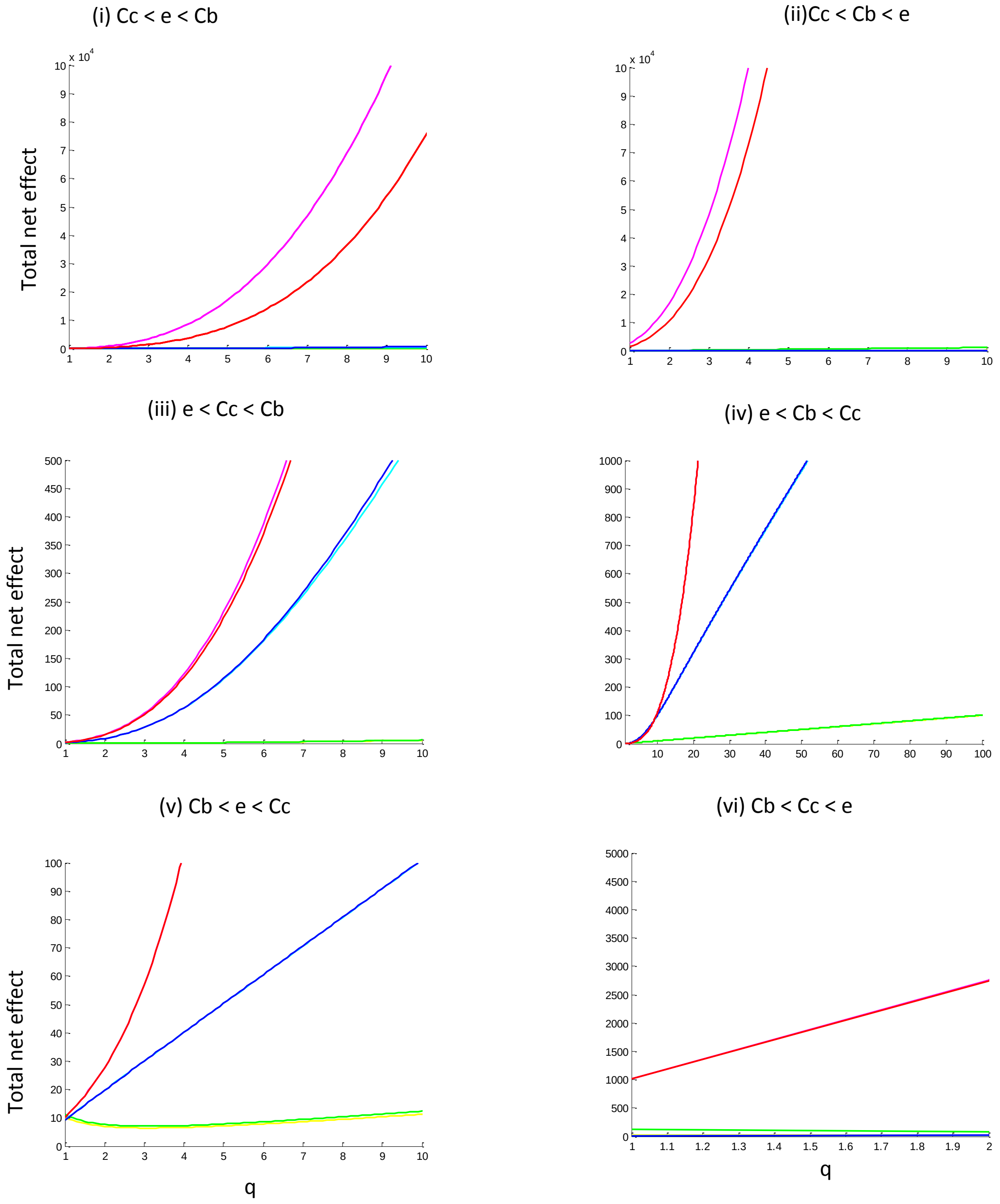
🟦 Species 5 (herbivore)

🟦 Species 6, 7 and 8 (herbivore)

🟪 Species 9 (carnivore)

🟥 Species 10, 11 and 12 (carnivore)

Figure H2(c) The ordering of the column sums for food web (c) with 6 different parameterisations. For graphs (iv) and (v) the column sum of the highly connected herbivore species (shown in light blue) is indistinguishable from the other herbivore species (shown in dark blue).



🟨 Species 1 (basal)

🟩 Species 2, 3 and 4 (basal)

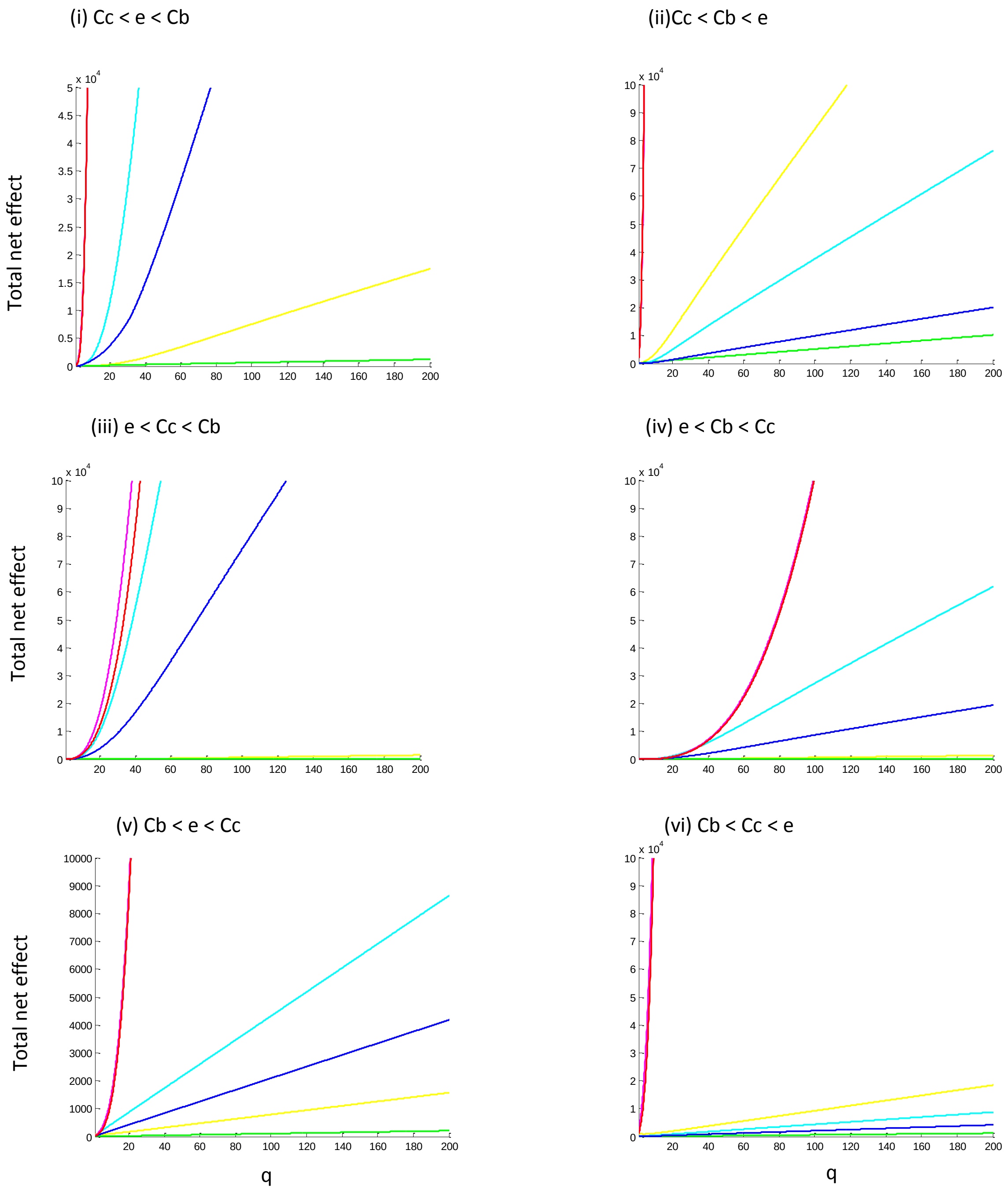
🟦 Species 5 (herbivore)

🟦 Species 6, 7 and 8 (herbivore)

🟪 Species 9 (carnivore)

🟥 Species 10, 11 and 12 (carnivore)

Figure H2(d) The ordering of the column sums for food web (d) with 6 different parameterisations. For graphs (iv), (v) and (vi) the column sum of the highly connected carnivore species (shown in pink) is indistinguishable from the other carnivore species (shown in red).



🟨 Species 1 (basal)

🟩 Species 2, 3 and 4 (basal)

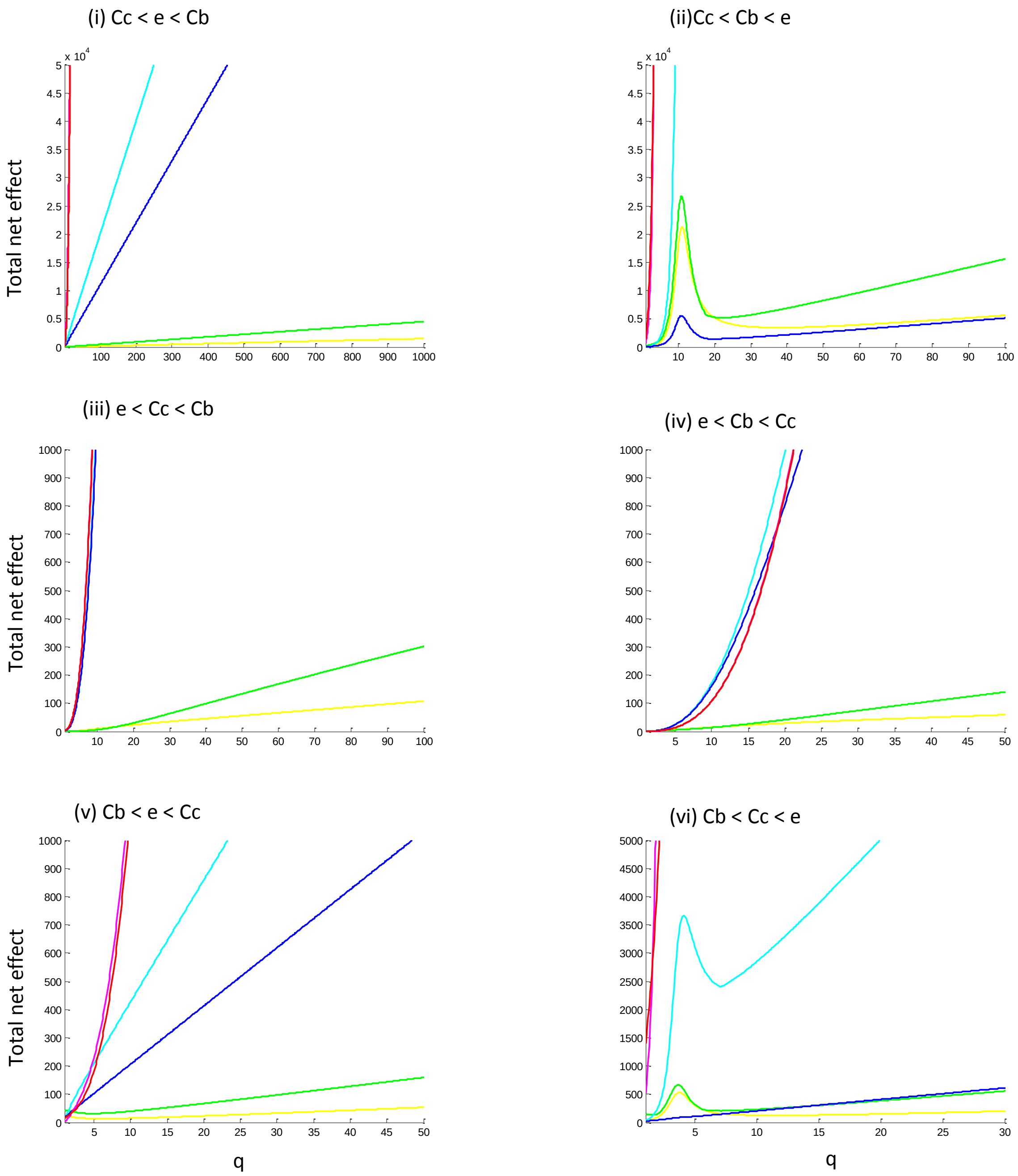
🟦 Species 5 (herbivore)

🟦 Species 6, 7 and 8 (herbivore)

🟪 Species 9 (carnivore)

🟥 Species 10, 11 and 12 (carnivore)

Figure H2(e) The ordering of the column sums for food web (e) with 6 different parameterisations. The highly connected herbivore species (preys upon all basal species and preyed upon by all carnivore species) is shown in light blue.



🟨 Species 1 (basal)

🟩 Species 2, 3 and 4 (basal)

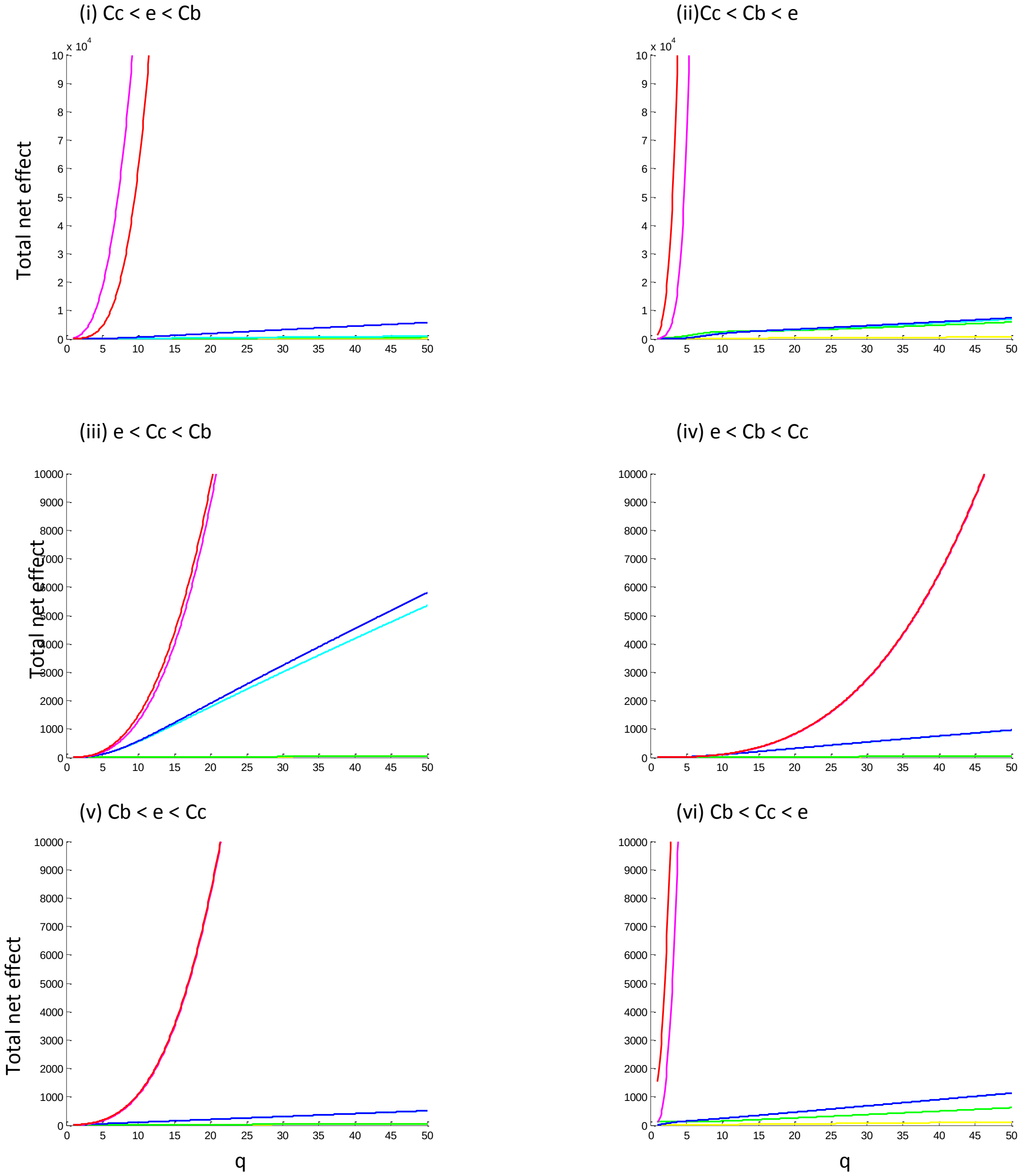
🟦 Species 5 (herbivore)

🟦 Species 6, 7 and 8 (herbivore)

🟪 Species 9 (carnivore)

🟥 Species 10, 11 and 12 (carnivore)

Figure H2(f) The ordering of the column sums for food web (f) with 6 different parameterisations. The highly connected basal species (preyed upon by all herbivore and carnivore species) is shown in yellow.



🟨 Species 1 (basal)

🟩 Species 2, 3 and 4 (basal)

🟦 Species 5 (herbivore)

🟦 Species 6, 7 and 8 (herbivore)

🟪 Species 9 (carnivore)

🟥 Species 10, 11 and 12 (carnivore)

Figure H2(g) The ordering of the column sums for food web (g) with 6 different parameterisations. The highly connected carnivore species (preys upon all herbivore and basal species) is shown in pink. For graphs (iv) and (v) the column sum for the highly connected carnivore species is indistinguishable from the column sum for the other carnivore species (shown in red).

Ordering of species for webs of different size structure and complexity

The columns sums for the seven food webs shown in Figures. 5.2-5.8 are examined graphically for $C_b = 1$, $C_c = 0.01$, $e = 0.1$ and $q = 100$.

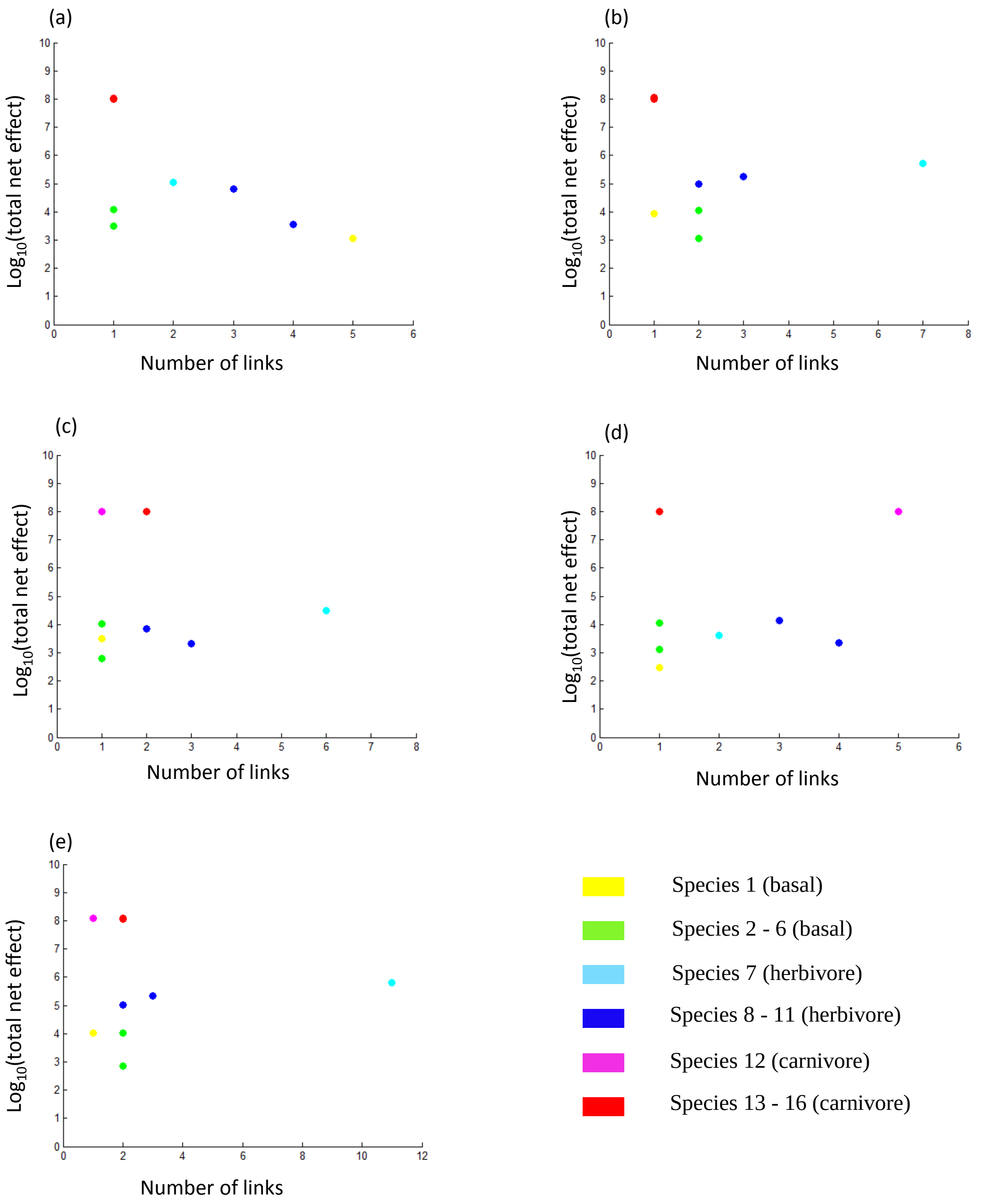


Figure I1 The relationship between a species total net effect and its linkage density for food webs 5.2(a) – (e) where there were 16 species with a basal, herbivore and carnivore species ratio of (6:5:5) and minimal complexity for cases:

(a) basal species 1 is preyed on by all herbivore species
(b) herbivore species 7 preys on all basal species
(c) herbivore species 7 is preyed upon by all carnivore species
(d) carnivore species 12 preys upon all herbivore species
(e) herbivore species 7 preys upon all basal species and is preyed upon by all carnivore species.

$C_b = 1$, $C_c = 0.01$, $e = 0.1$ and $q = 100$

N.B. In Figures (a) and (b) carnivore species 12 is indistinguishable from carnivore species 13 - 16

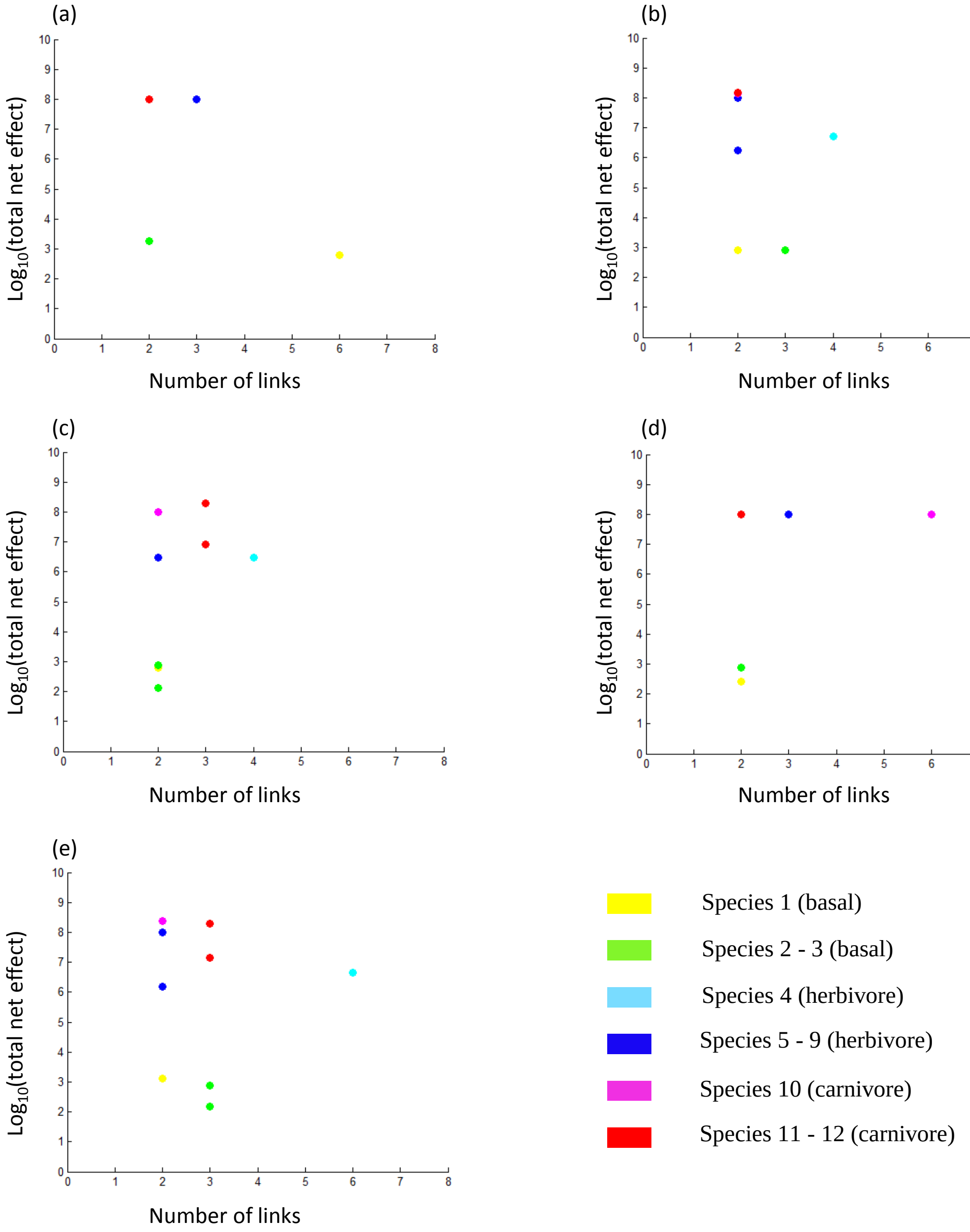


Figure I2 the relationship between a species total net effect and its linkage density for food webs 5.3(a)-(e) of size 12 with a basal, herbivore and carnivore species ratio of (1:2:1) and minimal complexity for cases:

- (a) basal species 1 is preyed on by all herbivore species
- (b) herbivore species 7 preys on all basal species
- (c) herbivore species 7 is preyed upon by all carnivore species
- (d) carnivore species 12 preys upon all herbivore species
- (e) herbivore species 7 preys upon all basal species and is preyed upon by all carnivore species.

$C_b = 1$,$C_c = 0.01$, $e = 0.1$ and $q = 100$

In Figure (a) species 4, 5, and 10 are indistinguishable from carnivore species 11-12.

In Figure (b) species 10 is indistinguishable from species 11-12.

In Figure (d) species 4 is indistinguishable from species 5-9.

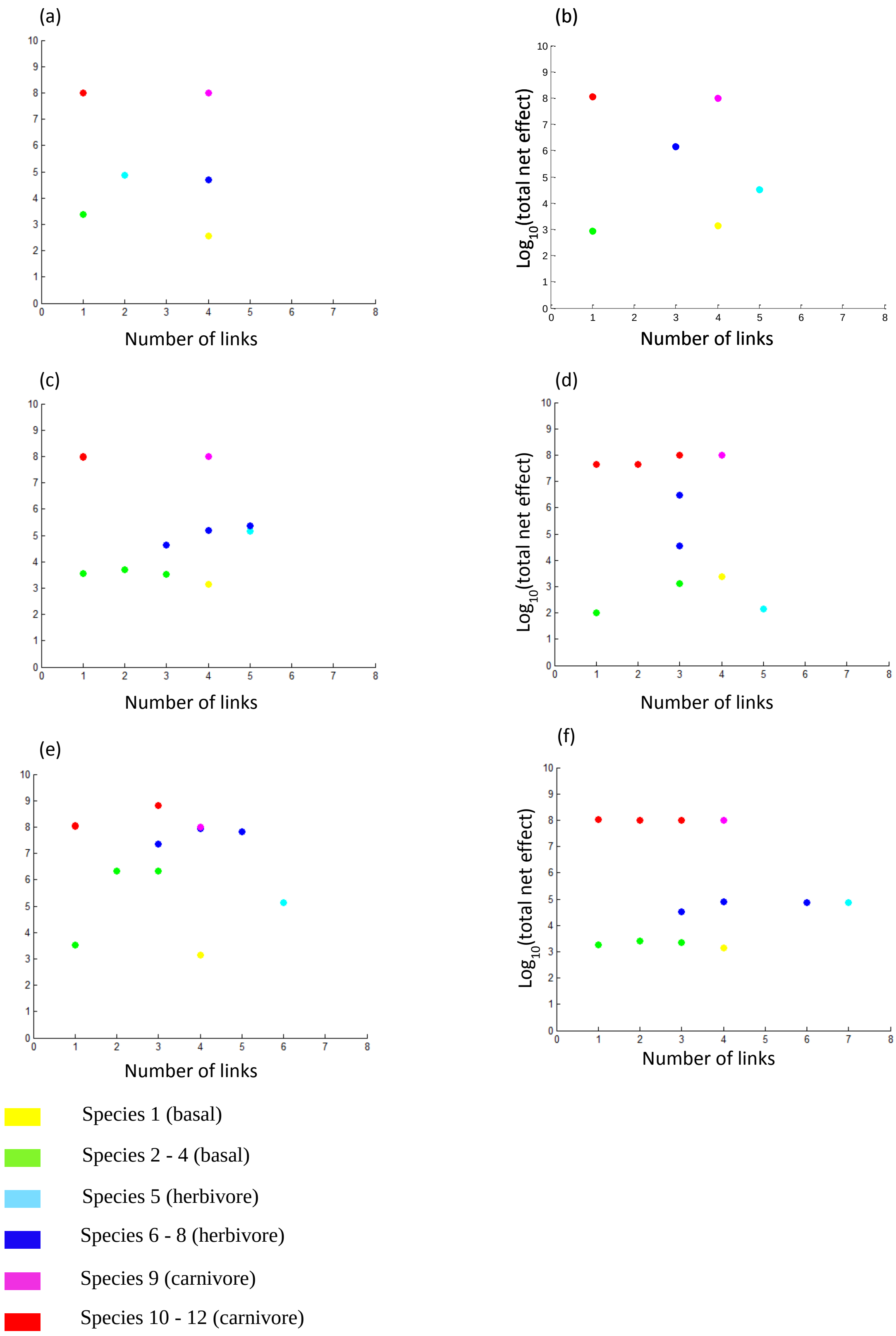


Figure. I3: the relationship between a species total net effect and its linkage density for food webs 5.4(a)-(f) where there were 12 species with a basal, herbivore and carnivore species ratio of (1:1:1) and varying web complexity.

C_b =1 ,C_c = 0.01, e = 0.1 and q = 100

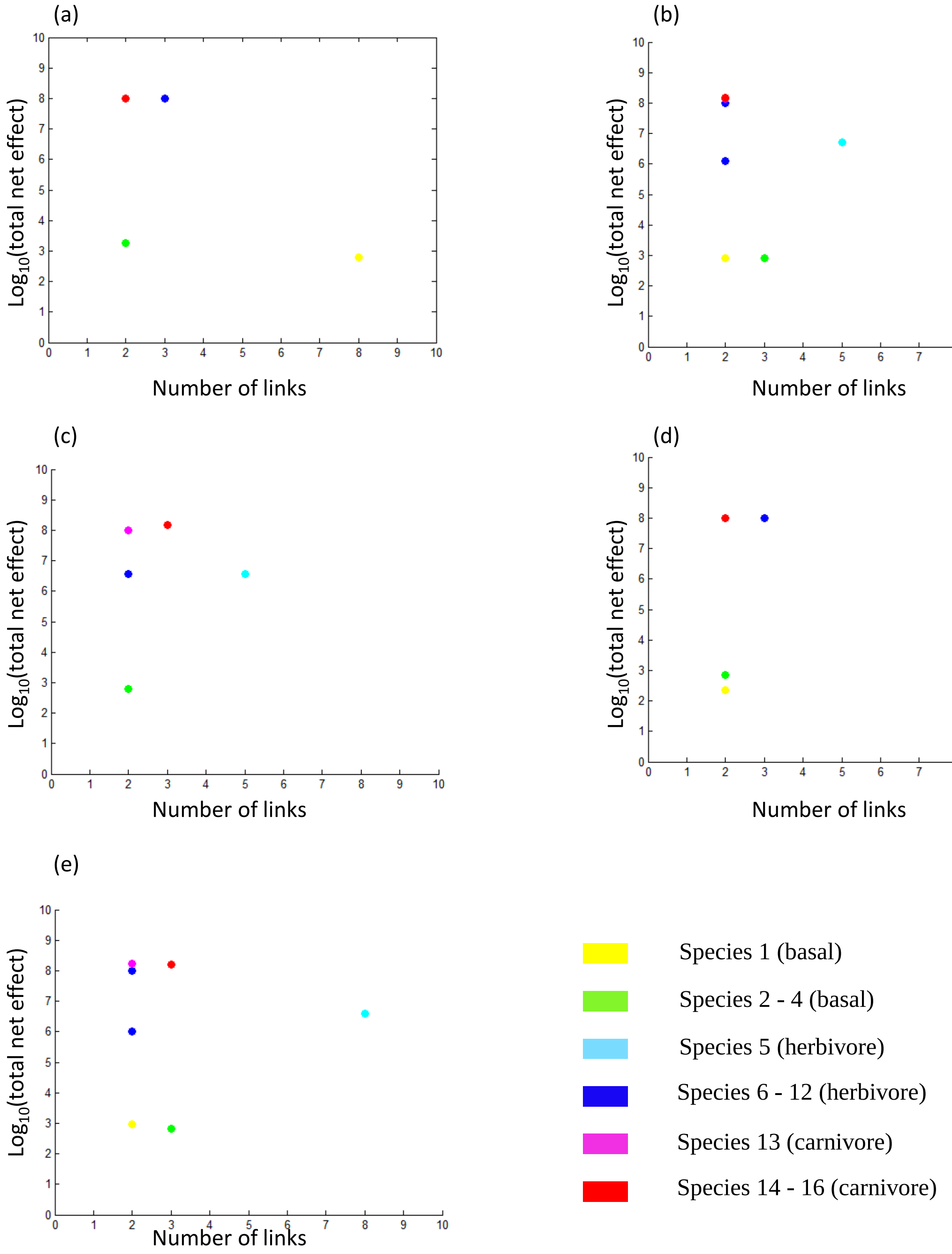


Figure. I4 The relationship between a species total net effect and its linkage density for food webs 5.5(a)-(e) where there were 16 species with a basal, herbivore and carnivore species ratio of (1:2:1) and minimal complexity for cases:

(a) basal species 1 is preyed on by all herbivore species
(b) herbivore species 7 preys on all basal species
(c) herbivore species 7 is preyed upon by all carnivore species
(d) carnivore species 12 preys upon all herbivore species
(e) herbivore species 7 preys upon all basal species and is preyed upon by all carnivore species.

C_b =1 ,C_c = 0.01, e = 0.1 and q = 100

In Figure (a) species 5, 6 and 13 are indistinguishable from species 14-16.

In Figure (b) species 13 is indistinguishable from herbivore species 14-16.

In Figure (d) species 5 is indistinguishable from herbivore species 6-12..

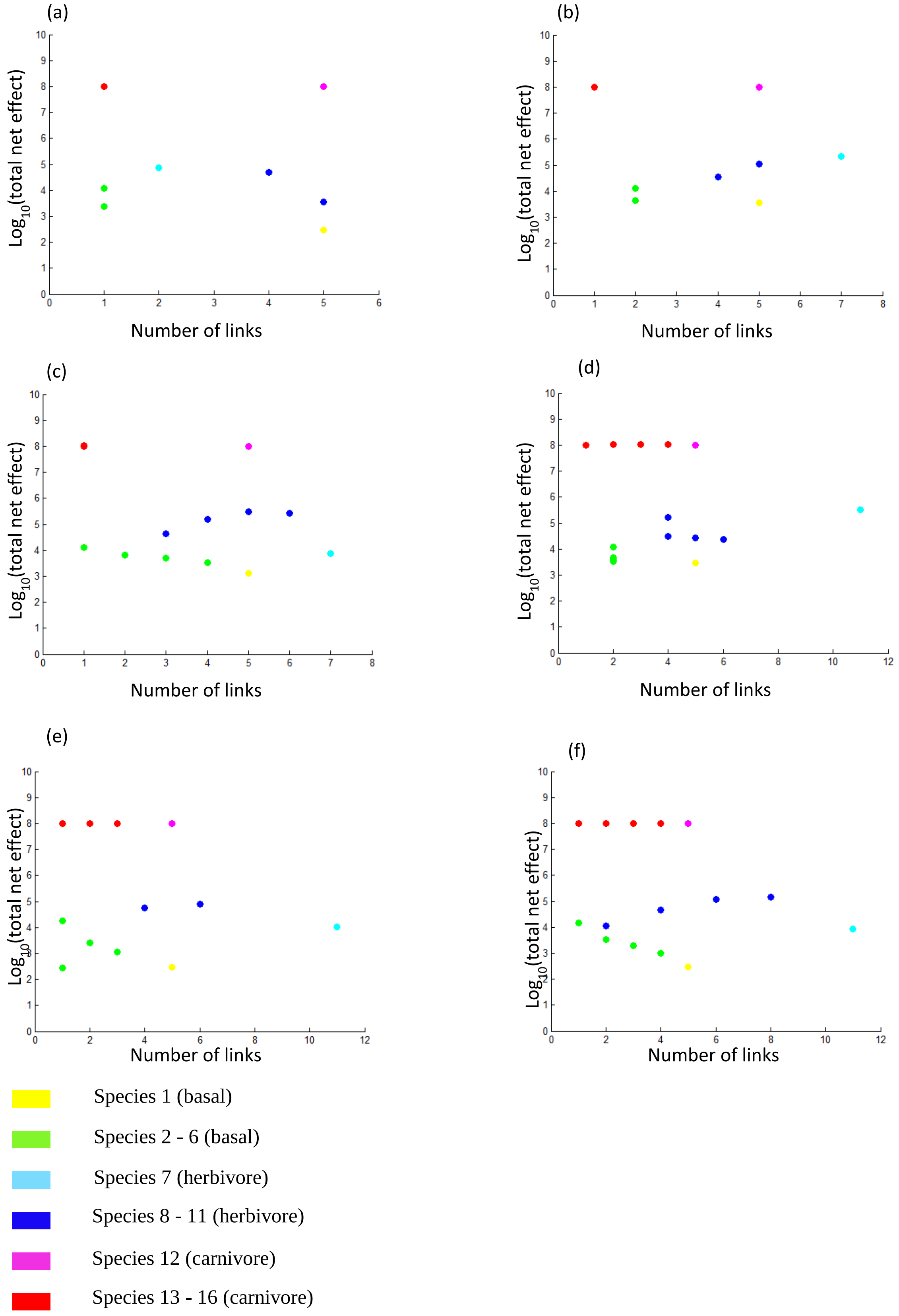


Figure I5 The relationship between a species total net effect and its linkage density for food webs 5.6(a)-(f) where there were 16 species with a basal, herbivore and carnivore species ratio of (6:5:5) and varying web complexity. C_b =1 ,C_c = 0.01, e = 0.1 and q = 100

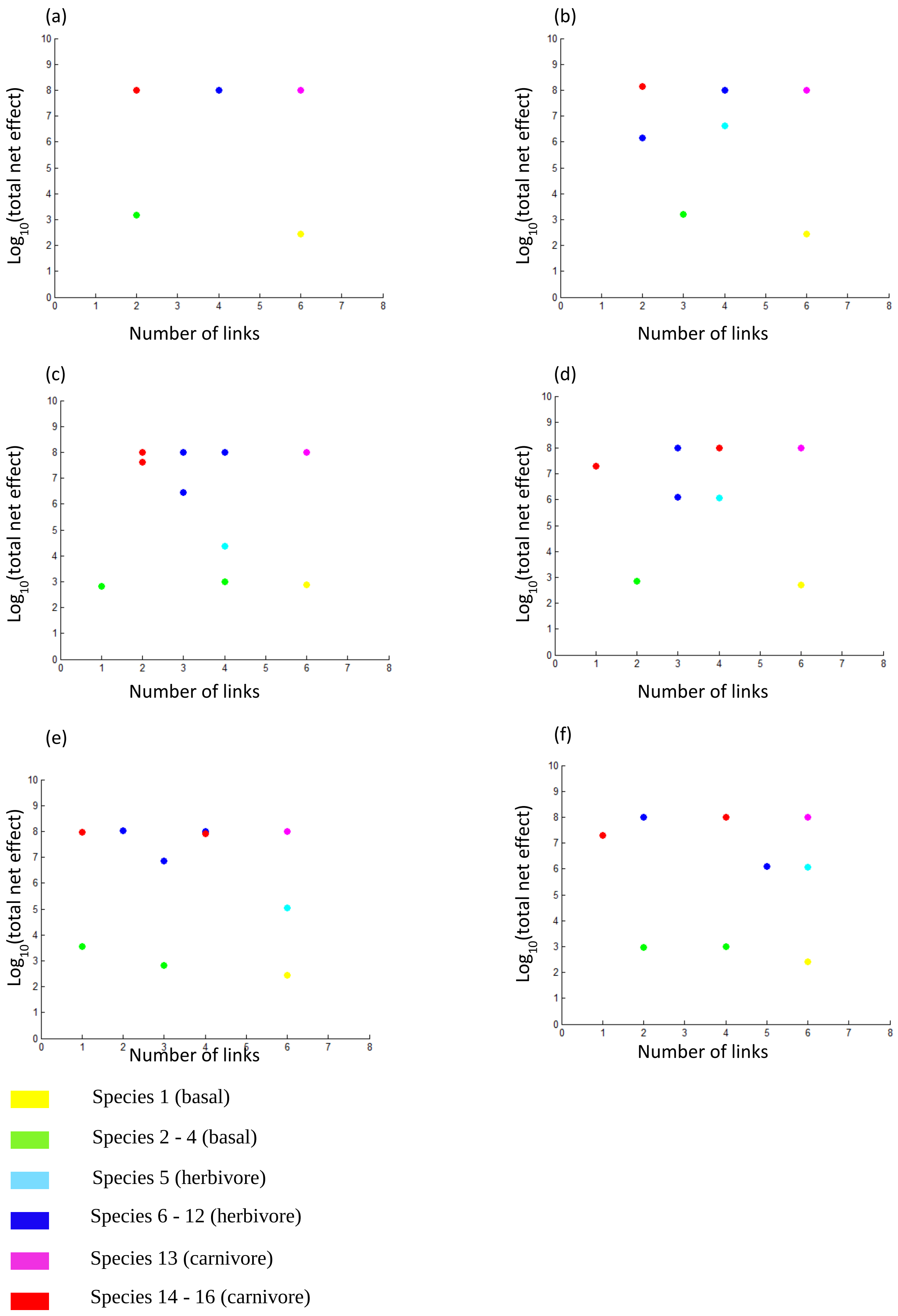


Figure I6 The relationship between a species total net effect and its linkage density for food webs 5.7(a)-(f) where there were 12 species with a basal, herbivore and carnivore species ratio of (1:2:1) and varying web complexity.

C_b =1 ,C_c = 0.01, e = 0.1 and q = 100

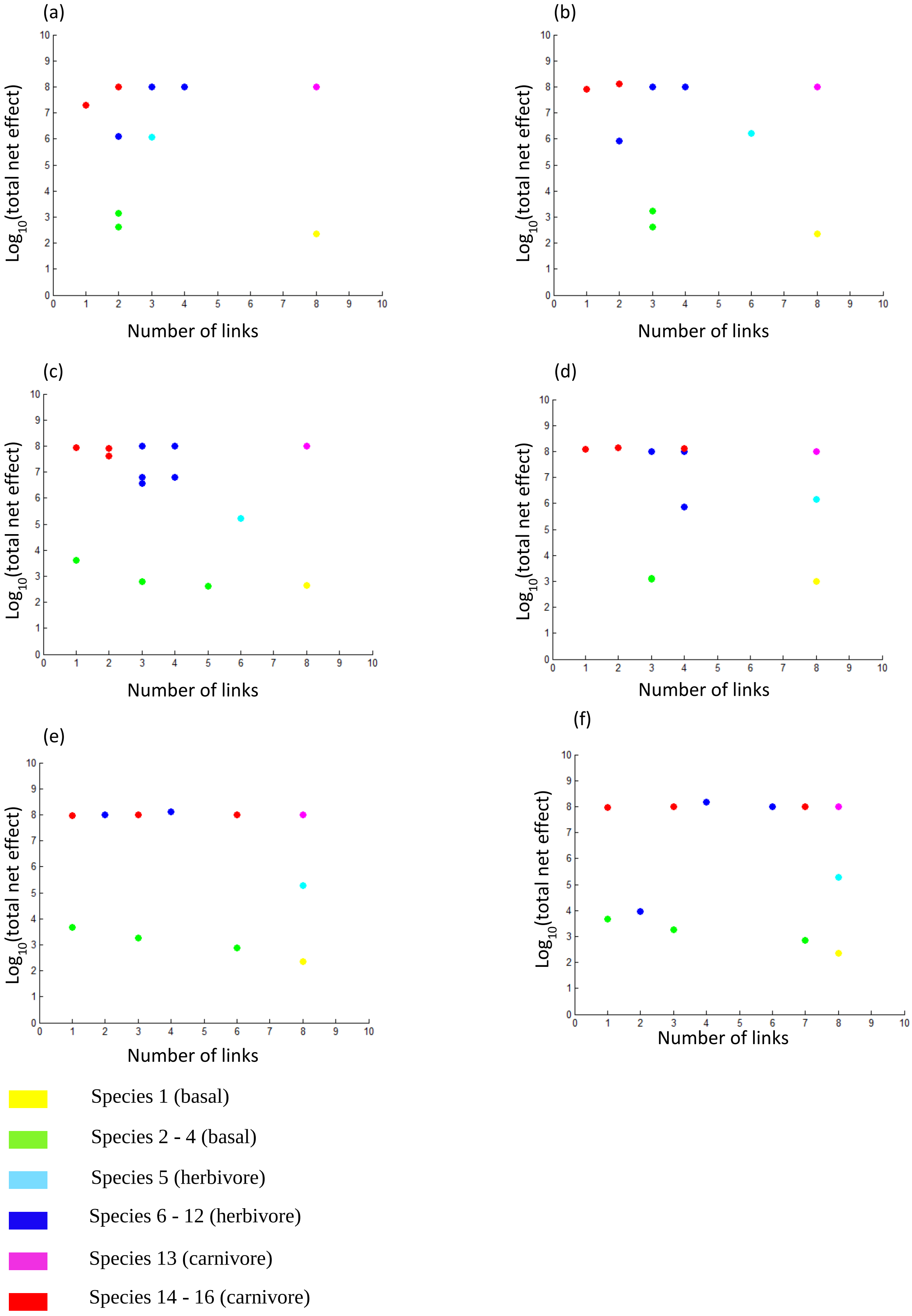


Figure I7 the relationship between a species total net effect and its linkage density for food webs 5.8(a)-(f) where there were 16 species with a basal, herbivore and carnivore species ratio of (1:2:1) and varying web complexity.

$C_b = 1$, $C_c = 0.01$, $e = 0.1$ and $q = 100$

APPENDIX J

Bar charts showing how the proportion of negative correlations varied with the number of links for each species for the set of food webs generated by the permutations of the 16 species food web.

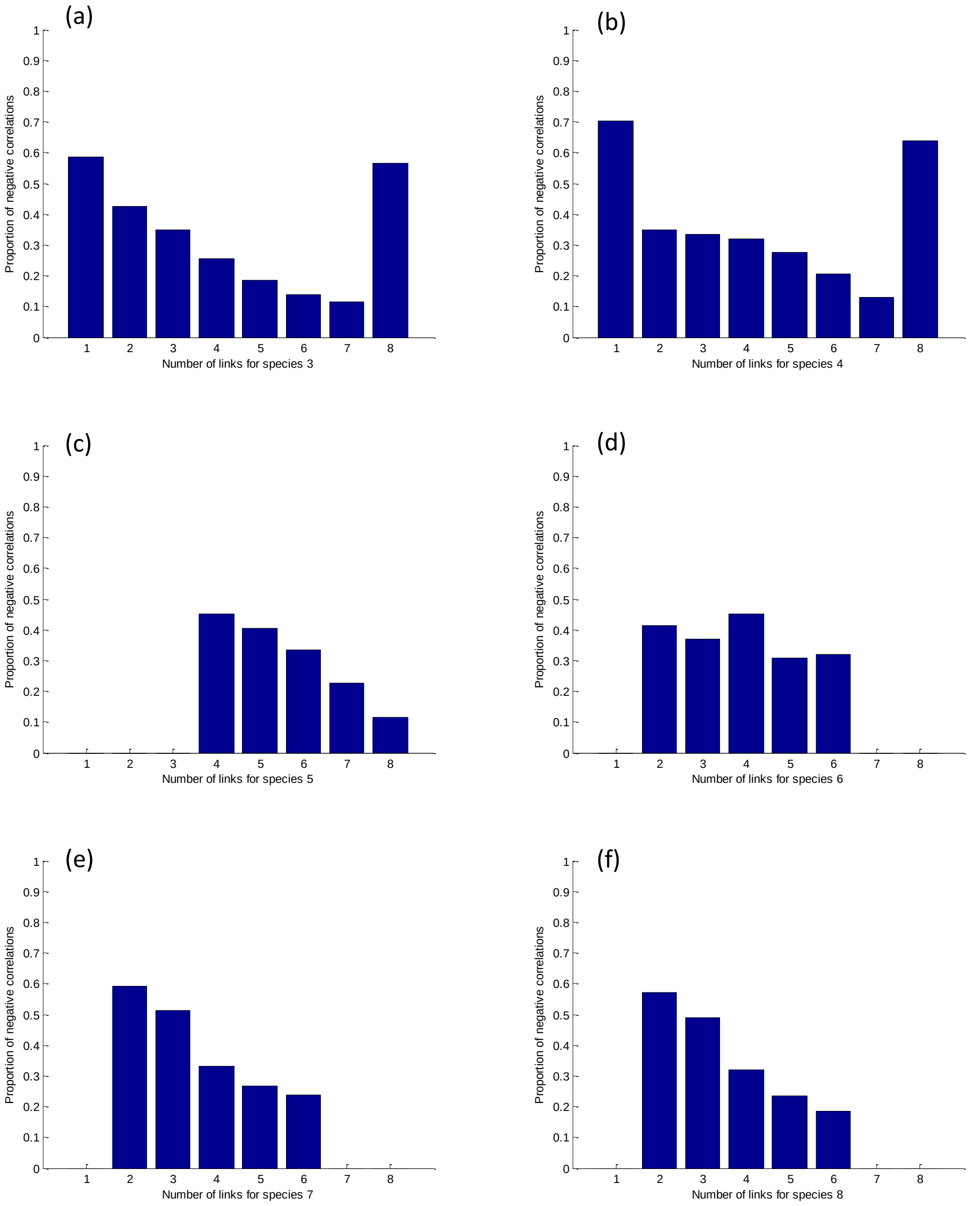


Figure J1(a) Basal trophic level: bar charts showing how the proportion of correlations between linkage density and total net effect with a value less than < -0.4 varies with the linkage density of species 3 – 8.

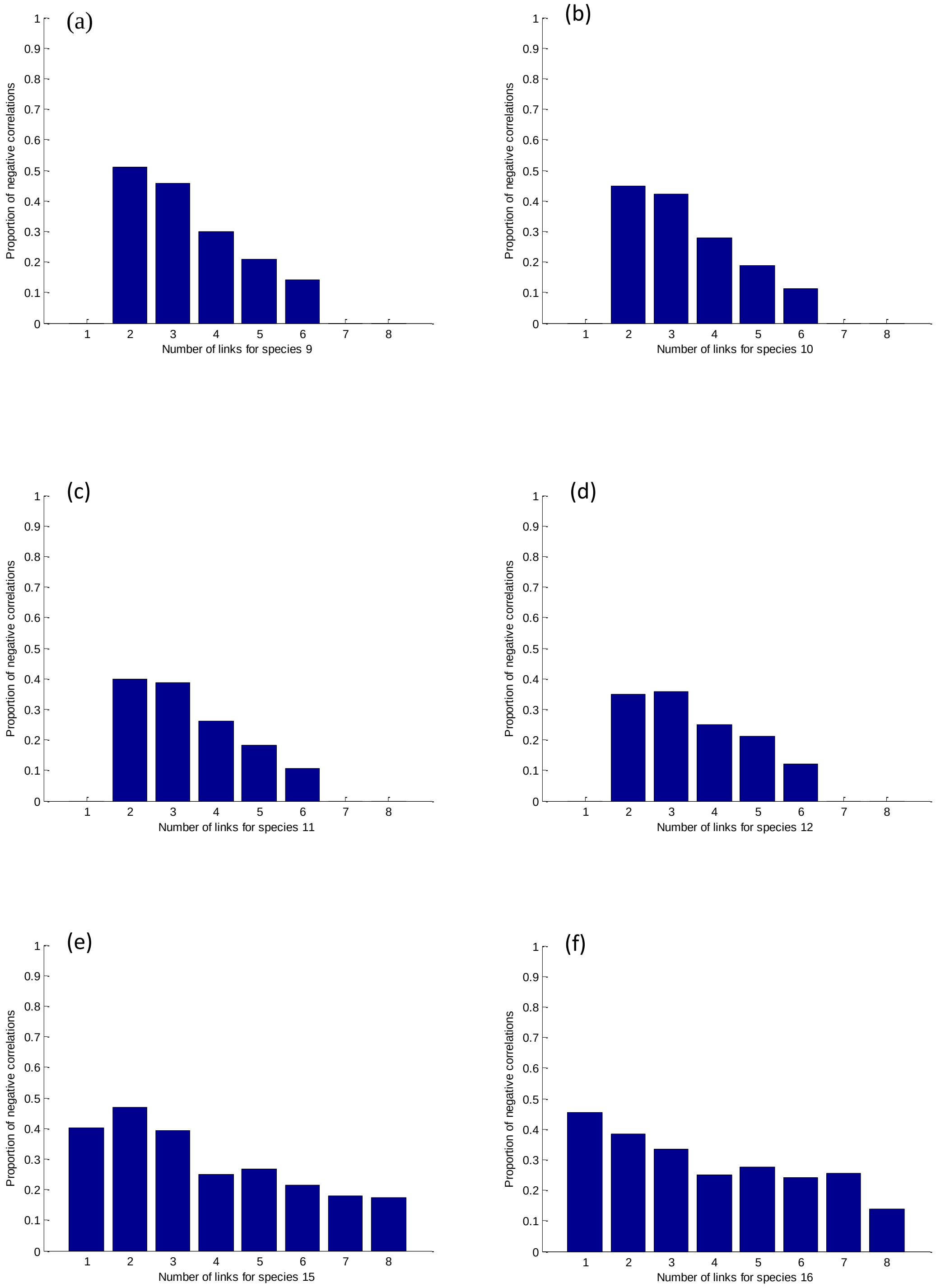


Figure J1(b) Basal trophic level: bar charts showing how the proportion of correlations between linkage density and total net effect with a value less than < -0.4 varies with the linkage density of species 9 – 12, 15 and 16.

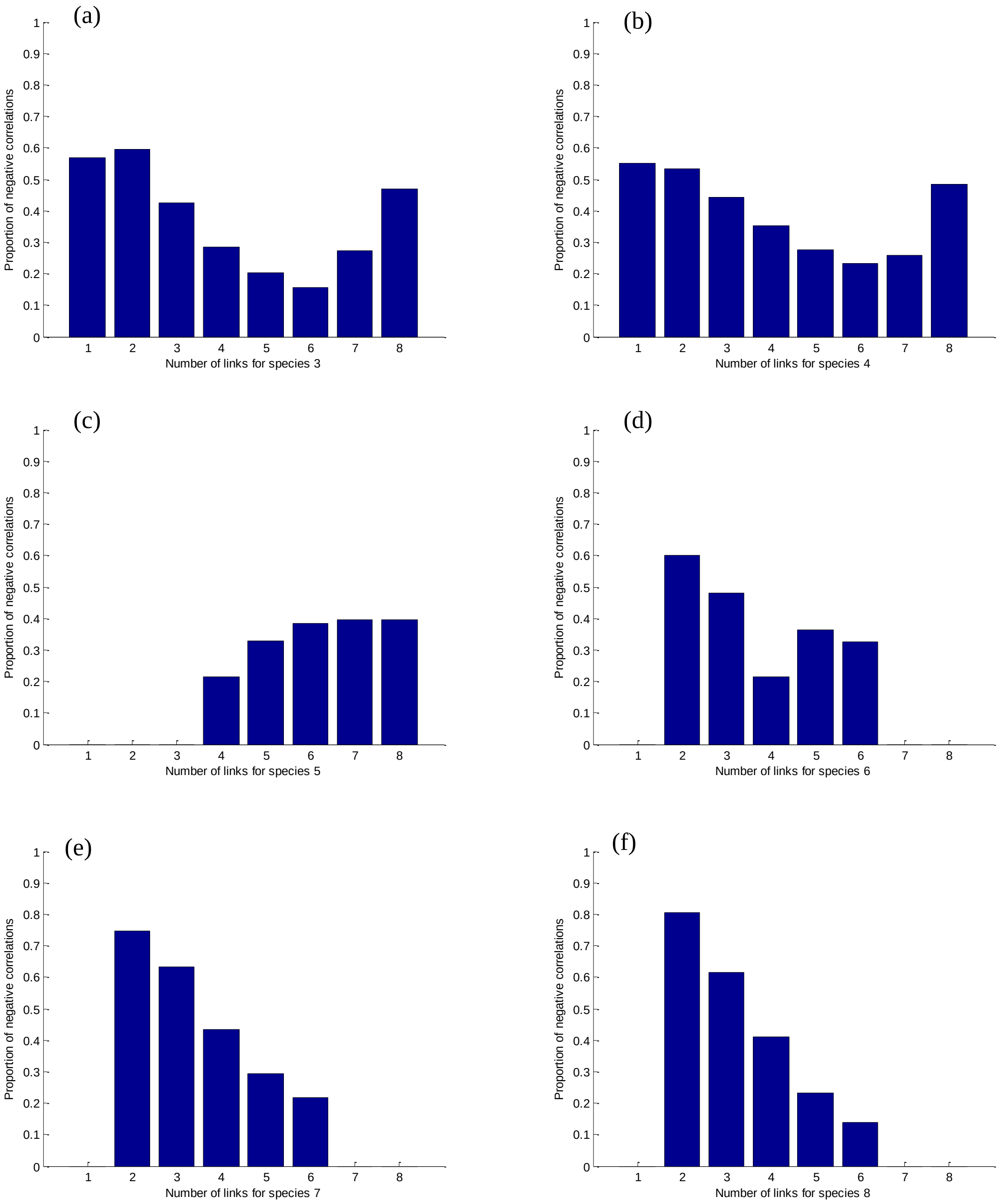


Figure J2(a) Herbivore trophic level: bar charts showing how the proportion of correlations between linkage density and total net effect with a value less than < -0.4 varies with the linkage density of species 3 – 8.

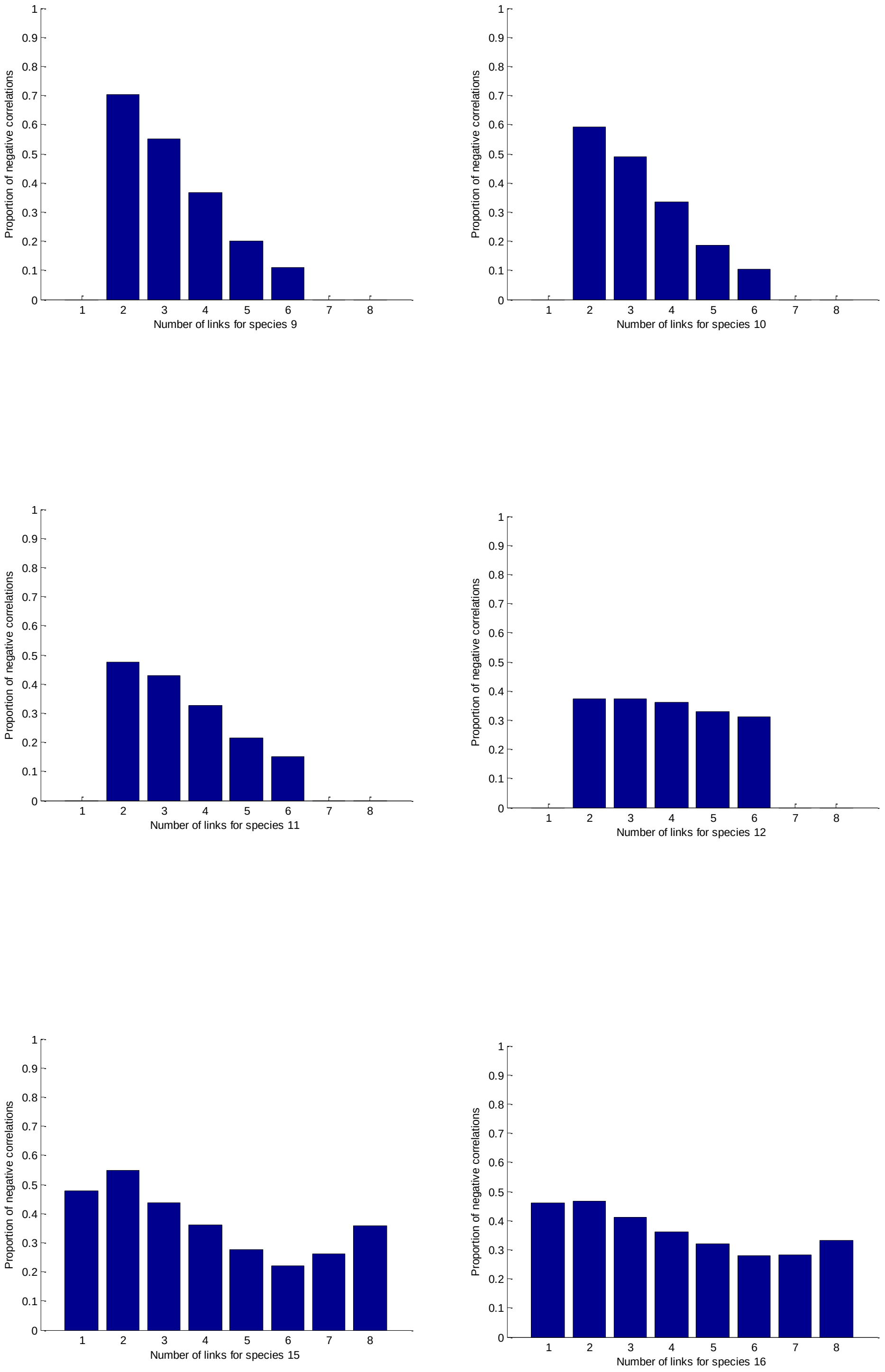


Figure J2(b) Herbivore trophic level: bar charts showing how the proportion of correlations between linkage density and total net effect with a value less than < -0.4 varies with the linkage density of species 9 – 12, 15 and 16.

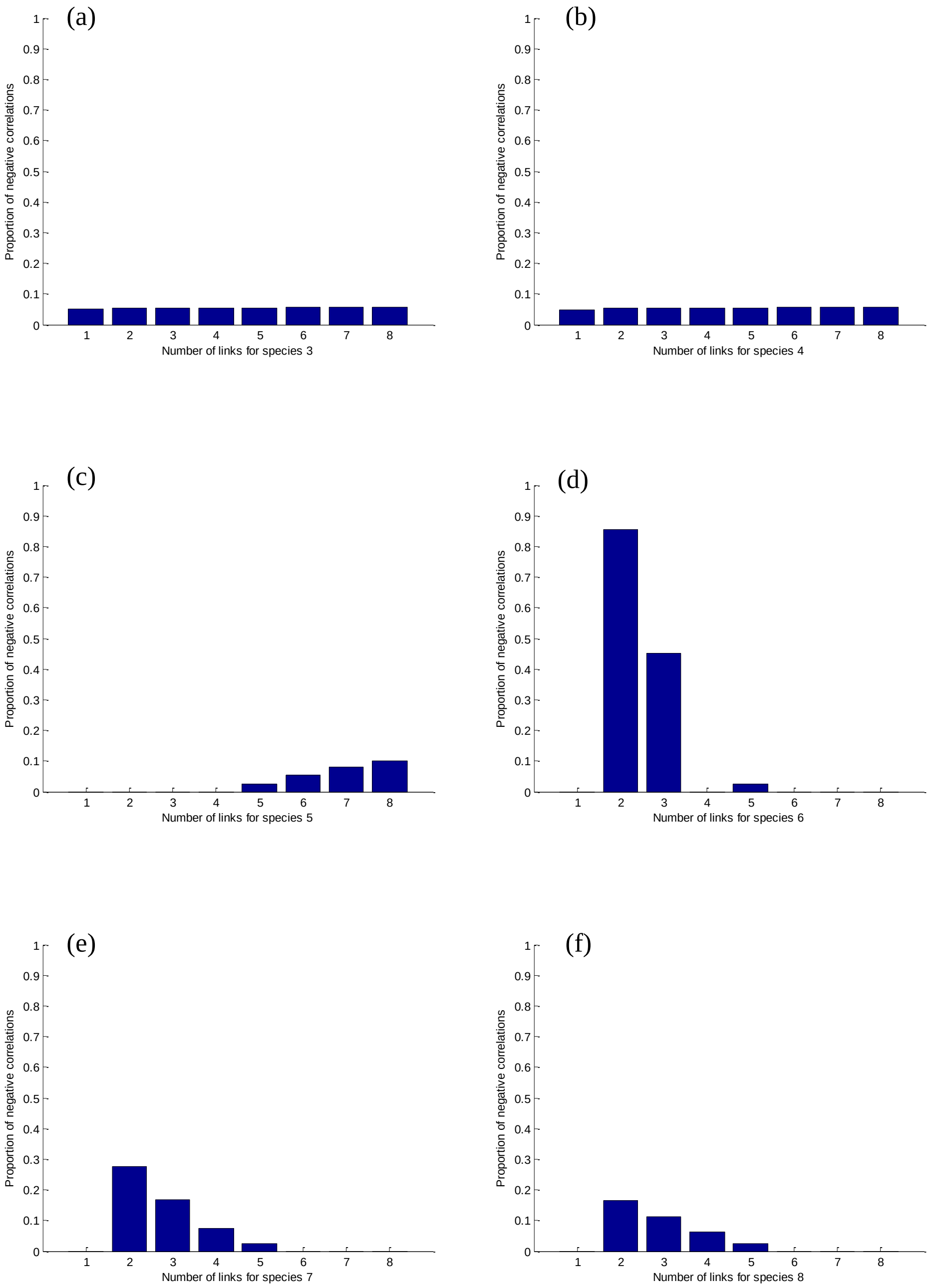


Figure J3(a) Carnivore trophic level: bar charts showing how the proportion of correlations between linkage density and total net effect with a value less than < -0.4 varies with the linkage density of species 9 – 12, 15 and 16.

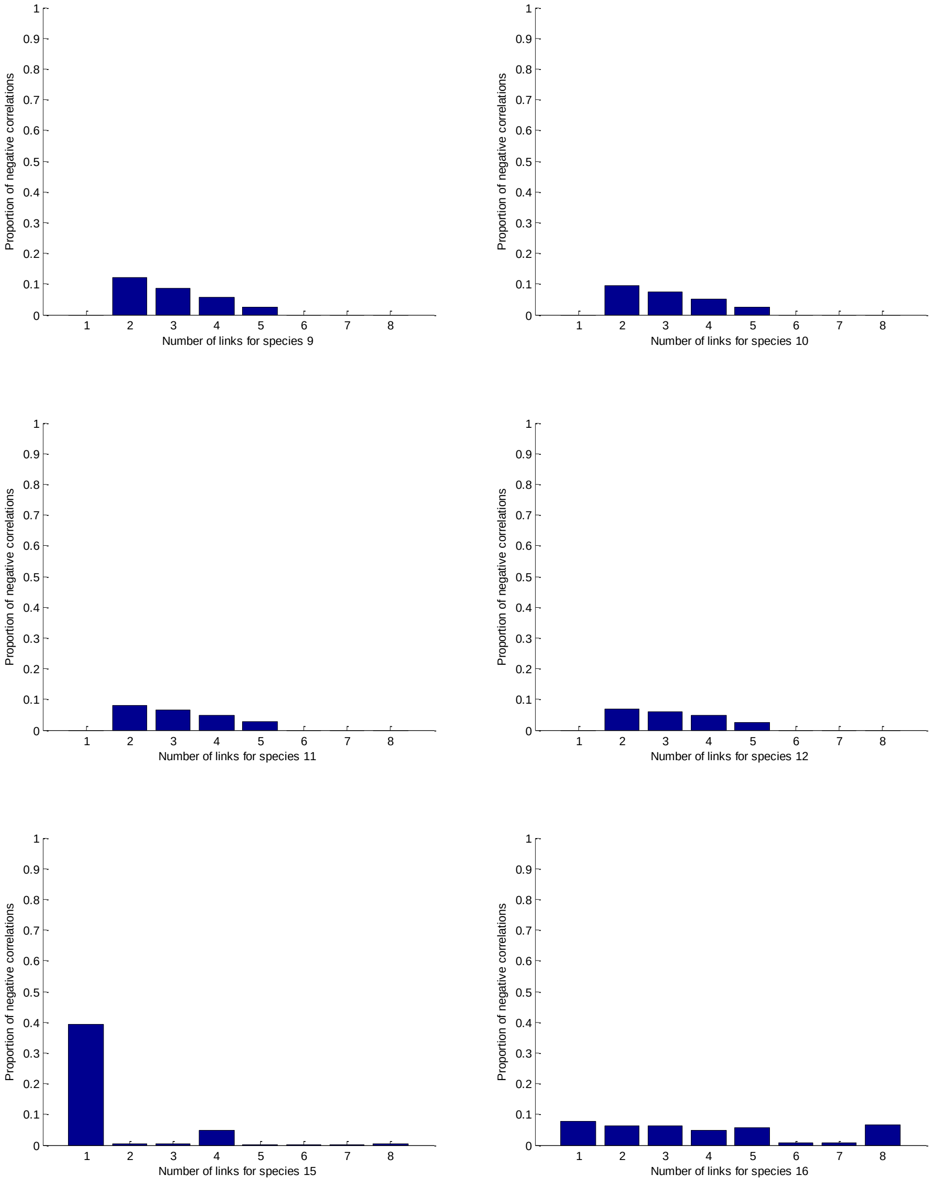


Figure J3(b) Carnivore trophic level: bar charts showing how the proportion of correlations between linkage density and total net effect with a value less than < -0.4 varies with the linkage density of species 1-8.

CHAPTER 6

GENERAL DISCUSSION

Main Findings

The work in this thesis explored the role of interaction strengths between species in food webs both empirically and theoretically. The study presented in Chapter 2 is the first to use the dynamic index and the newly developed intraspecific dynamic index to simultaneously obtain empirical estimates for both intraspecific and interspecific interaction strengths. These empirical measurements were made at the whole food chain scale comprising a novel experimental analysis of a simple three trophic level plant-herbivore-predator model system. In Chapter 3, a net effects analysis was used to investigate relationships between a species traits and its impact on the community; and in Chapters 4 and 5, the inverse community matrix was examined in detail to gain insight into the mechanisms underlying the observed relationships.

It is widely accepted that measuring interaction strengths between species empirically is problematic (Laska and Wootton 1998, Abrams 2001, Berlow et al. 2004, Wootton and Emmerson 2005) and the experiment to determine species intraspecific and interspecific interaction strengths (Chapter 2) highlighted this. Using food chains of different length and of varying initial species biomass densities revealed that interaction strength estimates can be affected by variation between individuals, non-linearities in interspecific interaction strengths, indirect effects and food chain structure. The interaction strengths estimated from the three-species food chain increased in both size and variation with trophic level but the variation associated with the estimates increased to the point that the aphid-lacewing and lacewing-lacewing estimates at the third trophic level were not informative. The ratio of intraspecific to interspecific interaction strength for the plant species was found to be small (a_{11} / a_{12} lay between -0.01 and -0.001) which is low compared to ratios used in previous theoretical studies (de Ruiter et al. 1995, Schmitz 1997, Jonsson and Ebenman 1998, Emmerson and Raffaelli 2004, Eklöf and Ebenman 2006, Neutel et al. 2007, Petchey et al. 2008b). However the plant-aphid-lacewing food chain that the estimates were derived from is not typical, in that aphids are a pest species that reproduce quickly, causing considerable damage to plants if the population is not kept in check by a variety of natural enemies (Hutchison and Hogg 1984, Aquilino et al. 2005). The ratio of intraspecific to interspecific interaction strength for basal species is expected to be higher in other systems, which could be checked using further applications of the dynamic and the intraspecific dynamic index.

Surprisingly, the estimate of basal intraspecific interaction strength was positive or negative depending on the presence or absence of higher trophic level consumers. It was not clear whether the differences in intraspecific interaction strength estimates were due to changes in plant conspecific interactions as observed in (Parmesan 2000, Alberti et al. 2008) or non-linearity in the plant-aphid interspecific interaction strength (Ruesink 1998, Case 2000, Sarnelle 2003, Vucic-Pestic et al. 2010).

In Chapter 3 it was found that, for model communities where interaction strengths between species were defined using an energetics approach, species with a large body size had a large impact on the community. This result supports previous findings for the Ythan Estuary (Montoya et al. 2005), and the Baltic Sea and Lake Vättern (Berg et al. 2011). A small press perturbation to large bodied species caused a large change in the equilibrium biomass abundances of the whole community. This relationship was strong and consistent, holding for all webs analysed. Chapter 4 showed that this positive relationship between a species body size and its total net effect is a consequence of the body-size based parameterisation of the community matrix and that the precise ordering of species with regard to their total net effect is dependent on relative values of the ecological efficiency parameter, predator-prey body mass ratios and intraspecific-interspecific interaction strength ratios. Information regarding ecological efficiency is relatively easy to find (Begon et al. 2009), and predator-prey body size ratios can be measured (Jennings and Warr 2003, Brose et al. 2005b, Brose et al. 2006a, Riede et al. 2011), but there is a lack of information regarding the empirical scaling of intraspecific and interspecific interaction strengths.

The nature of the relationship between species body size and its impact on the community at the population level depends on how population biomass density scales with body size. Numerical population density has been reported to scale with body mass according to a power law with an exponent between -1 and $-\frac{3}{4}$ (Peters 1983, Jonsson et al. 2005, White et al. 2007), if this observation holds, then biomass abundance would be invariant with body size or increase with body size and the positive relationship between body mass and total net effect persists at the population level. This result indicates that the conservation of large bodied species could be important for the persistence of strongly size-structured communities. However, although body size has been shown to be an important predictor for the impact that a species has on the community, it is not the only trait that can determine a species' role in the community. Body temperature, feeding strategy (e.g. predator, scavenger, grazer, filter feeder), resource type (e.g. herbivore, carnivore, omnivore detritivore), mobility, and environmental location have also been shown to contribute to the effect that a species has on the community in static food web models (Jacob et al. 2011).

Further information about how these traits affect the parameters in dynamic food web models (i.e. interspecific interaction strengths, intraspecific interaction strengths and the ecological efficiency) would better enable us to predict the response of communities to perturbations.

The relationship between a species linkage density and the impact it has on the community was found to be less consistent: in Chapter 3, out of 97 webs created using an assembly algorithm, a negative relationship between linkage density and net effects was detected for 38 webs. Comparison of the set of webs where a negative relationship was present and where it was not indicated that the set of webs for which the relationship was present had a statistically lower clustering coefficient and a higher average shortest path length. In Chapter 5, further analysis of the relationship using webs of size 12 and 16 (species) with varying structure and complexity found that negative correlations between linkage density and total net effects, at the whole web level (including all species in the web), were uncommon; the impact that a species had on its community was determined by its body size and any potential relationship between linkage density and total net effect did not affect this. Out of three studies that have examined the relationship between species linkage density and mean/total net effect (Montoya et al. 2005, O'Gorman et al. 2010, Berg et al. 2011), a negative relationship was present for the Ythan Estuary and Broadstone stream food webs (Montoya et al. 2005) and for mesocosm food webs in Lough Hyne (O'Gorman and Emmerson 2009), but no relationship was detected for the Baltic Sea and Lake Vättern food webs (Berg et al. 2011). The inconsistency of the relationship indicates that it is not a result of the body size based parameterisation of the community matrix.

Examining the relationship between species linkage density and total net effect within trophic levels where body size was held constant showed that for the basal and herbivore trophic levels, the relationship was frequently negative and rarely positive but the mechanism determining the nature of the relationship was unclear. The relationship was more likely to be negative in webs with low connectance, but this was not a definitive property and a negative relationship may or may not be present in a web with low connectance. The set of webs analysed contained webs that were identical in all respects: species richness, basal: herbivore: carnivore trophic ratios, interaction strengths, the linkage density of the most highly connected species and the linkage density of the most poorly connected species. The only difference permitted was in the arrangement of links of surrounding species and yet a negative relationship between linkage density and total net effect was present in some webs, but not in others, indicating that the negative relationship between linkage density and total net effect is a consequence of the pattern of interaction strengths in the surrounding web. The importance of web structure in determining stability and the response of a community to perturbations is well documented (McCann 2000, Neutel et al. 2002, Dambacher et al. 2003, Neutel et al. 2007).

Synthesis and Future Directions

In the broad context of food web ecology, the analyses presented in this thesis highlight issues regarding two important questions. First, is it possible to parameterise multispecies food web models directly using interaction strength estimates derived from empirical data? Second, in theoretical studies, how sensitive are the results to the underlying model?

Empirical Estimates of Interaction Strengths

Estimating the impact that species *j* has on species *i* requires measuring the population density of species *i* in response to changes in the population density of species *j*. Assuming that a model captures the behaviour of a system, an interaction strength estimate used to parameterise a particular model must be derived from the model in question (Laska and Wootton 1998, Berlow et al. 1999). The dynamic index used in Chapter 2 is an example of such an estimate; it is used to estimate the per capita/per unit mass effect of species *j* on species *i* per unit time in a discrete time Lotka-Volterra model (Laska and Wootton 1998). The experiment presented in Chapter 2 highlighted the difficulties in obtaining and interpreting empirical estimates based on population density measures. In just a simple three species food chain, non-linearities, indirect effects and context dependency in the estimates were observed.

To parameterise a non-linear functional response requires knowledge of the form of the functional response as well as the parameters. Once the form is established it is possible to estimate parameters by measuring changes in population densities for varying initial biomass densities (Ruesink 1998, Sarnelle 2003, Novak and Wootton 2010, Vucic-Pestic et al. 2010).

The problems associated with indirect effects are more difficult to overcome. The fundamental idea on which experiments are based is that we manipulate one variable (in this case the population density of species *j*), and record the impact that it has on the response variable (the population density of species *i*). Even if we exclude all other sources of variation we are still faced with the fact that the population densities of species *i* and species *j* are interdependent. In order to accurately measure the direct effect of species *j* on species *i* in a Lotka-Volterra model by applying a press perturbation to species *j*, it is necessary that the population density of species *j* is held constant at its new perturbed level i.e. species *j* is prevented from responding to changes in the population density of species *i* by either adding or removing individuals/biomass. If this method is extended to a community with *S* species then to measure the direct effect of species *j* on species *i* it is necessary that (within each treatment) the population density of all species is held constant (species *j* at the perturbed level and the other species at baseline levels) and only the population density of species *i* is permitted to respond (Nakajima and Higashi 1995). If the population densities of all species in the system (with the exception of the focal species) are not held constant then the experiment measures the net effect of species *j* on species *i* which includes indirect effects that are mediated through changes in population density of other species in the system. Indirect effects have been observed in many manipulation experiments (Wootton 1993, Werner and McPeek 1994, Menge 1995, O'Gorman et al. 2010). At present, controlling multiple species population densities in empirical systems is not possible, but measurements of population densities at frequent time intervals might give an indication of the timescale of direct and indirect effects (O'Connor et al. 2013). The development of novel techniques that allow frequent (ideally constant), non-destructive monitoring of population densities would advance our understanding of interaction strengths and should be a priority when designing manipulation experiments.

Evidence that interaction strengths between species are context dependent and can be altered by both environmental conditions and the composition of the surrounding community (Werner and Peacor 2003, Chapter 2, Alberti et al. 2008, Otto et al. 2008) raises doubts about the efficacy of interaction strength estimates in predictive models (Abrams 2001). A fundamental aim of model building in ecology is to provide information about the behaviour of a community when faced with novel perturbations; if the building blocks, that are pairwise interaction strengths, are highly sensitive to changes in the surrounding community then the predictive power of the model is lost. Further empirical information about the sensitivity of interaction strengths to abiotic and biotic conditions is required, along with information about the sensitivity of the underlying model to changes in interaction strengths (Berg et al. 2011).

Despite the numerous shortcomings discussed above it can still be argued that empirical manipulation experiments provide useful information for parameterising models. Novak et al. (2011) found that when examining community responses to press perturbations, the use of empirical estimates of interaction strengths to parameterise the community matrix provided greater certainty in the community response than using just qualitative entries. Currently, it is not possible to estimate all pairwise interaction strengths in a community accurately, but information regarding how interaction strengths scale across trophic levels and how intraspecific interaction strengths scale with interspecific interaction strengths would improve current models.

Model Sensitivity

Ecological systems are extremely complex so making simplifying assumptions is an essential part of model building. How these simplifying assumptions affect the outcomes of theoretical studies is an important question. Some important considerations include: functional responses, species resolution, ontogenetic shift, time scales and seasonality, omnivory, types of interactions (trophic, competitive, commensal or mutualistic), and units of measurement. The net effects analyses presented in Chapters 3, 4, and 5 were based on community matrices that were parameterised using a type I functional response and an energetics based approach via predator-prey body size ratios and allometric scaling. Interaction strengths were measured on a per unit biomass basis and interspecific competition was ignored.

Type I functional responses were used for their simplicity, analysis of the inverse community matrix is complex and near equilibrium (as in the case for a small press perturbation), non-linear functional responses are well described by a type I functional response (Case 2000). Ideally, for studies where dynamics are far from equilibrium, the effect of functional response on the outcomes of the study can by investigated by running models with alternative functional responses (Säterberg et al. 2013).

There is compelling empirical evidence that body size is important in describing the structure and dynamics of ecological communities (Cohen et al. 2003, Jonsson et al. 2005, Loeuille and Loreau 2005, Brose et al. 2006b, Riede et al. 2010) and the use of predator-prey body size ratios and allometric scaling to parameterise interaction strengths is potentially an important step towards the development of predictive models. The use of size-spectra models in fisheries have provided insights into the structure and functioning of marine communities and have had implications regarding fisheries management (Jennings et al. 2002, Shin et al. 2005, Andersen and Beyer 2006, Andersen et al. 2009, Plank and Law 2012, Blanchard et al. 2014). Incorporating elements of size-spectrum models into food web models can address problems associated with the assumption that all individuals of a species have an average body size and allow for ontogenetic shifts in diet (Andersen and Beyer 2006, Hartvig et al. 2011, Zhang et al. 2013). The relevance of body size based parameterisations of models in aquatic communities is clear, and there is evidence of size structuring in terrestrial communities (Memmott et al. 2000, Brose et al. 2006a, Riede et al. 2011). However, many trophic interactions within ecological communities are not typical predator-prey interactions and these often do not follow size based rules. In particular, host-parasitoid interactions, where small parasitoids consume much larger hosts, some benthic invertebrates, whose feeding method allows them to consume much larger prey and plant based herbivorous interactions, where small insect herbivores feed on large plants. These types of trophic interactions cannot be modelled using body size alone and incorporating such interactions into an energetics based framework is of great interest (Lafferty et al. 2008).

Interspecific competition between basal species was excluded from the models used in Chapters 2 and 4. This decision can be put into a broader context when we consider other types of interaction strengths in food web models: trophic, competitive, commensal or mutualistic. The incorporation of non-trophic links will change the structure of the community matrix which will, in turn, have consequences for the spread of indirect effects through the community and could potentially alter the response of a community to perturbations (Hosack et al. 2009). Examining the results of analyses using models with and without non-trophic interactions would determine the sensitivity of the results to the inclusion of non-trophic interactions and could provide insight into the mechanisms behind the set of observed results.

The choice of units is important when describing patterns in food webs. In a size structured community, if a community matrix is parameterised using predator-prey body size ratios then on a per unit mass basis, the entries in the community matrix decrease with increasing body size but on a per capita basis, the entries in the community matrix increase with increasing body size. This is just one example of how the units of measurement can affect observed relationships, and while it is easy to convert from per capita to per unit mass, inconsistency in the choice of units can obscure patterns and make comparisons between studies difficult.

In conclusion, theoretical models could potentially be improved by using experimental information to inform the scaling of interspecific interaction strengths (both trophic and non-trophic) and intraspecific interaction strengths across multiple trophic levels. This would require more experimental data that manipulates multiple species at multiple densities, that describes who interacts with whom and quantifies species population dynamics, at frequent intervals, through time. The Dynamic Index and the Intraspecific Dynamic Index used in Chapter 2 has the potential to provide such information.

As well as improving our understanding of ecological communities through empirical experiments, it is also possible to improve our understanding of ecological communities theoretically by examining the sensitivity of models to the underlying ecological assumptions. The importance of the scaling of interspecific and intraspecific interactions was highlighted in the Chapter 4 where it was shown that, in general, species with a large body size have a large impact on their surrounding community, however, it was also shown that the magnitude of a species' impact is constrained by the amount of intraspecific competition it is subject to. Whilst the scaling of interspecific interaction strengths and intraspecific interaction strengths is unknown, it would be beneficial to examine the sensitivity of models results to changes in the scaling of interspecific interaction strengths. Improved computing power will enable us to test multiple models side by side and examine the sensitivity of results to model choices.

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