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CHAPTER TWO

Interaction strength, food web topology, and the relative importance of species in food webs

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Abstract:

We established complex marine communities, consisting of over 100 species, in large subtidal experimental mesocosms. We measured the strength of direct interactions and the net strength of direct and indirect interactions between the species in those communities, using a combination of theoretical and empirical approaches. Theoretical estimates of interaction strength were derived from the interaction coefficient matrix, which was parameterised using allometric predator-prey relationships. Empirical estimates of interaction strength were quantified using the ln-ratio, which measures the change in biomass density of species A in the presence and absence of species B. We observed that highly connected species tend to have weak direct effects and net effects in our experimental food webs, whether we calculate interaction strength theoretically or empirically. We found a significant correlation between our theoretical and empirical estimates of direct effects and net effects. The net effects correlation was much stronger, indicating that our experimental communities were dominated by a mixture of direct and indirect effects. Re-calculation of the theoretical estimates of net effects after randomising predator and prey body masses did not affect the negative relationship with connectance. These results suggest that food web topology, which in this system is constrained by body mass, is overwhelmingly important for the magnitude of direct and indirect interactions and hence species importance in the face of biodiversity declines.

Keywords: dynamic index, indirect effects, community matrix, press perturbation, trophic links.

Introduction:

It is now generally accepted that biodiversity has a stabilising effect on natural ecosystems (see Ives & Carpenter (2007) for a review of empirical and theoretical studies, which include some destabilising effects of diversity). Diversity has been shown experimentally to have a positive effect on the temporal stability of community biomass (Caldeira *et al.* 2005; Tilman *et al.* 2006), decomposition (Dang *et al.* 2005), and parasitism (Tylianakis *et al.* 2006). An increasing number of experimental studies also show that diversity increases the resistance (Mulder *et al.* 2001; Kahmen *et al.* 2005) and resilience (Allison 2004; Steiner *et al.* 2006) of certain ecosystem properties to perturbations. Yet, Lotka-Volterra models based on randomly parameterised community matrices suggest that complexity should destabilise food webs (May 1973; Pimm & Lawton 1978). This implies that real food webs persist despite being unstable and far from equilibrium, or alternatively they have structures and properties that confer stability, in spite of complexity.

The patterning of interaction strengths between predators and prey in natural communities has attracted recent attention. Interaction strengths estimate the magnitude of the effect of one species on another (see Laska & Wootton (1998) for a review of experimental and theoretical approaches to measuring interaction strength). Studies on interaction strength typically measure the direct interaction between two species, but in this study we also examine the net effect of one species on another. The net effect is the sum of the direct and indirect effects of one species on another and can also be taken as a measure of interaction strength. Experiments (Paine 1992; Fagan & Hurd 1994) and theory based on empirical data (McCann *et al.* 1998; Neutel *et al.* 2002) have shown that real food webs are typically characterised by few strong interactions embedded in a majority of weak links. This arrangement of interaction strengths promotes community-level stability by generating negative covariances, which dampen the destabilising potential of strong consumer-resource interactions (McCann 2000; O'Gorman & Emmerson 2009). While the detrimental effects of keystone species loss are well documented (Paine 1966; Estes & Palmisano 1974), theoretical studies now suggest that the loss of weak interactors can be damaging for natural communities (Christianou & Ebenman 2005), particularly through their stabilising effects at the landscape level (Berlow 1999; Maser *et al.* 2007).

Recent theoretical investigations of large empirical food web data sets have also demonstrated the importance of weak interactions in maintaining the rich biodiversity of complex natural communities (Otto *et al.* 2007). It has been shown that highly connected species have weaker net effects than poorly connected species in some complex natural ecosystems (Montoya *et al.* 2005). As a result of this property, perturbations to species with fewer links should have larger net effects on the rest of the food web than perturbations to species with many links (Montoya *et al.* 2009). This suggests that complex communities with many highly connected species will be more stable to perturbations than simple communities. There is still much doubt as to whether or not this pattern occurs in nature, with several contradictory studies indicating that perturbations to highly connected species may in fact destabilise communities (Dunne *et al.* 2002; Coll *et al.* 2008). Consequently, there is a need to explore empirical patterns of interaction strength and their relationship to species connectance.

The biggest stumbling block towards validating predictions regarding the stabilising patterns of interaction strengths in natural systems is the lack of experimental tests of these theoretical predictions. Many theoretical studies use empirical data to inform their predictions, but theoretical interaction strengths are typically estimated in very different ways to those measured in field experiments (Laska & Wootton 1998; Wootton & Emmerson 2005). This introduces uncertainty over the feasibility of theoretical predictions and constrains their application in the real world. The lack of a direct comparison between theoretical and empirical estimates of interaction strength is a rate limiting step in our understanding of the consequences of biodiversity loss using dynamic systems models.

Testing the validity of theory is essential to confirm that the patterns predicted by community models are indeed the same as those found in nature. Our aim here was to make theoretical predictions about the strength of predator-prey interactions in a complex marine community (based on allometric predator-prey relationships) and to compare those predictions to the closest empirical measure of interaction strength that could be determined in a field setting. We chose to use large subtidal exclusion cages to achieve this goal. Exclusion cages have the potential to introduce some experimental artefacts (Stocker 1986; Benedetti-Cecchi & Cinelli 1997), but they also represent a balance between open and closed systems. Here, they facilitated an intricate exploration of species interactions in a relatively

controlled environment, whilst allowing benthic community assembly and ecosystem processes to occur against a semi-natural backdrop. We investigated the correlation between our theoretical and empirical estimates of interaction strength (for direct effects and net effects) and searched for common patterns that might contribute to the stability of this complex system.

Materials and Methods:

Study system and experimental design

To measure interaction strengths, we established an *in situ* mesocosm experiment in the shallow subtidal of Lough Hyne, a sheltered marine lake in Co. Cork, southwest Ireland (N 51˚29'52", W 9˚17'46"). Each mesocosm consisted of a subtidal cage, cylindrical in shape, 0.5m tall, with a diameter of 0.76m and a 5mm mesh size (benthic surface area = 0.45m^2). The mesocosms were sealed at both ends and weighted to the benthos by clean, stony substrate, which was spread across the bottom of each cage. This was sufficient to keep the mesocosms in place for the duration of the experiment due to the highly sheltered nature of Lough Hyne. This also meant that the starting conditions for each mesocosm were the same, except for the focal species we selected for manipulation in the experiment. We chose ten abundant benthic species (trophic roles including vertebrate and invertebrate predators, scavengers, and grazers) from the shallow subtidal of the Lough, for manipulation in the experiment. The species used were fish (black goby, *Gobius niger*; rock goby, *Gobius paganellus*; sea scorpion, *Taurulus bubalis*; shore rockling, *Gaidropsarus mediterraneus*; goldsinny wrasse, *Ctenolabrus rupestris*), crabs (shore crab, *Carcinus maenas*; velvet swimming crab, *Necora puber*), echinoderms (spiny starfish, *Marthasterias glacialis*; purple sea urchin, *Paracentrotus lividus*) and prawns (common prawn, *Palaemon serratus*). All of these species are locally common in Lough Hyne, reaching densities in the shallow subtidal during summer months that closely approximate the densities reached in our mesocosms, i.e. 1 individual per 0.45m^2 (Costello 1992; Crook *et al.* 2000; Verling *et al.* 2003; Yvon-Durocher *et al.* 2008).

The experiment consisted of eleven treatments: ten treatments contained the ten manipulated consumers, with one individual of one species in each cage; the eleventh treatment was a control cage, free of any manipulated species. Note that

these were the initial conditions. Once the treatments had been established, the cages were sealed and placed in the shallow subtidal, where benthic invertebrate species small enough to fit through the 5mm mesh were free to recruit naturally into the cages. There were three replicates of each treatment. This corresponds to a press experiment, where the densities of perturbed species are altered and maintained at predetermined levels throughout the experiment (see Bender, Case & Gilpin (1984) for an overview of press experiments and their application in community ecology). We repeated the experiment in two separate time blocks: 13th July-17th August 2006 (35 days) and 17th August-26th September 2006 (40 days). We used the same cages in each run of the experiment, scrubbing and washing the cages clean before the second experiment. Our aim was to estimate the mean direct effect and the mean net effect of all species within the mesocosm food webs a) theoretically, based on allometric predator-prey relationships; and b) empirically, based on changes in species biomass density in the presence/absence of all other species in the web.

We used two different sampling substrates to estimate the densities of benthic invertebrate species in the cages: a) settlement panels, which consisted of 100 × 100mm PVC squares, were used to estimate the density of sessile species in the mesocosms (sponges, bryozoans, calcareous polychaetes, bivalves); b) nylon pot scourers (approx. radius = 40mm; approx. height = 20mm) were used to estimate the density of mobile species within the mesocosms (amphipods, isopods, gastropods, polychaetes, etc.). The pot scourers are ideal for colonisation by benthic invertebrates and simulate the form and structure of coralline algae prevalent in the study system (O'Gorman *et al.* 2008). We measured the length of a linear dimension for every individual benthic invertebrate identified from the sampling substrates (n = 38,070). The body mass of each individual was then calculated from length-weight relationships established during the study (see Table S1).

We also noted that two small fish species (two-spot goby, *Gobiusculus flavescens*, and painted goby, *Pomatoschistus pictus*) were able to pass through the small mesh size of the cages. To estimate their densities, we carried out visual surveys on every cage in the experiment, counting the number of gobies seen in each cage over a five minute period. We also estimated the mean body size of these two fish species along the south shoreline of the Lough (n = 100 for both species). Combining all these data provided an estimate of mean density and mean body mass for most species in each of our 33 mesocosms, for both the August and September

experiments. Measuring the density or body mass of resources such as algae, CPOM, FPOM, and diatoms was problematic because of their small size. Therefore, we did not take any measurements for the basal resources. This does not affect the way we estimate interaction strength theoretically (see "*Theoretical estimates of interaction strength*" below), but it meant we could not calculate interaction strengths for the basal resources empirically.

Quantifying food web structure

We used a combination of gut content analysis and intensive literature research to establish the food web structure of the benthic cages for the August (Figure S1) and September (Figure S2) experiments. These composite food webs are built around all the species identified in the experiments (138 taxa in August; 122 taxa in September; see Table S2 for a complete list of taxa). Gut content analysis was carried out on the larger predators in the cages, i.e. manipulated species and the two small gobies (n = at least 30 guts per species). The remaining links were reviewed from the literature. Data from more than 200 publications (peer-reviewed journals and books) were standardised using the approach of Martinez (1991), i.e. a direct feeding link was assigned to any pair of species A and B within the benthic cages, whenever an investigator reported that A is likely to consume B in a typical year. This criterion was maintained throughout construction of the web and, for example, restricted the inclusion of prey links that may have occurred by chance through passive consumption. It should be noted that these webs describe the possible interactions between predators and prey, but we cannot confirm if these interactions actually take place in the experiments (see (Raffaelli & Hall 1996) for caveats of literature-based food webs). We calculated the number of trophic links for each species in the webs as the number of direct links to the species of interest, including both predators and prey (see Table S2).

Theoretical estimates of interaction strength

The theoretical measures of interaction strength characterising the mesocosm webs were calculated after Montoya *et al.* (2005), i.e. we used theory based on allometric predator-prey relationships to parameterise a community matrix, $\boldsymbol{A}$, for each of the food webs resolved in our experiments. The community matrix (or interaction coefficient matrix) is derived from the generalised Lotka-Volterra

equation and describes the average direct effect, a_{ij}, of one individual of a species on a single individual of another (unlike the Jacobian matrix, which describes the average direct effect of one individual of a species on the total population of another). The elements of the inverse community matrix following a sign reversal give the sum of the direct and indirect interactions between each species in the food web, i.e. the net effect (Bender *et al.* 1984; Yodzis 1988; Case 2000).

To theoretically estimate the direct interaction between a predator and its prey, ${}^{Th}a_{ij}$ we used the following power function:

$${}^{Th}a_{ij} = -b\left(\frac{M_j^{-0.25}}{s_j}\right)$$

where M_j is the body mass of predator j, s_j is the number of prey species consumed by predator j, the intercept b = 0.01 was arbitrarily defined (changing only the magnitude of the interaction strengths) and the exponent of -0.25 is based on allometric scaling relationships to approximate basal metabolic rate per unit biomass (Peters 1983; West *et al.* 1997; Brown & Gillooly 2003) (see Appendix S1 for a derivation of this equation). The superscripted *Th* denotes that this is a theoretically estimated measure of direct effects. Note that ${}^{Th}a_{ij}$ is derived from a feeding rate, $F_{ij} = -a_{ij}B_i^*B_j^*$, where B_i^* and B_j^* are equilibrium population biomasses of species i and j (see Neutel *et al.* 2002; Emmerson *et al.* 2005), so our resulting ${}^{Th}a_{ij}$ effects are expressed per unit biomass. To estimate the direct effect of each prey on its predator, ${}^{Th}a_{ji}$, we assumed an ecological efficiency, e, equal to 0.1 reflecting a 10% transfer of energy between trophic levels, hence ${}^{Th}a_{ji} = e \times {}^{Th}a_{ij}$ (Brown & Gillooly 2003). Note that the basal resources in the web have no prey, so their only direct effects in the system are calculated using this ecological efficiency. These values comprised the theoretically estimated elements of the community matrix. We then calculated the inverse of the community matrix, whose elements are typically given the notation $(a_{ij})^{-1}$ (Case 2000). By averaging across the absolute values in the columns of the inverse Community matrix, we obtained the mean absolute net effect per unit biomass of each species in the system, ${}^{Th}(a_{ij})^{-1}$. We calculated mean absolute net effects for both the August and September data sets. Note that the food webs were slightly different for these two months (see Figures S1 and S2) and average species body size also varied. Consequently, the theoretical estimates of interaction strength are not identical for the August and September experiments.

Empirical estimates of interaction strength

We determined the strength of species interactions empirically from our series of press experiments, comparing species changes in the presence/absence of each predator. Since our theoretical estimates of interaction strength deal with effects per unit biomass, we also quantified the empirical measures of interaction strength in units of biomass, calculated as $B = XM$, where X is the density of a given species (m^{-2}) and M is its body mass (mg). We used the dynamic index (Osenberg & Mittlebach 1996; Wootton 1997) to empirically measure the direct effect, ${}^{Em}a_{ij}$, between the manipulated species and each species in the mesocosm food webs:

$${}^{Em}a_{ij} = \frac{\ln\left(B_i^{+j} \big/ B_i^{-j}\right)}{B_j \; t}$$

where B_i^{+j} and B_i^{-j} are the biomass density of species i in the presence and absence of a predator j, B_j is the biomass density of the corresponding predator, and t is the duration of the experiment in days (similar to Brose *et al.* 2005). The superscripted *Em* denotes that this is an empirically estimated measure of direct effects. Note that the change in biomass density was only considered for species pairs where a direct predator-prey interaction takes place. Ideally, direct interaction strengths should be measured as the instantaneous growth rate of the focal species, but this is not possible in an experimental setting. Consequently, we divide through by time to obtain the growth rate of the focal species per unit of target species. These ${}^{Em}a_{ij}$ terms are directly comparable to the terms of the Community matrix, ${}^{Th}a_{ij}$ defined above. Similar to the community matrix, the dynamic index is derived from the generalised Lotka-Volterra equation (the discrete time version) (Laska & Wootton 1998). An assumption of the dynamic index is that all target species have the same initial densities. This assumption is met, as all mesocosms had the same starting conditions, i.e. empty, apart from the presence or absence of the focal (i.e. manipulated) species.

Measuring direct interaction strength is difficult. The duration of our experiments makes it unclear whether the response of species will be dominated by direct effects, indirect effects, or a mixture of the two. At the outset of the experiment, the response of each species will be dominated by direct effects. Over longer timescales indirect effects can feed back in a complex network of interacting species and hence differentiating between direct and indirect effects becomes

problematic (Wootton & Emmerson 2005). In our study system, the two experiments lasted for 35 and 40 days. This is insufficient time for entire generations of most species present to occur, but still long enough for indirect effects to become manifest, i.e. the density of a given species was not just affected directly through predation, but also indirectly through trophic (density-mediated) and non-trophic (trait-mediated) interactions (Schmitz 1997; Werner & Peacor 2003; O'Gorman *et al.* 2008). This is illustrated by the presence of positive as well as negative effects of predators on their prey when we calculate ${}^{Em}a_{ij}$. We also noted changes in the biomass density of species pairs that do not have a direct predator-prey link.

Given the highly reticulate nature of the mesocosm food webs (see Figures S1 and S2), a perturbation to just one species will have knock-on effects for virtually every species in the web. Consequently, we alter our use of the dynamic index to estimate the mean net effect (considering direct and indirect interactions) of each species in the community. First, we consider all species pairs, even if a direct predator-prey interaction does not take place. Also, we no longer divide through by time. This estimates the long-term change in abundance and is not a growth rate, thus it provides a measure of the net effect of each species, ${}^{Em}(a_{ij})^{-1}$, combining direct and indirect effects (see Laska & Wootton 1998). As such, these ${}^{Em}(a_{ij})^{-1}$ effects are comparable to the terms of the negative inverse of the community matrix, ${}^{Th}(a_{ij})^{-1}$ (Bender *et al.* 1984; Yodzis 1988; Schmitz 1997). It is important to note that in the empirical estimates of interaction strength, species *j* can have an indirect effect on species *i*, even if they are not linked along a food chain, because we are accounting for non-trophic interactions (e.g. interference competition, behavioural reactions). This is subtly different from the inverse community matrix, which only takes account of trophic interactions (i.e. direct interactions and density-mediated indirect interactions). As such, we can expect to see some differences in our comparison of theoretical and empirical estimates of interaction strength. If our experiment is dominated by direct effects, the correlation between our theoretical and empirical estimates of direct effects (${}^{Th}a_{ij}$ and ${}^{Em}a_{ij}$, respectively) should be strongest. If our experiment is dominated by net effects, the correlation between our theoretical and empirical estimates of net effects (${}^{Th}(a_{ij})^{-1}$ and ${}^{Em}(a_{ij})^{-1}$, respectively) should be strongest.

The design of the experiment facilitated a comparison of the biomass density of benthic invertebrate species in the presence and absence of the ten manipulated

species (by comparing each of the cages containing manipulated species to the mean of the control cages). However, it was also possible to obtain estimates of the direct/net effect of each benthic invertebrate species on every other species in the mesocosms. Since most benthic invertebrate species were absent from at least some of the cages, we were able to average across the biomass densities of every species in cages where a given benthic invertebrate species was present (B_i^{+j}) and compare this to the average of every species in cages where the same benthic invertebrate species was absent (B_i^{-j}). In this way, we were able to quantify the effects in each mesocosm attributable to a particular species and thus obtain estimates of the mean absolute direct/net effect of almost all species in the mesocosm webs (some species were present in all treatments and so we could not obtain a comparison with their absence).

Exploration of body mass patterns

To investigate the relative importance of interaction strength (determined by body mass) versus food web topology, we randomised the empirical pattern of body masses within the food webs (n = 1000 permutations). We calculated per unit biomass effects, using allometric predator-prey relationships to parameterise the community matrix $\boldsymbol{A}$ (as above). We then calculated the mean absolute net effect of each species (averaging across the 1000 permutations) in the inverse community matrix $\boldsymbol{A}^{-1}$. We also investigated the relationship between body size and number of trophic links, given that we know these food webs to be highly size structured, i.e. big species typically eat smaller species and so they are more likely to be highly connected.

Results:

Theoretical estimates of interaction strength

To test for patterns in the theoretically predicted net effects data, we first plotted the frequency distribution of absolute net effects. This reveals a clear skew towards weak effects, with relatively few strong interactions for both the August and September data sets (see Figure 1*A*-*B*). The frequency distribution of direct effects is similarly skewed towards weak effects, but this pattern is not shown. We also plotted the theoretical estimate of the mean absolute direct effect and net effect for each species (a measure of species impact in the system) as a function of the number of

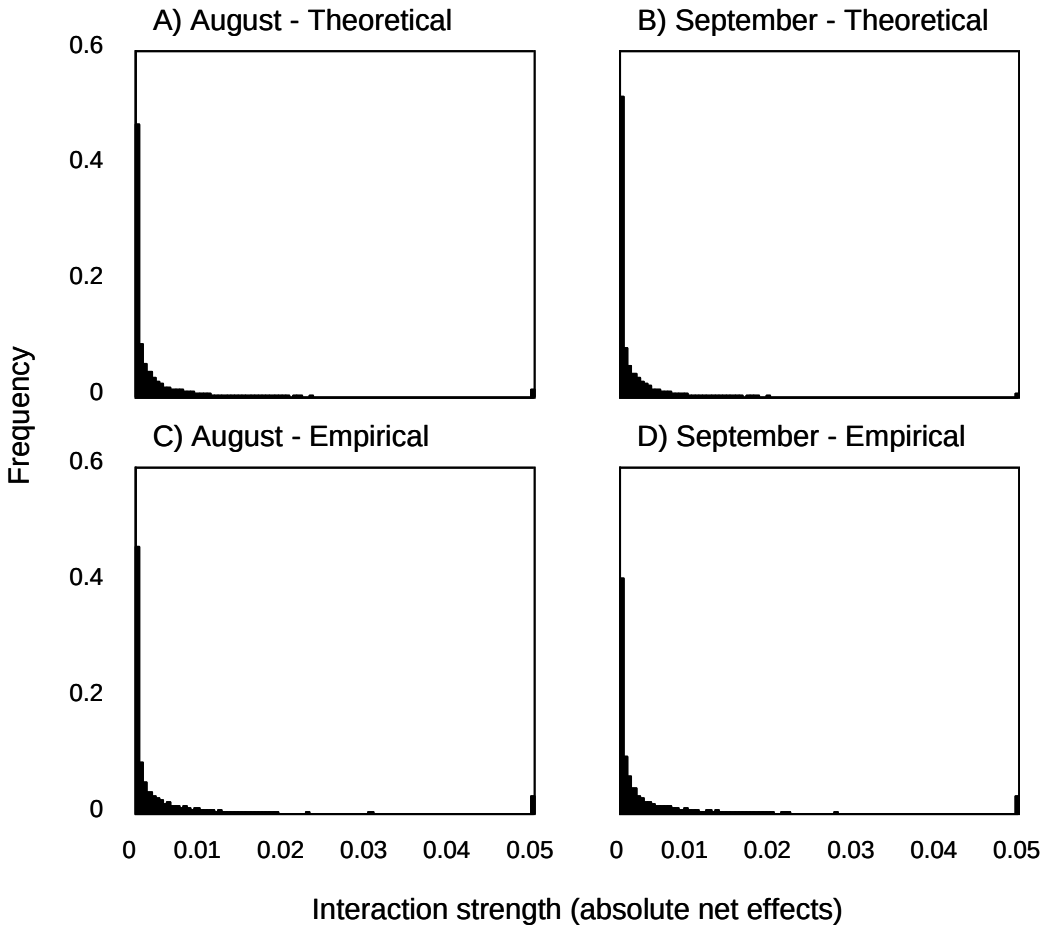

Figure 1. Frequency distribution of absolute net effects, measured (*A*-*B*) theoretically and (*C*-*D*) empirically for the two experimental time periods (i.e. the experiment ending in August and the experiment ending in September). The distribution of interaction strengths is highly skewed towards weak effects.

trophic links for that species. As the number of trophic links increased, the mean direct effect ($^{Th}a_{ij}$) of each species in the web decreased, and this relationship was highly significant for both August (Exponential regression: $F_{1,136} = 467.32$, $p < 0.001$, Figure 2*A*) and September (Exponential regression: $F_{1,120} = 419.76$, $p < 0.001$, Figure 2*B*). It should be noted that while the relationships in Figure 2*A*-*B* seem to be largely driven by some of the manipulated species (cloud of points in the lower right hand corner of the figure), significant negative relationships remain even if they are removed from the analysis for both August (Exponential regression: $F_{1,126} = 267.60$, $p < 0.001$) and September (Exponential regression: $F_{1,110} = 275.09$, $p < 0.001$). As the number of trophic links increased, the mean net effect ($^{Th}(a_{ij})^{-1}$) of each species in the web also decreased, and this relationship was highly significant for both August (Exponential regression: $F_{1,136} = 170.15$, $p < 0.001$, Figure 3*A*) and September (Exponential regression: $F_{1,120} = 175.64$, $p < 0.001$, Figure 3*B*). Again, highly significant negative relationships remain after the manipulated species are removed from the analysis for both August (Exponential regression: $F_{1,126} = 41.74$, $p < 0.001$) and September (Exponential regression: $F_{1,110} = 55.59$, $p < 0.001$).

Empirical estimates of interaction strength

We also plotted the frequency distribution of empirically measured net effects. Similar to the theoretical estimates, these are clearly skewed towards weak net effects for both the August and September experiments (see Figure 1*C*-*D*). Again, the frequency distribution of direct effects is similarly skewed towards weak effects, but this pattern is not shown. The empirical estimates of mean absolute direct effect ($^{Em}a_{ij}$) were considered as a function of the number of trophic links for each species. There was a significant negative relationship for both the August (Exponential regression: $F_{1,87} = 26.18$, $p < 0.001$, Figure 2*C*) and September (Exponential regression: $F_{1,79} = 26.20$, $p < 0.001$, Figure 2*D*) experiments. Note that the residual degrees of freedom vary in the empirical relationships because direct effects could not be calculated for all species (see Materials and Methods). If we remove the manipulated species from the analysis, the August relationship breaks down (Exponential regression: $F_{1,77} = 2.48$, $p = 0.119$), while a significant negative relationship remains for September (Exponential regression: $F_{1,69} = 6.31$, $p = 0.014$). The empirical estimates of mean absolute net effect ($^{Em}(a_{ij})^{-1}$) were also considered as a function of the number of trophic links for each species. There was a highly

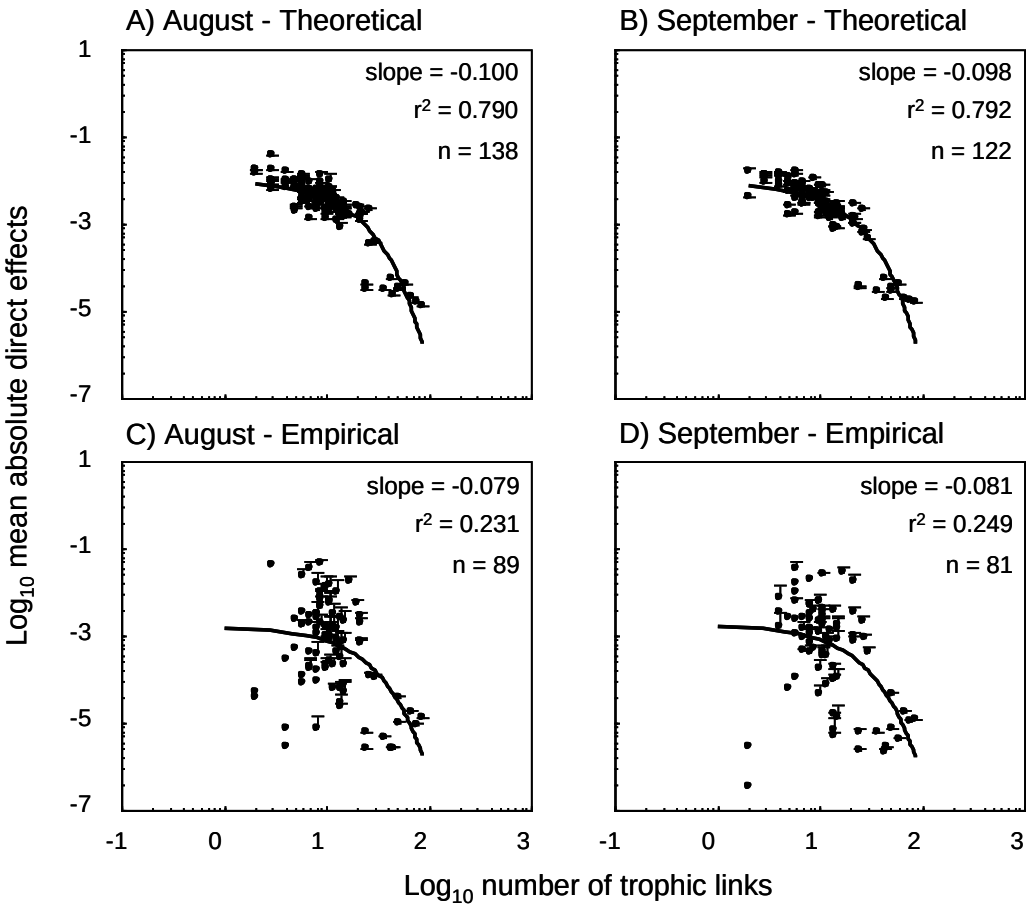

Figure 2. Mean absolute direct effect (+SE) of each species on all other species in the mesocosm food webs, plotted against number of trophic links (considering both predator and prey links for each species). Direct effects were calculated (*A-B*) theoretically, using allometric predator-prey relationships and (*C-D*) experimentally, as growth rates of predators for the two experimental time periods. Values are plotted on a log-log scale with an exponential line of best fit.

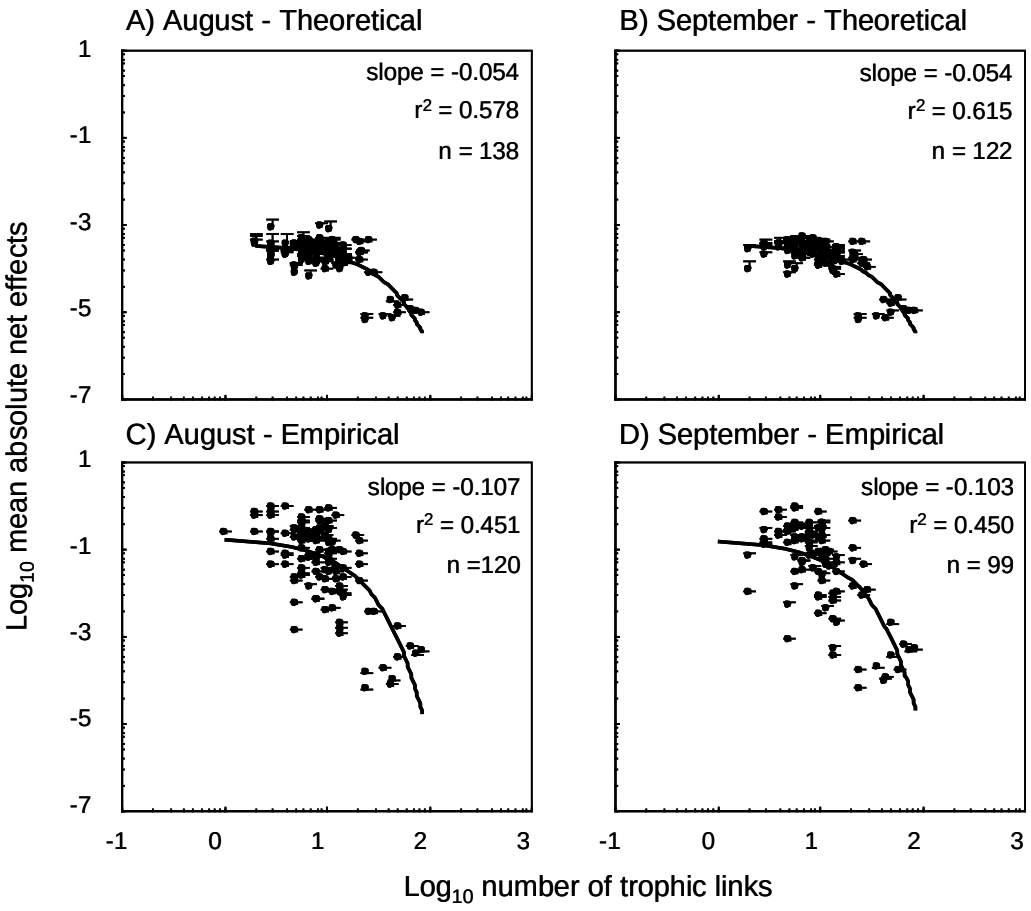

Figure 3. Mean absolute net effect (+SE) of each species on all other species in the mesocosm food webs, plotted against number of trophic links (considering both predator and prey links for each species). Net effects were calculated (*A-B*) theoretically, using allometric predator-prey relationships and (*C-D*) experimentally, in the presence/absence of predators/competitors for the two experimental time periods. Values are plotted on a log-log scale with an exponential line of best fit.

significant negative relationship for both the August (Exponential regression: $F_{1,119}$ = 96.74, p < 0.001, Figure 3*C*) and September (Exponential regression: $F_{1,98}$ = 79.43, p < 0.001, Figure 3*D*) experiments. Here, highly significant negative relationships remain even if the manipulated species are removed from the analysis for both August (Exponential regression: $F_{1,109}$ = 41.89, p < 0.001) and September (Exponential regression: $F_{1,88}$ = 41.26, p < 0.001).

Exploration of body mass patterns and correlations

We found a significant correlation between average species body size and the number of trophic links for both the August (Pearson's r = 0.550, p < 0.001) and September (Pearson's r = 0.573, p < 0.001) food webs. We also found a significant correlation between the theoretical and empirical estimates of mean absolute direct effects for both August (Pearson's r = 0.622, p < 0.001; Figure 4*A*) and September (Pearson's r = 0.669, p < 0.001; Figure 4*B*). There was a significant, but weaker correlation between total absolute direct effects for both August (Pearson's r = 0.328, p = 0.002) and September (Pearson's r = 0.400, p < 0.001). We found an even stronger correlation between the theoretical and empirical estimates of mean absolute net effects for both August (Pearson's r = 0.877, p < 0.001; Figure 4*C*) and September (Pearson's r = 0.886, p < 0.001; Figure 4*D*). Again, there was a significant, but weaker correlation between total absolute net effects for both August (Pearson's r = 0.661, p < 0.001) and September (Pearson's r = 0.735, p < 0.001). Lastly, when we compared the interaction strengths from our two experiments, we found significant correlations between the August and September estimates of ${}^{Th}a_{ij}$ (Pearson's r = 0.984 p < 0.001), ${}^{Th}(a_{ij})^{-1}$ (Pearson's r = 0.962, p < 0.001), ${}^{Em}a_{ij}$ (Pearson's r = 0.760, p < 0.001) and ${}^{Em}(a_{ij})^{-1}$ (Pearson's r = 0.906, p < 0.001) (see Figure S3 for these correlations). Note that all data were $\log_{10}$ transformed to meet the assumptions of normality for these correlations.

After randomising the pattern of body masses within each food web (n = 1000) and re-calculating net effects, we found a significant negative relationship between the mean absolute net effect of each species and the number of trophic links for both the August (Exponential regression: $F_{1,136}$ = 85.75, p < 0.001, Figure 5*A*) and September (Exponential regression: $F_{1,120}$ = 100.74, p < 0.001, Figure 5*B*) food webs.

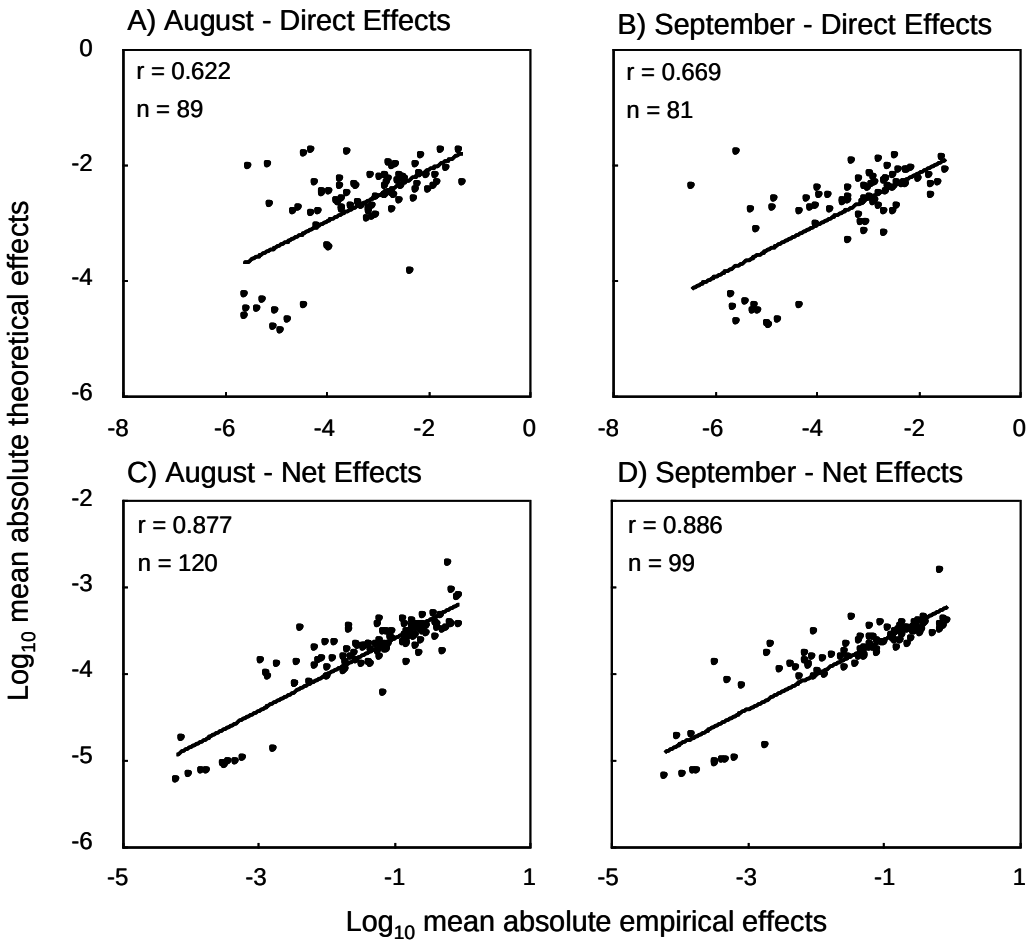

Figure 4. Correlations between theoretical and empirical estimates of (*A*-*B*) mean absolute direct effects and (*C*-*D*) mean absolute net effects for the August and September data sets. Values are plotted on a log-log scale with a power fitting.

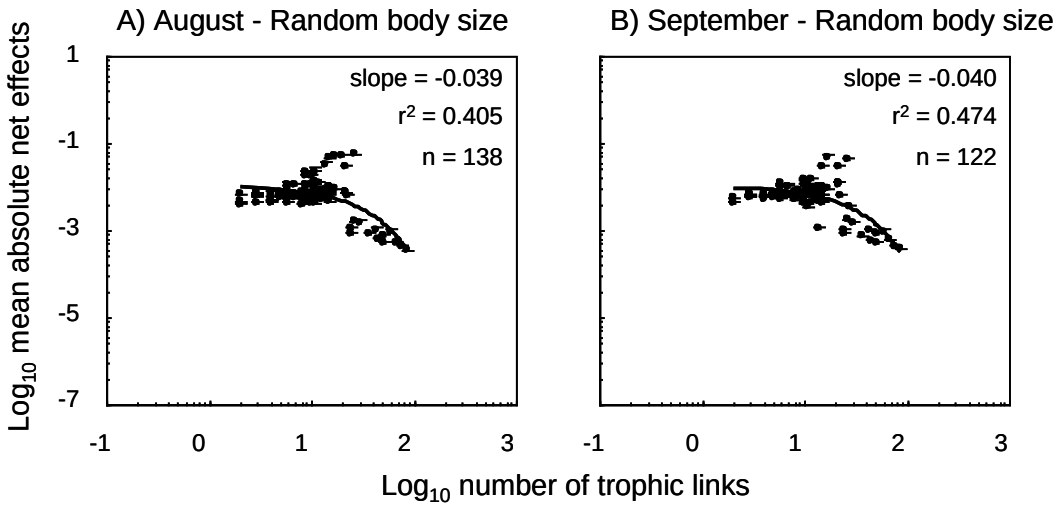

Figure 5. Mean absolute net effect (+SE) of each species on all other species in the mesocosm food webs, plotted against number of trophic links (considering both predator and prey links for each species). Net effects were calculated theoretically after random rewiring of predator and prey body masses for the two experimental time periods. Values are plotted on a log-log scale with an exponential line of best fit.

Discussion:

Our study confirms many of the interaction strength patterns found in other systems. Our theoretical and empirical estimates of net effects show a remarkably similar distribution of interaction strengths, which is highly skewed towards weak effects (see Figure 1). This arrangement of interaction strengths appears to be a fundamental blueprint for the stability of complex communities (McCann *et al.* 1998; Neutel *et al.* 2002), dampening the destabilising potential of strong consumer-resource interactions (McCann 2000). We also see a clear pattern of lower mean interaction strength (direct effects and net effects) for the more highly connected species, using both empirical and theoretical estimates (see Figures 2 and 3). Such effects manifest in theoretical explorations of other complex food webs, such as the Ythan Estuary and Broadstone Stream (Montoya *et al.* 2005), but have never been demonstrated empirically. This pattern appears to ensure that complex communities with many highly connected species will be more resilient to extinction perturbations than simple communities with fewer links (Montoya *et al.* 2009), most likely due to an increasing number of pathways for species to dampen impacts of population fluctuations (MacArthur 1955). Dunne *et al.* (2002) and Coll *et al.* (2008) have demonstrated that perturbations to highly connected species have the largest effect on the robustness of model food webs. While this initially appears to contradict our findings, it should be noted that the perturbation in these studies was extinction of highly connected species. If highly connected species tend to have weaker effects (as we have shown), then removal of these species should increase the mean interaction strength of the community, limiting the coexistence of many species (Kokkoris *et al.* 2002) and making the food web more sensitive to species removal (Dunne *et al.* 2002).

The pattern appears to be largely driven by the highly size-structured nature of the communities and the fact that body size is correlated to the number of trophic links. Here, highly connected species tend to be large and so have small direct/net effects per unit biomass in the community. As such, we argue that the general pattern demonstrated within the Lough Hyne system will be applicable to a wide range of size-structured communities, particularly marine and freshwater systems (Jennings *et al.* 2001; Jonsson *et al.* 2005). We caution that the relationship is less likely to be found in poorly size-structured communities, such as terrestrial food webs, where the direct/net effect per unit biomass of each species is likely to be consistent,

irrespective of its connectedness. We demonstrate however, that the relationship between number of trophic links and interaction strength remains even after removing the ten largest species from the current analysis. Here, we obtain two clouds of data in all the panels in Figures 2 and 3 as we are missing information on the direct/net effect of organisms with body sizes intermediate to the large manipulated species and the small benthic invertebrates that assembled through the small mesh size of the cages. Two exceptions are the painted and two spot gobies, which do bridge the gap in our regression lines in Figures 2 and 3. With more information on intermediate-sized species, it is likely that the relationships (and r^2 values) would be much stronger.

The weakest patterns are shown for the empirically estimated direct effects. Less than 25% of the variability in number of trophic links is explained by our empirically estimated direct effects. The relationship is weakest for the experiment ending in August, where the negative relationship breaks down with the removal of the ten largest species from the analysis. This suggests that other factors are diluting our estimation of the direct interaction between a predator and its prey, accentuated by the tightly fitting relationship between the theoretically predicted direct effects and the number of trophic links (see Figure 2). This is further illustrated by the considerably lower correlation between our theoretical and empirical estimates of direct effects, compared to net effects (see Figure 4). These results indicate that the duration of our experiments was indeed sufficient for indirect effects to become manifest and that the experimental food webs are dominated by a mixture of direct and indirect effects. Consequently, our empirical measures of net effects offer a clearer insight into the interactions taking place in the system.

It is recognised that biodiversity-ecosystem functioning (BEF) research needs to evolve from a largely confirmatory science to a more predictive discipline (Naeem & Wright 2003). Central to that dictum is the need for unifying patterns in natural systems that can be identified, measured, and predicted within the logistical constraints of the natural world. Such an approach will require the integration of sub-disciplines (Ives *et al.* 2005), including BEF research and investigations of predator-prey interactions (PPI), which ultimately describe food webs. A concerted research effort has demonstrated that the patterning of interaction strengths between predators and their prey is a vital ingredient in the successful functioning of complex ecosystems (McCann *et al.* 1998; Neutel *et al.* 2002; Emmerson & Raffaelli 2004;

Montoya *et al.* 2005; O'Gorman & Emmerson 2009). Like so much of BEF research, however, there is a large disparity between these studies in the methods used for calculating interaction strength, both within and between theoretical and empirical investigations. To promote an integration of BEF and PPI research as a predictive science, we need to concentrate our efforts on standardising methodologies in all aspects of the discipline.

In this study, we show the predictive power of the community matrix for estimating the strength of species interactions in real food webs. With information on the body size and diet of all the species in our webs, we were able to estimate the strength of the interactions (direct and indirect) between all species. The interaction strengths predicted using this modelling approach are correlated to empirical measurements of interaction strength taken in the field over two separate time periods (particularly for the net effects). Importantly, the method we used for predicting interaction strengths theoretically is closely matched to our empirical measurement of interaction strengths (although they do differ in several assumptions, which are discussed below). Schmitz (1997) demonstrated that the inverse community matrix could be used to predict the outcome of field press experiments. Those results, in conjunction with our study, highlight the potential importance of the inverse community matrix in predicting knock-on effects of perturbations in natural food webs, through complex chains of trophic interactions.

While our study shows the large manipulated species have the weakest effects per unit biomass in the system, it is also interesting to examine the taxa with the strongest effects. Perhaps surprisingly, predatory polychaetes (particularly the Syllidae and Nereidae), hydroids, cyclopoid copepods, some amphipods (Corophiidae and Dexaminidae), and micro-gastropods had the strongest mean interaction strength per unit biomass. Nereid polychaetes have previously been shown to play an important role in structuring soft-bottom communities (Commito 1982). Deposit feeding amphipods are known to have dramatic effects on the abundance of important basal resources (Gerdol & Hughes 1994). Copepods serve as major grazers of phytoplankton (Turner 2004) and as an important link between microbial and pelagic food webs (Roff *et al.* 1995). Small hydroids and gastropods can be extremely abundant in shallow marine benthic communities and are likely to have large impacts on the system through suspension feeding and grazing. Little is known about their importance in an overall food web context and their role as strong

interactors in the experimental food webs described here highlights the need for detailed study of such species.

It should be noted that there are sources of error involved in the estimation of both the theoretical and empirical effects. For the theoretical estimates, we assumed a 10% transfer of energy between trophic levels to estimate the direct effect of each prey on its predator. This assumption is based on the second law of thermodynamics, which implies a low efficiency of energy transfer between trophic levels (Brown & Gillooly 2003). Empirical measurements of the transfer efficiency of energy between trophic levels often range from 5-15% (Lindeman 1942; Slobodkin 1962; Pauly & Christensen 1995), although this can vary depending on the system and the type of organism (Turner 1970; Slobodkin 2001). In the absence of more detailed data for individual predator-prey pairs, a 10% transfer of energy is a reasonable approximation. The value of the intercept in the power function is arbitrarily defined. This will not change the qualitative nature of the negative relationship between the net effects and number of trophic links, but it can affect the magnitude of the interaction strengths. While our theoretical and empirical estimates of direct effects were of the same order of magnitude, our theoretical estimates of net effects tended to be an order of magnitude lower than our empirical estimates of net effects. Changing the value of the intercept would correct this difference. We also accept that the use of a metabolic scaling exponent of -0.25 (derived from $M^{0.75}$ divided through by mass, to express effects in units of biomass; see Appendix S1) can be contentious (Kozlowski & Konarzewski 2004) and works best when spanning body sizes from whales to microbes (West *et al.* 1997). But we contend that the body sizes of organisms in our study still span over 10 orders of magnitude. This is comparable to Tuesday Lake, one of the best defined food webs in the literature, which finds body mass-abundance relationships that agree with a metabolic scaling of 0.75 (or -0.25 per unit biomass) (Jonsson *et al.* 2005).

In the empirical estimates of direct effects, the units of time used in the dynamic index are undefined. We chose to measure the duration of the experiment in days, but the magnitude of the empirical direct effects would be different if we had chosen weeks or hours. Again, this does not alter the qualitative, only the quantitative nature of the results. The empirical estimates of net effects also incorporate non-trophic, as well as trophic, interactions. This is different from the theoretical estimates of net effects, which do not take account of non-trophic

interactions in the food webs. It is compelling that we find the same patterns, and indeed a strong correlation between the theoretical and empirical estimates of interaction strength, over two separate time periods, in spite of these issues (see Figure 4). This also suggests that the presence of non-trophic interactions in the empirical measures of interaction strength is not sufficiently important to overwhelm the patterns shown in the theoretical estimates, in spite of previous evidence highlighting the importance of (non-trophic) trait-mediated indirect interactions (Schmitz *et al.* 2004; Preisser *et al.* 2005; O'Gorman *et al.* 2008).

Lastly, it should be noted that net effects measure the combined contribution of every species present in a system on a particular species, in response to a manipulation of another species. Thus, each net effect is uniquely associated with the species composition of the community in which it is measured. We also acknowledge that stochastic processes associated with these complex natural communities will lead to variation in species composition, which is impossible to control for experimentally. This can lead to misinterpretation of the empirical net effects and probably accounts for much of the unexplained variability in the relationships with the number of trophic links. In addition, our experimental design necessitated that each sub-community began with a different manipulated species in isolation. The extent to which the net effects would change for the aggregate communities shown in Figures S1 and S2 is unknown and beyond the scope of the present study. Future studies could examine the extent to which a species' mean net effect in the community changes with the addition or removal of highly connected species.

Interestingly, we find that the pattern of decreasing mean net effects with increasing number of trophic links still holds when we randomise the body sizes used to theoretically predict interaction strength (see Figure 5). Given two predators of equal size, we would expect the more highly connected predator to have weaker net effects because of s_j in our equation for ${}^{Th}a_{ij}$. By randomising body size, however, we would expect some cases where highly connected predators are very small and so possess weak net effects. This implies that the strength of direct trophic interactions (and hence the empirical pattern of body mass) is not the factor driving the magnitude of the net effects (Yodzis 1988). Rather, the pattern of net effects seems to be intrinsically linked to the topology of the food web. The definitive test of this would be to randomise topology and see if the pattern between net effects and

number of trophic links is destroyed. To randomise topology is to completely change the interacting species and the structure of the food webs under investigation however, and this is no longer a viable comparison with our other estimates of species net effects.

Many studies have quantified the importance of structured hierarchies for the determination of food web topology (Williams & Martinez 2000; Petchey *et al.* 2008). In this context, food web structure reflects the topological arrangement of interaction strengths, which are also known to be size structured. Whilst, the arrangement of direct effects, determined by the empirical pattern of predator and prey body mass, has been shown to affect food web stability (Emmerson & Raffaelli 2004; Brose *et al.* 2005; Otto *et al.* 2007), here the identity of the predators and their prey and their respective body masses also contribute to food web topology. This suggests a deficit in our understanding of food web structure and function and implies that there is a need to integrate dynamic and topological approaches for predicting the behaviour of complex systems, which is currently missing (although see Petchey *et al.* 2008). The approach presented here provides a way of identifying the relative importance of species in a food web context. We have been able to show that there is a strong relationship between empirical and theoretical patterns in the same complex natural food web, which is worthy of further exploration in a wider range of experimental systems. Such a multi-system approach to predicting changes in species importance and the magnitude of species interactions would be an extremely useful tool in conservation biology.

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Appendix S1. Derivation of the power function shown in the Materials and Methods, "*Theoretical estimates of interaction strength*": $^{Th}a_{ij} = -b\left(\frac{M_j^{-0.25}}{s_j}\right)$.

To estimate the strength of trophic interactions per unit biomass, we used allometric theory and the formulation of De Ruiter *et al.* (1995). These authors assumed that, at equilibrium, the terms of the Jacobian matrix, $\boldsymbol{C}$, ($c_{ij} = a_{ij}B_i^*$) are equivalent to the terms from a steady state model developed by Hunt *et al.* (1987), so that:

$$a_{ij}B_i^* = -\left(\frac{F_{ij}}{B_j^*}\right) \qquad \text{Eq. (1)}$$

Here, a_{ij}, represents a per unit biomass effect of species j on species i, B_i^* and B_j^* represent the biomass densities of species i and species j, respectively, and F_{ij} represents the per unit biomass feeding rate of species j on species i. The general relationship between body size and density reported by Peters (1983) and predicted by metabolic theory (Brown & Gillooly 2003) is $X \sim M^{-1}$, assuming that this represents an estimate of the equilibrium population size for each species. Thus, $B = X \times M = M^{-1} \times M^{1} = M^{0}$. We assumed that the per unit biomass feeding rate of species j, F_j, could be approximated by the mass specific metabolic rate, defined as $M_j^{-0.25}$ (Peters 1983; West *et al.* 1997; Brown & Gillooly 2003; see also Otto *et al.* 2007). Predator j must spread its feeding effort across a range of prey, belonging to the set Ω_j, and hence we defined the preference p_{ij} of predator j for prey i (where $i \in \Omega$) as being proportional to prey biomass abundance in the set Ω_j, so that:

$$p_{ij} = \frac{B_i}{\sum_{i\in\Omega}^{s} B_i} = \frac{M_i^0}{\sum_{i\in\Omega}^{s} M_i^0} = \frac{1}{s_j} \qquad \text{Eq. (2)}$$

Here, s defines the number of prey species of predator j. Therefore, predator j spreads its feeding effort evenly among its prey. The per unit biomass feeding rate of species j on species i is defined as:

$$F_{ij} = F_j p_{ij} = M_j^{-0.25}\left(\frac{1}{s_j}\right) = \frac{M_j^{-0.25}}{s_j} \qquad \text{Eq. (3)}$$

By rearranging Eq. (1) above we can estimate the per unit biomass effect of species *j* on species *i*, so that:

$$a_{ij} = -\left(\frac{F_{ij}}{B_i^* B_j^*}\right) \qquad \text{Eq. (4)}$$

By combining Eq. (3) and Eq. (4), and substituting the allometries for biomass, we find:

$$a_{ij} = -\frac{\left(\frac{M_j^{-0.25}}{s_j}\right)}{M_i^0 M_j^0} = -\frac{M_j^{-0.25}}{s_j} \qquad \text{Eq. (5)}$$

Therefore, the per unit biomass effects of species *j* on species *i* can be estimated simply by the mass specific metabolic rate of predator *j* divided by the number of prey species of predator *j*.

Table S1. Length-weight (*L-W*) relationships used to estimate body size of all taxa identified in the experiment. For taxa with no *L-W* relationship, we identified the closest taxa in terms of body shape and used that *L-W* relationship as a substitute (see Table S2 for a list of *L-W* relationships used for each species in the food web). Length (x) is measured in mm. Weight (y) is measured in mg.

Code	Taxa	*L-W* Relationship	r^2
LW1	*Carcinus maenas* [1]	$y = 0.2668x^{2.9545}$	0.9693
LW2	*Ctenolabrus rupestris* [2]	$y = 0.0057x^{3.181}$	0.9734
LW3	*Gaidropsarus mediterraneus* [2]	$y = 0.0008x^{3.3972}$	0.9847
LW4	*Gobius niger* [2]	$y = 0.0074x^{3.0788}$	0.9320
LW5	*Gobius paganellus* [2]	$y = 0.0014x^{3.4672}$	0.9356
LW6	*Marthasterias glacialis* [3]	$y = 0.3088x^{2.7417}$	0.9187
LW7	*Necora puber* [1]	$y = 0.2989x^{2.9639}$	0.9204
LW8	*Palaemon serratus* [4]	$y = 0.0014x^{3.3838}$	0.9201
LW9	*Paracentrotus lividus* [5]	$y = 1.2774x^{2.737}$	0.9398
LW10	*Taurulus bubalis* [2]	$y = 0.0032x^{3.3258}$	0.9604
LW11	*Gobiusculus flavescens* [2]	$y = 0.0004x^{3.7234}$	0.9612
LW12	*Pomatoschistus pictus* [2]	$y = 0.0039x^{3.1954}$	0.9733
LW13	*Alvania* spp. [6]	$y = 0.1391x^{2.71}$	0.9877
LW14	*Anomia ephippium* [7]	$y = 0.0304x^{2.9244}$	0.9428
LW15	*Aora gracilis* [8]	$y = 0.0018x^{3.2994}$	0.9202
LW16	Aoridae [8]	$y = 0.0031x^{2.8427}$	0.9596
LW17	*Bittium reticulatum* [6]	$y = 0.1224x^{2.3117}$	0.9831
LW18	*Buccinum undatum* [6]	$y = 0.0958x^{3.0601}$	0.9804
LW19	Cardiidae [7]	$y = 0.1084x^{3.0951}$	0.9870
LW20	*Chlamys varia* [7]	$y = 0.0508x^{3.036}$	0.9893
LW21	*Clathrina coriacea* [9]	$y = 0.2909x^{1.9999}$	0.9541
LW22	*Crassicorophium* spp. [8]	$y = 0.0046x^{3.1972}$	0.9491
LW23	*Crisia* spp. [9]	$y = 0.00004x^{2.6928}$	0.9691
LW24	Cumacea [4]	$y = 0.0101x^{1.9552}$	0.8806
LW25	*Epilepton clarkiae* [7]	$y = 0.0959x^{2.8774}$	0.9805
LW26	Foraminifera [9]	$y = 0.1598x^{3.2349}$	0.9801
LW27	*Galathea squamifera* [8]	$y = 0.0284x^{4.3903}$	0.9353
LW28	*Hiatella arctica* [4]	$y = 0.053x^{2.9161}$	0.9540
LW29	*Janua pagenstecheri* [9]	$y = 0.1117x^{3.0229}$	0.9314
LW30	*Lembos websteri* [8]	$y = 0.0037x^{2.6724}$	0.9806
LW31	*Lysianassa ceratina* [8]	$y = 0.0096x^{3.0979}$	0.9877
LW32	Melitidae [8]	$y = 0.004x^{3.095}$	0.9598
LW33	*Microdeutopus anomalus* [8]	$y = 0.0016x^{3.3615}$	0.9685

LW34	*Musculus discors* [7]	$y = 0.0986x^{2.7968}$	0.9766
LW35	Mysidae [4]	$y = 0.0006x^{3.2529}$	0.9236
LW36	Nudibranchia [9]	$y = 0.0096x^{2.8116}$	0.9726
LW37	*Ophiothrix fragilis* [10]	$y = 0.4875x^{2.9185}$	0.9435
LW38	*Ophiura ophiura* [10]	$y = 0.2936x^{2.5329}$	0.9603
LW39	Ostracoda [9]	$y = 0.1738x^{4.2678}$	0.7896
LW40	*Parvicardium exiguum* [7]	$y = 0.1104x^{3.0932}$	0.9786
LW41	*Parvicardium ovale* [7]	$y = 0.1018x^{3.1784}$	0.9900
LW42	*Parvicardium scabrum* [7]	$y = 0.1103x^{3.0607}$	0.9870
LW43	Pectinidae [7]	$y = 0.0698x^{2.8284}$	0.9871
LW44	*Perinereis cultrifera* [9]	$y = 0.0015x^{3.0023}$	0.9733
LW45	*Pilumnus hirtellus* [1]	$y = 0.1324x^{2.963}$	0.9438
LW46	*Platynereis dumerilii* [9]	$y = 0.0113x^{2.2781}$	0.8051
LW47	Polychaeta [9]	$y = 0.0021x^{2.395}$	0.8612
LW48	*Pomatoceros* spp. [11]	$y = 0.0029x^{2.781}$	0.9688
LW49	*Rissoa* spp. [6]	$y = 0.1532x^{2.3992}$	0.9691
LW50	*Tubulipora liliacea* [9]	$y = 0.0504x^{2.5072}$	0.9272

For each taxon, length is measured as:

[1] Widest part of the carapace.

[2] Tip of the mouth to the base of the tail (straight line along the midline).

[3] Centre of the oral surface to the tip of the longest arm.

[4] Tip of the rostrum to the base of the telson (straight line along the top surface of the animal).

[5] Diameter of the test.

[6] Straight line from the apex to the base.

[7] Straight line from the umbo to the ventral margin.

[8] Tip of the head to the base of the abdomen (straight line along the top surface of the animal).

[9] Straight line along the longest dimension.

[10] Diameter of the oral disc (all legs frequently damaged).

[11] Line following the ridge from the tip of the operculum to the base of the tube.

Table S2. Names and codes for all 150 taxa identified in the two mesocosm experiments. A code for the length-weight (*L-W*) relationship used to estimate the body mass of each taxon is provided (see Table S1 for the *L-W* relationships that correspond to each code). The number of trophic links (*TL*) and trophic height (*TH*) of each taxon are also presented for the two experiments (ending in August and September).

Code	Taxa	*L-W*	*TL* Aug	*TL* Sep	*TH* Aug	*TH* Sep
1	*Carcinus maenas*	LW1	31	33	5.12	5.20
2	*Ctenolabrus rupestris*	LW2	61	55	5.23	5.32
3	*Gaidropsarus mediterraneus*	LW3	41	40	5.88	6.00
4	*Gobius niger*	LW4	74	62	4.74	4.89
5	*Gobius paganellus*	LW5	81	69	5.17	5.32
6	*Marthasterias glacialis*	LW6	19	23	6.04	6.09
7	*Necora puber*	LW7	22	23	5.58	5.67
8	*Palaemon serratus*	LW8	49	47	4.35	4.48
9	*Paracentrotus lividus*	LW9	5	5	2	2
10	*Taurulus bubalis*	LW10	43	35	4.88	4.98
11	*Gobiusculus flavescens*	LW11	43	38	3.72	3.53
12	*Pomatoschistus pictus*	LW12	56	56	3.51	3.76
13	*Abra alba*	LW25	8	9	2	2
14	*Acanthocardia echinata*	LW19	7		2	
15	*Acanthocardia tuberculata*	LW19	6		2	
16	*Aequipecten opercularis*	LW43	15	13	2.68	2.63
17	*Alvania beani*	LW13	8	8	2	2
18	*Alvania semistriata*	LW13	5		2	
19	*Ammonicera rota*	LW49	3		2	
20	*Anomia ephippium*	LW14	15	15	2	2
21	*Aora gracilis*	LW15	13	13	3.07	3.07
22	*Apherusa bispinosa*	LW32	6	6	2	2
23	*Apseudes latreillei*	LW24	8	8	2	2
24	*Apseudes talpa*	LW24	6	6	2	2
25	*Asterina phylactica*	LW6		14		3.57
26	*Bittium reticulatum*	LW17	21	20	2.81	2.78
27	*Boreotrophon truncatus*	LW18	5		2	
28	*Buccinum undatum*	LW18		11		3.71
29	Calanoida	LW24	20		2	
30	*Callopora lineata*	LW21	5	5	2	2
31	*Caprella acanthifera*	LW16	8		2	
32	*Caprella equilibra*	LW16	11		3.30	
33	*Caprella linearis*	LW16	8	8	3.47	3.47
34	*Ceradocus semiserratus*	LW32	3	3	2	2
35	*Cerastoderma edule*	LW19		10		3.21
36	*Cerithiopsis tubercularis*	LW17	13	12	2.50	2
37	Chironomidae spp.	LW47	8	8	2	2
38	*Chlamys varia*	LW20	10	10	2	2
39	*Circulus striatus*	LW26	6		2	
40	*Clathrina coriacea*	LW21	7	8	2	2
41	*Cliona celata*	LW21	11		2	
42	*Coriandria fulgida*	LW49	11	11	2	2

43	*Crassicorophium bonnellii*	LW22	13	12	2	2
44	*Crassicorophium crassicorne*	LW22	15	14	2	2
45	*Crisia denticulata*	LW23	11		2	
46	*Crisia eburnea*	LW23	9		2	
47	*Cuthona A*	LW24	2		3.67	
48	Cyclopoida	LW39	21	18	2.50	2
49	*Cythere lutea*	LW39	6	6	2	2
50	*Dexamine spinosa*	LW32	7	7	2	2
51	*Dexamine thea*	LW32	4	4	2	2
52	*Elasmopus rapax*	LW32	6	6	2	2
53	*Elysia viridis*	LW36	3	3	2	2
54	*Epilepton clarkiae*	LW25	10	11	2	2
55	*Epitonium clathrus*	LW18		2		3.67
56	*Ericthonius brasiliensis*	LW22	15	15	2.36	2.36
57	*Ericthonius punctatus*	LW22	15	15	2.36	2.36
58	*Eubranchus farrani*	LW36	2	2	3.67	3.67
59	*Exogone gemmifera*	LW47	5	6	2	2
60	*Foraminifera A*	LW26	10	10	2	2
61	*Foraminifera B*	LW26	10	10	2	2
62	*Foraminifera C*	LW26	6	6	2	2
63	*Foraminifera D*	LW26	5	5	2	2
64	*Foraminifera E*	LW26		6		2
65	*Foraminifera F*	LW26	9	9	2	2
66	*Foraminifera G*	LW26	8		2	
67	*Galathea squamifera*	LW27	25	22	3.61	3.41
68	*Gammaropsis maculata*	LW16	5	5	2	2
69	*Gammarus locusta*	LW32	8		2	
70	*Gammarus zaddachi*	LW32	6		2	
71	*Gastropod A*	LW49	3		2	
72	*Gibbula umbilicalis*	LW18		9		2.50
73	*Halacarellus basteri*	LW24	5	6	2	2
74	Harpacticoida	LW24	25	24	2	2
75	*Hiatella arctica*	LW28	12	13	2	2
76	Hydrozoa	LW23	14	14	2.79	2.79
77	*Idotea A*	LW24	9	6	2.75	2
78	*Idotea B*	LW24	10	7	2.75	2
79	*Janua pagenstecheri*	LW29	8	9	2	2
80	*Lasaea rubra*	LW25	8	8	2	2
81	*Lembos websteri*	LW30	17	17	2.61	2.61
82	*Leptocheirus tricristatus*	LW16	7	7	2	2
83	*Leptochelia savignyi*	LW24	7		2	
84	*Leptocythere pellucida*	LW39	5	5	2	2
85	*Leptomysis lingvura*	LW32	7	7	2	2
86	*Loxoconcha rhomboidea*	LW39	12	12	2	2
87	*Lysianassa ceratina*	LW31		5		2
88	*Melita palmata*	LW32		9		2
89	*Microdeutopus anomalus*	LW33	11	11	2	2
90	*Microprotopus maculatus*	LW16	6	5	2.71	2
91	*Modiolula phaseolina*	LW34	19	21	3.00	2.71
92	*Munna kroyeri*	LW24	8	8	2	2
93	*Musculus discors*	LW34	19	21	3.00	2.71
94	*Mytilus edulis*	LW34	19	21	3.00	2.71
95	*Nannastacus unguiculatus*	LW24	7	6	2.67	2.50
96	Nematoda spp.	LW47	15	15	2	2

97	*Nereis A*	LW47	10		2	
98	*Omalogyra atomus*	LW26	3	3	2	2
99	*Onoba semicosta*	LW49	9	8	2.57	2.40
100	*Ophiothrix fragilis*	LW37		13		2
101	*Ophiura ophiura*	LW38		24		3.69
102	*Ostracod A*	LW39	8	8	2	2
103	*Ostracod B*	LW39	5	5	2	2
104	*Ostracod C*	LW39		4		2
105	*Paradoxostoma variabile*	LW39	10	10	2	2
106	*Parvicardium exiguum*	LW40	12	14	2	2
107	*Parvicardium ovale*	LW41	13	15	2	2
108	*Parvicardium scabrum*	LW42	13	15	2	2
109	*Perinereis cultrifera*	LW44		10		2
110	*Phtisica marina*	LW16	9		3.04	
111	*Phyllodocid A*	LW47	8	9	3.17	2.75
112	*Pilumnus hirtellus*	LW45	27	28	3.63	4.02
113	*Platynereis dumerili*	LW46	11	11	2.57	2
114	*Pomatoceros lamarcki*	LW48	13	13	2	2
115	*Pomatoceros triqueter*	LW48	13	13	2	2
116	*Pontocypris mytiloides*	LW39	7	7	2	2
117	*Pseudoparatanais batei*	LW24	7	7	2	2
118	*Rissoa parva*	LW49	16	15	2.44	2
119	*Rissoa sarsi*	LW49	15	15	2	2
120	*Rissoella diaphana*	LW49	13	13	2	2
121	*Rissoella opalina*	LW49	12	12	2	2
122	*Sabella pavonina*	LW47	8		2	
123	*Sagitta elegans*	LW47	13	11	3.08	2.80
124	*Scrupocellaria* spp.	LW23	11		2	
125	*Semicytherura nigrescens*	LW39	6	6	2	2
126	*Serpulid A*	LW48	12	12	2	2
127	*Siriella armata*	LW35	10	10	3.00	2.71
128	*Skenea serpuloides*	LW26	3	3	2	2
129	*Spirorbis A*	LW29	5	6	2	2
130	*Stenothoe marina*	LW16	7	7	3.39	3.39
131	*Syllidae A*	LW47	3	4	3.67	3.67
132	*Syllidae B*	LW47	3	4	3.67	3.67
133	*Tapes aureus*	LW25	6	6	2	2
134	*Tomopteris helgolandica*	LW47	2		4.00	
135	*Tritaeta gibbosa*	LW32	3	3	2	2
136	*Tryphosella sarsi*	LW31	2		2	
137	*Tubulipora liliacea*	LW50	4		2	
138	*Turbellaria A*	LW47	5	5	2	2
139	*Typosyllis prolifera*	LW47	3		3.67	
140	*Xestoleberis aurantia*	LW39	11	11	2	2
141	Algae	NA	55	54	1	1
142	Bacteria	NA	62	55	1	1
143	Cladocerans	NA	9	8	1	1
144	CPOM	NA	54	53	1	1
145	Diatoms	NA	70	138	1	1
146	FPOM	NA	98	86	1	1
147	Microphytobenthos	NA	50	50	1	1
148	Phytoplankton	NA	41	34	1	1
149	Cyprid larvae	NA	8		1	
150	Hymenopteran larvae	NA	1		1	

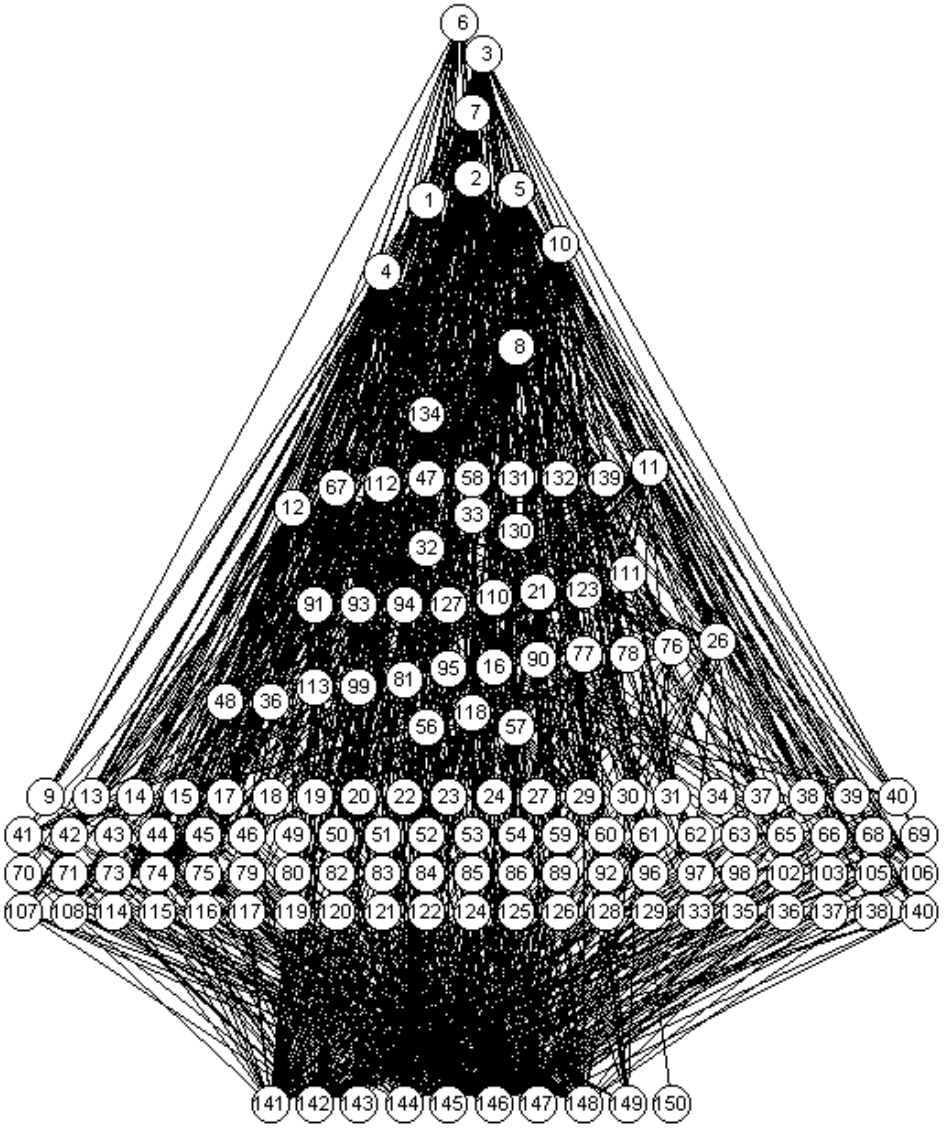

Figure S1. Composite mesocosm food web for the experiment ending in August. We calculated chain-averaged trophic height (*TH*) as the average trophic position of a species in all food chains of which it is a part. The ten basal resources at the foot of the web have *TH* = 1. The four long parallel rows have *TH* = 2. All other taxa are arranged in the vertical plane according to their *TH*. A list of the taxa that correspond to each number in the web (along with their linkage density and *TH*) can be found in Table S2.

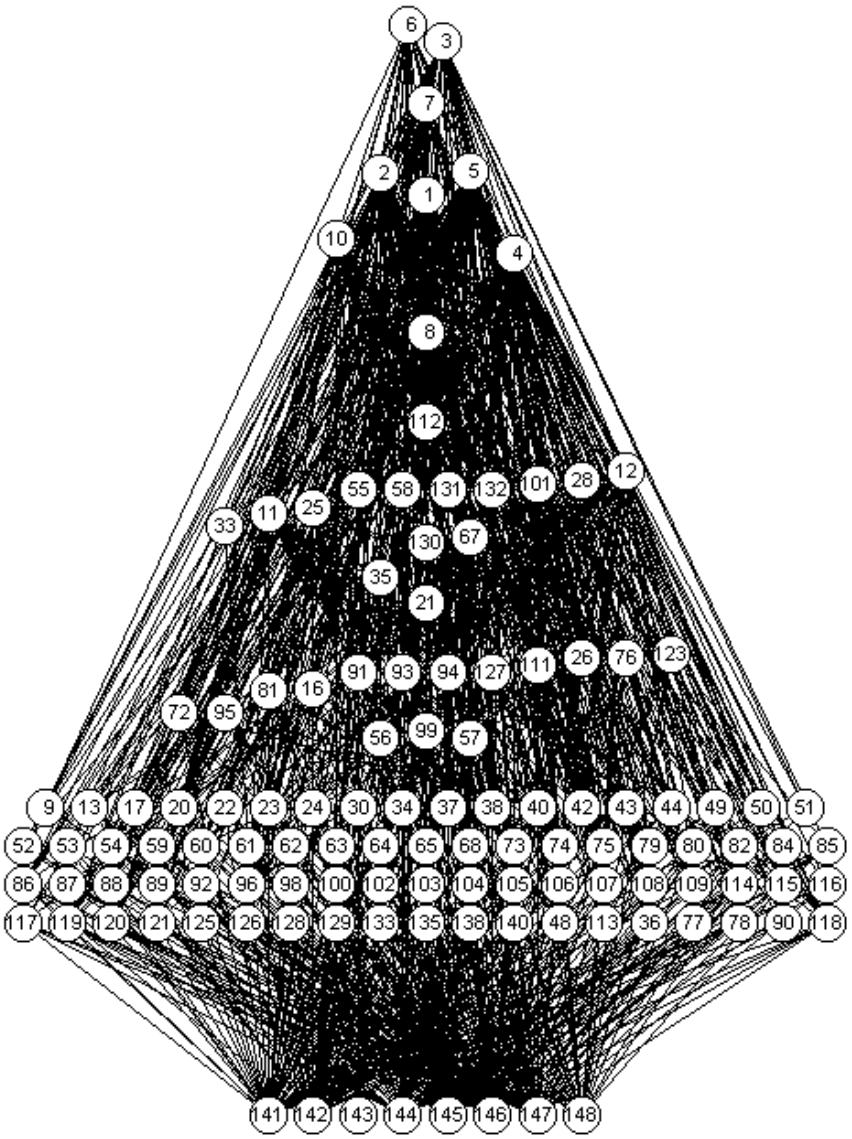

Figure S2. Composite mesocosm food web for the experiment ending in September. All other details are the same as Figure S1.

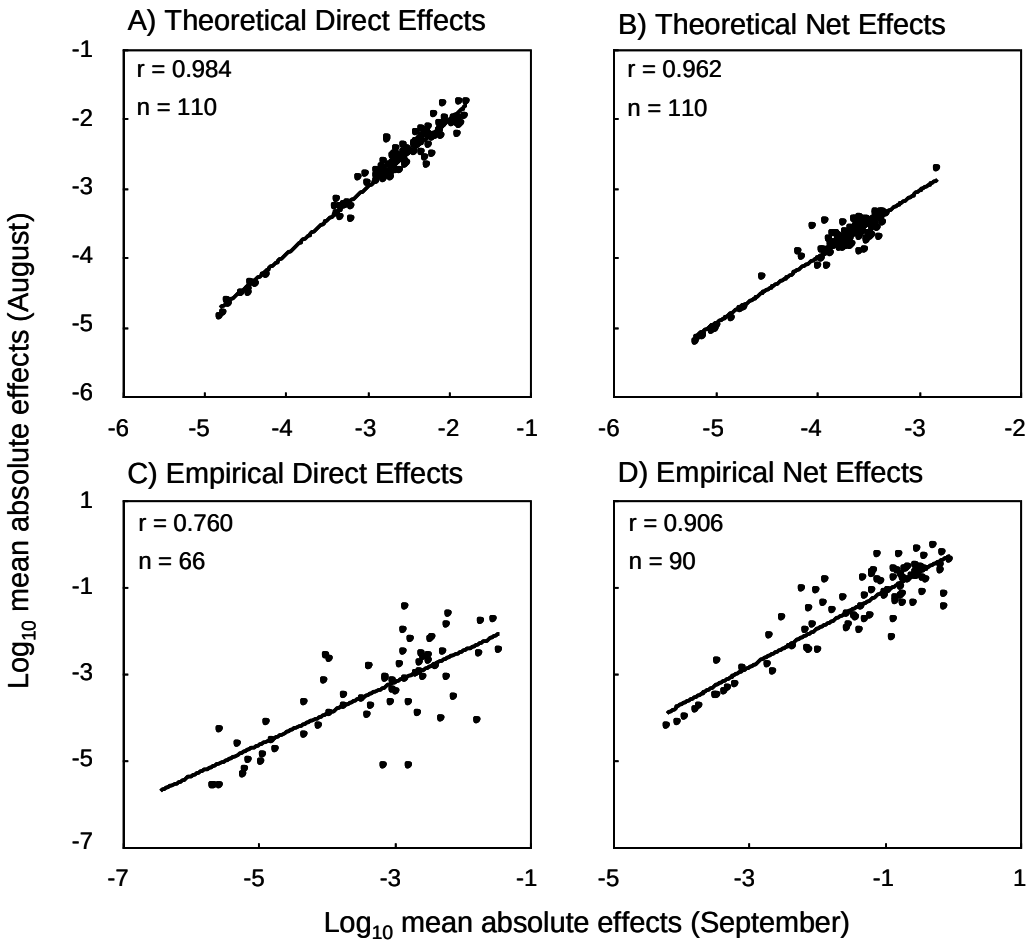

Figure S3. Correlation between August and September estimates of interaction strength.