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CHAPTER THREE

Perturbations to trophic interactions and the stability of complex food webs

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Abstract:

The pattern of predator-prey interactions is thought to be a key determinant of ecosystem processes and stability. Complex ecological networks are characterised by distributions of interaction strengths that are highly skewed, with many weak and few strong interactors present. Theory suggests that this pattern promotes stability as weak interactors dampen the destabilising potential of strong interactors. Here, we present an experimental test of this hypothesis and provide empirical evidence that the loss of weak interactors can destabilise communities in nature. We ranked ten marine consumer species by the strength of their trophic interactions. We removed the strongest and weakest of these interactors from experimental food webs containing more than 100 species. Extinction of strong interactors produced a dramatic trophic cascade and reduced the temporal stability of key ecosystem process rates, community diversity and resistance to changes in community composition. Loss of weak interactors also proved damaging for our experimental ecosystems, leading to reductions in the temporal and spatial stability of ecosystem process rates, community diversity and resistance. These results highlight the importance of conserving species to maintain the stabilising pattern of trophic interactions in nature, even if they are perceived to have weak effects in the system.

Keywords: interaction strength, dynamic index, predator-prey interactions, biodiversity and ecosystem functioning, temporal and spatial variability.

Introduction:

For decades, scientists have argued over the natural phenomena that allow complex communities to persist in nature (Elton 1958; May 1973; McCann 2000). Randomly assembled communities become less stable with increasing complexity (May 1973; Pimm & Lawton 1978), but natural communities are finely structured (Emmerson & Raffaelli 2004; Brose *et al.* 2006b), displaying properties that promote stability in spite of complexity (De Ruiter *et al.* 1995). Experiments (Paine 1992; Fagan & Hurd 1994; Wootton 1997) and theory based on empirical data (McCann *et al.* 1998; Neutel *et al.* 2002) have shown that real food webs are characterised by few strong interactions embedded in a majority of weak links. It is thought that this non-random arrangement of interaction strengths promotes community-level stability by generating negative covariances, which suppress the destabilising effect of strong consumer-resource interactions (McCann 2000). Theoretical studies provide overwhelming support for the idea that the pattern of strong and weak predator-prey interaction strengths confers stability to food webs (McCann *et al.* 1998; Neutel *et al.* 2002; Emmerson & Yearsley 2004; Rooney *et al.* 2006), however, these predictions have never been tested experimentally in natural systems.

One difficulty in testing the importance of interaction strength patterns for the stability of real food webs is the disparity between empirical and theoretical estimates of stability. Theoretical studies often assume that a system is stable only if it is governed by stable equilibrium dynamics (Gardner & Ashby 1970; May 1973; De Ruiter *et al.* 1995; Neutel *et al.* 2002). Consequently, stability is often measured as the system's ability to defy change, i.e. resilience or resistance (McCann 2000). In contrast, laboratory and field experiments rarely possess a well-defined equilibrium, so it is difficult to measure resilience or resistance (Ives *et al.* 2000). Given the highly variable nature of population dynamics, empirical studies often rely on measures of variability as indicators of system stability (Fukami *et al.* 2001; Morin & McGrady-Steed 2004; Dang *et al.* 2005; Steiner 2005; Weigelt *et al.* 2008). The two approaches are not necessarily contradictory (Tilman 1996), but the challenge for explorations of stability in real ecosystems is to bridge the gap between theory and experiment.

To investigate how a change in the pattern of species interactions might disrupt food web stability, we first empirically quantified the strength of *per capita* interactions individually for a set of ten marine consumer species (see *Materials and*

Methods). These consumers included both vertebrates and invertebrates and are characteristic of the shallow subtidal food web found along the temperate east Atlantic seaboard (Hayward & Ryland 1995). We ranked these species based on their average *per capita* effects, measured in isolation, classifying them as either strong or weak interactors (Figure 1), i.e. species that have, on average, either strong or weak feeding/behavioural interactions with their prey/competitors. In a second experiment, using large subtidal cages that included all ten consumers (and hence a range of interspecific interactions and multiple predator effects), we allowed natural food webs to develop over a six month period (with in excess of 100 species of benthic invertebrates). Based on the classification of species as either strong or weak interactors, we then removed the two and three strongest and weakest interactors from the mesocosms using a fully factorial experimental design (see *Materials and Methods*). We examined the consequences for the structural and functional components of our experimental ecosystems and their stability in time and space. We measured ecosystem process rates (primary and secondary production) and community-level properties (community diversity and stability). We chose to quantify temporal and spatial variability as measures of dynamic stability, and resistance as a measure of the system's ability to defy change. This approach facilitates a comparison of our results with both empirical and theoretical definitions of stability (McCann 2000).

Materials and Methods:

Experimental design

The experiments were carried out in an array of subtidal mesocosms at Lough Hyne in southwest Ireland. The mesocosms were placed on stony substrate, in shallow water (1-2m), on the south shoreline of the Lough. They were secured to the benthos by spreading clean stony substrate across the bottom of each cage. Lough Hyne is a highly sheltered sea lough, and the weight of substrate in the cages was sufficient to keep them in place for the duration of the experiments. Consequently, the study site was not cleared or disturbed in any other way. Each mesocosm used in the experiments consisted of a large 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 mesh size of the mesocosms was sufficiently small to contain the manipulated species, while allowing small benthic invertebrates from lower trophic levels to

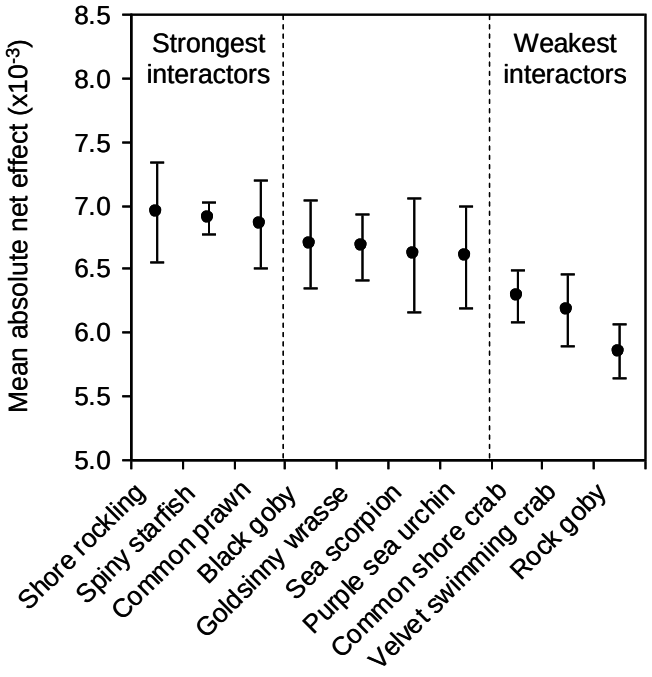

Figure 1. Categorisation of ten marine consumers as strong or weak interactors. The mean absolute net effect (± SE) of the ten manipulated species on the rest of the mesocosm communities was measured using the dynamic index (Wootton 1997). We chose the three strongest and three weakest interactors for manipulation in the final phase of the experiment.

recruit naturally into the cages (see Figure S1 and Table S1 for details of the food web). The study consisted of two experiments: (1) single species impacts, where the aim was to identify the strongest and weakest interactors from our ten chosen consumers; and (2) interaction strength manipulation, where we removed the strongest and weakest interactors from intact communities. The design of these two experiments is now discussed in greater detail.

Experiment 1: Single species impacts

33 mesocosms were used in this experiment. To identify strong and weak interactors, we added single consumers to empty benthic cages and quantified the net *per capita* impact of our manipulated species on the rest of the mesocosm community that recruited into those cages. We employed a randomised block design, with three blocks of eleven treatments placed in the shallow subtidal at depths of 1m, 2m, and 3m at low spring tide. Within each block, we had ten monocultures of our manipulated species (one individual per cage) and one empty cage (for comparison in the absence of the manipulated species). The position of these treatments within the block was randomly assigned. The experiment ran from 17/08/06 to 26/09/06 (40 days). The net impacts of these predators were quantified using the dynamic index (Wootton 1997):

$$a_{ij} = \frac{\ln\left(X_i^{+j} / X_i^{-j}\right)}{X_j \,.\, t}$$

where X_i^{+j} and X_i^{-j} are the density of species i in the presence and absence of manipulated species j, X_j is the density of the manipulated species and t is the duration of the experiment in days. The manipulated species had positive as well as negative effects on benthic invertebrates. They also had effects on species that they do not feed on directly. This implies that the 40 day duration of the experiment was sufficient for indirect effects to take place and so a_{ij} represents the net (direct plus indirect) effect of the manipulated species. Since the interactions for each manipulated species are a mixture of positive and negative values (which tend to cancel each other out), we obtained the absolute value of each net effect to better represent the magnitude of a species' impact on the community. Thus, we calculated the mean absolute net effect for each of our ten manipulated species (Figure 1).

Experiment 2: Interaction strength manipulation

24 mesocosms were used in this experiment, which was divided into two phases. *(a) Community assembly.* In this phase of the experiment, each mesocosm contained one individual of all ten manipulated species, i.e. the starting point of all 24 mesocosms was the same and any mortalities among these predators were replaced as they were observed. Small benthic invertebrates were free to recruit naturally into the cages and so similar communities were allowed to develop over a six month period (comparable to the food web in Figure S1). We arranged the cages into four blocks of six cages in the shallow subtidal, parallel to the shore, with two blocks each at depths of 1m and 2m at low spring tide. The community assembly period ran for 195 days from 05/10/06 to 18/04/07. *(b) Manipulation.* We removed species based on the strength of their interactions (Figure 1) and examined the effects on ecosystem structure, functioning, and stability. The six treatments that we employed were: (1) 10 species community ($W^{+}S^{+}$), i.e. an intact community; (2) two weakest interactors removed ($W^{-2}S^{+}$); (3) three weakest interactors removed ($W^{-3}S^{+}$); (4) two strongest interactors removed ($W^{+}S^{-2}$); (5) three strongest interactors removed ($W^{+}S^{-3}$); (6) all strong and weak interactors removed ($W^{-}S^{-}$), i.e. only intermediate interactors present. These six treatments were randomly assigned within each of the four blocks. The experiment ran for a further 230 days from 18/04/07 to 04/12/07.

Measures of ecosystem process rates

All sampling substrates used to estimate primary and secondary production were attached to the inside of the cages at the outset of the experiment and sacrificially sampled at each sampling session, i.e. the sampling substrates represent independent measurements of primary and secondary production, but non-independence among sampling times. Therefore, they constitute a repeated measures design (Underwood 1997). Primary productivity was measured by quantifying the square root of chlorophyll *a* (mg/m^2) on glass slides using the spectrophotometric method (Parsons *et al.* 1984). The square root of chlorophyll *a* has been shown to be a good approximation for primary productivity (Friedrichs *et al.* 2009). The slides mostly consisted of small green and red algae, although small fucoids occasionally settled as well. We assessed secondary production in the mesocosms using: (a) settlement panels (100 × 100mm PVC squares) to quantify sessile species (sponges,

bryozoans, calcareous polychaetes, etc.); and (b) nylon pot scourers (approx. radius = 40mm; approx. height = 20mm) to quantify mobile species (amphipods, isopods, gastropods, polychaetes, etc.). We calculated the density of every species identified on these substrates. We also measured the length of every individual identified (n = 228,163) and estimated its corresponding body mass using length-weight relationships defined for all species (Table S2). We used the square root of chlorophyll *a* as a surrogate for primary production and biomass density (body mass × density) as a surrogate for secondary production. All the manipulated species in the cages, as well as the benthic invertebrate community, had access to the sampling substrates and so could contribute to our measurements of primary and secondary production.

Statistical analysis

We employed a general linear model (GLM) to analyse the data, with primary and secondary production, Shannon diversity, and Whittaker's index of beta-diversity as response variables. This analysis corresponded to a fully factorial two-way ANOVA for repeated measures, including the main effects and interaction terms for the presence/absence of strong interactors and presence/absence of weak interactors, with the addition of a single main effect term for block. We split the analysis to examine responses pre- and post-treatment, i.e. during the community assembly phase (pre-treatment) and after the interaction strength manipulations were initiated (post-treatment). There were three repeated measurements pre-treatment (Dec 06, Feb 07 and Apr 07) and three repeated measurements post-treatment (Jun 07, Aug 07 and Dec 07). It was not possible to analyse temporal and spatial CV using the repeated measures design. This is because a comparison across the seasons is implicit in the temporal CV analysis and there is only one measurement per season in the spatial CV analysis. Consequently, we employed a three-way ANOVA with temporal and spatial CV as response variables and presence/absence of strong interactors, presence/absence of weak interactors, and treatment as factors (with the addition of block as a single main effect term in the temporal CV analysis). We applied a $\log_{10}$ transformation to the secondary production data and a square root transformation to the temporal CV data to meet the assumptions of normality and homogeneity of variance. To analyse the data in a balanced statistical design, we grouped the treatments according to number of species removed, i.e. we carried out

one GLM on $W^{+}S^{+}$, $W^{-2}S^{+}$, $W^{+}S^{-2}$, and $W^{-}S^{-}$ and one GLM on $W^{+}S^{+}$, $W^{-3}S^{+}$, $W^{+}S^{-3}$, and $W^{-}S^{-}$. This approach permitted us to investigate whether effects were consistent for both two and three strong or weak interactors removed. Note that block was a significant main effect for the 2 and 3 species removals in the analysis of secondary production and temporal CV of primary production. We are accounting for block in all the models however.

Results:

There were no significant effects on primary or secondary production during the community assembly phase of the experiment, i.e. pre-treatment. This suggests that the ecosystem process rates of the mesocosm communities were sufficiently similar before the interaction strength manipulations were applied. The removal of strong interactors produced a dramatic trophic cascade (Figure 2). Secondary production increased after the interaction strength manipulations were applied, i.e. post-treatment, in the absence of two ($F_{1,9}$ = 5.119, p = 0.050) and three ($F_{1,9}$ = 6.802, p = 0.028) strong interactors. As a consequence of the community-level increase in the biomass density of benthic invertebrates, primary production declined post-treatment in the absence of two ($F_{1,9}$ = 5.214, p = 0.048) and three ($F_{1,9}$ = 6.902, p = 0.027) strong interactors. The removal of weak interactors had no significant effects on primary or secondary production.

We found significant effects of the interaction strength manipulations on the stability of the mesocosm communities (Figure 3 and 4*A*-*B*). First, we examined the coefficient of variation (CV) for the different ecosystem process rates within each replicate mesocosm over time as a measure of temporal stability (Dang *et al.* 2005; Steiner 2005). Note that high variability equates with instability. For the three species removals, we found that if only strong or weak interactors were present in the community, the temporal variability of secondary production increased (strong×weak: $F_{1,21}$ = 5.555, p = 0.028; Figure 3*A*-*B*). The temporal variability of primary production was significantly lower after two ($F_{1,21}$ = 9.811, p = 0.005) and three ($F_{1,21}$ = 10.045, p = 0.004) strong interactors were removed (Fig 3*C*-*D*). We also investigated spatial stability (CV across replicates within each sampling period) as a measure of consistency in the ecosystem processes of the replicate communities (Fukami *et al.* 2001; Morin & McGrady-Steed 2004; Weigelt *et al.* 2008). Here, the removal of two ($F_{1,16}$ = 5.123, p = 0.038) and three ($F_{1,16}$ = 11.090, p = 0.004) weak

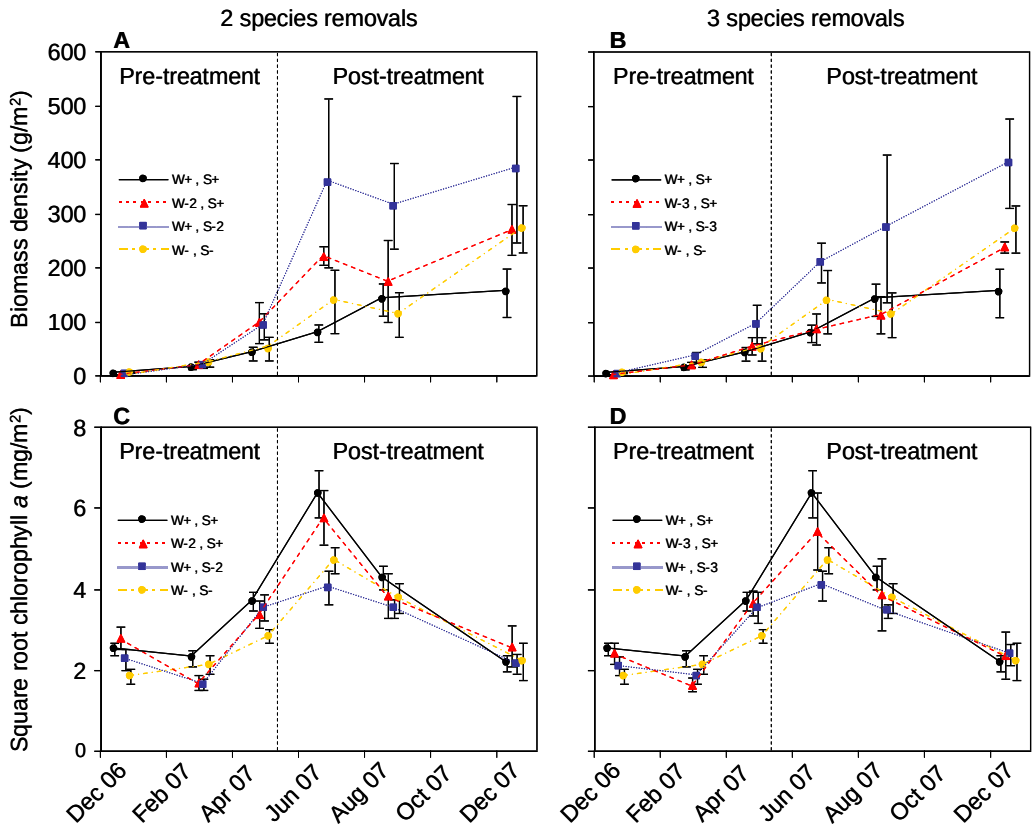

Figure 2. Ecosystem process rates in the experiment. Levels of secondary production (*A-B*) and primary production (*C-D*) in the experimental mesocosms (± SE) at each of six different sampling sessions. Three of these were before the interaction strength manipulation (pre-treatment), with three after (post-treatment). In the key, $W^{+}S^{+}$ = an intact community; $W^{-2}S^{+}$ = two weakest interactors removed; $W^{-3}S^{+}$ = three weakest interactors removed; $W^{+}S^{-2}$ = two strongest interactors removed; $W^{+}S^{-3}$ = three strongest interactors removed and; $W^{-}S^{-}$ = all strong and weak interactors removed. Data was transformed for statistical analyses, but original values are shown here for clarity.

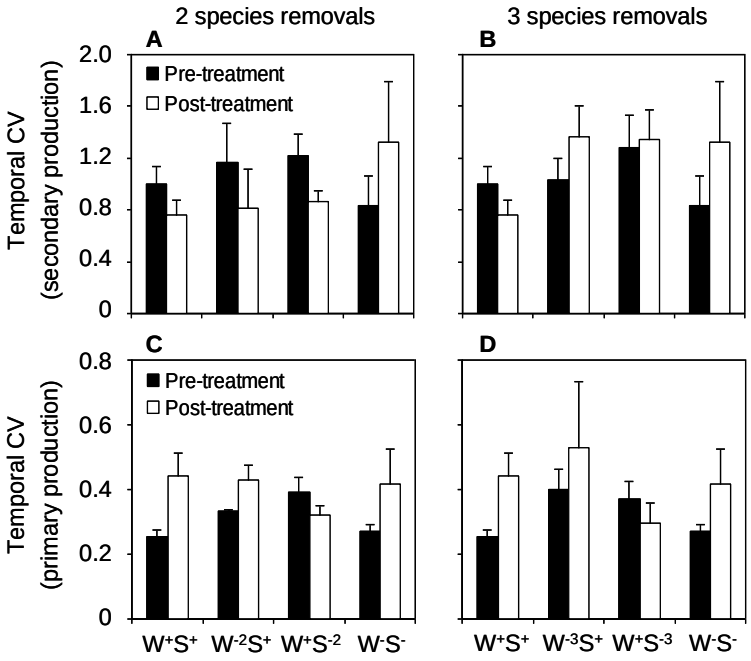

Figure 3. Temporal stability effects in the experiment. These effects were measured as the coefficient of temporal variation (temporal CV; ± SE) of secondary production (*A-B*) and primary production (*C-D*). Black bars indicate that stability effects are before the interaction strength manipulation (pre-treatment); white bars indicate that stability effects are after the manipulation (post-treatment). $W^{+}S^{+}$ = an intact community; $W^{-2}S^{+}$ = two weakest interactors removed; $W^{-3}S^{+}$ = three weakest interactors removed; $W^{+}S^{-2}$ = two strongest interactors removed; $W^{+}S^{-3}$ = three strongest interactors removed and; $W^{-}S^{-}$ = all strong and weak interactors removed. Data was transformed for statistical analyses, but original values are shown here for clarity.

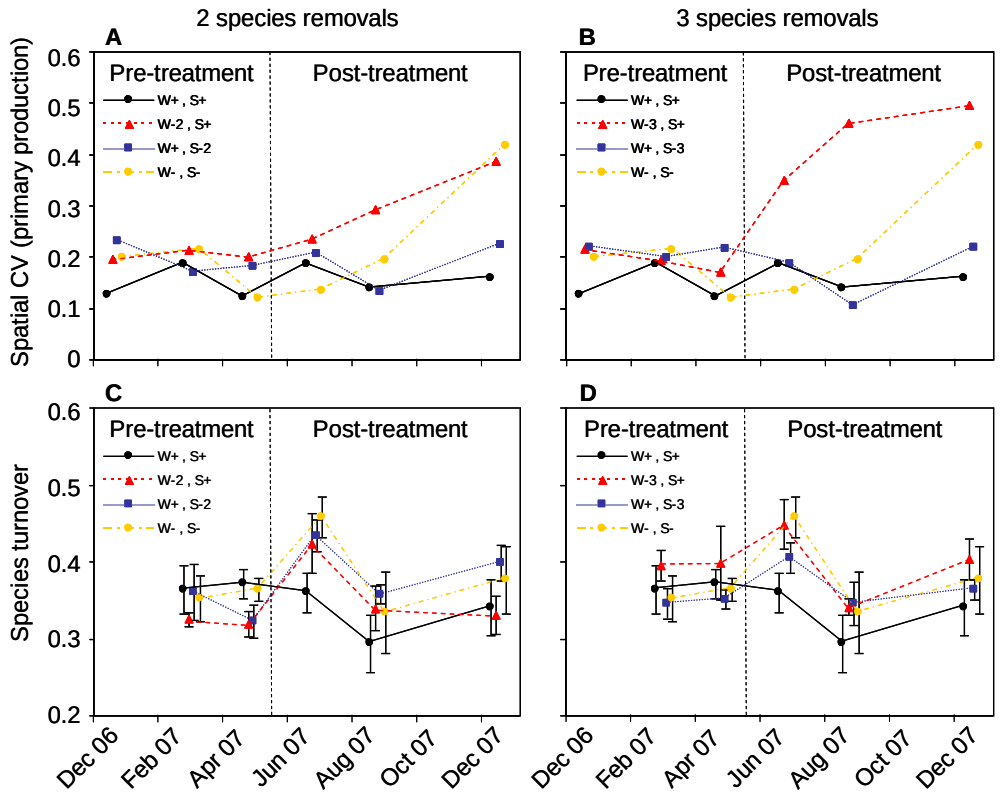

Figure 4. Spatial stability and resistance of the mesocosm communities. (*A-B*) Spatial stability effects in the experiment measured as the coefficient of spatial variation (spatial CV) of primary production. Each data point represents a single measure calculated across the replicates within each treatment. Therefore, no y-axis error bars are included in the plot. (*C-D*) Resistance of the experimental mesocosm communities to invasions and extinctions, measured as the species turnover (beta-diversity) between consecutive sampling sessions. December 06 was the first sampling session, so there is no comparison for species turnover in this month. In the key, $W^{+}S^{+}$ = an intact community; $W^{-2}S^{+}$ = two weakest interactors removed; $W^{-3}S^{+}$ = three weakest interactors removed; $W^{+}S^{-2}$ = two strongest interactors removed; $W^{+}S^{-3}$ = three strongest interactors removed and; $W^{-}S^{-}$ = all strong and weak interactors removed.

interactors increased the spatial variability of primary production (Figure 4*A*-*B*), i.e. there was greater spatial heterogeneity between the communities. This effect was most pronounced in the three species removals (weak×treatment: $F_{1,16} = 9.420$, $p = 0.007$). Furthermore, when we considered spatial variability in the three species removals, we found that the presence of the weak interactors significantly reduced the destabilising effect of the strong interactors (strong×weak: $F_{1,16} = 6.326$, $p = 0.023$).

Lastly, we examined the effect of the interaction strength manipulations on the diversity of the mesocosm communities. First, we used the Shannon-Wiener index as a measure of richness and evenness in the community. We found no significant diversity effects during the community assembly phase. We found inconsistent effects post-treatment, with removal of two weak interactors ($F_{1,9} = 9.417$, $p = 0.013$) and three strong interactors ($F_{1,9} = 7.166$, $p = 0.025$) reducing the diversity of our experimental ecosystems. We also measured Whittaker's index of beta-diversity, β_w, to examine compositional changes in the communities within a given treatment through time. Here, $\beta_w = (s/\alpha)-1$, where s is the total number of species in a replicate community over two consecutive sampling sessions and α is the average species richness of the two samples. A high turnover of species in the community equates with low resistance to species invasions or extinctions and hence β_w is used here as a measure of resistance (Pimm 1984; McCann 2000). We found no significant species turnover effects during the community assembly phase. Again, we found inconsistent effects post-treatment, with the loss of two strong interactors ($F_{1,9} = 5.199$, $p = 0.049$) and three weak interactors ($F_{1,9} = 5.381$, $p = 0.046$) leading to increased species turnover in the mesocosm communities (Fig 4*C*-*D*).

Discussion:

Natural ecosystems are a complex tangle of interactions, with 95% of species typically no more than three links apart (Williams *et al.* 2002). This natural complexity persists against the odds (Gardner & Ashby 1970; May 1973) because it is governed by fundamental laws and principles that confer stability. One of the most widely accepted of these principles is the pattern of species interactions (Paine 1992; Fagan & Hurd 1994; McCann *et al.* 1998; McCann 2000; Neutel *et al.* 2002; Emmerson & Raffaelli 2004). There is a tendency to consider biodiversity loss in terms of taxonomic identities or functional roles, yet every species can also be

considered as a node in a complex web of interactions. Each node contributes to the overall balance of interactions, whether it is a strong or weak interactor. Given the highly inter-connected nature of food webs (Williams *et al.* 2002; Figure S1), any loss of biodiversity could contribute to a ripple effect, changing the pattern of interaction strengths, and thus threatening to unbalance the stability conferred by this pattern (McCann 2000; Emmerson & Raffaelli 2004).

Here, for the first time in an experimental study, we have explicitly manipulated species based on the strength of their interactions in nature. We have shown that removal of strong interactors can produce dramatic trophic cascades. The loss of just two or three strongly interacting predators led to a massive increase in secondary production, which subsequently caused a reduction in the energy available to the food web through the primary productivity of our experimental ecosystems (Figure 2). Here, secondary production increased as benthic invertebrates were released from heavy predation pressure, due to removal of the strong interactors. Since many of the benthic invertebrates are grazers, this led to a knock-on effect on primary productivity, i.e. an increased density of grazers, and hence grazing pressure, led to a reduction in primary productivity. It should be noted that this effect is largely driven by a suppression of primary productivity in the absence of strong interactors during the summer months. These effects suggest that strong interactors are analogous to keystone species, which typically have effects disproportionately large relative to their abundance (Paine 1966; Estes & Palmisano 1974; Power *et al.* 1996). Fluctuations in population biomass are commonplace and compensatory reactions among species can maintain aggregate biomass (Tilman 1996). The changes in primary and secondary production shown here are community-level responses however, suggesting that the insurance effect (Yachi & Loreau 1999) of community diversity is not sufficient to overwhelm the impacts of strong interactors. Trophic cascades like this can alter energy flow, community composition, habitat provision, and lead to secondary extinctions (Mills *et al.* 1993; Power *et al.* 1996; Eklof & Ebenman 2006).

While the loss of weak interactors from our experimental food webs did not lead to cascading effects, their importance in an ecosystem-level context should not be underestimated. They appear to play a vital stabilising role in the delivery of key ecosystem process rates by reducing the variability associated with both primary and secondary production (Figure 3*A*-*B* and 4*A*-*B*). Crucially, when strong interactors

were present in the community without a sufficient number of weakly interacting species around them, the temporal variability of secondary production and the spatial variability of primary production increased. The lowest levels of variability in these ecosystem process rates could be found when the normal pattern of strong and weak interactors was restored. It is clear from these results that when strong interactors lack a sufficient buffer of weakly interacting species to dampen their destabilising potential (McCann *et al.* 1998), they can disrupt patterns of species interactions, undermining ecosystem functioning and the structures that allow complex communities in nature to persist (Pimm 1984; Dang *et al.* 2005; Kahmen *et al.* 2005; Steiner 2005).

There is also a suggestion that weak interactors may be destabilising in the absence of strong interactors. In our mesocosm communities, there was high temporal variability of secondary production when weak interactors were present in the community without the three strongest interactors (Figure 3*B*). This implies that strong interactors are also important for stability. Indeed, the highest levels of stability were consistently seen in the intact communities, which contained both strong and weak interactors. As we have seen above, some strong interactors are necessary to maintain the productivity of the system or else cascading effects occur (Figure 2). Many weak interactors are also required to reduce the destabilising effect of the strong interactors, most likely through predator interference, e.g. weak interactors may limit predation by strong interactors, through behavioural (i.e. trait-mediated) interactions and competition for resources (Siddon & Witman 2004; O'Gorman *et al.* 2008).

It must be noted that the measure of stability discussed above, i.e. variability, is not directly comparable to many of the theoretical studies that suggest a stabilising pattern of few strong and many weak interactions (e.g. De Ruiter *et al.* 1995; McCann *et al.* 1998; Neutel *et al.* 2002). In theoretical studies, stability is typically defined as the return-time of a system to equilibrium, or the degree to which a variable changes, after a perturbation. Consequently, we also investigated Shannon diversity and species turnover as measures of the degree to which our experimental communities were perturbed from equilibrium. We see that any disruption to the normal pattern of strong and weak interactors has the potential to upset the community dynamics. Loss of either strong or weak interactors led to a reduction in Shannon diversity, as well as increased species turnover within the experimental

communities. High turnover can be attributed to an increased number of species invasions and/or secondary extinctions as a result of the interaction strength manipulations. Consequently, these results suggest that loss of either strong or weak interactors reduced the resistance of the community to changes in species composition. This highlights the need to preserve the natural pattern of predator-prey interactions to maintain the ability of natural ecosystems to resist change (McCann 2000; Rooney *et al.* 2006).

Our experimental design led to the gradual development of communities during a six month pre-treatment phase. All mesocosms in this phase contained the full complement of manipulated consumer species and, therefore, the communities that developed were quite similar. Subtle differences exist between the mesocosms in this pre-treatment phase, which may be due to mortality of some manipulated species between sampling sessions or small differences in the body size of the individuals added to the mesocosms. These pre-treatment differences are unlikely to carry over to the interaction strength manipulation phase. For example, the communities with the lowest temporal variability pre-treatment have the highest temporal variability post-treatment (Figure 3*A*-*D*). Additionally, we found no significant differences between the treatments in the community assembly phase of the experiment. This suggests that any observed pre-treatment differences are minimal and do not influence post-treatment results.

Lastly, the effects on temporal variability of primary production in this experiment initially appear counterintuitive to our arguments above. Here, temporal variability of primary production was high in the intact community (Figure 3*C*-*D*). This effect was driven by the seasonality of primary production however, with the normal seasonal cycle of primary production (high in summer; low in winter), leading to high temporal variability. The removal of strong interactors led to a significant reduction in temporal variability by diminishing the summer high in primary productivity. Consequently, our measure of ecosystem similarity, spatial variability of primary production, quantified stability effects that were not obscured by the seasonality of primary production.

Through these experimental manipulations, we have shown that strong interactors are analogous to keystone species, driving productivity in our ecosystems through cascading effects (Paine 1966; Estes & Palmisano 1974). We have also shown that extinction of either strong or weak interactors can have detrimental

effects on diversity and stability, as the stabilising natural pattern of trophic interactions breaks down (McCann *et al.* 1998; Rooney *et al.* 2006). The strong and weak interactors that were removed in this experiment all represent well connected consumers (see Figure S1 and Table S1). It would be interesting to investigate whether effects are consistent for the removal of poorly connected species (specialists) and basal species. On the basis of our experimental results, we contend that any loss of biodiversity has the potential to upset the delicate balance of interactions in natural food webs, whether the species lost are strong or weak interactors. Our results emphasise the need to conserve biodiversity, and thus the pattern of species interactions, as a means of maintaining ecosystem structure and functioning and the stable provision of ecosystem services.

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Table S1. Key to the taxa in the mesocosm food web shown in Figure S1. The number of trophic links (*TL*) and trophic height (*TH*) of each taxon are also provided.

Code	Taxa	Common name	*TL*	*TH*
1	*Carcinus maenas*	Common shore crab	55	3.09
2	*Ctenolabrus rupestris*	Goldsinny wrasse	85	3.16
3	*Gaidropsarus mediterraneus*	Shore rockling	65	3.24
4	*Gobius niger*	Black goby	96	3.14
5	*Gobius paganellus*	Rock goby	105	3.14
6	*Marthasterias glacialis*	Spiny starfish	52	3.26
7	*Necora puber*	Velvet swimming crab	31	3.13
8	*Palaemon serratus*	Common prawn	33	3.09
9	*Paracentrotus lividus*	Purple sea urchin	46	2
10	*Taurulus bubalis*	Sea scorpion	5	3.16
11	*Gobiusculus flavescens*	Two-spot goby	80	3.05
12	*Pomatoschistus pictus*	Painted goby	67	3.08
13	*Abra alba*	White furrow shell	10	2
14	*Acanthocardia echinata*	Prickly cockle	12	2
15	*Acanthochitona crinitus*	(chiton)	5	2
16	*Aequipecten opercularis*	Queen scallop	9	2
17	*Alvania beani*	(gastropod)	14	2
18	*Alvania semistriata*	(gastropod)	14	2
19	*Amphilochus manudens*	(amphipod)	8	2.46
20	*Anomia ephippium*	Saddle oyster	15	2
21	*Aora gracilis*	(amphipod)	10	2
22	*Apherusa bispinosa*	(amphipod)	5	2
23	*Apseudes latreillei*	(tanaid)	6	2
24	*Apseudes talpa*	(tanaid)	6	2
25	*Ascidiella aspersa*	Dirty sea squirt	6	2
26	*Asterina phylactica*	(starfish)	13	2.71
27	*Bittium reticulatum*	Needle whelk	22	2.69
28	*Buccinum undatum*	Common whelk	14	3.08
29	Calanoida	(copepod)	24	2
30	*Callopora lineata*	(bryozoan)	5	2
31	*Caprella acanthifera*	(caprellid)	12	2.40
32	*Caprella equilibra*	(caprellid)	12	2.40
33	*Caprella linearis*	(caprellid)	12	2.40
34	*Ceradocus semiserratus*	(amphipod)	6	2
35	*Cerastoderma edule*	Common cockle	7	2
36	*Cerithiopsis tubercularis*	(gastropod)	13	2.40
37	*Chironomidae spp.*	(chironomid)	7	2
38	*Chlamys varia*	Variegated scallop	9	2
39	*Circulus striatus*	(gastropod)	10	2
40	*Clathrina coriacea*	(sponge)	15	2
41	*Coriandria fulgida*	(gastropod)	15	2
42	*Crassicorophium bonnellii*	(amphipod)	12	2
43	*Crassicorophium crassicorne*	(amphipod)	12	2
44	*Crisia denticulata*	(bryozoan)	11	2
45	*Cumacea A*	(cumacean)	11	2
46	*Cuthona sp.*	(gastropod)	5	2
47	Cyclopoida	(copepod)	22	2.20
48	Cyprid larvae	(cyprid)	5	1
49	*Cythere lutea*	(ostracod)	11	2

50	*Dexamine spinosa*	(amphipod)	9	2
51	*Dexamine thea*	(amphipod)	9	2
52	*Disporella hispida*	(bryozoan)	5	2
53	*Dysidea fragilis*	(sponge)	15	2
54	*Elasmopus rapax*	(amphipod)	8	2
55	*Electra pilosa*	Hairy sea mat	7	2
56	*Elysia viridis*	Green Elysia	6	2
57	*Emarginula fissura*	(gastropod)	8	2.33
58	*Epilepton clarkiae*	(bivalve)	10	2
59	*Epitonium clathrus*	Common wentletrap	6	2
60	*Ericthonius brasiliensis*	(amphipod)	12	2
61	*Ericthonius punctatus*	(amphipod)	12	2
62	*Eubranchus farrani*	(gastropod)	5	2
63	*Exogone gemmifera*	(polychaete)	6	2
64	*Foraminifera A*	(foraminiferan)	10	2
65	*Foraminifera B*	(foraminiferan)	10	2
66	*Foraminifera C*	(foraminiferan)	10	2
67	*Foraminifera D*	(foraminiferan)	10	2
68	*Foraminifera E*	(foraminiferan)	10	2
69	*Foraminifera F*	(foraminiferan)	10	2
70	*Foraminifera G*	(foraminiferan)	10	2
71	*Galathea squamifera*	Black squat lobster	26	3.02
72	*Gammaropsis maculata*	(amphipod)	8	2.20
73	*Gammarus locusta*	(amphipod)	8	2
74	*Gammarus zaddachi*	(amphipod)	8	2
75	*Gibbula umbilicalis*	Flat top shell	9	2.33
76	*Halacarellus basteri*	(sea mite)	3	2
77	Harpacticoida	(copepod)	24	2
78	*Hiatella arctica*	Wrinkled rock borer	15	2
79	Hymenopteran larvae	(hymenopteran)	1	1
80	*Iothia fulva*	(gastropod)	11	2.57
81	*Idotea A*	(isopod)	11	2.57
82	*Idotea B*	(isopod)	4	2
83	*Janua pagenstecheri*	(spirorbid)	10	2
84	*Lasaea rubra*	(bivalve)	11	2
85	*Lembos websteri*	(amphipod)	11	2
86	*Leptocheirus tricristatus*	(amphipod)	11	2
87	*Leptochelia savignyi*	(tanaid)	7	2
88	*Leptocythere pellucida*	(ostracod)	11	2
89	*Leptomysis lingvura*	(mysid)	6	2
90	*Loxoconcha rhomboidea*	(ostracod)	11	2
91	*Lysianassa ceratina*	(amphipod)	5	2
92	*Melita palmata*	(amphipod)	8	2
93	*Microdeutopus anomalus*	(amphipod)	9	2
94	*Microprotopus maculatus*	(amphipod)	6	2.33
95	*Modiolula phaseolina*	Bean horse mussel	22	2.36
96	*Monia patelliformis*	Ribbed saddle oyster	14	2
97	*Munna kroyeri*	(isopod)	10	2.33
98	*Musculus discors*	Green crenella	22	2.36
99	*Mytilus edulis*	Common mussel	22	2.36
100	*Nannastacus unguiculatus*	(cumacean)	7	2.33
101	Nematoda spp.	(nematode)	11	2
102	*Nereis sp.*	(polychaete)	10	2
103	*Odostomia plicata*	(gastropod)	6	2
104	*Omalogyra atomus*	(gastropod)	10	2
105	*Onoba semicosta*	(gastropod)	11	2.25
106	*Ophiothrix fragilis*	Common brittle star	13	2

107	*Ophiura ophiura*	Serpent star	32	2.88
108	*Ostracod A*	(ostracod)	11	2
109	*Ostracod B*	(ostracod)	11	2
110	*Ostracod C*	(ostracod)	11	2
111	*Paradoxostoma variabile*	(ostracod)	11	2
112	*Parvicardium exiguum*	(bivalve)	14	2
113	*Parvicardium ovale*	(bivalve)	14	2
114	*Parvicardium scabrum*	(bivalve)	14	2
115	*Perinereis cultrifera*	(polychaete)	9	2
116	*Phyllodocidae sp.*	(polychaete)	6	2
117	*Pilumnus hirtellus*	Hairy crab	36	3.08
118	*Platynereis dumerilii*	(polychaete)	10	2
119	*Podocoryne borealis*	(hydrozoa)	9	2.50
120	*Pomatoceros lamarcki*	(serpulid polychaete)	12	2
121	*Pomatoceros triqueter*	(serpulid polychaete)	12	2
122	*Pontocypris mytiloides*	(ostracod)	11	2
123	*Pseudoparatanais batei*	(tanaid)	6	2
124	*Retusa truncatula*	(gastropod)	7	2
125	*Rissoa parva*	(gastropod)	15	2.40
126	*Rissoa sarsi*	(gastropod)	15	2.40
127	*Rissoella diaphana*	(gastropod)	15	2
128	*Rissoella opalina*	(gastropod)	15	2
129	*Sabella pavonina*	(sabellid)	11	2
130	*Sagitta elegans*	Arrow worm	8	2.64
131	*Scrupocellaria* spp.	(bryozoan)	12	2
132	*Semibalanus balanoides*	Northern rock barnacle	8	2.53
133	*Semicytherura nigrescens*	(ostracod)	11	2
134	*Serpulid A*	(serpulid)	11	2
135	*Siriella armata*	(mysid)	8	2.64
136	*Skenea serpuloides*	(gastropod)	10	2.33
137	*Spirorbis A*	(spirorbid)	10	2
138	*Spirorbis B*	(spirorbid)	10	2
139	*Stenothoe marina*	(amphipod)	6	2
140	*Syllidae A*	(polychaete)	4	2
141	*Syllidae B*	(polychaete)	4	2
142	*Tapes aureus*	(bivalve)	12	2
143	*Tectura virginea*	(gastropod)	10	2.25
144	*Tomopteris helgolandica*	(polychaete)	8	2
145	*Tritaeta gibbosa*	(amphipod)	6	2
146	*Tryphosella sarsi*	(amphipod)	3	2
147	*Tubulipora liliacea*	(bryozoan)	5	2
148	*Turbellaria A*	(flat worm)	5	2
149	*Typosyllis prolifera*	(polychaete)	4	2
150	*Vitreolina philippi*	(gastropod)	4	3.44
151	*Xestoleberis aurantia*	(ostracod)	11	2
152	Algae	Algae	89	1
153	Bacteria	Bacteria	53	1
154	Cladocerans	Cladocerans	8	1
155	CPOM	CPOM	98	1
156	Diatoms	Diatoms	74	1
157	FPOM	FPOM	112	1
158	Microphytobenthos	Microphytobenthos	80	1

Table S2. 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. Weight (y) is measured in mg. Length (x) is measured in mm.

Taxa	***L-W* Relationship**	r^2
Carcinus maenas	$y = 0.2668x^{2.9545}$	0.9693
Ctenolabrus rupestris	$y = 0.0057x^{3.181}$	0.9734
Gaidropsarus mediterraneus	$y = 0.0008x^{3.3972}$	0.9847
Gobius niger	$y = 0.0074x^{3.0788}$	0.9320
Gobius paganellus	$y = 0.0014x^{3.4672}$	0.9356
Marthasterias glacialis	$y = 0.3088x^{2.7417}$	0.9187
Necora puber	$y = 0.2989x^{2.9639}$	0.9204
Palaemon serratus	$y = 0.0014x^{3.3838}$	0.9201
Paracentrotus lividus	$y = 1.2774x^{2.737}$	0.9398
Taurulus bubalis	$y = 0.0032x^{3.3258}$	0.9604
Gobiusculus flavescens	$y = 0.0004x^{3.7234}$	0.9612
Pomatoschistus pictus	$y = 0.0039x^{3.1954}$	0.9733
Alvania spp.	$y = 0.1391x^{2.71}$	0.9877
Anomia ephippium	$y = 0.0304x^{2.9244}$	0.9428
Aora gracilis	$y = 0.0018x^{3.2994}$	0.9202
Aoridae	$y = 0.0031x^{2.8427}$	0.9596
Ascidiella aspersa	$y = 0.1159x^{2.3628}$	0.8922
Bittium reticulatum	$y = 0.1224x^{2.3117}$	0.9831
Buccinum undatum	$y = 0.0958x^{3.0601}$	0.9804
Cardiidae	$y = 0.1084x^{3.0951}$	0.9870
Chlamys varia	$y = 0.0508x^{3.036}$	0.9893
Clathrina coriacea	$y = 0.2909x^{1.9999}$	0.9541
Crassicorophium spp.	$y = 0.0046x^{3.1972}$	0.9491
Cumacea	$y = 0.0101x^{1.9552}$	0.8806
Dysidea fragilis	$y = 0.1435x^{1.9328}$	0.8442
Epilepton clarkiae	$y = 0.0959x^{2.8774}$	0.9805
Foraminifera	$y = 0.1598x^{3.2349}$	0.9801
Galathea squamifera	$y = 0.0284x^{4.3903}$	0.9353
Hiatella arctica	$y = 0.053x^{2.9161}$	0.9540
Janua pagenstecheri	$y = 0.1117x^{3.0229}$	0.9314
Lembos websteri	$y = 0.0037x^{2.6724}$	0.9806
Lysianassa ceratina	$y = 0.0096x^{3.0979}$	0.9877
Melitidae	$y = 0.004x^{3.095}$	0.9598
Microdeutopus anomalus	$y = 0.0016x^{3.3615}$	0.9685
Musculus discors	$y = 0.0986x^{2.7968}$	0.9766
Mysidae	$y = 0.0006x^{3.2529}$	0.9236
Nudibranchia	$y = 0.0096x^{2.8116}$	0.9726
Ophiothrix fragilis	$y = 0.4875x^{2.9185}$	0.9435
Ophiura ophiura	$y = 0.2936x^{2.5329}$	0.9603
Ostracoda	$y = 0.1738x^{4.2678}$	0.7896
Parvicardium exiguum	$y = 0.1104x^{3.0932}$	0.9786
Parvicardium ovale	$y = 0.1018x^{3.1784}$	0.9900
Parvicardium scabrum	$y = 0.1103x^{3.0607}$	0.9870

Pectinidae	$y = 0.0698x^{2.8284}$	0.9871
Perinereis cultrifera	$y = 0.0015x^{3.0023}$	0.9733
Pilumnus hirtellus	$y = 0.1324x^{2.963}$	0.9438
Platynereis dumerilii	$y = 0.0113x^{2.2781}$	0.8051
Polychaeta	$y = 0.0021x^{2.395}$	0.8612
Pomatoceros spp.	$y = 0.0029x^{2.781}$	0.9688
Rissoa spp.	$y = 0.1532x^{2.3992}$	0.9691
Scrupocellaria spp.	$y = 0.00004x^{2.6928}$	0.9691
Tubulipora liliacea	$y = 0.0504x^{2.5072}$	0.9272

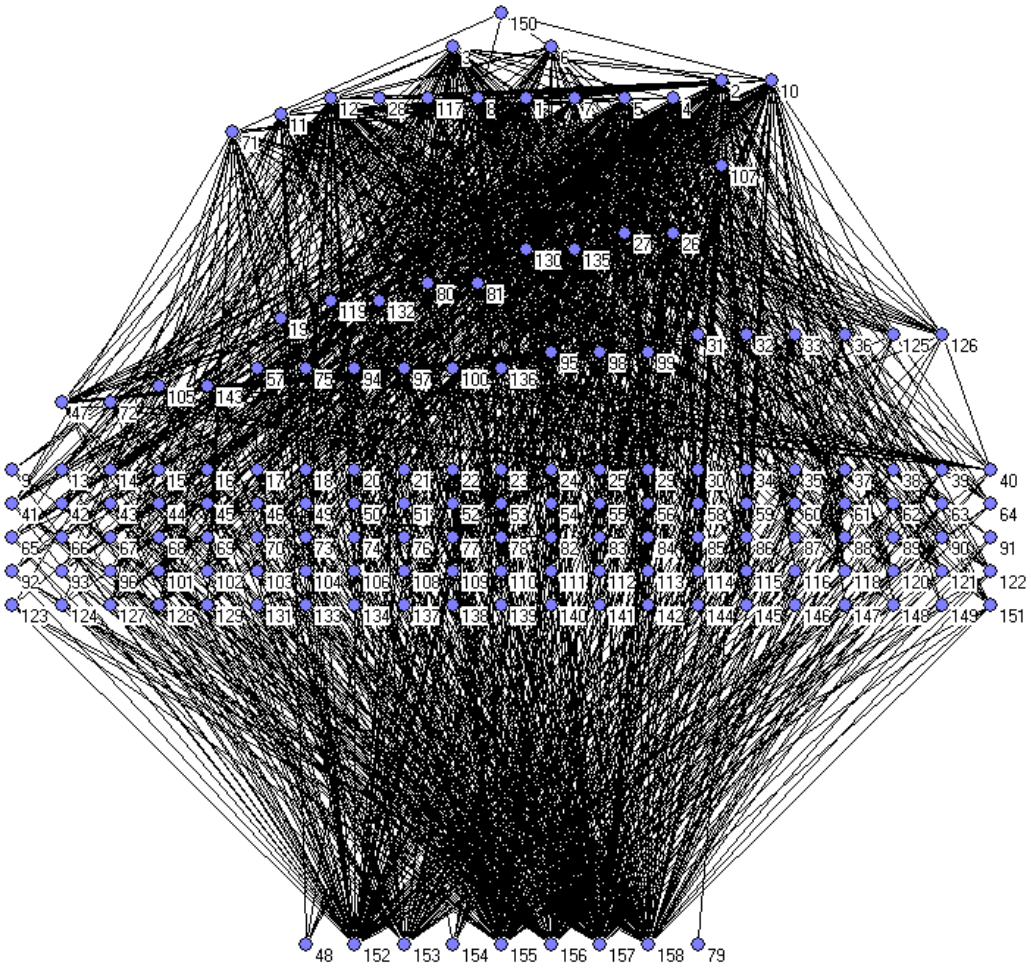

Figure S1. Core web of species interactions over all the experimental mesocosms**.** We calculated prey-averaged trophic height (*TH*) as 1 + the average trophic position of all prey species. The nine basal resources at the foot of the web have *TH* = 1. The five long parallel rows have *TH* = 2. All 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 S1. Note that species 150 at the top of the web is a parasitic gastropod (feeding on brittle stars). Taxa 48 and 79 at the foot of the web are non-feeding larvae.