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*Research article*

# Stable motifs delay species loss in simulated food webs

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Some three-species motifs (unique patterns of interactions between three species) are both more stable when modelled in isolation and over-represented in empirical food webs. This suggests that these motifs may reduce extinction risk for species participating in them, ultimately stabilising the food web as a whole. We test whether a species' time to extinction following a perturbation is related to its participation in stable and unstable motifs and assess how motif roles co-vary with a species' degree or trophic level. We found that species' motif roles are related to their times to extinction following a disturbance. Specifically, having a larger proportion of the motif role made up by the omnivory motif was associated with longer times to extinction, even though the omnivory motif is less stable than the others when modelled in isolation. While motif roles were associated with extinction risk, they also varied strongly with degree and trophic level. This means that these simpler measures of a species' role may be sufficient to roughly predict which species are most vulnerable to disturbance (though motif roles can be used to refine these predictions), but that studies of species' motif participation can also reasonably comment on vulnerability to extinction.

Keywords: competition, disturbance, omnivory, species roles, three-species chain

## Introduction

The connections between food-web structure and the extinction risk of species within the food web have interested ecologists since at least the 1970s (May 1972). Although large, randomly-connected networks are unlikely to retain all species after small perturbations (Gardner and Ashby 1970, May 1972), several non-random structures that might stabilise food webs (allowing all species to persist) have been identified. These structural features include nestedness (Allesina and Tang 2012, Sauve et al. 2014), modularity (Thébault and Fontaine 2010, Sauve et al. 2014) and skewed distributions of link strengths (McCann et al. 1998, Gross et al. 2009, Rooney and McCann 2012, Wootton and Stouffer 2016a).

Although important, these global-scale properties (properties of the network as a whole, Fig. 1) can mask important differences in network structure (Simmons et al. 2019) and do not provide information about differences between species within the

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**(A)** Multiple scales of network descriptors

## Global scale
### (whole network)



Species richness (S) = 9
Link richness (L) = 11
Connectance (C = L/S$^2$) = 0.123

## Meso scale
### (direct + indirect ints)



Motif participation:

| | | | |
|---|---|---|---|
| A: 6 | 1 | 1 | 2 |
| B: 6 | 0 | 2 | 5 |

All motifs indicated for A.
Motif colours as in Fig. 1B.

## Fine scale
### (single dimension)



Trophic level: A = 3, B = 2

Degree: A = 3, B = 5

Global scale measures describe the network as a whole, but do not give information about differences between species within a food web.

Meso-scale structures, such as motifs, capture direct and close indirect interactions between species, describing differences between species. Species A appears in each of the four motifs found in this network, but species B appears in more total instances of three-species motifs.

Fine-scale descriptions of a species' role such as trophic level (height in the food web) and degree (number of interaction partners) provide less detail than motif roles. Note that fine-scale descriptions and motifs are related: species B has a higher degree and participates in more motifs than species A.

**(B)** Key motifs and extinction risk

### Some motifs are more stable than others



Left: Direct competition
Middle: Apparent competition
Right: Three-species chain

Omnivory

There are 13 possible three-species motifs in food webs (grey trios of circles). Four motifs (coloured) have higher stability (probability of retaining all species) in simulations.

### Stable motifs have ecological meanings

Direct competition: two predators share prey. By changing the prey population, predators affect each other indirectly. E.g., owls and hawks share rodent prey. A decline in owls could allow rodents to increase, benefitting hawks.

Apparent competition: two prey share a predator. By changing the predator population, prey affect each other indirectly. E.g., introduced rabbits can increase introduced fox populations, leading to greater predation on Australian marsupials.

Three-species chain: a predator eats an intermediate consumer, which eats a prey. By changing the intermediate consumer population, the predator and prey affect each other indirectly. E.g., declining sea otter populations lead to sea urchin booms, in turn causing declines in kelp.

### Omnivory motif: direct and indirect effects

Omnivory: a predator eats an intermediate consumer and a prey, and the intermediate consumer eats the prey. Note that, *sensu* Thompson *et al.* (2007), the prey does not need to be a basal resource. All three species affect each others' populations directly and indirectly (by modifying the populations of other species in the motif).

Omnivory is less stable when modelled in isolation than the other stable motifs, but more stable than the remaining seven three-species motifs (far left).

All four stable motifs tend to be over-represented in empirical food webs, compared to random networks of the same size.
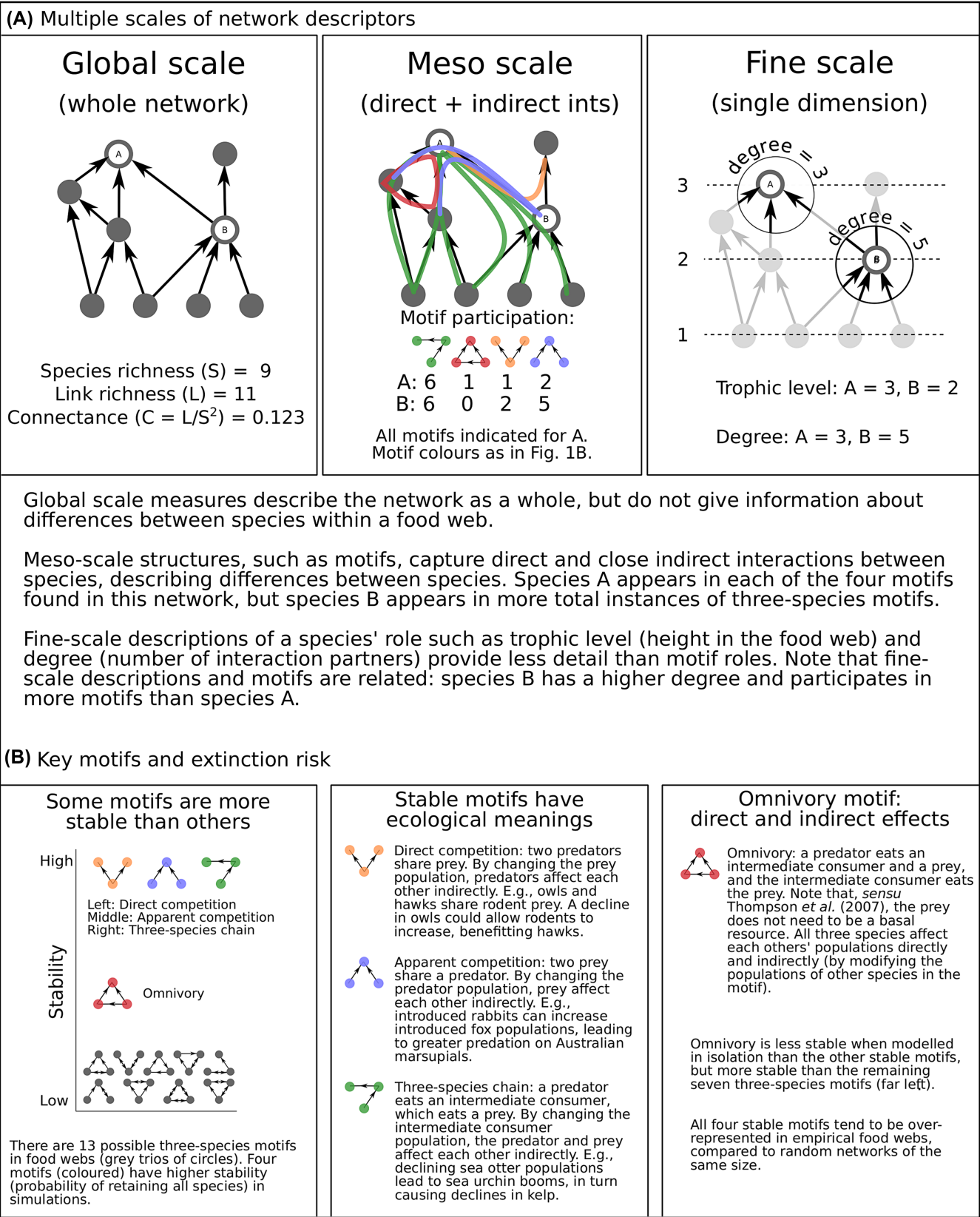
Figure 1. A brief introduction to motifs.

same network (Cirtwill et al. 2018). Two networks with the same connectance and similar values of nestedness and modularity may still have quite different meso-scale (i.e. more detailed than global-scale) arrangements of links. These meso-scale structures, described by frequencies of *motifs* (unique patterns of *n* interacting species), define the local neighbourhood of a focal species and reflect its direct and close indirect interactions (Fig. 1). As three-species motifs are the best studied, particularly with respect to stability (Stouffer et al. 2007, Borrelli 2015, Borrelli et al. 2015, Giling et al. 2019), we also focus on this size of motif.

In addition to providing species-level information on network structure, there are early indications that some mesoscale structures may tend to stabilise food webs (Prill et al. 2005, Borrelli et al. 2015, Monteiro and Faria 2016). This possibility is supported by the fact that empirical food webs tend to contain more three-species chains and either more omnivory (sensu Thompson et al. 2007) motifs or more apparent competition and direct competition motifs than random networks (Stouffer et al. 2007). These four motifs (out of 13 total three-species motifs) make up, on average, about 95% of all three-species motifs in food webs (Stouffer and Bascompte 2010). The high frequencies of these four motifs in observed networks suggest that they may be beneficial to the network containing them or, in other words, that more stable motifs appear more frequently in empirical food webs because unstable motifs are more likely to disappear as the species within them go extinct (Borrelli 2015, Borrelli et al. 2015) or links between species are lost (Tylianakis et al. 2010).

When modelled in isolation, three species arranged in three-species chain, apparent competition, direct competition and omnivory motifs are more likely to all persist than trios of species arranged in other motifs (Borrelli 2015). By damping perturbations and maintaining more constant populations of the species participating in them, these 'stable' motifs may contribute to the stability of the network as a whole (Borrelli 2015). The greater chances of maintaining all species in a stable motif could explain the over-representation of these motifs in empirical food webs if species and interactions in less-stable motifs are more likely to be 'pruned' from empirical communities over time. We expect that stable structures will endure for longer than unstable ones, and so it is not surprising that stable structures should be over-represented in empirical communities (Borrelli et al. 2015).

'Stability' broadly refers to the tendency of a community to retain or return to a particular state, but it is a multifaceted concept incorporating resistance, resilience, asymptotic stability, variability and robustness (Donohue et al. 2013). 'Disturbance' is similarly multifaceted, including short- or long-term and species-specific or community-wide disturbances, each with a different effect on a given metric of stability (Donohue et al. 2013, Radchuk et al. 2019). Here, we focus on a dynamic measure of stability after a permanent disturbance – the time to extinction for all species in the network after a single species is removed (primary extinction). Given these early indications that some motifs are more

stable than others, we may also expect that a species' role – here defined as the frequency with which it participates in different motifs – could affect its probability of extinction following a perturbation. Specifically, we expect that species participating more frequently in the stable motifs identified by Borrelli (2015) are less likely to go extinct than species whose roles are dominated by other motifs.

Testing the hypothesis that participation in stable motifs will decrease a species' likelihood of extinction is complicated by the fact that species' motif roles are not independent of other aspects of fine-scale network structure. In particular, a species' degree (number of predators and prey) is likely to strongly affect its motif role. The more interaction partners a species has, the more motifs it can participate in (Fig. 1). Species with higher degrees can therefore likely participate in a wider variety of motifs, as well as participate more frequently in the four common, stable motifs. Likewise, species with different trophic levels tend to have different motif roles (Cirtwill and Eklöf 2018). As well as these correlations between simple network measures and motif roles, species with high in-degrees (more prey) or lower trophic levels are also generally less likely to go extinct (Cirtwill et al. 2018). This means that relationships between motif roles and extinction risk could be describing relationships between degree and/or trophic level and both extinction risk and motif roles. This possibility should be taken into account when interpreting any such relationship between motif roles and extinction.

Here, we investigate the relationship between species roles and extinction risk by simulating the removal of species from simulated networks at stable equilibria. We test 1) whether species' roles are related to their time to extinction following the removal of another species in the network and 2) if so, which motifs show the strongest correlations with time to extinction. Because of the non-independence of different network measures, we also test 3) whether these correlations are driven by potential relationships between species' participation in various motifs and simpler definitions of species roles (degree, trophic level). Taken together, the results we obtain for these tests show that species are generally consistent in their vulnerability to disturbances, regardless of the location in the network of that disturbance, and this vulnerability is shaped by both motif roles and other network parameters.

## Methods

### Generating networks and extinctions

#### Generating food webs
We simulated a suite of food webs based on the probabilistic niche model, which assigns predator–prey links based on the body–mass ratios between individuals of different species (Williams and Martinez 2000, Delmas et al. 2017). The meso-scale structure of niche-model networks closely mimics that of empirical food webs (Stouffer et al. 2007). To ensure that we captured a variety of realistic community sizes and structures, we generated networks ranging between 50 and 100

species (in steps of 10) with connectance values between 0.02 and 0.2 (in steps of 0.02). The range of network sizes was chosen to reflect moderately well-sampled empirical webs while working within our computational limits, while the range of connectance values was chosen to cover that observed in most empirical food webs (Dunne et al. 2002). We generated a total of 100 networks with each combination of parameters, for a total of 6000 networks (Supporting information). All networks were generated using the function *'nichemodel'* within the Julia language package BioEnergeticFoodWebs (Delmas et al. 2017, 2019). If a simulated network contained any disconnected species (species without predators or prey) or disconnected components (a group of species connected amongst themselves but not to the rest of the network), the network was rejected and a new network simulated. Finally, networks where the path lengths between each species and a basal resource could not be resolved (i.e. trophic levels were undefined) were rejected and new networks simulated.

After generating the network structure, we simulated community dynamics using the function 'simulate' from the Julia language package 'BioEnergeticFoodWebs' (Delmas et al. 2017, 2019). This function uses the bio-energetic model of Yodzis and Innes (1992) adapted to food webs (Williams et al. 2007), including density dependence and type 2 functional responses for all species (please see Delmas et al. 2017 for full details). All non-basal species were designated as vertebrates to ensure a good match between metabolic and predator–prey body-mass ratio values. Metabolic rates in the bio-energetic model are based on each species' body mass (i.e. mass of a single individual). We assigned relative body masses based on each species' trophic level. Trophic levels, in turn, were calculated based on the food-web structure provided by the niche model. Specifically, we use the shortest trophic level (STL), i.e. the shortest path between the species and a basal species (Hairston and Hairston 1993). After basal species were assigned a body mass of 1, we used a predator–prey body-mass ratio of 3.065 to calculate the relative body masses of higher trophic levels. We selected this ratio based on the estimate for vertebrates (averaged across ecosystem and metabolic types) in Brose et al. (2006). We excluded reported body-mass ratios for invertebrates as these could include parasites and parasitoids, which are generally smaller than their prey, and because interactions among vertebrates are better represented in the food-web literature than interactions involving invertebrates.

The persistence of each species in our simulated networks also depends on its population biomass. We randomly assigned initial population biomasses (i.e. cumulative biomass across all individuals of a species) for each species from a uniform distribution [0,1]. Note that population biomasses and individual body masses are not calculated on the same scale. We then simulated community dynamics for 1000 time steps to obtain an equilibrium community. We use an equilibrium community to ensure that secondary extinctions are caused by the initial disturbance (i.e. removal of a species) and not due to existing disequilibrium. To ensure that species did not 'recover' from unrealistically low biomasses during the simulation, we considered a species extinct if it dropped below an arbitrary threshold

biomass of $1 \times 10^{-5}$. When simulating initial (i.e. pre-perturbation or equilibrium) dynamics, we rejected any network where one or more species dropped below this biomass threshold. Consumers were assumed to have no preferences such that the consumption rate $w_{ij}$ of predator $i$ eating prey $j$ is equal to $1/n$, where $n$ is the number of prey for predator $i$. If the network did not reach an equilibrium with all species persisting for 1000 time steps, a new set of initial population biomasses was applied and the simulation repeated until an equilibrium with all species persisting was obtained. If a stable equilibrium still had not been reached after 100 sets of randomly-assigned initial biomasses, we discarded the network and simulated another to replace it.

### Calculating species roles

We were interested in whether species' roles at equilibrium are related to their response to a perturbation, in this case the removal of another species in the network. We defined each species' role as the number of times it appears in each unique three-species motif, following Stouffer et al. (2012) and Cirtwill and Stouffer (2015). Note that each set of three interacting species forms exactly one motif (Cirtwill et al. 2018). Our main focus is on how different motifs might affect extinction risk, but we also consider how the different positions species may take within a motif could provide extra information on vulnerability to extinction. We expect that appearing more frequently in stable motifs (three-species chain, apparent and direct competition, and omnivory) will correlate with lower extinction risk while appearing more frequently in unstable motifs (those containing two- or three-species loops) will be associated with higher extinction risk. Note that cannibalistic links were ignored when calculating motif frequencies within a network and species' roles, although they were included when calculating connectance. As well as these 'raw' motif roles, we calculated 'species-normalised' motif roles for each species by dividing the number of appearances in each motif by the total number of times the species appears in any motif (as in Cirtwill and Stouffer (2015); this total is expected to strongly correlate with degree). Finally, we also calculated 'network-normalised' motif roles, defined as the Z-score ($Z_{imn}$) of a focal species i's participation in motif m compared to full set of species in network n (Eq. 1):

$$Z_{imn} = \frac{x_{imn} - \mu_{mn}}{\sigma_{mn}} \tag{1}$$

where $x_{imn}$ is the observed count of motif m in the role of species $i$ in network $n$, $\mu_{mn}$ is the mean count of motif m in the roles of all species in network $n$, and $\sigma_{mn}$ is the standard deviation of the count of motif $m$ in network $n$. The species normalisation allows us to test whether trends in stability with motif participation are due to differences in the total number of motifs a species appears in, while the network normalisation allows us to test whether trends in stability are related to how unusual a species' motif participation is relative to other species in its community, rather than which specific motifs a species participates in.

### Perturbing networks

After identifying species' roles in the equilibrium networks, we perturbed the networks by removing a single species. After this removal, community dynamics were simulated for 50 rounds of 10 time-steps (500 time-steps total). After each round, any species with a biomass below our threshold of $1 \times 10^{-5}$ was considered to have gone extinct and its biomass was set to 0. We recorded the biomass of each species after each round, as well as the round in which any additional extinctions occurred. Although the BioEnergeticFoodWebs package does allow for rewiring following extinctions, we chose not to allow rewiring because this would change species' motif profiles. After 500 time-steps, we reset the network to its original state (including all species). We then removed a new species and again simulated community dynamics. We repeated this process until all species had served as the initial removal. We then calculated the mean time to extinction across all removals as an overall measure of each species' vulnerability (Supporting information). Species which did not go extinct in a given simulation were assigned an extinction time of 500. Time to extinction was highly correlated across removals in all combinations of S and C, indicating that this is a robust measure.

### Statistical analysis

#### Is motif participation related to persistence?

We are interested in whether the set of motifs in which a species appears at 'equilibrium' is related to its persistence (here defined as time to extinction following the removal of another species). To address this question, we can consider the motif participation role as a whole or the relationships between participation in each motif and persistence. The first approach provides a more holistic view of the relationship between meso-scale structure and extinction risk, while the second may identify specific meso-scale structures with especially strong relationships to persistence.

#### Motif participation as a whole

To test whether motif participation as a whole is related to persistence, we fit a series of PERMANOVAs relating the Bray–Curtis dissimilarity in species' motif participation vectors to their persistence times per se and Mantel tests relating dissimilarity in species' motif participation to dissimilarity in their persistence times (see Supporting information for details). Due to computational constraints, we fit one PERMANOVA and one Mantel test per combination of network size and connectance (60 combinations). We repeated these sets of PERMANOVAs and Mantel tests for each version of motif participation vectors (counts, species-normalised and network-normalised; 180 of each test in total).

Because the assumption of equal variability that underlies a PERMANOVA test was not met (Supporting information), the results of these tests are indicative but not conclusive. Further, because of this violation of assumptions, we did not use PERMANOVAs to test whether motif roles including positions were related to time to extinction. The Mantel tests did not suffer from the same violation of assumptions but also mask which motif participation vectors are associated with high or low extinction risk; we therefore consider these tests likewise indicative but not conclusive. We therefore present the results of these tests in the Supporting information only.

#### Participation in particular motifs

For a more detailed perspective on relationships between motif participation and persistence, we fit linear mixed-effect models including the effect of each motif separately. Since the motifs containing loops (two-way interactions or three-species loops) are rare in both empirical systems (Stouffer et al. 2007) and our simulated networks (means $8.99 \times 10^{-4}$–2.06%) and are all unstable when modelled in isolation (Borrelli 2015), we pool these loop-containing motifs into an 'other' group (see Supporting information for details about how each version of motifs were pooled). We considered each stable motif (apparent competition, direct competition, omnivory and three-species chain) individually.

For each version of motif participation (count, frequency or Z-score), we fit a linear mixed-effect model (LMM) of the form (Eq. 2):

$$\tau_{in} \approx \alpha_i + \delta_i + o_i + \chi_i + \omega_i + S_n : C_n + N_n \qquad (2)$$

where $\tau_{in}$ is the mean time to extinction (persistence) of species i belonging to network n, $\alpha_i$, $\delta_i$, $o_i$ and $\chi_i$ are the species' participation in the apparent competition, direct competition, omnivory and three-species chain motifs (respectively), $\omega_i$ is the species' participation in the unstable/'other' motif group, $S_n : C_n$ is a random effect of the size and connectance of network n, and $N_n$ is a random effect of belonging to network n. The random effect of global network structure controls for differences in mean persistence between, for example, highly-connected and weakly-connected networks. The random effect of network ID controls for the fact that all species in the same network have the same pool of motifs to participate in and are therefore non-independent. These models indicate whether each motif is positively or negatively correlated with persistence time, and how much variation in persistence time can be explained by each version of motif participation. We fit the LMMs using the R (<www.r-project.org>) function *lmer* from the package 'lmerTest' (Kuznetsova et al. 2017) and calculated variance explained using the function *r.squaredGLMM* from the package 'MuMIn' (Bartón 2015).

Note that, in the species-normalised motif participation vectors, the frequencies of all motifs must sum to 1 and are therefore not independent. Participation in the count and Z-score motifs also may not be independent (e.g. species which participate in especially many interactions may have high counts and Z-scores of several motifs). To illustrate these potential interdependences, we also present the correlations among all motifs for each version of motif participation, calculated using the function *'lmer'* as above. To obtain more detail about the relationships between motif participation

and persistence time, we repeated the analyses above while defining roles based on a species' participation in each unique position (e.g. top, middle and bottom species in a three-species chain) in each motif. As we are most interested in relationships between persistence and the apparent competition, direct competition, omnivory and chain motifs, we grouped all positions in other motifs into an 'other' category, similar to the way we pooled 'other' motifs above. We calculated raw count, species-normalised and network-normalised roles including positions as above.

Adding context: how does motif participation relate to simple roles?

To interpret the results of the analyses above, especially the LMMs, we must bear in mind the potential for motif participation to reflect differences in degree, trophic level and global network structure. To establish this context, we therefore fit a series of linear models (LMs) relating degree, trophic level, network size and connectance to each version of the motif role (Supporting information). These LMs also included a random effect of global network structure. For ease of interpretation, we once again grouped the loop-containing motifs into an 'other' group. When using species-normalised motifs, we removed the 'other' motifs from the model to avoid a rank-deficient model matrix. As with the relationship between motif participation and persistence time, we repeated the analyses above for roles including positions within each of our focal motifs.

To complete this background, we fit a regression of persistence against degree, trophic level and their interaction, as well as a random effect of global network structure (Supporting information). These regressions are intended only to confirm whether our simulations show the expected increase in persistence with degree and decrease in persistence with trophic level.

## Results

### Participation in stable motifs was related to persistence

When defining participation based on counts, increased participation in any stable motif except for omnivory was correlated with longer persistence following species removal (Supporting information). Regressions against motif participation explained only 5.8% of variation in persistence time (fixed effects only). When defining roles based on positions within each motif, increased participation in any of the positions in the omnivory motif was correlated with shorter time to extinction while increased participation in any position in the apparent competition, direct competition and three-species chain motifs was associated with longer persistence (Supporting information). Roles including positions explained the same amount of variation in persistence time as roles including whole motifs.

When defining participation based on frequencies, greater participation in the omnivory, three-species chain and apparent competition motifs was correlated with longer persistence,

while the frequency of the direct competition motif was not significantly associated with persistence (Supporting information). However, the amount of variance in persistence time explained by frequencies was extremely low (0.5%; fixed effects only). The amount of variance in persistence time explained by roles including motif positions was substantially higher (8.1%; fixed effects only). Persistence time increased with the frequency of appearing in the bottom position in the apparent competition motif, the top position of the direct competition motif and the middle position of the three-species chain motif (Fig. 2, Supporting information).

When defining participation based on Z-scores, unusually high participation in the omnivory motif was associated with shorter persistence while unusually high participation in any other motif was associated with longer persistence (Supporting information). The amount of variance in persistence explained by trends in Z-score participation was lower than that explained by counts but higher than that explained by frequencies (2.2%; fixed effects only). The amount of variance in persistence explained by Z-scores of appearing in different positions was higher than that explained by participation in whole motifs (4.9%; fixed effects only). Unusually high participation in the bottom position in the apparent competition motif, either position in the direct competition motif, and middle position in the three-species chain were associated with longer persistence (Supporting information).

### Motif participation was related to simpler roles

As expected, a higher degree was associated with higher counts and higher Z-scores of any motif (Supporting information). A higher degree was also associated with higher counts of all positions and higher Z-scores of all positions except for the bottom and middle positions of the three-species chain (Supporting information). A higher frequency of omnivory was also associated with higher degree, while the converse was true for all other motifs. A higher frequency of any position in the omnivory motif was likewise associated with higher degree, as were higher frequencies of both positions in the apparent competition motif and top positions in the direct competition and three-species chain motifs (Fig. 3). Raw motif participation explained almost all variance in degree, while the correlation between network-normalised (Z-score) motif participation and degree was weaker. Based on these correlations, raw motif participation provides mostly the same information given by degree while species-normalised and network-normalised motif participation are likely to provide more independent information.

The relationships between trophic level and participating in different motifs or positions were extremely weak for all versions of motif participation (Supporting information). While there were some significant relationships, these trends explain so little variation in trophic level that motif participation and trophic level are likely to convey almost entirely different information about a species' place in the network.
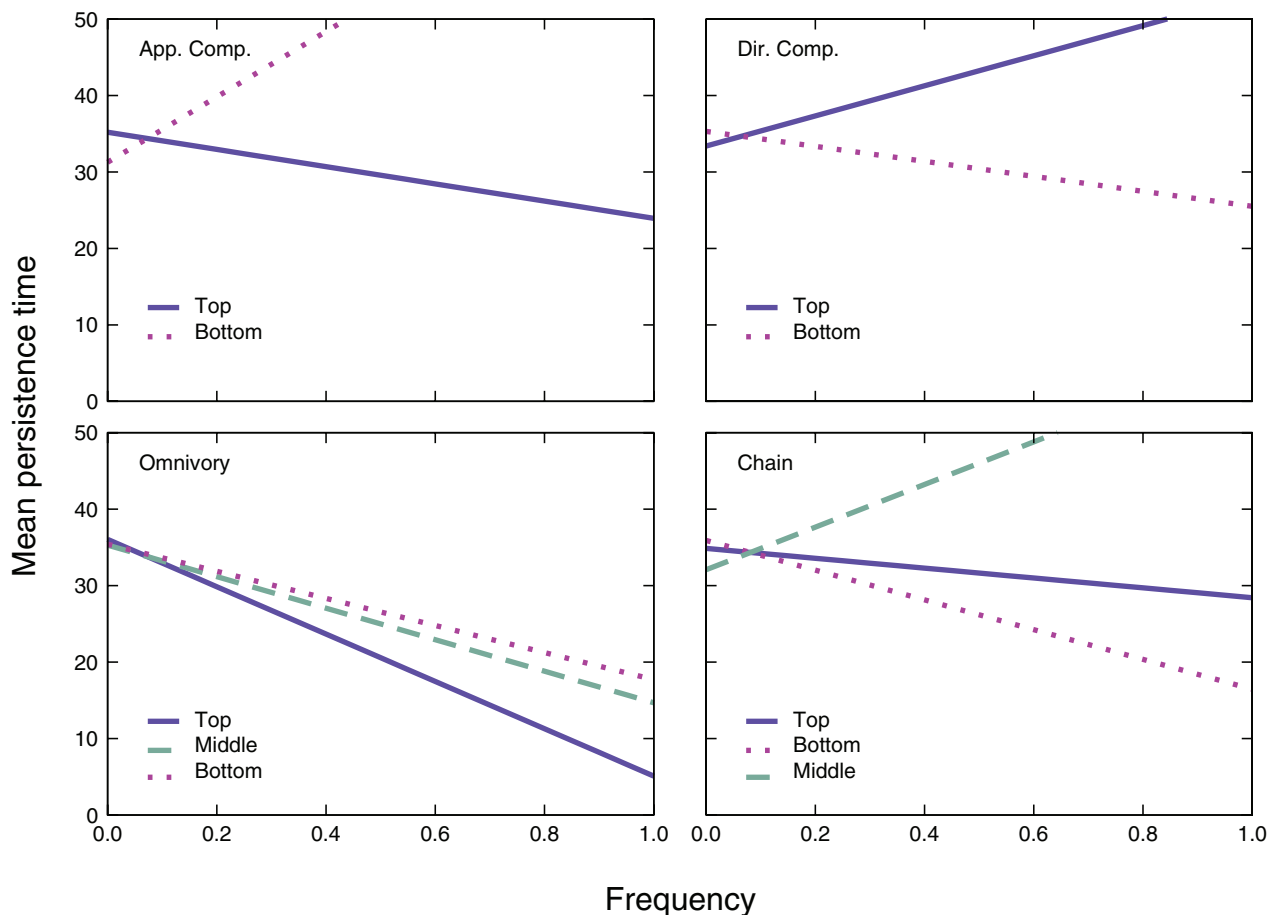
Figure 2. Mean persistence time was significantly related to the frequency of appearing in different motif positions (marginal $R^2 = 0.081$, Supporting information). The figure is based on the fixed effects in a regression of persistence against participation in positions in the apparent competition, direct competition, omnivory, three-species chain and motifs, with all positions in the 'other' (loop-containing; not shown) motifs grouped, as well as random effects of global network structure and network ID. Top positions have prey but no predators within the motif, bottom positions have predators but no prey within the motif, and middle positions have both prey and predators within the motif. We show the marginal effects of increasing frequencies of each position. As position frequencies must sum to 1, we weighted participation in other motifs by their mean values.

### Persistence was related to simpler roles

Simple roles (degree and trophic level) together explained a moderate amount of variation in persistence ($R^2_m = 0.211$, $R^2_c = 0.232$). Species with higher degrees and lower trophic levels tended to have longer mean times to extinction (Supporting information). However, a negative interaction term means that an increase in degree is less beneficial for species with high trophic level (Fig. 4).

### Discussion

We found that times to extinction were tightly correlated across removals. Although the exact length of time a species persists after disturbance likely depends on the threshold for extinction chosen, the correlation of times to extinction for a given threshold suggests that the position of a focal species within a network can affect its risk of extinction following a disturbance regardless of where in the network the

disturbance is applied. This result also justifies our use of mean times to extinction across removals as a measure of a species' overall risk.

Taken together, our results show that motif roles are related to mean times to extinction. Species-normalised (frequency) motif roles including participation in different positions explained the most variation in time to extinction. As expected, participation in positions in the apparent competition, direct competition and three-species chain were especially associated with longer times to extinction.

### Times to extinction are highly consistent

The consistency of species' times to extinction across removals in our simulations suggests that some species are more likely to go extinct than others due to their position within a network. This complements other work identifying sets of species which are more vulnerable to extinction due to their traits (Curtsdotter et al. 2011, Ryser et al. 2019). Since
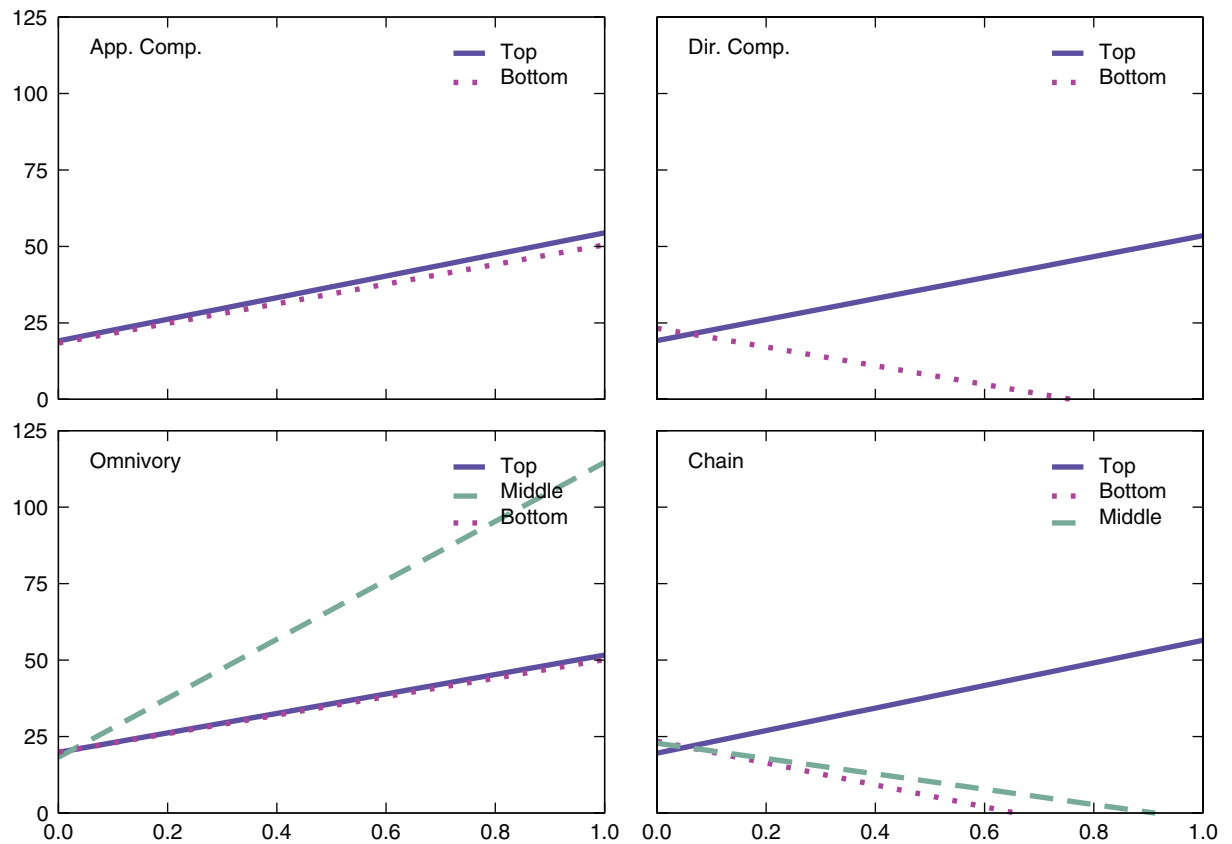
Figure 3. Species-normalised (frequency) roles explained a great deal of variation in species' degrees (marginal $R^2 = 0.729$, Supporting information). The frequencies of the bottom position in the direct competition motif and the bottom and middle positions in the three species chain decreased with increasing degree while the frequencies of the other positions in our focal motifs increased. We show the marginal effects of increasing frequencies of each position. As position frequencies must sum to 1, we weighted participation in other motifs by their mean values.

the trophic level and degree of the species being removed can also affect which species, if any, go secondarily extinct (Dunne et al. 2002, Wootton and Stouffer 2016b), the properties of both disturbed and non-disturbed species affect the ways in which extinctions can cascade through a food web.

The stronger correlation of time to extinction in larger, more-connected networks, as well as the somewhat shorter mean times to extinction in these webs (Supporting information) may be due to the greater number of short pathways by which an extinction somewhere in the web can affect a focal species. These short pathways are more likely to have strong effects on the population dynamics of species along them than the longer indirect pathways in poorly-connected networks (Jordán et al. 2006, Jordán and Scheuring 2012). These stronger effects in turn likely explain why more secondary extinctions in large or highly-connected webs are due to indirect effects rather than direct loss of a prey or predator (Wootton and Stouffer 2016b).

These strong correlations of times to extinction may also be related to the extinction threshold we chose. If we used an arbitrarily lower threshold, species would likely persist longer before being declared extinct and more species would not reach

the threshold for extinction. With fewer extinctions detected, we might not observe such consistency across removals or such strong relationships between species roles and extinction risk.

## Motif roles relate to extinction risk

Overall, our results show that species' motif roles were related to their time to extinction after a disturbance. As species-normalised motif roles including positions explained most variation in time to extinction, we focus on those results below. Note however, that in all cases the counts, frequencies or Z-scores of the four motifs which are most stable in isolation (Borrelli 2015) were also most strongly associated with persistence time. This supports earlier work suggesting that these motifs are most common in empirical networks (Stouffer et al. 2007) because the species which participate in them tend to persist longer and are therefore more likely to be extant when a food-web is sampled (Borrelli et al. 2015).

Species tended to have longer times to extinction if their roles contained higher frequencies of the bottom position in the apparent competition motif, top position in the direct competition motif or middle position in the three-species
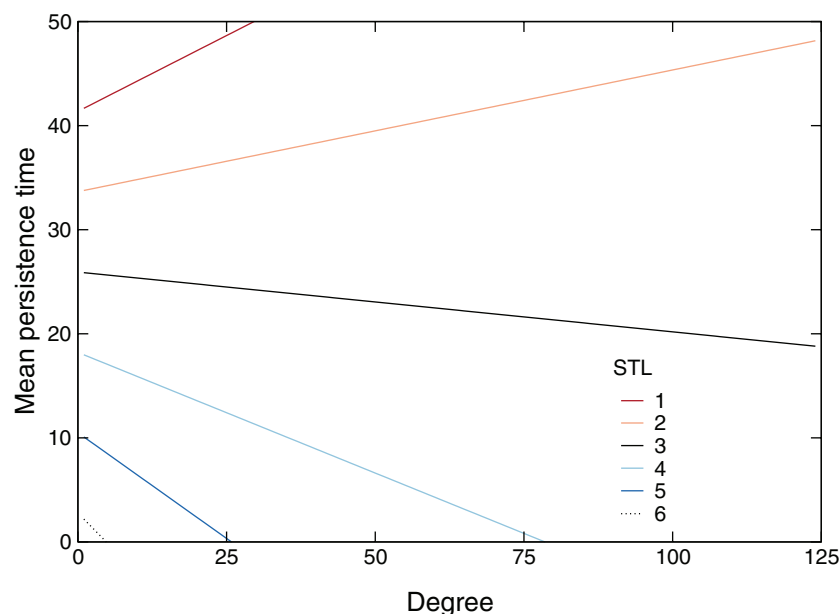
Figure 4. Persistence time was strongly related to degree, trophic level and their interaction (marginal $R^2 = 0.211$, Supporting information). Mean persistence time increased with increasing degree for species at low trophic levels (STL 1–2) but decreased with increasing degree for species at high trophic levels (STL > 2). The figure is based on the fixed effects in a regression of persistence against degree, trophic level, their interaction and a random effect of global network structure. We also give the marginal $R^2$ for the regression (fixed effects only).

chain. Higher frequencies of all other positions, notably all positions in the omnivory motif, were associated with shorter mean persistence times. For direct competition, these associations may be due to an underlying association between motif roles and degree. Higher degree was associated with longer persistence time and species-normalised roles explained a large amount of the variation in degree, and the associations between frequencies of positions in the direct competition motif and persistence match their associations with degree. The benefit of participating frequently in the top position may therefore be due to an underlying effect of degree.

In other cases, however, the association between the frequency of a position and persistence is opposite to what would be expected based on the position's association with degree, while trophic level was not strongly associated with motif roles (Supporting information). This indicates that motifs and simpler measures of species roles provide some independent information about extinction risk. For example, higher frequencies of all positions in the omnivory motif were associated with shorter times to extinction *despite* being associated with higher degree. This is consistent with Borrelli (2015)'s finding that omnivory motifs are less likely to be stable than the chain and competition motifs. Earlier work has shown that the omnivory motif can be stable or unstable under different conditions and may or may not increase the overall stability of an entire food web (McCann and Hastings 1997, Emmerson and Yearsley 2004, Borrelli 2015, Monteiro and Faria 2016). Our results suggest that omnivory motifs may not benefit the species within them even if they do tend to benefit the network as a whole. This could be related to the distribution of link strengths within a food web. In small (3–5 species) model communities and soil food webs, weak

interactions only promote stability if omnivory is present (Neutel et al. 2002, Emmerson and Yearsley 2004) and the loss of the omnivorous species dramatically reduces stability (Emmerson and Yearsley 2004). In our terms, this suggests that when the top species in an omnivory motif is lost, the other species in the motif will tend to have substantially shorter times to extinction. Species participating in many omnivory motifs are unlikely to always occupy the top position and may, therefore, be strongly affected by the loss of other species within the same motif.

## Moving forward with motifs

As motif roles become more common as tools for ecologists wishing to understand how species' positions within networks are related to their traits (Cirtwill and Eklöf 2018), taxonomy (Stouffer et al. 2007) and position in space or time (Baker et al. 2015), it is natural to wonder how these roles might relate to a species' response to disturbance. Our results suggest that participation in the three-species chain, apparent competition and direct competition motifs promote longer persistence after a disturbance, while the omnivory motif may indicate more rapid extinction. However, interpreting these trends is complicated by strong relationships between motif roles and degree, which itself promotes longer persistence after a disturbance.

Because relationships between motif roles and degree appear even when considering the proportion of species roles made up by each motif, as in Baker et al. (2015), Cirtwill and Stouffer (2015) and Simmons et al. (2019), normalising motif roles based on the total number of motifs does not control for differences in species' roles due to degree. The papers

cited above explicitly aim to control for differences due to the total number of motifs in which a species appears (which depends upon the degrees of the focal species and those of its interaction partners) rather than degree per se. However, this distinction is subtle (hence our use of 'species-normalisation' to describe the proportional roles) and future authors should take great care that they are not using the sum of motifs as a substitute for degree as our results show that these quantities are not interchangeable. Rather, our results suggest that both motif roles and simpler measures of network structure can provide information about a species' response to disturbance. Motifs may be particularly useful when comparing species with similar degrees or trophic levels: the multi-dimensional nature of the motif role allows it to capture information which is lost in single-value measures, and participation in the omnivory motif shows a relationship to extinction risk which cannot be explained based on degree or trophic level. Alternatively, future work exploring interactions between motifs and simple roles could improve our ability to predict extinction risk. For example, although we treated basal and non-basal species the same in this analysis, basal resources are not subject to all of the same threats as consumers. In particular, our simulation assigns basal resources a positive intrinsic growth rate to reflect the assumption that a basal resource will, having reached a particular habitat, have all of the resources (water, nitrogen, etc.) it needs. In situations where basal resources may lack resources (e.g. in highly degraded soils or drought-prone areas), this assumption may not be met and basal resources will be at greater risk than in our simulations.

As previous work shows that traits of both the disturbed and responding species affect extinction risk (Wootton and Stouffer 2016a) and that disturbance of basal resources can have particularly strong effects (Scherber et al. 2010), adding the trophic levels of both disturbed and focal species to future analyses may improve our predictions. Likewise, interactions between motif participation and population biomasses could also affect how motifs relate to extinction risk. This could occur if species with high or low biomasses tend to appear in certain motifs more frequently or if participating in certain motifs assists species to be stable at different biomasses; future studies designed to separate these possibilities could strongly contribute to our mechanistic understanding of the relationships between network structure and persistence. While the interpretation of motif roles remains challenging, our results suggest that they are nevertheless a valuable tool and that the omnivory motif in particular may be useful when predicting responses to future disturbances.

## Speculation and alternative viewpoints

We note that our simulations reflect only body-mass structured vertebrate food webs. Testing whether these results hold true for other types of networks (e.g. invertebrate food-webs not structured by body mass) will require alternative simulation approaches; however, the increasing availability of highly-resolved empirical data for interactions among invertebrates (Waldner and Traugott 2012) should allow researchers to

create such simulations and test the generality of our results in the near future. Different network-building mechanisms are likely to result in networks with different motif frequencies overall. This will lead to species roles with different frequencies of each motif. Nevertheless, as our four focal motifs are the most common in a variety of empirical networks (Stouffer et al. 2007) we expect that they will remain important regardless of the type of food web under investigation.

We also note that our choice of extinction threshold is, in the absence of a best-practice consensus, arbitrary. The choice of a lower threshold would permit species to remain extant at lower biomasses and lengthen times to extinction for the species most prone to reach low biomasses, therefore requiring longer and more computationally-expensive simulations to detect differences in extinction risk between species. A lower extinction threshold might also reduce the impact of degree on persistence time as species would be more likely to retain all of their interaction partners, although the influence of very rare prey is minimal when interaction strengths are weighted by abundance as we have done here. Despite this overall decrease in extinction if we used a longer threshold, we do not expect that which motifs are associated with persistence would change. The species which most rapidly go extinct under our current threshold should also be the first to reach a lower threshold (excepting spurious recoveries of rare species between threshold values), leading to similar associations between motifs and extinction risk.

## Author contributions

**Alyssa R. Cirtwill**: Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (lead); Project administration (equal); Software (supporting); Visualization (lead); Writing – original draft (equal); Writing – review and editing (equal). **Katherine L. Wootton**: Conceptualization (equal); Investigation (equal); Methodology (supporting); Software (lead); Writing – original draft (equal); Writing – review and editing (equal).

## Data availability statement

Code used to simulate food webs and disturbance dynamics are available from the Zenodo Digital Repository: <https://doi.org/10.5281/zenodo.6377974> (Cirtwill and Wootton 2022).

## Supporting information

The Supporting information associated with this article is available with the online version.

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