

# Feedback spectra of soil food webs across a complexity gradient, and the importance of three-species loops to stability

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**Abstract** It has been shown that in real food webs, the strongest omnivorous feedback, a three-link positive feedback, is a good indicator of system stability, suggesting that the strongest positive feedback in a food web could be the Achilles heel of stability. However, the complete spectrum of feedbacks in observed food webs has never been analyzed. Here, we have quantified all the feedbacks in 32 soil food webs along a complexity gradient, including trophic feedbacks and feedbacks resulting from recycling of organic matter. We found that, although the maximum omnivorous feedback was rarely the strongest positive feedback in a system, it stood out over longer and stronger feedbacks as the indicator of stability. The results emphasize the importance of small substructures in complex networks.

**Keywords** Food webs · Loop weight analysis · Feedback · Omnivory

## Introduction

One of the main challenges for ecological research is to understand how ecological structure contributes to

ecosystem stability. Key to stability are feedbacks in an ecosystem (Levins 1974, 1975). Positive feedbacks reinforce deviations from a steady state and are usually destabilizing while negative feedbacks dampen deviations from steady state and are usually stabilizing. The balance of positive and negative feedbacks within an ecosystem determines its stability.

Studies of hypothetical food webs have shown that omnivorous interactions affect stability, with a greater amount of omnivory corresponding to greater instability (Pimm and Lawton 1978). Observations on real food webs have revealed specific patterns in the strength of species<sup>1</sup> interactions (de Ruiter et al. 1995), resulting in feedbacks from longer omnivorous chains of interactions being typically weaker (Neutel et al. 2002). This patterning has been shown to be crucial for ecosystem stability (Neutel et al. 2002, 2007). The maximum weight of omnivorous feedback loop decreases as the number of the species forming the loop increases, so that the heaviest omnivorous feedback of a food web always consists of three species (where weight refers to the geometric mean strength of interactions in a loop and omnivorous refers to feeding on different trophic levels in a food chain—see “Methods”). Neutel et al. (2007) find that this heaviest three-species feedback, which is always positive, is a good indicator of food-web stability: the weaker this three-species feedback, the less self-damping, negative feedback, is needed from competition within the species to make the system stable. They suggest that the maximum positive feedback in a predator–prey system is the “Achilles heel” of a food web.

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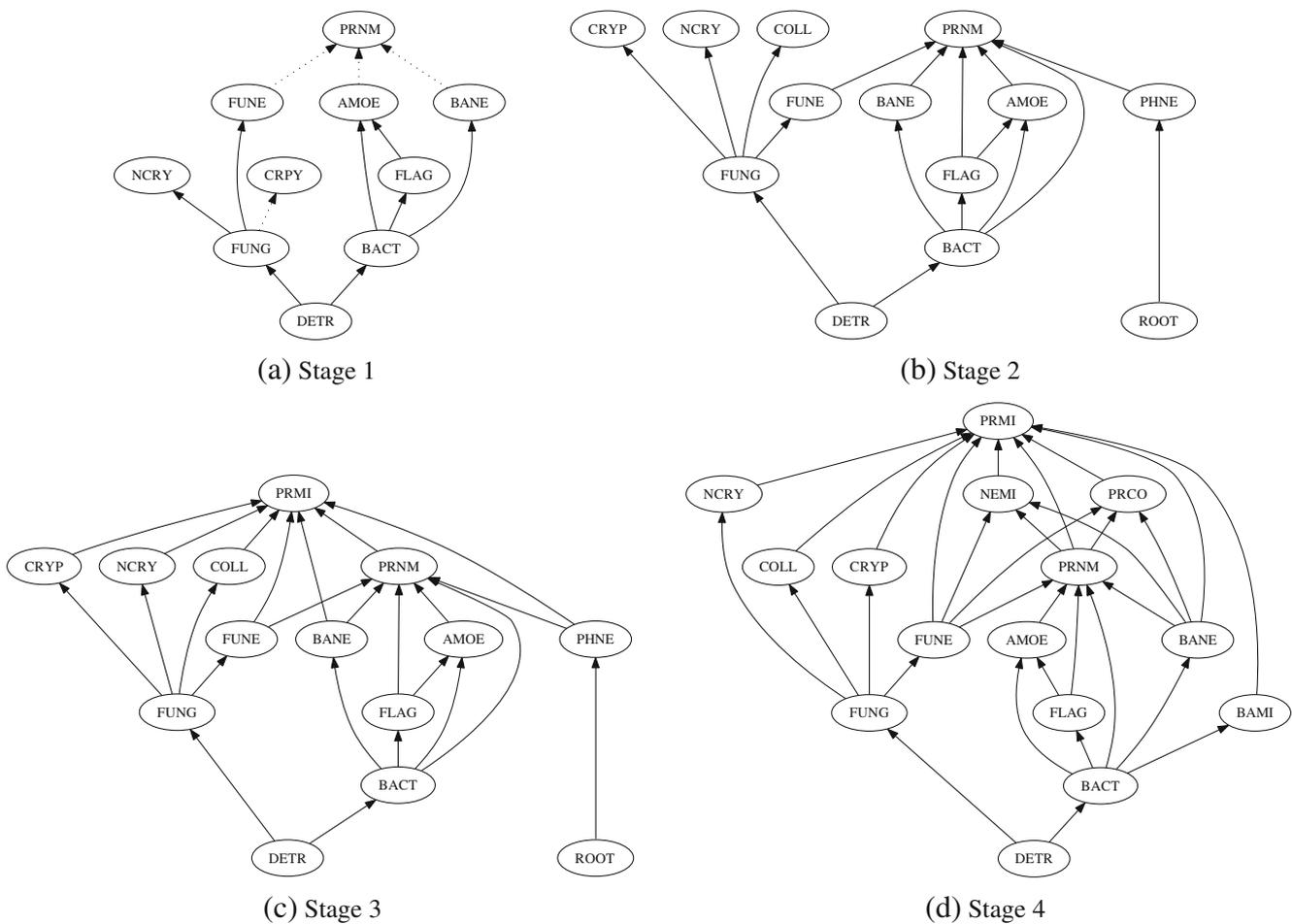
<sup>1</sup>In this study, we use the term species in a broad sense to refer to trophic groups of functionally similar species.

Neutel et al. (2007) only analyze two-species and omnivorous loops which form a small subset of all the feedbacks in a food web. Here, we quantify complete feedback “spectra” of the same soil food webs studied by Neutel et al. (2007) in order to explore feedback-stability relationships in more detail. We describe the relationship between maximum weights of the feedback loops with their lengths (number of species that form the feedback) for four categories of feedback loops: all loops, omnivorous loops, trophic loops (which contain the omnivorous loops), and detrital loops (which contain non predator–prey effects resulting from the recycling of dead organic matter). Our main questions are: what is the relation between maximum loop weight

and loop length for these different categories of feedback, is the three-species feedback always the heaviest positive feedback, and are there other feedbacks which are more important for stability than the three-species omnivorous feedback?

## Methods

Our analysis was carried out on the 32 soil food webs from Neutel et al. (2007), which represent two series of below-ground communities (Fig. 1). Each series consists of four stages in chronosequences of primary



**Fig. 1** Representative food-web diagrams of the four stages, from the two chronosequences of primary vegetation succession analyzed by Neutel et al. (2007). Labels refer to the trophic groups: *DETR* detritus, *ROOT* roots, *BACT* bacteria, *FUNG* fungi, *BANE* bacteriophagous nematodes, *PHNE* phytophagous nematodes, *FUNE* fungivorous nematodes, *FLAG* flagellates, *NCRY* noncryptostigmatic mites, *CRPY* cryptostigmatic mites, *COLL* collembola, *AMOE* amoebae, *PRNM* predatory nemo-

todes, *PRMI* predatory mites, *PRCO* predatory collembolans, *NEMI* nematophagous mites. Dotted lines in (a) indicate interactions present in only one of the series. Functional groups are similar to previous studies (de Ruiter et al. 1995) on soil systems. Earthworms and enchytraeidae were not measure by Neutel et al. (2007), in contrast to earlier soil studies, and were therefore not included in the webs

vegetation succession with each stage represented by four food-web replicates. The complexity of the food webs increases over this successional gradient (Neutel et al. 2007). The number of species increases, from eight to ten in the first stage to 16 to 17 in the fourth (Fig. 1). Detritus is also included within the food webs as a trophic group (de Ruiter et al. 1995; Neutel et al. 2007). The maximum food chain length of these webs varied between three and six, comparable to ranges found both into aquatic and terrestrial webs (Schoener 1989).

In our study, the two series were grouped together, so each successional stage contained eight food webs. Following Neutel et al. (2007) the interaction strengths and loop weights were calculated from their observational data. The dynamics of the populations were described by Lotka–Volterra-type equations:

$$\frac{dX_i}{dt} = X_i \left( b_i + \sum_{j=1}^n c_{ij} X_j \right) \tag{1}$$

Where  $X_i$  is the population density,  $b_i$  is the specific rate of increase or decrease of group  $i$  (for consumers it is the natural non-predatory, non-density dependent mortality), and  $c_{ij}$  is the interaction coefficient between species  $i$  and  $j$ . Interaction strengths  $\alpha_{ij}$  were defined as the entries of the Jacobian community matrices (May 1972), being the partial derivatives  $\alpha_{ij} = \frac{\partial \dot{X}_i}{\partial X_j}$  evaluated at equilibrium. The off diagonal Jacobian elements evaluated at equilibrium (denoted by \*). Values for the interaction strengths were derived from the energetics following the method of de Ruiter et al. (1995). In this procedure, equilibrium population sizes  $X_i^*$  and  $X_j^*$ , were assumed to be equal to the observed annual mean population sizes  $B_i$  and  $B_j$  and average annual feeding  $F_{ij}$  were calculated. With the species in the Jacobians ordered from the top predator on the first row and column, to the most basal group on the last row and column, the effect of a consumer  $j$  on resource  $i$ , and is given by:  $\alpha_{ij} = c_{ij} X_i^* = -\frac{F_{ij}}{B_j}$  with  $i > j$ . The effect of a resource  $i$  on its consumer  $j$  and is given by  $\alpha_{ij} = c_{ij} X_{ij}^* = \frac{e_i F_{ji}}{B_j}$  with  $i < j$ , where  $e_i$  is a biomass conversion efficiency ( $0 < e_i < 1$ ) of consumer  $j$ .

The effect of a population on itself (intraspecific competition),  $i = j$  was expressed as a proportion  $s$  of total specific natural death  $d_j$  implying that  $c_{ii} = \frac{s_i d_i}{B_i}$  and  $b_i = (1 - s_i) d_i$  and is given by:

$$\alpha_{ii} = c_{ii} X_i^* = -s_i d_i \tag{2}$$

The Jacobian elements for the detritus group were calculated using a modified Lotka–Volterra equation (following de Ruiter et al. 1995):

$$\begin{aligned} \frac{dX_D}{dt} = & R_d + \sum_{i=1}^n d_i X_i + \sum_{i=1}^n \sum_{j=1}^n (1 - e_j^{ass}) c_{ij} X_i X_j \\ & - \sum_{j=1}^n c_{Dj} X_D X_j \end{aligned} \tag{3}$$

where  $R_d$  is the input of allochthonous material,  $e_i^{ass}$  is the assimilation efficiency of the group  $j$  ( $0 < e_j^{ass} < 1$ ). The effect of a population  $j$  on detritus is:

$$\alpha_{Dj} = d_j - \frac{F_{Dj}}{B_j} + \sum_{k=1}^n (1 - e_j^{ass}) \frac{F_{kj}}{B_j} + \sum_{k=1}^n (1 - e_k^{ass}) \frac{F_{jk}}{B_j} \tag{4}$$

The effect of detritus on itself (diagonal element) is:

$$\alpha_{DD} = - \sum_{j=1}^n e_j^{ass} \frac{F_{Dj}}{B_D} \tag{5}$$

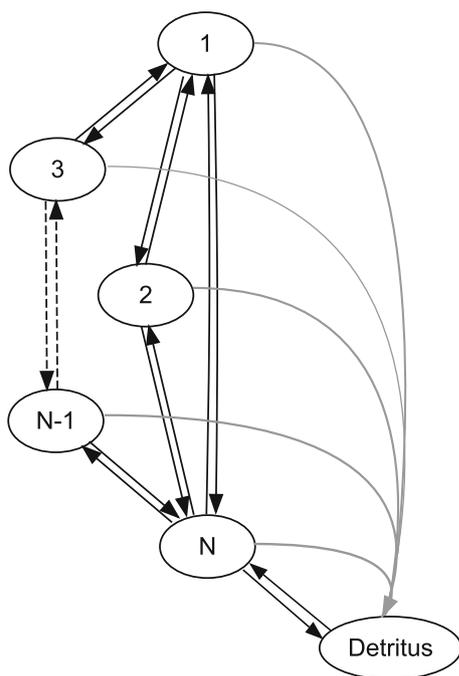
Loop weights  $w_k$ , containing  $k$  species, were calculated by taking the geometric mean of the absolute values of the Jacobian elements  $\alpha_{ij}$  in a feedback loop, relative to the mass specific non-predatory loss rates  $d_i$  of the functional groups in the loop (Neutel et al. 2007):

$$w_k = \left| \frac{\alpha_{i_1 i_2} \alpha_{i_2 i_3} \dots \alpha_{i_k i_1}}{d_{i_1} d_{i_2} \dots d_{i_k}} \right|^{\frac{1}{k}} \tag{6}$$

The geometric mean of the elements in a loop as a measure of weigh feedback was introduced by Neutel et al. (2002), to relate feedback to criterion of quasi diagonal dominance of the community matrix, which is a sufficient condition for stability, which enables a comparison of loops of different lengths in relation to the self-damping (diagonal strength) of the matrix. In order to allow comparisons with the dimensionless stability measure  $s$ , which indicates a proportion of total natural death  $d_i$ , Neutel et al. (2007) scale the feedback weights to the natural death rate  $d_i$  making the loop weight also dimensionless. Apart from the weight, the sign of the feedback was determined, defined as the sign of the product of Jacobian elements which formed the loop (Levins 1974; Hofbauer and Sigmund 1988). The loop length is defined as the number of species  $k$  within the loop. The maximum loop weight of loops of length  $k$  was denoted  $W_k$ .

Stability (the ability to return to steady state post perturbation) was determined using the diagonal

values of the community matrix as a control parameter, following Neutel et al. (2002, 2007). Specifically the stability measure was the multiplier of the diagonal for which all the real parts of the eigenvalues of the Jacobian were negative, so that  $\alpha_{ii} = -sd_i$  where  $s$  is the stability measure, and  $d_i$  is the natural non-predatory mortality. This measure represents the minimal amount of intraspecific (that is intragroup) loss as a proportion of total non-predatory loss. Food webs that required less intraspecific competition (lower values of the self-damping term  $s$ ) were called “more stable.” The detritus diagonal element was fully determined



**Fig. 2** An example food web, with trophic interactions given by the *black arrows*. Detrital interactions resulting from flow from species to the detrital pool are given in *gray*. The *dashed arrows* represent a possible predation chain containing any number of species. Omnivorous loops contain a chain, where species 1 feeds on species 2, extending up to  $N$  species, where the  $N$ th species is also eaten by species 1. Note that in our definition of omnivory, there must be feeding on different trophic levels within a single predation chain, thus the loop from species  $1 \rightarrow 2 \rightarrow N \rightarrow N-1 \rightarrow 3 \rightarrow 1$  is not considered an omnivorous loop in our analysis because it consists of two joined predatory chains. However this loop is a trophic loop. For each omnivorous or trophic chain of length  $N$  ( $N > 2$ ), there are two different feedback loops. For the omnivorous loops, there is one loop in the direction of the chain, which consists of  $N-1$  predator–on–prey interactions with one prey–on–predator interaction. The other corresponding omnivorous loop is in the opposite direction, consisting of one predator–on–prey interaction, and  $N-1$  prey–on–predator interactions. Detrital loops are formed by at least one detrital interaction, shown by the gray arrow. Unlike omnivorous and trophic loops, detrital loops do not have a loop in the opposite direction

by the predator–prey feeding rates Eq. 5 and so was not included in the diagonal control parameter which measures stability.

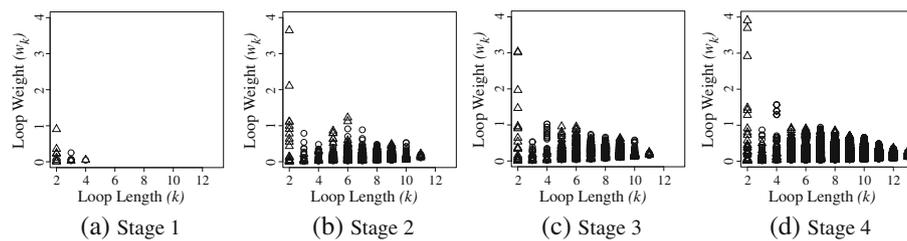
To obtain the most direct information, our stability analysis was based on the exact interaction strength values, unlike Neutel et al. (2007) who averaged stability over a number of Jacobians obtained from randomly sampling interaction strengths from intervals around the calculated values.

In our analysis, four different categories of loops were distinguished: all loops, omnivorous loops, trophic loops, and detrital loops (Fig. 2). The category “all loops” contained all the feedback loops in the food web (excluding loops of length one, which represent self-damping due to intraspecific competition). The trophic and detrital loop categories are the mutually exclusive sub-categories of this all-loop category. Trophic loops were defined as consisting of combinations of species-on-food-source and food-source-on-species relationships. Omnivorous loops as defined by Neutel et al. (2002), refer to single-chain omnivory as shown in Fig. 2 by the loop given by species 1 to species 3 extending up to species  $N$ . Three-species trophic loops are by definition always omnivorous loops (Fig. 2), however trophic loops of longer loop length may contain both omnivorous and non-omnivorous loops. Detrital loops were defined as containing one or more non-trophic effects—positive effects that species have on the detritus pool through flow to detritus of dead organisms or unassimilated feeding (see DeAngelis et al. 1989; de Ruiter et al. 1995). The distribution of loop weights along the axis of loop length is called the loop spectrum.

## Results

We found that for all 32 food webs, there was a general but non-monotonic decrease of maximum loop weight with increasing loop length (Fig. 3). Loops of length two always contained the heaviest loop (Fig. 3). The food webs showed an increase in the total numbers of loops along the complexity gradients (Fig. 3), with a mean number of 162 loops in the first successional stage (8–10 species), 1,994 in the second (12–14 species), 6,090 in the third (14 species), and 43,190 in the fourth (16–17 species). The omnivorous feedback loops previously studied by Neutel et al. (2007), formed only 0.4% of the total number of loops we found.

The number of trophic loops relative to detrital loops changed along the gradient. In the low complexity webs of the first successional stage, 58.8% of all the loops were detrital while in the second to last stage this



**Fig. 3** Relation between length ( $k$ ) and weight ( $w_k$ ) of positive (*open circles*) and negative (*open triangles*) feedback loops, along a complexity gradient. The spectra shown are representative of each of the successional stages

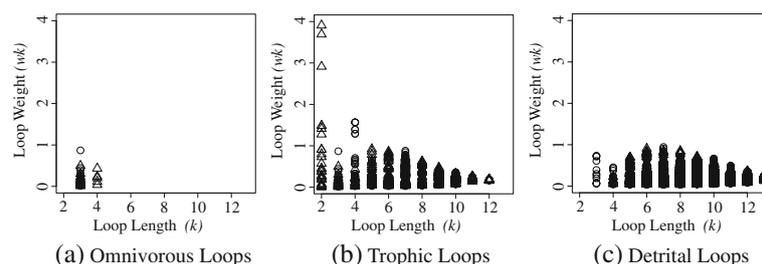
percentage was 83.0%, 90.3%, and 89.7%, respectively, showing a clear increase between the first and subsequent stages in the proportions of detrital loops.

Trophic loops showed a general decrease of loop weight with increasing loop length, (Fig. 4b). Loops of length two were always the heaviest (see Neutel et al. 2002). The maximum weight of trophic loops, longer than length two, occurred at a loop length of mean 3.9 with the heaviest positive loop occurring at a shorter loop length of mean 3.6, compared to mean 4.5 for negative loops. Detrital maximum loop weights had a spectrum closer to a normal-type functional form (Fig. 4c). The detrital loop weights were higher than the trophic loop weights, with a mean at 5.2, a positive loop mean at 3.9 and a negative loop mean at 5.6. Over all successional stages and loop categories, the proportion of negative and positive loops was roughly equal. The distribution of loop weights within each loop length for positive and negative loops varies, with no consistent pattern. Omnivorous maximum loop weight decreased with loop length, the maximum being always a positive loop of length three (Fig. 4a), as was found previously by Neutel et al. (2007). For none of the webs, apart from the simplest stage webs, was this maximum omnivorous feedback loop the heaviest loop in the system, nor was it the heaviest positive loop.

Although the heaviest omnivorous three-species loops did not represent the heaviest positive loop in

the system, they did correlate strongly with stability ( $R^2 = 0.686$ , Table 1), as was found by Neutel et al. (2007), Fig. 5. Note that we use the term stability to refer to the minimum level of intraspecific competition needed for food-web stability. This definition means that a high value of our stability measure corresponds to food webs that we would regard as less stable, since they need more competition within the species (more “self-damping”). There were other strong correlations at high loop lengths for both detrital ( $R^2 = 0.713$ ) and trophic ( $R^2 = 0.624$ ) loops, however, in these cases the long loop length that correlated well with stability depended purely on the (sub)set of food webs taken. For example, for each of the four successional stages, the high correlations occurred at loop lengths 6, 9, 10, and 11 respectively, and these loop lengths were not correlated with any food web property (e.g., maximum loop length). Conversely the strong correlation between three-species omnivorous loop weight and stability was a general relation, i.e., did not depend on the (sub)set taken.

The constituent species of the heaviest three-species omnivorous loops were predatory nematodes, bacteriophageous nematodes and bacteria for 21 of the 32 food webs, as found by Neutel et al. (2007). When present predatory nematodes were in the heaviest omnivorous loop; the heaviest omnivorous loop of for the simplest webs consisted of amoeba–flagellates–bacteria. In the



**Fig. 4** Relation between length ( $k$ ) and weight ( $w_k$ ) of positive (*open circles*) and negative (*open triangles*) feedback loops, for the different loop categories representative of stage four (see

overall spectrum shown in Fig. 3d). Shown are omnivorous loops (a), trophic loops (b), and detrital loops (c)

**Table 1** Adjusted  $R^2$  values for linear regressions performed between stability  $s$  (where stability refers to the minimum level of intraspecific competition required for food-web stability) and

maximum loop weight ( $W_k$ ) for loops of different length ( $k$ ) and sign ( $W_k^+$  is the maximum positive loop of length  $k$ ,  $W_k^-$  negative)

Loop Length $k$	All loops			Omnivorous			Trophic			Detritus		
	$W_k$	$W_k^+$	$W_k^-$	$W_k$	$W_k^+$	$W_k^-$	$W_k$	$W_k^+$	$W_k^-$	$W_k$	$W_k^+$	$W_k^-$
Any > 2	-0.017	0.395	-0.018	0.686	0.686	0.085	0.032	0.428	0.028	0.270	0.270	0.312
2	0.024	NA	0.024	0.024	NA	0.024	0.027	NA	0.027	NA	NA	NA
3	0.160	0.160	0.683	0.686	0.686	0.683	0.686	0.686	0.683	0.114	0.114	NA
4	0.249	0.248	0.227	0.202	NA	0.202	0.123	0.123	0.202	0.197	0.195	0.157
5	0.138	0.048	0.138	NA	NA	NA	0.090	0.097	0.090	0.116	0.042	0.116
6	0.277	0.432	0.278	NA	NA	NA	0.199	0.291	0.108	0.277	0.349	0.278
7	0.469	0.469	0.357	NA	NA	NA	0.507	0.507	0.478	0.469	0.469	0.357
8	0.341	0.269	0.485	NA	NA	NA	0.557	0.500	0.288	0.341	0.269	0.485
9	0.439	0.604	0.439	NA	NA	NA	0.429	0.466	0.429	0.439	0.604	0.439
10	0.449	0.449	0.376	NA	NA	NA	0.624	0.595	0.615	0.449	0.449	0.376
11	0.409	0.427	0.375	NA	NA	NA	0.564	0.611	0.487	0.409	0.427	0.375
12	0.713	0.673	0.634	NA	NA	NA	-0.078	-0.020	-0.078	0.713	0.673	0.634
13	0.581	0.511	0.570	NA	NA	NA	NA	NA	NA	0.581	0.511	0.570
14	-0.055	-0.146	-0.055	NA	NA	NA	NA	NA	NA	-0.055	-0.146	-0.055
15	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

For the total of 32 food webs, the four categories are All Loops, Omnivorous Loops, Trophic Loops, and Detrital Loops. The correlation with stability and maximum loop weight for any loop length longer than two is given by the first row. All  $R^2$  correlations have a significance of over 95%, and at least three sample points for each entry. The maximum omnivorous loop weights, omnivorous three-species loop weights, and trophic three-species loop weights all refer to the same loops, so have the same strong correlations. NA is used when loops did not occur at a given loop length, or when there were not enough points ( $< 3$ ) to perform the analysis

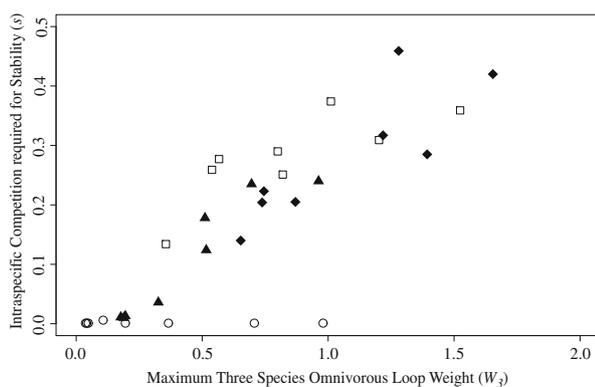
most complex webs the heaviest loops consisted of predatory nematodes, bacteriophagous nematodes and then either predatory collembolans or nematophagous mites. There was more variety for the constituent species for the heaviest overall trophic loop, although predatory mites and fungi were both contained in 19 of

the 32 of these webs. In terms of positioning in the web, the heaviest omnivorous loops were well connected within the food webs, whereas the overall heaviest loops tended to be more peripheral.

The overall heaviest positive feedback did not correlate well with stability, nor did any maximum weight of any other loop category or length. Interestingly, the omnivorous three-species loop was often not even the heaviest positive three-species feedback. In 27 of the 32 food webs, the heaviest three species loops were detrital, consisting of three positive interactions. However, these detrital loops did not correlate with stability ( $R^2 = 0.114$ ), emphasizing the importance of trophic interactions within food webs.

## Conclusions

We presented the first quantification of all the feedbacks for a set of observed food webs. We found that while maximum loop weight did not decrease monotonically with loop length, longer loops were still relatively weak, confirming the results of Neutel et al. (2002). We showed a shift in the proportion of detrital versus trophic loops, as complexity and successional age of the food webs increased (Odum 1971). We found that within the multitude of positive and negative feedback



**Fig. 5** Relationship between maximum loop weight and stability of the successional stage 1 (open circles), 2 (open squares), 3 (closed triangles), and 4 (closed diamonds) which are all represented by four replicates from two different sites. Stability was measured as the level of intraspecific competition needed for stability; high intraspecific competition values correspond to less stable ecosystems. Values were based on the exact community matrix elements. All quantities are dimensionless

loops, three-species omnivorous loops stood out in their relationship with stability, with stronger loops corresponding to lower food-web stability. These loops were not the heaviest positive feedback loops, unlike the suggestion by Neutel et al. (2007), nor were the heaviest (positive or negative) feedback loops correlated with stability.

There has been much work on the importance of small substructures within complex networks (Neutel et al. 2007; Williams et al. 2002; Allesina and Pascual 2008; Holt and Polis 1979; Huxel et al. 2002). Omnivory has long been thought to be destabilizing Pimm and Lawton (1978). Our results emphasize the importance of omnivory, but also suggest that it is not so much the number or length of omnivorous chains that contributes to instability, but rather the strength of feedback in the smallest omnivorous feedback loop that is critical for stability. It is intriguing that within the multitude of feedbacks this three species loop is so important. Since it is not the dominant positive feedback, what is it that makes it key to the dynamics of the whole network?

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