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ORIGINAL PAPER

# Patterns in intraspecific interaction strengths and the stability of food webs

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**Abstract** A common approach to analyse stability of biological communities is to calculate the interaction strength matrix. Problematic in this approach is defining intraspecific interaction strengths, represented by diagonal elements in the matrix, due to a lack of empirical data for these strengths. Theoretical studies have shown that an overall increase in these strengths enhances stability. However, the way in which the pattern in intraspecific interaction strengths, i.e. the variation in these strengths between species, influences stability has received little attention. We constructed interaction strength matrices for 11 real soil food webs in which four patterns for intraspecific interaction strengths were chosen, based on the ecological literature. These patterns included strengths that were (1) similar for all species, (2) trophic level dependent, (3) biomass dependent, or (4) death rate dependent. These four patterns were analysed for their influence on (1) ranking food webs by their stability and (2) the response in stability to variation of single interspecific interaction strengths. The first analysis showed that ranking the 11 food webs by their stability was not strongly influenced by the choice of diagonal pattern. In contrast, the second analysis showed that the response of food web stability to variation in single interspecific interaction strengths was sensitive to the choice of diagonal pattern. Notably, stability could increase using one pattern and decrease using another. This result asks for deliberate approaches to choose diagonal element values in order to make predictions on how particular species, interactions, or other food web parameters affect food web stability.

**Keywords** Food web stability · Interaction strength matrix · Intraspecific interaction strength · Press perturbations

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## Introduction

The stability of ecological communities expresses how resistant or resilient a community is to disturbances. Examples of disturbances are changes in the environment (e.g. in nutrient availability, soil acidity), changes in climatic conditions (e.g. in rainfall, temperature), or disturbances caused by humans (e.g. pollution, fire). Resistance can be expressed in terms of how strongly a community responds to a disturbance, for example in terms of population variation, or in terms of the loss of species. Resilience can be expressed in terms of the ability and rate with which a community can return to its original state from before the disturbance. In studies of community stability, much attention has been given to food web stability, in which the community is defined in terms of trophic interactions, i.e. interactions between consumers and resources, leaving out other types of ecological interactions, like competition, mutualism, and facilitation.

A common approach to measure food web stability is to calculate the Jacobian matrix, in this context called the interaction strength matrix, which is derived from population dynamical models of the species in the community (May 1972; 1973; Yodzis 1988). Stability of the interaction strength matrix is measured with the maximum of the real parts of all eigenvalues, the inverse being a measure for the rate with which a food web recovers from a disturbance (Pimm and Lawton 1977, 1978). The interaction strength matrix is stable if this maximum real part of the eigenvalues is negative and unstable if it is positive. The interaction strength matrix

approach has been used in forming theories on a wide range of topics in community ecology, such as the occurrence of omnivory (Pimm and Lawton 1978), the maximum length of food chains (Pimm and Lawton 1977; Hairston and Hairston 1993; Moore et al. 1993), and the effects of nutrient enrichment (Rosenzweig 1971). It has also been used to investigate how patterns in the strengths of the interspecific interactions, which are represented by the off-diagonal elements of the interaction strength matrix, might be related to stability (Yodzis 1981; de Ruiter et al. 1995; Neutel et al. 2002; Berlow et al. 2004; Emmerson and Raffaelli 2004), and to investigate which species and/or interactions are important to stability (Yodzis 1988; Neutel et al. 2002; Montoya et al. 2009; Allesina and Tang 2012).

Methods and approaches to construct the interaction strength matrix for food webs have developed over the past decades, but these have primarily focused on the values for interspecific interaction strengths. Initially, these values were obtained by randomly drawing them all from the same intervals (May 1972, 1973). This random assignment became more realistic when more plausible, asymmetric intervals were chosen to draw random values from (Pimm and Lawton 1978), so that negative effects were two orders of magnitude stronger than the positive effects. Later, inspired by empirical studies on food webs (Paine 1980; Wootton 1994), interaction strength matrices were derived from observations on real food webs (de Ruiter et al. 1995; Schmitz 1997; McCann et al. 1998; Emmerson and Raffaelli 2004; Banašek-Richter et al. 2009).

Much less attention though has been paid to how to define and represent the intraspecific interaction strengths in the interaction strength matrices. Intraspecific interaction strengths are the diagonal elements of the interaction strength matrix and represent per capita effects of species on itself, e.g. via density-dependent effects, also referred to as self-regulation, self-limitation, or intraspecific interference. Two problems arise when one wants to define the intraspecific interaction strengths. First, it is unclear which species are self-regulated and which are not, thus, which diagonal elements of the interaction strength matrix should be assigned negative values and which not. Second, how is the actual value of the strength of the self-limitation (compared with interspecific interaction strength) determined?

Given the scarcity of data on intraspecific interaction strengths, diagonal element values have been mostly obtained by randomly drawing negative values from plausible intervals, with some exceptions (Schmitz 1997). May (1972) simply chose a constant negative value for intraspecific interaction strengths 'to set a timescale'. Yodzis (1988) assumed that the negative intraspecific interaction strengths should be much stronger (i.e. four orders of magnitude) for basal species than for higher trophic level species. Furthermore, intervals have been proposed that relate intraspecific interaction strength to both trophic level and population size (Berg et al. 2011) or to specific death rates (de Ruiter et al. 1995; Neutel et al. 2002).

The choice of diagonal strength is important for the outcome of stability analyses. It is well known that the stronger the negative strengths on the diagonal, the more likely the matrix will be stable (May 1972; Yodzis 1981; Haydon 1994). However, besides the importance of the numerical values of intraspecific interaction strengths, the way in which these values vary between species, that is, the pattern of the values of intraspecific interaction strengths as distributed over the food web species, might also be important to food web stability. For example, Yodzis (1981) varied the strength of intraspecific interference and the frequency with which it occurred in the consumer species populations and showed that both influence food web stability. Furthermore, the relation between particular inter- and intraspecific interaction strengths is important for stability as well, as can be seen from the mathematical criterion quasi-diagonal dominance (QDD) for matrix stability. This criterion states that stability depends on how the diagonal value relates to its associated off-diagonal values within each row (Hofbauer and Sigmund 1988) and was used in Neutel et al. (2002).

Whether a food web is stable or unstable in itself is not always the main interest; it is also interesting to quantify whether a food web is 'more stable' than another food web, in which 'more stable' means a larger absolute value (more negative) for the maximum (negative) real part of the eigenvalues, correlating, for example, with a faster return time after a disturbance. One could compare stability of food webs that are derived from different systems, e.g. from different sites or ecosystems (Moore et al. 2004; Rip and McCann 2011), or derived from the same system, but with different parameters for the interaction strengths, for example representing the effects of environmental change (Neutel et al. 2007), or perturbations of particular species or species interactions (Yodzis 1988; Montoya et al. 2009; Rip and McCann 2011). Stability comparisons between food webs have also been made to investigate what kinds of patterns in interaction strengths are important for real food webs (DeAngelis 1975; Yodzis 1981; de Ruiter et al. 1995; Neutel et al. 2002; Emmerson and Raffaelli 2004). Studies on responses of food web stability to applied disturbances, or 'press perturbations', have mostly focused on the role of particular species or interactions on food web stability (Yodzis 1988; de Ruiter et al. 1995; Rip and McCann 2011). In all such studies, the focus is on 'relative' differences in stability: the exact stability values are of minor importance. It is therefore important to know how the pattern in intraspecific interaction strengths influences these 'relative' differences in food web stability.

The objective of the present study was to determine the influence of the pattern in intraspecific interaction strengths on food web stability, when stability comparisons are made between interaction strength matrices. The study was carried out

using 11 soil food webs for which the interspecific interaction strengths could be derived from observations (Hendrix et al. 1986; Hunt et al. 1987; Andrén et al. 1990; de Ruiter et al. 1993; Neutel et al. 2007). For the values of the intraspecific interaction strengths, four patterns were selected from the ecological literature. These patterns included diagonal element values that were (1) the same for all species (May 1972, 1973), (2) trophic level dependent (Yodzis 1988), (3) biomass dependent (Berg et al. 2011), or (4) death rate dependent (de Ruiter et al. 1995; Neutel et al. 2002). These four patterns were analysed for their influence on (1) ranking food webs by their stability and (2) the response in stability to variation of single interspecific interaction strengths. The question in the present study was whether the choice of a particular pattern may affect the outcome of such stability analyses in principle ways. For example, regarding the first stability analysis, if one choice of pattern in intraspecific interaction strengths, applied to two food webs, indicates that food web X is 'more stable' than food web Y, will this ranking in stability be the same if another choice of pattern is applied to these two food webs? Regarding the second stability analysis, if one choice of pattern in intraspecific interaction strengths, applied to one food web, indicates that increasing a specific interspecific interaction strength increases food web stability, will this also hold true for another choice of pattern on the diagonal?

## Methods

### Food web data and construction of the interaction strength matrix

The analyses were carried out using data from 11 real soil food webs. Data available for these 11 food webs included biomasses, death rates, and biomass conversion (from resource to consumer) efficiencies. To construct food webs, species were aggregated in (trophic) functional groups, based on species life history characteristics and diet (Hunt et al. 1987; Moore and Hunt 1988). The number of functional groups in the 11 food webs ranged from 12 to 19. See the Appendix (Tables 5 and 6) for more detailed information on the data used.

Interspecific interaction strengths, $\alpha_{ij}$ ($i \neq j$), were derived from measured biomasses, death rates, and biomass conversion efficiencies (cf. de Ruiter et al. 1995). For intraspecific interaction strengths, $\alpha_{ii}$, we selected from the literature four patterns to define these (Table 1), from here on referred to as *diagonal definitions*. Definition A is based on May (1972), representing a diagonal with diagonal values that are equally distributed. Definition B is based on Yodzis (1988), which represents a more asymmetric diagonal: the values for basal species (in our case detritus and roots, see Appendix) have much larger negative values than the consumer species. Definition C is based on Berg et al. (2011) and assumes that intraspecific interaction strength is proportional to the biomass of the species, where definition D assumes that it is proportional to the death rate of the species (De Ruiter et al. 1995).

The stability metric calculated in all analyses was the maximum real part of the eigenvalues of the interaction strength matrix, denoted here with Re($\lambda$). When comparing stability of food webs, a food web is called 'more stable' than another food web if its Re($\lambda$) is more negative. Here, we use the term 'more stable' to indicate that Re($\lambda$) of one food web is smaller than the Re($\lambda$) of another food web. For example, if two food webs are both unstable (both Re($\lambda$)>0), we still call the food web with the smallest Re($\lambda$) 'more stable', in the sense that this food web is 'closer' to being stable.

### Comparing stability between different food webs

Stability of the interaction strength matrices of the 11 food webs was assessed for all four diagonal definitions (Table 1). This stability analysis also included two types of variations within these diagonal definitions. First, the value of $g_i$ (see Table 1) that determines the value of $\alpha_{ii}$ was either fixed as the middle value of the proposed interval (Table 1) or drawn from the proposed interval. This first type of variation was applied to all four diagonal definitions. Second, the soil food web data enabled to estimate a diagonal value for the detrital component in the food web; therefore, the analyses were carried out either with this empirically derived value for the diagonal element for detritus (see Appendix, Table 7) or by choosing a value prescribed by the selected diagonal definition (Table 1). This second variation was only applied to diagonal definitions A, B, and C (Table 1). For diagonal definition D, the empirically derived diagonal element for detritus was used because this definition is based on species death rates, for which detritus does not have. These two variations led to a total of 14 types of diagonal patterns that were used in this analysis (3(definitions A, B, and C)×2($g_i$ fixed or drawn)×2(detritus derived or prescribed)+1 (definition D)×2($g_i$ fixed or drawn)=14).

For each food web, 1000 interaction strength matrices were generated, for which the interspecific interaction strengths $\alpha_{ij}$ were sampled from the uniform distribution (0, $2\alpha_{ij}$) where $\alpha_{ij}$ is the empirically derived value; this allowed for variations in these elements so that a more robust stability value was obtained (cf. Neutel et al. 2007). These 1000 matrices were used to calculate an average stability value for Re($\lambda$) for each of the 14 diagonal patterns. The 11 food webs were ranked from 'most stable' to 'least stable', that is, from the smallest value for Re($\lambda$) to the largest value of Re($\lambda$). Subsequently, similarity of stability rankings was tested in a pairwise manner with Spearman's rank correlation coefficient $\rho$ for each of the diagonal definitions between (1) diagonal elements with fixed $g_i$ and diagonal elements with drawn $g_i$ (with the detrital

**Table 1** The four diagonal definitions, i.e. the four patterns in intraspecific interaction strength elements, $\alpha_{ii}$, selected from the literature. Values of $g_i$ were either set to a fixed value (*column Fixed*) or drawn from uniform distributions (*column Drawn*). For diagonal definitions A, B, and C, the detritus diagonal element could either be as prescribed by the definition or empirically derived (cf. Moore et al. 1993). For definition D, only the empirically derived detritus diagonal element was used

| Diagonal definition | Description | $\alpha_{ii}$ value | Value of $g_i$ | |
|---|---|---|---|---|
| | | | Fixed | Drawn |
| A | Similar[a] | $\alpha_{ii}=-g_i$ | $g_i=1$ | $g_i\in(0,\ 2)$ |
| B | Trophic level dependent[b] | $\alpha_{ii}=-g_i$ | $g_i=5.5$ for basal species and $g_i=0.00055$ for consumers | $g_i\in(1,\ 10)$ for basal species and $g_i\in(0.0001,\ 0.001)$ for consumers |
| C | Biomass dependent[c] | $\alpha_{ii}=-g_iB_i$ | $g_i=1$ for basal species and $g_i=0.1$ for consumers | $g_i\in(0,\ 2)$ for basal species and $g_i\in(0,\ 0.2)$ for consumers |
| D | Death rate dependent[d] | $\alpha_{ii}=-g_id_i$ | $g_i=0.1$ | $g_i\in(0,\ 0.2)$ |

[a] May (1972)

[b] Yodzis (1988)

[c] Berg et al. (2011)

[d] De Ruiter et al. (1995)

diagonal element either prescribed or empirically derived, see Table 1) and between (2) detritus diagonal element prescribed by the definition (Table 1) and empirically derived (with $g_i$ either fixed or drawn, see Table 1). Furthermore, for the four diagonal definitions for which values of $g_i$ were fixed and for which in definitions A, B, and C the detritus diagonal elements were prescribed by the selected diagonal definitions (Table 1), we determined Kendall's coefficient of concordance $W$, with $W=1$ if rankings are completely similar and $W=0$ if rankings are completely dissimilar. With this test, the overall agreement of stability rankings for these four specific diagonal patterns was tested.

### Response in food web stability to variation in single interspecific interaction strengths

For each food web, single (nonzero) interspecific interaction strengths $\alpha_{ij}$ were varied from 0 to $2\alpha_{ij}$ in 100 runs, holding all other elements the same (i.e. fixed to their originally calculated values). For each run, the matrix stability metric Re($\lambda$) was calculated. This was done for the four diagonal definitions with fixed values for $g_i$ and with the detritus diagonal elements prescribed by the selected diagonal definitions for definitions A, B, and C (Table 1); for definition D, the empirically derived diagonal element for detritus was used. To see the similarities and dissimilarities in the responses in stability for these four diagonal definitions, we carried out a two-step analysis. First, the response in stability to the variation in $\alpha_{ij}$ was categorized according to its 'strength' by using four thresholds. These four thresholds were defined in terms of >5, >10, >25, and >50 % change in Re($\lambda$), relative to the original value of Re($\lambda$) (i.e. the Re($\lambda$) associated with the original value of $\alpha_{ij}$). When the response was below a 5 % change in Re($\lambda$) relative to the original value of Re($\lambda$), the response was denoted as 'no response'. If varying an $\alpha_{ij}$ caused a response in Re($\lambda$) larger than the threshold for one of the four diagonal definitions, the $\alpha_{ij}$ was selected for further analysis. Second, for each selected $\alpha_{ij}$ and for each threshold, we tested similarities in responses of Re($\lambda$) between the diagonal definitions in a pairwise manner with Spearman's rank correlation coefficient $\rho$. For this, we defined three categories of similarities and dissimilarities in responses in Re($\lambda$): (1) *consistent* ($\rho\geq0.9$): Re($\lambda$) shows no or similar responses for both diagonal definitions when varying $\lambda$; (2) *inconsistent* ($\rho<0.9$): the responses in Re($\lambda$) are principally different for the two diagonal definitions, including cases that Re($\lambda$) shows a response for one diagonal definition and no response for the other diagonal definition or that Re($\lambda$) shows a monotonous change (increase or decrease) for one diagonal definition while Re($\lambda$) shows a discontinuous response (with an increasing and a decreasing part—see for example Fig. 2) for the other diagonal definition; and (3) *opposing* ($\rho<0$): the responses in Re($\lambda$) are completely contrasting, i.e. Re($\lambda$) increases for one diagonal definition while Re($\lambda$) decreases for the other diagonal definition. Thus, the opposing responses are a subset of the inconsistent responses.

## Results

### Comparing stability between different food webs

The Spearman's rank correlation coefficients $\rho$ between two stability rankings of Re($\lambda$), based on the four diagonal definitions and their two variations, are given in Table 2. Stability

**Table 2** Values of Spearman's rank correlation coefficient $\rho$. All 11 food webs were ranked from 'most stable' (smallest Re($\lambda$)) to 'least stable' (largest Re($\lambda$)) for all four diagonal definitions A, B, C, and D (Table 1). Values are the outcome of the pairwise comparison between two food web rankings of one diagonal definition for which values of $g_i$ were fixed or drawn (see Table 1; for both the detritus diagonal element prescribed by the definition and the detritus diagonal element empirically derived (cf. Moore et al. 1993)) and between two food web rankings of one diagonal definition for which the detritus diagonal element was prescribed by the definition or empirically derived (cf. Moore et al. 1993; for both $g_i$ fixed and $g_i$ drawn, see Table 1)

| | Correlation between fixed and drawn values | | Correlation between defined and empirically derived detritus | |
|---|---|---|---|---|
| | Prescribed detritus | Empirically derived detritus | Fixed $g_i$ values | Drawn $g_i$ values |
| Diagonal definition | | | | |
| A | 0.75 | 0.95 | 0.68 | 0.67 |
| B | 1.00 | 0.99 | 1.00 | 0.99 |
| C | 1.00 | 1.00 | 1.00 | 1.00 |
| D | – | 0.99 | – | – |

A: Similar: $\alpha_{ii}=-g_i$ with $g_i=1$ or $g_i$ drawn from the interval (0,1) for all species (May 1972); B: Trophic level dependent: $\alpha_{ii}=-g_i$ with $g_i=5.5$ or $g_i$ drawn from (1, 10) for basal species and $g_i=0.0005$ or $g_i$ drawn from (0.0001, 0.001) for higher trophic level species (Yodzis 1988); C: Biomass dependent: $\alpha_{ii}=-g_iB_i$ with $g_i=1$ or $g_i$ drawn from (0, 2) for basal species and $g_i=0.1$ or $g_i$ drawn from (0, 0.2) for higher trophic levels species, where $B_i$ is the equilibrium population size (biomass) of the species (Berg et al. 2011); D: Death rate dependent: $\alpha_{ii}=-g_id_i$ with $g_i=0.1$ or $g_i$ is drawn from (0,0.2) in which $d_i$ is the annual specific death rate of the population (de Ruiter et al. 1995; Neutel et al. 2002)

rankings for which values of $g_i$ were either fixed or drawn (see Table 1) were similar for the four diagonal definitions, for both detritus diagonal element prescribed by the definitions (all $P<0.05$; no $\rho$ for definition D for prescribed detritus diagonal element because only empirically derived values were used) and for the detritus diagonal element empirically derived (all $P<0.05$). Stability rankings for which the detritus diagonal element was either prescribed or empirically derived were similar for the three diagonal definitions A, B, and C, for both fixed values of $g_i$, and for randomly drawn values of $g_i$ (all $P<0.05$; no $\rho$ for definition D because only empirically derived values were used).

As an example, rankings of Re($\lambda$) of the 11 food webs for the four definitions with fixed $g_i$ and for definitions A, B, and C with the detritus diagonal element prescribed by the definition (Table 1) are given in Table 3. According to Kendall's coefficient of concordance, the stability rankings for these four specific diagonal patterns were similar ($W=0.91$, $P<0.001$). There were inconsistencies though, the largest inconsistency being from the food web from the second succession stage at Schiermonnikoog, which is ranked 9 for diagonal definitions A and D but ranked 4 for diagonal definitions B and C. Other inconsistencies were smaller. For example, the food web of Horseshoe bend CT was ranked as 'most stable' (ranked 1) by the three diagonal definitions A, B, and D, and ranked as second 'most stable' (ranked 2) by diagonal definition C.

## Response in food web stability when varying single interspecific interaction strengths

The response in food web stability to the variation of (nonzero) single interspecific interaction strengths $\alpha_{ij}$ over the interval (0, $2\alpha_{ij}$) is given in Table 4. The table summarizes the frequencies of the selected $\alpha_{ij}$ for the four thresholds (5, 10, 25, and 50 %) and the frequencies of $\alpha_{ij}$ with inconsistent or opposing responses between the diagonal definitions. The frequency of interactions that produced >5 % change in Re($\lambda$) relative to the original Re($\lambda$) value in one of the four diagonal definitions varied between 23 (Horseshoe bend CT) and 75 % (Kjettslinge B120); that is, for some food webs, more than half of the total number of interactions showed a response for any of the four diagonal definitions. Some food webs had a relatively high number of $\alpha_{ij}$ that were selected for the 50 % threshold, such as the two food webs from the two sites of the Kjettslinge Experimental Farm. From the selected $\alpha_{ij}$, a large proportion also produced inconsistent responses. On average, the percentage inconsistent $\alpha_{ij}$ (within the selected $\alpha_{ij}$) was 81, 79, 73, and 64 % for thresholds of 5, 10, 25, and 50 %, respectively. Moreover, the percentage opposing $\alpha_{ij}$ (within the selected $\alpha_{ij}$) was 10, 11, 12, and 16 % for thresholds of 5, 10, 25, and 50 %, respectively. In summary, of the total of 816 (nonzero) $\alpha_{ij}$ analysed, 419 showed a response in Re($\lambda$) of more than 5 %, of which 349 showed an inconsistent response and 57 an opposing response in Re($\lambda$) between diagonal definitions. Also, there were 184 $\alpha_{ij}$ with a response in Re($\lambda$) of more than 50 %, of which 127 showed an inconsistent response and 41 an opposing response in Re($\lambda$) between diagonal definitions. Two examples of inconsistencies in the response of Re($\lambda$) for the four diagonal definitions to varying a single interspecific interaction strength are given in Figs. 1 and 2. In Fig. 1, this is for the relatively large negative effect $\alpha_{10,2}$ (caused by predatory nematodes feeding on phytophageous nematodes) in the food web of the second

**Table 3** Ranking and values of Re($\lambda$) for the 11 food webs and for each of the four diagonal definitions for which $g_i$ was fixed (see Table 1) and the detritus diagonal element was prescribed by the definition (except for diagonal definition D, for which detritus diagonal element was empirically derived). Values are based on mean stability values ($n$= 1000). All 11 food webs were ranked from 'most stable' (smallest Re($\lambda$), ranked 1) to 'least stable' (largest Re($\lambda$), ranked 11) for all four diagonal definitions A, B, C, and D (Table 1)

| | Ranking | | | | Re($\lambda$) | | | |
|---|---|---|---|---|---|---|---|---|
| Diagonal definition | A | B | C | D | A | B | C | D |
| Central plains[a] | 6 | 6 | 5 | 4 | −0.813 | 0.169 | 0.059 | −0.014 |
| Horseshoe bend CT[b] | 1 | 1 | 2 | 1 | −0.941 | 0.002 | −0.008 | −0.111 |
| Horseshoe bend NT[b] | 3 | 3 | 1 | 3 | −0.924 | 0.029 | −0.010 | −0.074 |
| Kjettslinge B0[c] | 4 | 5 | 6 | 5 | −0.831 | 0.155 | 0.083 | 0.015 |
| Kjettslinge B120[c] | 7 | 7 | 7 | 7 | −0.807 | 0.171 | 0.110 | 0.040 |
| Lovinkhoeve Int[d] | 8 | 9 | 9 | 8 | −0.717 | 0.286 | 0.259 | 0.070 |
| Lovinkhoeve Con[d] | 10 | 10 | 10 | 10 | −0.521 | 0.478 | 0.463 | 0.262 |
| Schiermonnikoog 1[e] | 2 | 2 | 3 | 2 | −0.930 | 0.007 | 0.007 | −0.097 |
| Schiermonnikoog 2[e] | 9 | 4 | 4 | 9 | −0.621 | 0.045 | 0.019 | 0.125 |
| Schiermonnikoog 3[e] | 5 | 8 | 8 | 6 | −0.815 | 0.177 | 0.168 | 0.024 |
| Schiermonnikoog 4[e] | 11 | 11 | 11 | 11 | −0.185 | 0.816 | 0.812 | 0.602 |

A: Similar: $\alpha_{ii}=-g_i$ with $g_i$=1 or $g_i$ drawn from the interval (0, 1) for all species (May 1972); B: Trophic level dependent: $\alpha_{ii}=-g_i$ with $g_i$=5.5 or $g_i$ drawn from (1, 10) for basal species and $g_i$=0.0005 or $g_i$ drawn from (0.0001, 0.001) for higher trophic level species (Yodzis 1988); C: Biomass dependent: $\alpha_{ii}=-g_iB_i$ with $g_i$=1 or $g_i$ drawn from (0, 2) for basal species and $g_i$=0.1 or $g_i$ drawn from (0, 0.2) for higher trophic levels species, where $B_i$ is the equilibrium population size (biomass) of the species (Berg et al. 2011); D: Death rate dependent: $\alpha_{ii}=-g_id_i$ with $g_i$=0.1 or $g_i$ is drawn from (0,0.2) in which $d_i$ is the annual specific death rate of the population (de Ruiter et al. 1995; Neutel et al. 2002)

[a] Central plains experimental range (Hunt et al. 1987)

[b] Horseshoe bend experimental farm conventional tillage (CT) and no tillage (NT) (Hendrix et al. 1986)

[c] Kjettslinge Experimental Farm barley field with no fertilizer (B0) and with fertilizer (B120) (Andrén et al. 1990)

[d] Lovinkhoeve Experimental Farm integrated farming (Int) and conventional farming (Con) (de Ruiter et al. 1993)

[e] Schiermonnikoog primary succession stage 1, stage 2, stage 3, and stage 4 (Neutel et al. 2007)

succession stage at Schiermonnikoog (Neutel et al. 2007), and in Fig. 2 for the relatively small positive effect $\alpha_{2,10}$ (caused by microbivorous macroarthropods being the resource for predatory arthropods) in the food web of the fertilized barley site (B120) at the Kjettslinge Experimental Farm (Andrén et al. 1990). Note that a decrease in the $y$-value (Re($\lambda$)) indicates an increase in stability for all four diagonal definitions. Figure 1 shows that increasing $\alpha_{10,2}$ in the Schiermonnikoog food web from twice its original negative value to 0 led to an increase in stability (decrease in Re($\lambda$)) using diagonal definitions A and D and a decrease in stability (increase in Re($\lambda$)) using definitions B and C. Figure 2 shows that increasing $\alpha_{2,10}$ in the Kjettslinge food web caused 'no' response of stability using definition A, a small decrease in stability (increase in Re($\lambda$)) using definition C, an increase in stability (decrease in Re($\lambda$)) over a low range of $\alpha_{2,10}$ values, and a decrease in stability at the higher $\alpha_{2,10}$ values using definition B, which was also seen when using definition D, but then in a weaker manner. Furthermore, definition B showed for most part of the $\alpha_{2,10}$ range a decrease in stability, whereas definition D showed for most part of the $\alpha_{2,10}$ range an increase in stability.

## Discussion

The objective of the present study was to determine the influence of the pattern in intraspecific interaction strengths on food web stability, when stability comparisons are made between interaction strength matrices. By using four different patterns, or diagonal definitions, we analysed the influence on (1) ranking food webs by their stability and (2) the response in stability to variation of single interspecific interaction strengths.

In the first analysis, we looked at potential differences in rankings of food webs by their stability, both within diagonal definitions as well as between diagonal definitions. For the two variations that we investigated within diagonal definitions, that is, between fixed and drawn values for $g_i$ (see Table 1) and between the detritus diagonal element prescribed by the definition and empirically derived, we saw no significant differences in rankings. Also, there were no large differences in stability rankings of food webs between the four diagonal definitions. This means that the choice of diagonal elements does not strongly influence the stability rankings of food webs. Note that this only holds for the stability *rankings* of food webs; the *values*

**Table 4** The total number of interspecific interaction strengths $\alpha_{ij}$ per food web (Total); the number of selected $\alpha_{ij}$ for which at least one of the four diagonal definitions showed respectively a more than 5, 10, 25, or 50 % change in stability (S); the number of $\alpha_{ij}$ that caused inconsistent responses in Re($\lambda$) between diagonal definitions (I); and the number of $\alpha_{ij}$ that caused opposing responses in Re($\lambda$) between diagonal definitions (O)

| | Total | 5 % | | | 10 % | | | 25 % | | | 50 % | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | S | I | O | S | I | O | S | I | O | S | I | O |
| Central plains[a] | 94 | 42 | 37 | 5 | 38 | 33 | 5 | 21 | 16 | 2 | 14 | 9 | 2 |
| Horseshoe bend CT[b] | 47 | 11 | 11 | 0 | 6 | 6 | 0 | 2 | 2 | 0 | 0 | 0 | 0 |
| Horseshoe bend NT[b] | 47 | 19 | 19 | 0 | 15 | 15 | 0 | 6 | 6 | 0 | 0 | 0 | 0 |
| Kjettslinge B0[c] | 93 | 64 | 64 | 18 | 57 | 57 | 18 | 47 | 47 | 18 | 38 | 38 | 18 |
| Kjettslinge B120[c] | 93 | 70 | 69 | 18 | 62 | 61 | 16 | 49 | 48 | 15 | 33 | 32 | 10 |
| Lovinkhoeve Int[d] | 94 | 40 | 28 | 2 | 32 | 20 | 2 | 22 | 10 | 1 | 17 | 6 | 0 |
| Lovinkhoeve Con[d] | 92 | 35 | 18 | 0 | 29 | 12 | 0 | 19 | 2 | 0 | 14 | 0 | 0 |
| Schiermonnikoog 1[e] | 41 | 18 | 18 | 1 | 12 | 12 | 0 | 7 | 7 | 0 | 7 | 7 | 0 |
| Schiermonnikoog 2[e] | 59 | 42 | 38 | 7 | 37 | 31 | 7 | 28 | 23 | 7 | 23 | 19 | 7 |
| Schiermonnikoog 3[e] | 70 | 49 | 48 | 7 | 33 | 32 | 7 | 26 | 25 | 7 | 17 | 16 | 4 |
| Schiermonnikoog 4[e] | 86 | 29 | 1 | 0 | 26 | 0 | 0 | 17 | 0 | 0 | 12 | 0 | 0 |

[a] Central plains experimental range (Hunt et al. 1987)

[b] Horseshoe bend experimental farm conventional tillage (CT) and no tillage (NT) (Hendrix et al. 1986)

[c] Kjettslinge Experimental Farm barley field with no fertilizer (B0) and with fertilizer (B120) (Andrén et al. 1990)

[d] Lovinkhoeve Experimental Farm integrated farming (Int) and conventional farming (Con) (de Ruiter et al. 1993)

[e] Schiermonnikoog primary succession stage 1, stage 2, stage 3, and stage 4 (Neutel et al. 2007)

of Re($\lambda$) were different for different diagonal definitions (Table 3).

It is not clear why the diagonal pattern does not influence stability rankings of food webs more strongly. It might be that stability rankings of food webs are mainly driven by the food web architecture, i.e. in terms of the number of trophic groups and frequency of interactions, and/or the differences in the values of the interspecific interaction strengths rather than differences in the values of the intraspecific interaction strengths. This hypothesis could be tested for example by generating random matrices that differ in their interspecific interaction strength values but that share the same network topology; if the stability rankings of these random matrices are the same for different diagonal patterns, this would confirm that network topology is more important for stability rankings than diagonal patterns. However, one should note that randomized food webs are very different from food webs that are based on empirical data in terms of their stability (De Ruiter et al. 1995). Preferably, analyses with randomized food webs should be complemented with analyses based on food webs derived from empirical data. For example, stability of food webs that have the same number of species could be compared for different diagonal patterns to rule out or confirm that this number influences the effect of diagonal patterns on stability rankings.

The result of our first analysis implies in practice that if one wants to compare stability between different food webs, and only qualitative differences are of main interest (e.g. is food web X more stable than food web Y?), then it is likely that any (reasonable) choice of diagonal elements will reveal the most important differences in stability. One can consider though to repeat the analysis using different approaches to define the diagonal elements, for example to investigate more precisely how the relation between inter- and intraspecific interaction strengths influences stability. For example, the most notable difference in stability rankings in Table 3 could be found for the food web of the second succession stage of Schiermonnikoog: definitions A and D ranked this food web as less stable than definitions B and C. Definitions B and C have in common that they assign more negative values to basal species. Thus, the differences in rankings might reflect the contribution to stability of interactions in which basal species are involved.

In the second analysis, the results can be summarized as that it is not uncommon to see large or fundamental differences in responses in Re($\lambda$) to variation of single interspecific interaction strengths between different diagonal definitions. More than half of the 816 (nonzero) $\alpha_{ij}$ caused a response of >5 % change in Re($\lambda$), 349 $\alpha_{ij}$ caused inconsistent responses in Re($\lambda$) between diagonal definitions, of which 57 were opposing. Inconsistent and opposing responses were found in all 11 food webs for this threshold of 5 %. For the other thresholds (10, 25, and 50 %), we found inconsistent and opposing responses as well. Thus, inconsistent responses can be found for both interactions

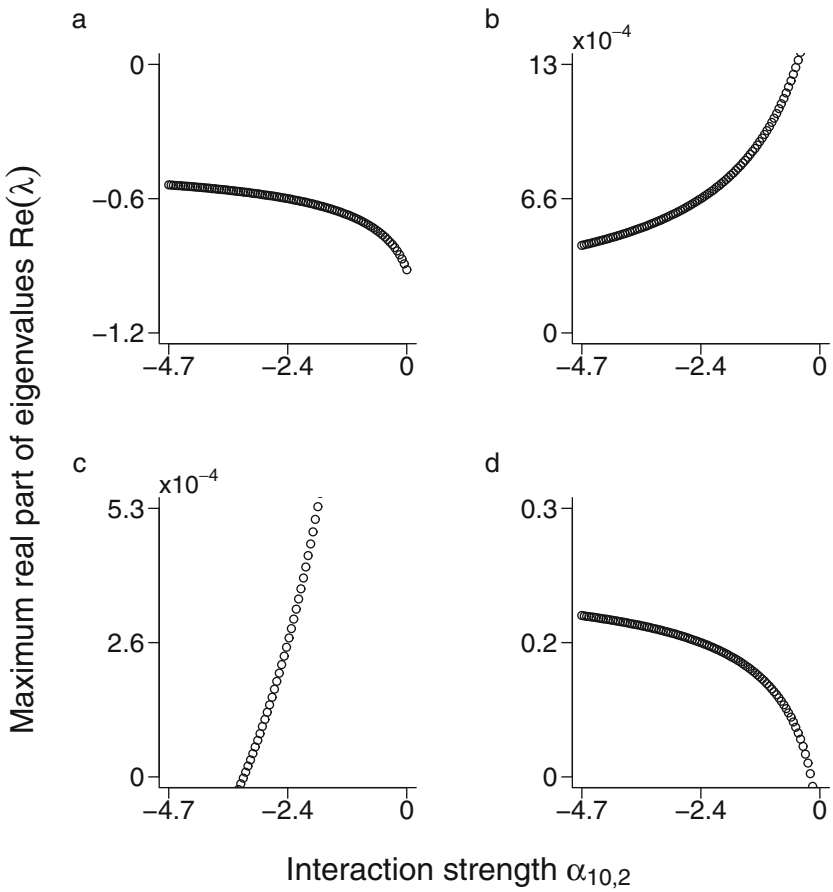


**Fig. 1** Inconsistencies in the response of food web stability to varying the negative interaction strength $\alpha_{10,2}$ for the four diagonal definitions A, B, C, and D (**a**–**d**; see Table 1). Interaction strength $\alpha_{10,2}$ is generated by the feeding of predatory nematodes on phytophageous nematodes in the food web of the second succession stage at the island of Schiermonnikoog (Neutel et al. 2007). *X-axes* are scaled from $2\alpha_{10,2}$ to 0, with $\alpha_{10,2}=-2.37$ as its original interaction strength value. *Y-axes* are scaled for each stability method from 0 to 2Re(λ). Decreasing *y*-values indicate increases in stability for all diagonal definitions. Note that for each diagonal definition, the stability value associated with the original interaction strength value is somewhat different from the stability value used in the ranking analysis (Table 3). This is due to the sampling process that was used to generate average stability values for the ranking analysis. **a** Similar: $\alpha_{ii}=-g_i$ with $g_i=1$ or $g_i$ drawn from the interval (0, 1) for all species (May 1972). **b** Trophic level dependent: $\alpha_{ii}=-g_i$ wit h $g_i=5.5$ or $g_i$ drawn from (1, 10) for basal species and $g_i=0.0005$ or $g_i$ drawn from (0.0001, 0.001) for higher trophic level species (Yodzis 1988). **c** Biomass dependent: $\alpha_{ii}=-g_iB_i$ with $g_i=1$ or $g_i$ drawn from (0, 2) for basal-species and $g_i=0.1$ or $g_i$ drawn from (0, 0.2) for higher trophic levels species, where $B_i$ is the equilibrium population size (biomass) of the species (Berg et al. 2011). **d** Death rate dependent: $\alpha_{ii}=-g_id_i$ with $g_i=0.1$ or $g_i$ is drawn from (0,0.2) in which $d_i$ is the annual specific death rate of the population (de Ruiter et al. 1995; Neutel et al. 2002)

that have a weak influence on stability and interactions that have a strong influence on stability.

These results imply that in this second type of comparative analysis, where the response of a single interaction strength on food web stability is analysed, the outcome of the analysis is highly sensitive to the choice of pattern in diagonal elements. The goal of studies that use this type of analysis is to find general relations between particular species, or particular interactions between species, and food web stability. These studies have been carried out for a wide array of ecosystems, using different kinds of empirical and theoretical approaches (de Ruiter et al. 1995; Montoya et al. 2009; Rip and McCann 2011). Our results show that the outcome of such analysis is influenced by the choice of pattern in diagonal elements, to the extent that an interaction strength can be found to be stabilizing for one diagonal pattern while destabilizing for another diagonal pattern. This means that when the intraspecific interaction strengths are unknown, or when there is no data available for these strengths, and these strengths are defined in a more or less random manner, it is problematic to make general predictions on the effect of certain interactions, or related parameters, on food web stability. The least one can do in such analysis is to repeat the analysis using different patterns for the intraspecific interaction strengths to increase confidence on the results. In such studies, special attention could be paid to how the value of a particular species interaction $\alpha_{ij}$ is related to its associated diagonal element

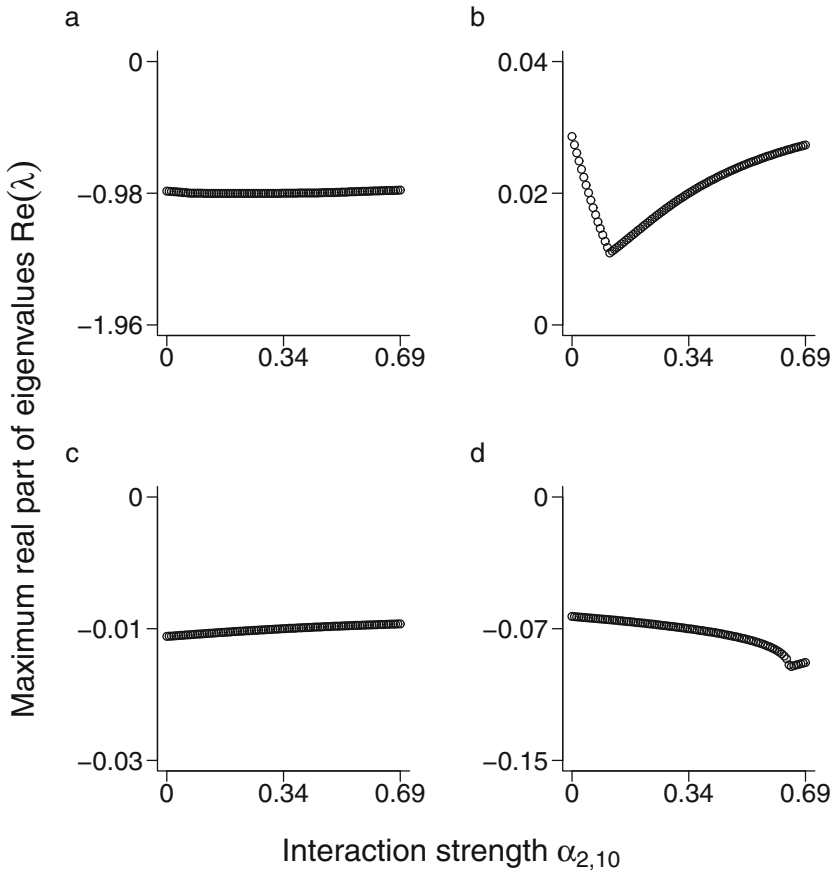


**Fig. 2** Inconsistencies in the response of food web stability to varying the positive interaction strength $\alpha_{2,10}$ for the four diagonal definitions A, B, C, and D (**a**–**d**; see Table 1). Interaction strength $\alpha_{2,10}$ is generated by microbivorous macroarthropods being the resource for predatory arthropods in the food web from the barley field at the Kjettslinge Experimental Farm with the use of fertilizer (Andrén et al. 1990). *X-axes* are scaled from 0 to 2 $\alpha_{2,10}$, with $\alpha_{2,10}$=0.34 as its original interaction strength value. *Y-axes* are the same as in Fig. 1. **a** Similar: $\alpha_{ii}=-g_i$ with $g_i$=1 or $g_i$ drawn from the interval (0, 1) for all species (May 1972). **b** Trophic level dependent: $\alpha_{ii}=-g_i$ with $g_i$=5.5 or $g_i$ drawn from (1, 10) for basal species and $g_i$=0.0005 or $g_i$ drawn from (0.0001, 0.001) for higher trophic level species (Yodzis 1988). **c** Biomass dependent: $\alpha_{ii}=-g_iB_i$ with $g_i$=1 or $g_i$ drawn from (0, 2) for basal species and $g_i$=0.1 or $g_i$ drawn from (0, 0.2) for higher trophic levels species, where $B_i$ is the equilibrium population size (biomass) of the species (Berg et al. 2011). **d** Death rate dependent: $\alpha_{ii}=-g_id_i$ with $g_i$=0.1 or $g_i$ drawn from (0,0.2) in which $d_i$ is the annual specific death rate of the population (de Ruiter et al. 1995; Neutel et al. 2002)

$\alpha_{ii}$, considering the quasi-diagonal dominance criterion (Hofbauer and Sigmund 1988).

To summarize, our first result shows that data constraints on diagonal strength patterning do not hamper the assessment of overall food web stability. Our second result, however, shows that a better knowledge about the patterns in intraspecific interactions is necessary for the interpretation of how particular species, interactions, or other food web parameters affect food web stability. Our conclusions are based on analyses in which we used empirical data of soil food webs. The generality of the results could be tested by repeating the analyses with food webs from other ecosystems for which empirical data is available that can be used to construct interaction strength matrices. In addition, we conducted our analyses with four diagonal definitions that we encountered in the ecological literature. Besides that the diagonal could be defined in a different way, the four chosen diagonal definitions can be somewhat different for other food webs, which might affect the results as well. For example, the asymmetry in diagonal values in diagonal definition B (trophic level dependent, Yodzis 1981) changes with the number of basal species: the more basal species, the less asymmetric these values are. Similarly, aquatic systems have a reverse biomass pyramid compared to soil systems; if diagonal definition C (biomass dependent, Berg et al. 2011) is used, top predators will thus have larger negative diagonal values than diagonal values of lower trophic groups, which is the other way around in soil food webs. Thus, how general our results are for other diagonal patterns is an open question.

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## Appendix

**Table 5** Averaged yearly biomasses (kg C $ha^{-1}$ $year^{-1}$) for the functional groups of the 11 food webs

| | Central plains[a] | Horseshoe bend CT[b] | Horseshoe bend NT[b] | Kjettslinge B0[c] | Kjettslinge B120[c] | Lovinkhoeve Int[d] | Lovinkhoeve Con[d] | Schiermonnikoog 1[e] | Schiermonnikoog 2[e] | Schiermonnikoog 3[e] | Schiermonnikoog 4[e] |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Microorganisms | | | | | | | | | | | |
| Bacteria | 304 | 690 | 440 | 740 | 900 | 245.75 | 227.5 | 1.14 | 4.72 | 18.75 | 17.82 |
| Saprophytic fungi | 63 | 150 | 160 | 1500 | 2300 | 3.28 | 2.13 | 0.03 | 0.13 | 0.21 | 0.29 |
| Mycorrhizae | 7 | – | – | – | – | – | – | – | – | – | – |
| Protozoa | | | | | | | | | | | |
| Amoebae | 3.78 | 50 | 40 | 110 | 34 | 18.90 | 11.53 | 0.01 | 0.03 | 0.20 | 0.35 |
| Flagellates | 0.16 | – | – | – | – | 0.63 | 0.53 | 0.0003 | 0.004 | 0.04 | 0.11 |
| Nematodes | | | | | | | | | | | |
| Herbivores | 2.9 | 0.5 | 0.4 | 0.18 | 0.29 | 0.36 | 0.19 | 0.000004 | 0.003 | 0.0009 | 0.0003 |
| Bacteriovores | 5.8 | 1.4 | 0.46 | 0.45 | 0.5 | 0.36 | 0.30 | 0.00006 | 0.01 | 0.04 | 0.07 |
| Fungivores | 0.41 | 0.08 | 0.12 | 0.2 | 0.12 | 0.13 | 0.08 | 0.000168 | 0.004 | 0.02 | 0.006 |
| Omnivores | 0.65 | – | – | – | – | – | – | – | – | – | – |
| Predators | 1.08 | – | – | 0.44 | 0.44 | 0.06 | 0.06 | 0.00003 | 0.03 | 0.009 | 0.005 |
| Arthropods | | | | | | | | | | | |
| Herbivorous herbage arthropods | – | – | – | 0.1 | 0.14 | – | – | – | – | – | – |
| Predatory herbage arthropods | – | – | – | 0.15 | 0.19 | – | – | – | – | – | – |
| Microbivorous macroarthropods | – | – | – | 0.25 | 0.25 | – | – | – | – | – | – |
| Predatory macroarthropods | – | – | – | 0.49 | 0.49 | – | – | – | – | – | – |
| Predatory mites | 0.16 | 0.04 | 0.2 | 0.18 | 0.28 | 0.08 | 0.06 | – | 0.0009 | 0.02 | 0.08 |
| Nematophageous mites | 0.16 | – | – | – | – | 0.007 | 0.004 | – | – | 0.00008 | 0.01 |
| Cryptostigmatic mites | 1.68 | 0.22 | 0.8 | – | – | 0.003 | 0.007 | 0.00005 | 0.01 | 0.02 | 0.13 |
| Noncryptostigmatic mites | 1.36 | 0.39 | 0.9 | – | – | 0.04 | 0.02 | 0.0002 | 0.06 | 0.07 | 0.08 |
| Bacteriovorous mites | – | – | – | – | – | 0.0003 | 0.001 | – | – | – | 0.0005 |
| Collembolans | 0.46 | 0.09 | 0.3 | 0.17 | 0.17 | 0.38 | 0.47 | – | 0.002 | 0.06 | 0.07 |
| Predatory collembolans | – | – | – | – | – | 0.008 | 0.03 | – | – | – | 0.001 |
| Annelids | | | | | | | | | | | |
| Enchytraeids | – | 0.3 | 0.1 | 4.2 | 3.4 | 0.21 | 0.43 | – | – | – | – |
| Earthworms | – | 20 | 100 | 13 | 13 | 63.53 | – | – | – | – | – |
| Basal groups | | | | | | | | | | | |
| Detritus | 3000 | 8400 | 6000 | 22,400 | 32,000 | 2500 | 2500 | 4 | 25 | 250 | 2500 |
| Roots | 300 | 200 | 250 | 500 | 700 | 350 | 300 | 225 | 900 | 900 | 675 |

[a] Central plains experimental range (Hunt et al. 1987)

[b] Horseshoe bend experimental farm conventional tillage (CT) and no tillage (NT) (Hendrix et al. 1986)

[c] Kjettslinge Experimental Farm barley field with no fertilizer (B0) and with fertilizer (B120) (Andrén et al. 1990)

[d] Lovinkhoeve Experimental Farm integrated farming (Int) and conventional farming (Con) (de Ruiter et al. 1993)

[e] Schiermonnikoog primary succession stage 1, stage 2, stage 3, and stage 4 (Neutel et al. 2007)

**Table 6** Death rates (year$^{-1}$) of the trophic groups, based on literature data (Hunt et al. 1987; De Ruiter et al. 1993)

| | Death rates |
|---|---|
| Microorganisms | |
| Bacteria | 1.20[a] |
| Saprophytic fungi | 1.20[a] |
| Mycorrhizae | 2.00 |
| Protozoa | |
| Amoebae | 6.00[b] |
| Flagellates | 6.00 |
| Nematodes | |
| Herbivores | 1.08 |
| Bacteriovores | 2.68 |
| Fungivores | 1.92 |
| Omnivores | 4.36 |
| Predators | 3.00[c] |
| Arthropods | |
| Herbivorous herbage arthropods | 1.84 |
| Predatory herbage arthropods | 1.84 |
| Herbivorous macroarthropods | 1.84 |
| Microbivorous macroarthropods | 1.84 |
| Predatory macroarthropods | 1.84 |
| Predatory mites | 1.84 |
| Nematophageous mites | 1.84 |
| Cryptostigmatic mites | 1.20 |
| Noncryptostigmatic mites | 1.84 |
| Bacteriovorous mites | 1.84 |
| Collembolans | 1.84 |
| Predatory collembola | 1.84 |
| Annelids | |
| Enchytraeids | 5.00 |
| Earthworms | 2.40 |
| Basal groups | |
| Roots | 1.00 |

[a] In food webs of the Kjettslinge Experimental Farm barley fields: 0.10

[b] In food webs of the Kjettslinge Experimental Farm barley fields: 1.00

[c] In food webs of the central plains experimental range (Hunt et al. 1987): 1.60

**Table 7** Empirically derived detritus diagonal values (cf. Moore et al. 1993) for the 11 food webs

| Empirically derived detritus | |
|---|---|
| Central plains[1] | −0.733 |
| Horseshoe bend CT[b] | −0.741 |
| Horseshoe bend NT[b] | −0.871 |
| Kjettslinge B0[c] | −0.108 |
| Kjettslinge B120[c] | −0.062 |
| Lovinkhoeve Int[d] | −0.994 |
| Lovinkhoeve Con[d] | −0.660 |
| Schiermonnikoog 1[e] | −1.325 |
| Schiermonnikoog 2[e] | −1.180 |
| Schiermonnikoog 3[e] | −0.404 |
| Schiermonnikoog 4[e] | −0.050 |

[a] Central plains experimental range (Hunt et al. 1987)

[b] Horseshoe bend experimental farm conventional tillage (CT) and no tillage (NT) (Hendrix et al. 1986)

[c] Kjettslinge Experimental Farm barley field with no fertilizer (B0) and with fertilizer (B120) (Andrén et al. 1990)

[d] Lovinkhoeve Experimental Farm integrated farming (Int) and conventional farming (Con) (de Ruiter et al. 1993)

[e] Schiermonnikoog primary succession stage 1, stage 2, stage 3, and stage 4 (Neutel et al. 2007)

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