Evolutionary Ecology Research, 2004, **6**: 1145–1166

Reliability characteristics of natural functional group interaction webs

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ABSTRACT

We compare the reliability of interaction webs for functional groups derived from extensive field data. Reliability is the probability of a web continuing to function despite the failure of one or more functional groups. Interaction webs are diagrams of all the trophic and non-trophic relationships between groups. Functional groups are suites of species with similar roles in an ecosystem and, importantly, mediate the relationship between biodiversity and the functioning of ecosystems. How they interact will thus have major ecological consequences. We reveal interactions between groups by simple and partial Mantel tests and determine link type by applying sets of logical rules to the Mantel test results. We then calculate the reliability of the resulting interaction webs. We also derive the reliabilities for webs of different link types because web topology affects reliability, not just the number of groups and links. Using the qualities of sink webs derived from these interaction webs, we illustrate the overall patterns in the relationships between reliability and other web characteristics. We compare these with the relationships in food-webs. We demonstrate the relation of reliability to principal components representing the information common to web characteristics other than reliability. We show that reliabilities for webs of interactions between functional groups are very high, at least as high as those for food-webs, and that they show similar relationships to other web characteristics. Nevertheless, in our natural setting, it is the number of groups and the number of links a web has that most affects reliabilities. However, they also differ more between webs of different link types, where topology differs, than between sites. Thus, in nature, the reliability of webs of interactions between functional groups will depend on both web size and topology. This means that their contribution to mediating the relationship between biodiversity and ecosystem function will also depend on both web and topology.

Keywords: arthropods, biodiversity, ecosystem function, grasslands, plants, structure, topology.

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INTRODUCTION

We examine the reliability of networks of functional groups. This is just part of our interest in the interrelationships of functionally defined species groups. We want to detect how these relationships differ between habitats and ecosystems (Perner *et al.*, 2003; Voigt *et al.*, 2003; Voigt and Perner, 2004). Functional groups are important because they mediate relationships between diversity and ecosystem function (Bengtsson, 1998). There is no direct link between these phenomena, but they may be linked by the functioning of organisms (cf. Jones and Lawton, 1995; McCann, 2000). Implementing an approach based on functional groups is particularly important because of the effects of global environmental changes on the structure and functioning of ecosystems (Blondel, 2003).

Functional groups

Functional groups are polyphyletic suites of species (Steneck, 2001) carrying out the same ecosystem process (Blondel, 2003). The same processes operate in most ecosystems of similar type. Using functional groups frees comparison of system behaviour from dependence on the presence of particular species. Functional groups allow comparison between sites with different species compositions. They even allow comparison between biogeographic regions with no species in common.

Many criteria can be used for assigning species to groups. They may include species roles in ecosystem engineering as well as feeding mechanisms and morphology (Anderson, 1995; Woodward and Cramer, 1996). The exact choice of criteria depends on the questions asked (Körner, 1994). It also depends on the information available for species. But stringent mathematical or statistical definitions (Martinez, 1996; Bengtsson, 1998; Blondel, 2003) are often impossible. This is because the detailed information necessary is unavailable for all species in multi-species data sets. Ecologists need not ignore or discard these data. Ecologists can define functional groups *a priori* and examine their interactions for meaningful and useful patterns.

Interaction webs

Interactions between species, or groups, produce networks. Among networks, food-webs are familiar ecological examples. However, food-webs contain only trophic interactions. These are the influence of natural enemies and their victims on each other's abundance. Interaction webs are networks that capture other links. They include not only trophic interactions and competitive-facilitation effects (Paine, 1980), but also the effects that species exercise as ecosystem engineers (Anderson, 1995). Such non-trophic, non-competitive effects are common (Ohgushi, 1997; Price, 2002) but ignored by food-web studies. Some lepidopteran larvae roll up leaves and so provide refuges from predators for other species. Leaf rolls thus influence the population dynamics of these other species (Fukui, 2001). Similarly, the colonization of grassland by woody perennials provides anchorage points for orb webs. This produces an increase in the abundance of the spider species that produce webs (Borges and Brown, 2001).

We know that our webs omit potentially important groups. This is true even though they include large numbers of species. However, no webs are all-inclusive, even those containing hundreds of species (Müller *et al.*, 1999; Schönrogge and Crawley, 2000; Henneman and Memmott, 2001; Lewis *et al.*, 2002). All webs are also necessarily based on temporally and spatially limited data. They are nevertheless useful. They describe and visualize patterns within and between ecosystems.

It is very difficult to observe the links between numerous functional groups directly. This is especially so when each group contains very many species. However, many large sets of long-term abundance data exist for numerous species. These are valuable compilations of how population abundances vary and covary. Such data sets were not assembled for producing webs. Identifying interactions from them thus requires complex statistical techniques. We use simple and partial Mantel tests to detect similarity in the patterns of changes in abundance (Mantel, 1967; Legendre and Fortin, 1989; Legendre and Legendre, 1998). We then apply sets of logical rules to the results of Mantel tests (Legendre and Troussellier, 1988; Legendre, 1993). Using matrices in this way has the advantage of simultaneously comparing the changes in abundance of numerous species.

Reliability

Reliability is a static property of networks. It depends on topology, on how groups join together. It differs fundamentally from properties derived only from the numbers of nodes and links, such as connectance. Reliability theory originated in engineering and process management. It deals with the determinants of successful operation of complex systems (Barlow and Proschan, 1965; Aggarwal, 1993; Molnár, 1995). Buildings, production lines and power distribution all form networks composed of nodes (structural elements, factories, or power producers and consumers). Links between these nodes represent flows (stress, product and electricity). Reliability analysis determines the probability of a network continuing to function when failure of one or more nodes interrupts flows.

In ecological networks, nodes are species or groups of species. Links represent various influences between these nodes. In food-webs, links represent matter and energy flow between species. Food-webs are the only ecological networks so far analysed for reliability (Jordán and Molnár, 1999; Jordán *et al.*, 1999, 2003). However, links exist whenever one species, or functional group, affects another. We are interested in the interrelationships of functional groups. We therefore apply reliability analysis to networks in which the nodes are functional groups. The links are the mutual influences on population abundances between groups. There are thus two ecological equivalents of node failure. The first is the weakening of the interaction between groups to a value below a given threshold. The second is the disappearance of the species in the group by extinction or phenology. We investigate whether webs of interactions between functional groups have high or low reliabilities similar in size to those for food-webs (Jordán and Molnár, 1999). We also examine whether reliabilities for our webs relate to other web characteristics in the same way as for food-webs. We discuss the major influences on these relationships. We determine how different types of links affect reliability. Moreover, we examine whether web reliabilities differ between sites or relate to ecological differences.

METHODS

Sites and species

The data came from two grasslands on Triassic limestone near Jena, Germany. These sites are at 11.6°E, 50.9°N and 145 m above sea level. Leutratal is dominated by the grasses *Bromus erectus* Huds. and *Brachypodium pinnatum* (L.) P.B. *Sesleria varia* (Jacq.) Wettst. is abundant in the dryer parts. Steudnitz is 18 km further north. It is similar to Leutratal but was subject to industrial pollution until 1990. Heinrich *et al.* (1998, 2001) give detailed descriptions of both sites. Müller *et al.* (1978), Heinrich (1984) and Perner (1997) report the considerable research at these sites.

Data on species abundance came from collections made by colleagues and students. These collections cover several years within a 24-year period. They were made at three locations within each of the two sites. Abundance of plant species was assessed by the Braun-Blanquet method (Kent and Coker, 1994) on a regular program (Heinrich *et al.*, 1998, 2001). Arthropod abundance was determined by standardized sweep net sampling (Köhler, 1987) on a similar program (Heinrich *et al.*, 1998; Perner *et al.*, 2003). We included all available data in the analysis.

Functional groups

We uniquely assigned species to ecologically defined functional groups using readily available information (Perner *et al.*, 2003; Voigt *et al.*, 2003; Voigt and Perner, 2004). We classified producers by combinations of growth habit, structure and life span. Invertebrates were grouped according to their foraging characteristics (Table 1). Some species fall into different categories at different stages of development (Steneck, 2001). These species we placed in the group that had the greatest influence on the local ecosystem. Thus, Tachinidae (Diptera) were placed with ‘parasitoids’. Their larvae are likely to have greater local effects than the mobile adults. In addition, the diets of some species vary with place or opportunity. We therefore classified these species according to their predominant foraging behaviour in the collection sites. We classified Ensifera species as ‘attacking chewers’, although some can be partially omnivorous. This classification into functional groups disrupts taxa. Species of the same taxon may well fall into different functional groups. Species of the same taxon can also fall into different trophic levels.

Interaction webs

We constructed webs from interaction links between functional groups identified in the abundance data. We used a statistical technique that successfully reveals such relationships (Voigt and Perner, 2004). We improved normality of variances of the plant data by square root transformation. Arthropod data were log-transformed. We then tabulated these data for each functional group within each site. The rows of Table 1 represent collection locations and years. The columns give the abundance for each species within the functional group. Each cell of the table therefore records the abundance of a single species, year and collection locality within one of the sites. We then calculated a matrix of dissimilarities between the rows of the table based on species abundances in the columns. This matrix represents the pattern of changes in abundance over locations and years for all the species in the group.

Table 1. The numbers of individuals and species collected in Leutratal and Steudnitz grouped into functional groups (cf. Voigt and Perner, 2004)

			Steudnitz		Leutratal	
Trophic level	Code	Functional group	Species	Individuals	Species	Individuals
Producers			**132**		**193**	
	paf	annual forbs	38		18	
	pgr	grasses	17		18	
	pmo	mosses	18		40	
	ppf	perennial forbs	44		86	
	pwp	woody plants	15		31	
Herbivores			**348**	**44 642**	**544**	**95 214**
	hcw	stage-specific chewers	144	2 977	217	22 173
	hlc	lifetime chewers			11	4 832
	hmi	miners	67	9 751	134	6 461
	hts	cell-tissue suckers	60	5 287	72	16 864
	hvs	vascular suckers	77	26 627	110	44 884
Carnivores			**245**	**17 992**	**168**	**3 173**
	cac	attacking chewers			5	488
	cbs	biting suckers	56	2 957	119	2 087
	cch	chewing hunters	74	1 160		
	cpa	parasitoids	17	145	33	302
	csh	sucking hunters	11	936	11	296
	cws	web-spinners	87	12 794		

To determine the existence of a link we applied simple and partial Mantel tests (Mantel, 1967; Legendre and Legendre, 1998; Fortin and Gurevitch, 2001). A link between two functional groups exists whenever $p < 0.05$ for the Mantel correlations (r_M) between their matrices (Voigt and Perner, 2004). If r_M between two functional groups is high, the abundances of their constituent species change in similar ways over locations and years. The value $p = 0.05$ is a useful threshold value. It is not part of null-hypothesis testing. There is thus no need to use a correction for multiple comparisons.

Simple Mantel correlations do not fully characterize a link, however. This is because relationships between groups may arise for several reasons. Each set of reasons produces a different type of relationship. A link may exist between groups A and B because one directly affects the other. Alternatively, C may affect both A and B, and other pathways exist. We distinguished these link types by using partial Mantel tests and applying four sets of logical rules (Legendre and Troussellier, 1988; Legendre, 1993; Voigt and Perner, 2004). Partial Mantel tests determine the significance of interactions between two groups while holding constant the influence of a third (analogous to partial Pearson or Kendal correlations). The logical rules derive from the value, rank and significance of two sets of correlations. The first is $r_{M\,PH}$, $r_{M\,PC}$ and $r_{M\,HC}$ (r_M for all pair-wise combinations of functional groups from producer (P), herbivore (H) or carnivore (C) categories). The second is the values of $\boldsymbol{r}_{\mathrm{M\,HC}}$ relative to $\boldsymbol{r}_{\mathrm{M\,HC.P}}$, $\boldsymbol{r}_{\mathrm{M\,PC}}$ to $\boldsymbol{r}_{\mathrm{M\,PC.H}}$ and $\boldsymbol{r}_{\mathrm{M\,PH}}$ to $\boldsymbol{r}_{\mathrm{M\,PH.C}}$. The notation XY.Z means the partial effect of X on Y while controlling for their relationships with Z. Each of the four sets of logical rules defines a possible link type or model.

Links can belong to more than one type just as it is possible for partial correlations to be high in more than one direction. This would occur when groups B and C greatly affect group A. Interactions probably occur between species and groups in the same trophic level. Thus, horizontal links probably exist too. We omitted horizontal links because the sets of logical rules based on Mantel-like comparisons of more than three matrices (e.g. Manly, 1986) are highly complex and occasionally ambiguous. Horizontal links are rarely included in food-web studies.

We constructed webs using the links identified. Each web was of a single type because it included only links that fit a certain model. Some of the links in such webs may also fit other models (Voigt and Perner, 2004). Analysis of these webs allowed us to examine how links of different types affect reliability. Together, webs compiled from links of different types show all the interactions to be stronger than our threshold. The real ecosystem contains all such links. They must all be included to examine the reliability of the complete system. Therefore, we combined all the links into a single complete web for each site (the two webs analysed in Voigt and Perner, 2004). All these webs are related because the complete web contains no more links than those in constituent webs. They might thus be expected to have similar properties. Nevertheless, despite their origins, their reliabilities may differ if they have different topologies. Even webs with the same number of nodes and same connectance have widely divergent reliabilities (Jordán and Molnár, 1999). We tested this possibility since it would be of great ecological importance if true. It suggests that the reliabilities of natural interaction webs involving functional groups depend on the number and particular arrangement of the different link types they contain. This, in turn, would change their role in mediating between diversity and the functioning of ecosystems. For simplicity and to avoid confusion, we refer to eight 'models'. These eight are collectively the webs derived from different models and their associated complete web from each site.

To characterize the models fully, we compiled all their constituent sink webs. These are webs where only one species or group ultimately receives all flows (Cohen, 1978). The sink is a top carnivore or herbivore without predators. Sink webs were also necessary to compare the reliabilities of interaction webs with those for food-webs. Only Jordán and Molnár (1999) have derived reliability for food-webs and they did this only from sink webs.

Sink webs characterize the model from which they are constructed. However, those from the same model need not have the same structure or reliability (Jordán and Molnár, 1999). The difference between sink webs reflects the size and structural diversity of the original model. It is, itself, a model character. All the sink webs are related because our models share functional groups between sites. For the same reason they are also mutually related within sites. A consequence of this relatedness is that some sink webs from different models are structurally identical. They nonetheless characterize different models. Deleting these identical sink webs is thus invalid. To do so would remove similarities between models. It would artificially inflate differences between models. Minimizing differences is conservative. It ensures that any differences we find occur despite the relatedness of the models.

Reliability

The reliability of a network is the probability that sinks remain connected to at least one source if nodes randomly fail with a certain probability. We assumed that sinks do not fail (Jordán and Molnár, 1999). Webs with a single sink disconnect as soon as the links break between the single sink and the producers because of the failure of a base, or intervening, node. In webs with more than one sink, different definitions are possible. The weak definition is that webs fail when only one sink is disconnected. The intermediate definition is that failure occurs when 50% or more sinks detach. The strong definition is that webs fail only when all sinks become detached. We used the strong definition under which web failure is least likely. This represents a true, complete, failure.

In principle, each web node has its own failure probability. However, computational difficulties currently prevent calculation of reliabilities on this basis. We therefore used fixed and equal failure probabilities for all nodes (Jordán and Molnár, 1999). To be able to compare reliabilities of interaction webs with those for food-webs, we used the same failure probability, $p = 0.01$ (Jordán and Molnár, 1999). However, reliabilities tend to be very high with this value. They therefore do not fall accurately into size categories. The category widths are not much bigger than the rounding errors of individual values. To avoid this problem, we also used failure probabilities of 0.1 and 0.3. These two values reveal more clearly the relationships between reliability and other web characteristics.

The directedness of links is a key distinction between food- and interaction-webs. In food-webs, matter and energy flow in a single direction to a defined sink (e.g. a top predator). Flows in interaction webs are practically undirected. Reliable flows are much more difficult to define. They might be determined between several sets of nodes but this is a large and complex subject. Therefore, we assumed trophic flow to enable comparison with food-web reliabilities. We calculated the trophically directed component of reliability using the equation:

$$R = 1 - \sum_{i=1}^{n-1} \binom{n-1}{i} p^i q^{((n-1)-i)} F_i$$

The value p is the failure probability (= 0.01, 0.1 or 0.3) and q is the probability of not failing (= $1 - p = 0.99$, 0.9 or 0.7). The total number of nodes is n (and $n - 1$ is thus the number of deletable nodes). F_i is the 'fatal ratio', the ratio of the number of sets of i deleted points that result in disconnection between sources and sinks to the total number of sets of i deleted points (Jordán and Molnár, 1999; Jordán *et al.*, 2003).

Analysis

We compared the patterns of reliability in interaction webs of functional groups and in food-webs. To do this we plotted the values of various web characteristics against reliability classes (Jordán and Molnár, 1999). Calculation of web characteristics used conventional definitions. However, we also calculated vertical, as well as normal, connectance because our webs omit horizontal links. Vertical connectance is unbiased by the omission of horizontal links. It equals the number of links existing as a proportion of all possible vertical links. For functional group webs, the 'predator–prey ratio' is the ratio of groups with only links to lower trophic groups to those that have links upwards. This is the ratio of the numbers of groups with only incoming links (in-degrees) to the number that also have outgoing links (out-degrees) (cf. Jordán and Molnár, 1999). This ratio measures how much groups at the top of the web interact with species in more than one lower group. The proportion of 'specialists' equals the proportion of groups having an 'in-degree' of one. Such groups have only one link to a lower trophic level. This measures the proportion of groups in which species interact with species in only one lower group. We estimated the 'specialization range' as the standard deviation of the mean number of in-degrees. Webs with high specialization-ranges have more varied structure than those with low values. We derived reliability classes of <0.9, 0.901–0.96, 0.9601–0.97, 0.9701–0.98, 0.9801–0.99 and 0.9901–1.00 using only the reliabilities calculated with a 0.3 failure probability. This gave the greatest separation of reliability values. The two lowest classes are broad in order to avoid many non-empty classes with small numbers of values.

We examined the null hypothesis of no relationship between reliabilities and each of the other web characteristics. We used Kendal rank correlations because reliability and many of the web characteristics are proportions. They are therefore non-normally distributed. Multiple pair-wise correlations of these data are misleading. Most web characteristics ultimately derive from the number of nodes and links. In consequence, the measures are not independent of each other. To escape this problem we used principal component analysis (PCA). This technique also determines the major factors influencing the reliabilities of our webs. It extracts independent axes from the primary (numbers of nodes and links) and derived web characteristics. The web characteristics were standardized. This ensured that those with quantitatively larger values (e.g. number of nodes) did not overly influence the analysis. We then identified the major PCA axes as those collectively explaining more than 75% of the variance in the constellation of web characteristics. Afterwards we determined the relationship of reliability to these PCA axes.

We tested the null hypothesis that reliabilities did not differ between models or between sites with a nested analysis of variance (ANOVA). This design was needed because sink webs derive from site-specific models. Reliabilities of sink webs are thus non-independent within and between models. Standard ANOVA therefore underestimates within-sample variance and so inflates *F*-values (Underwood, 1997). We removed this effect by first calculating the residuals after multi-regression against variables denoting degree of relation between sink webs. We then carried out the ANOVA on these residuals (Stearns, 1983).

RESULTS

Species abundances, functional groups and models

The data included the abundances of 267 producer species (autotrophs). There were 686 species of arthropod herbivore (139,856 individuals). There were also 363 species of arthropod carnivore (21,165 individuals) (Table 1). Numerous species occurred in both sites. The sum of the site totals was therefore greater than the overall total. These species formed 16 functional groups. There were 14 functional groups at each site. However, Leutratal had one fewer carnivore group and one more herbivore group than Steudnitz. Most of the groups at the two sites were the same. However, Leutratal had no web-spinners (cws) and attacking chewers (cac) rather than chewing hunters (cch). Steudnitz lacked lifetime chewers (hlc). Leutratal had more significant links than Steudnitz. In both sites, the logical rules identified significant links of types 1 (m1), 2 (m2) and 4 (m4). No significant links fulfilled the rules for model 3. Overall, most links were of type 4 (39). There were fewer model 1 (30) and model 2 (24) links.

Interaction webs

The complete model for Leutratal (l-c) was the largest. It contained 14 functional groups and 52 links (Fig. 1). The smallest was the m4 model for Steudnitz with five groups and seven links (Fig. 2). We derived 17 sink webs from the four Leutratal models and 14 from the four in Steudnitz. These sink webs are identified by a code of the form 'l-m1-cac'. The first element indicates the site (l or s). The second is the model from which they derive (c, m1, m2

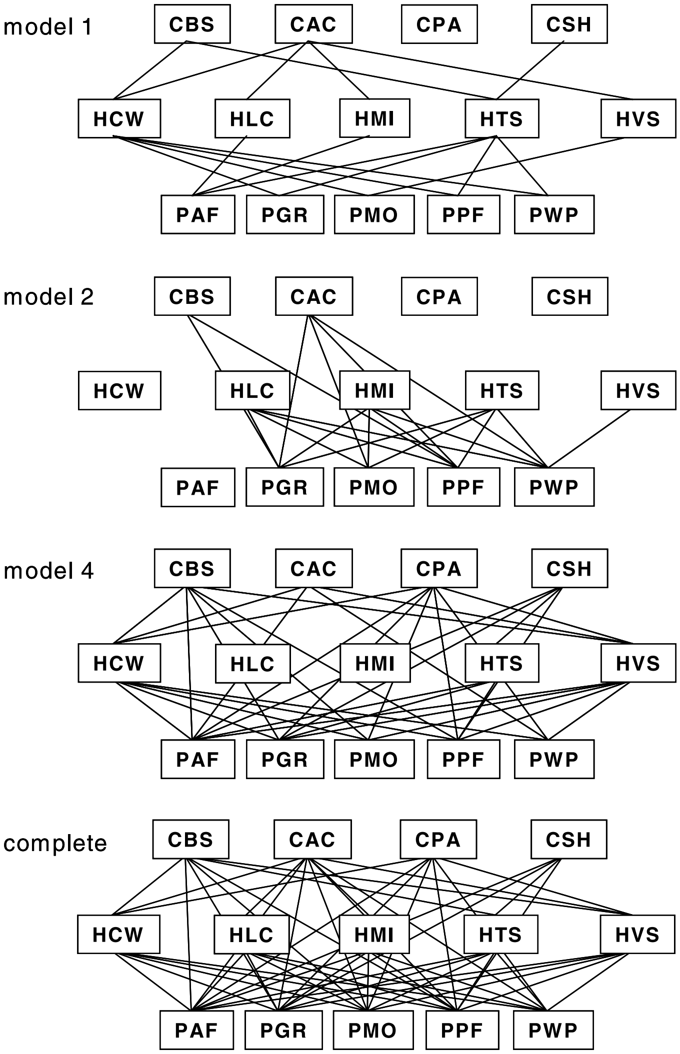


Fig. 1. Interaction webs of functional groups for Leutratal: Models 1, 2 and 4 and the complete web produced by combining them. Models 1, 2 and 4 incorporated from Voigt and Perner (2004). Copyright © Island Press.

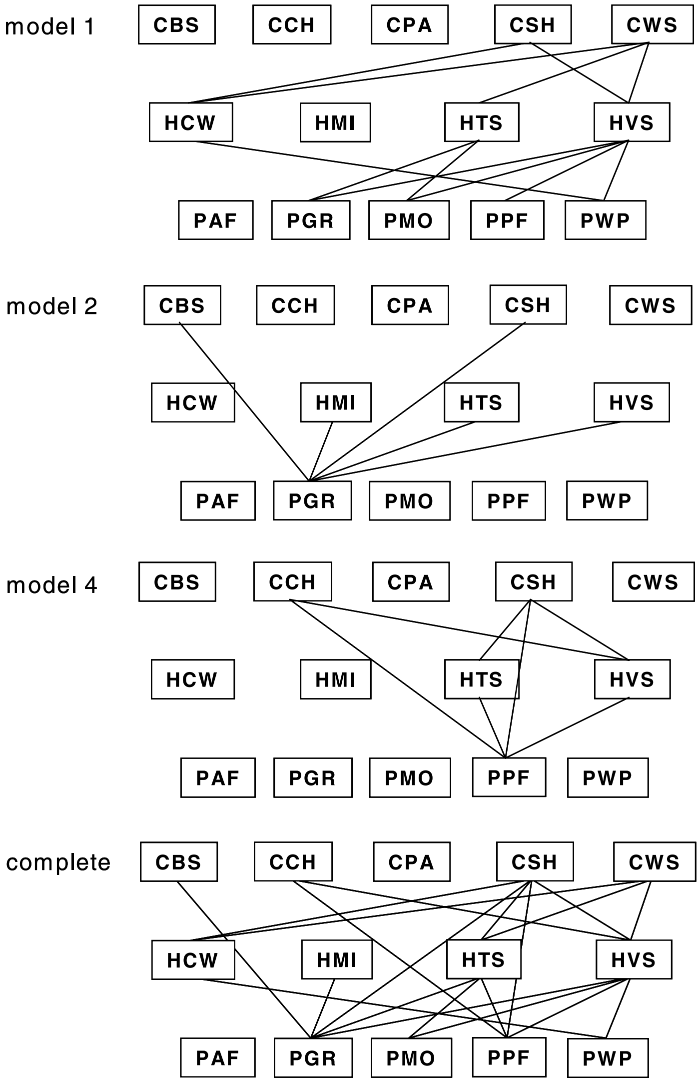


Fig. 2. Interaction webs of functional groups for Steudnitz: Models 1, 2 and 4 and the complete web produced by combining them. Models 1, 2 and 4 incorporated from Voigt and Perner (2004). Copyright © Island Press.

or m4). The third element is the identity of the sink species. Of these 31 sink webs, nine were c, five m1, eleven m2 and six were m4. The largest was of 10 nodes and 29 links (for l-c-cac). The smallest had a single pair of nodes and a single link (Fig. 3).

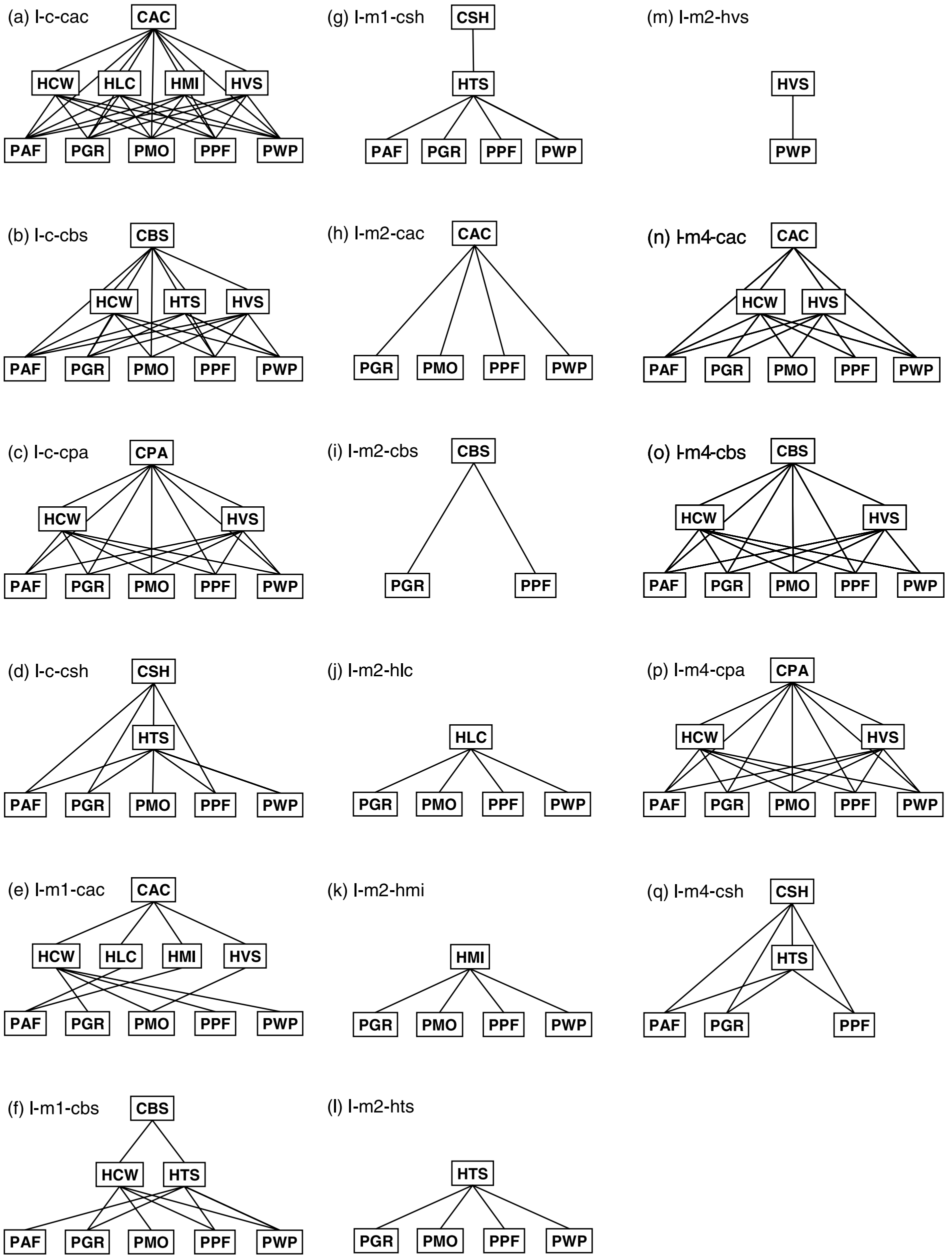
Reliability and analysis

There were very close correlations between the reliabilities of sink webs calculated with the three different node failure probabilities (r = 0.970–0.998). We therefore only analysed reliabilities calculated with $p = 0.3$. This produces the clearest patterns of relationship (Table 2).

Table 2. Reliability values for full model and sink interaction webs of functional groups for Leutratal and Steudnitz

Site	Model	Description	Sink group	Reliability
Leutratal	Model 1	full model		0.9806
		sink	cac	0.9424
		sink	cbs	0.9054
		sink	csh	0.6943
	Model 2	full model		0.9919
		sink	cac	0.9919
		sink	cbs	0.9100
		sink	hlc	0.9919
		sink	hmi	0.9919
		sink	hts	0.9919
		sink	hvs	0.7000
	Model 4	full model		0.9975
		sink	cac	0.9896
		sink	cbs	0.9970
		sink	cpa	0.9975
		sink	csh	0.9862
	Complete	full model		0.9975
		sink	cac	0.9975
		sink	cbs	0.9974
		sink	cpa	0.9975
		sink	csh	0.9901
Steudnitz	Model 1	full model		0.9387
		sink	csh	0.8413
		sink	cws	0.9467
	Model 2	full model		0.7000
		sink	cbs	0.7000
		sink	csh	0.7000
		sink	hmi	0.7000
		sink	hts	0.7000
		sink	hvs	0.7000
	Model 4	full model		0.7000
		sink	cch	0.7000
		sink	csh	0.7000
	Complete	full model		0.9873
		sink	cbs	0.7000
		sink	cch	0.9043
		sink	csh	0.9929
		sink	cws	0.9455
		sink	hmi	0.7000

Leutratal sink webs



Steudnitz sink webs

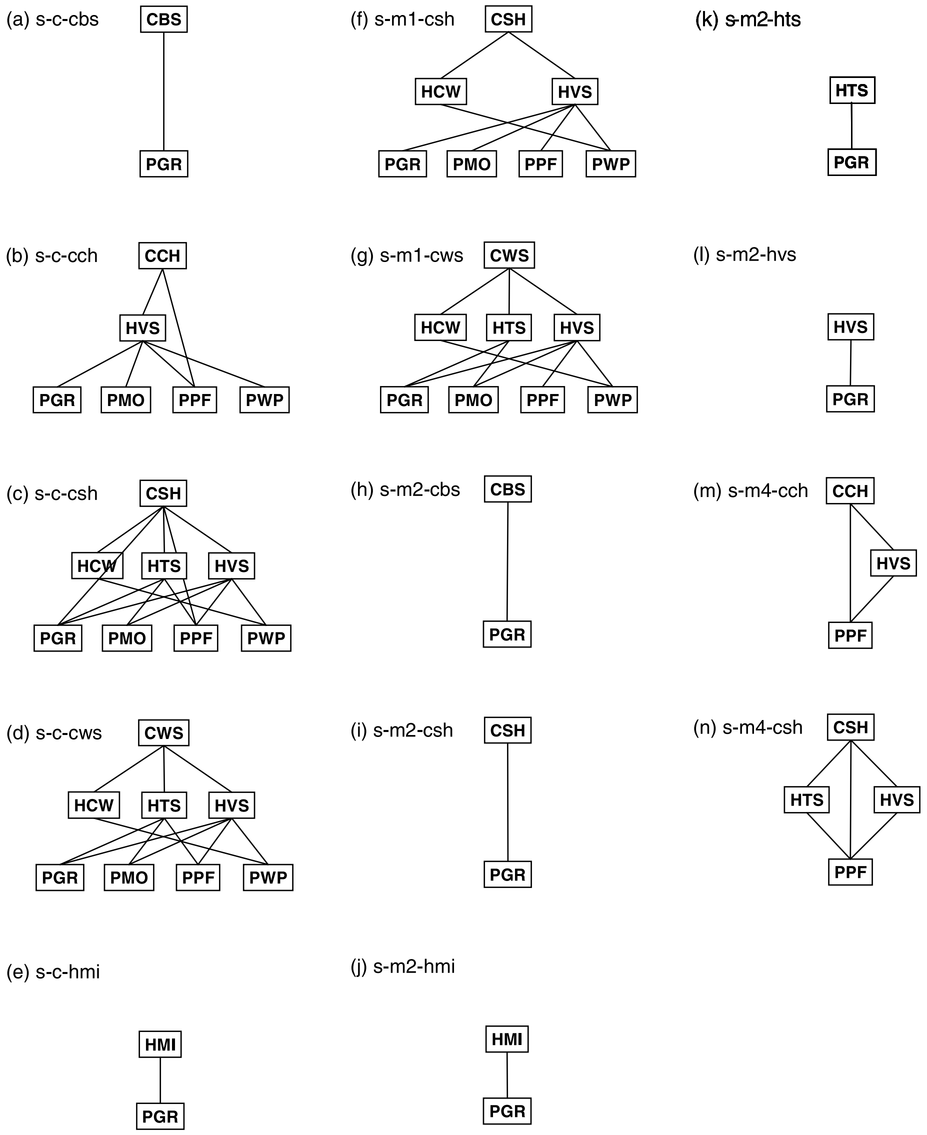
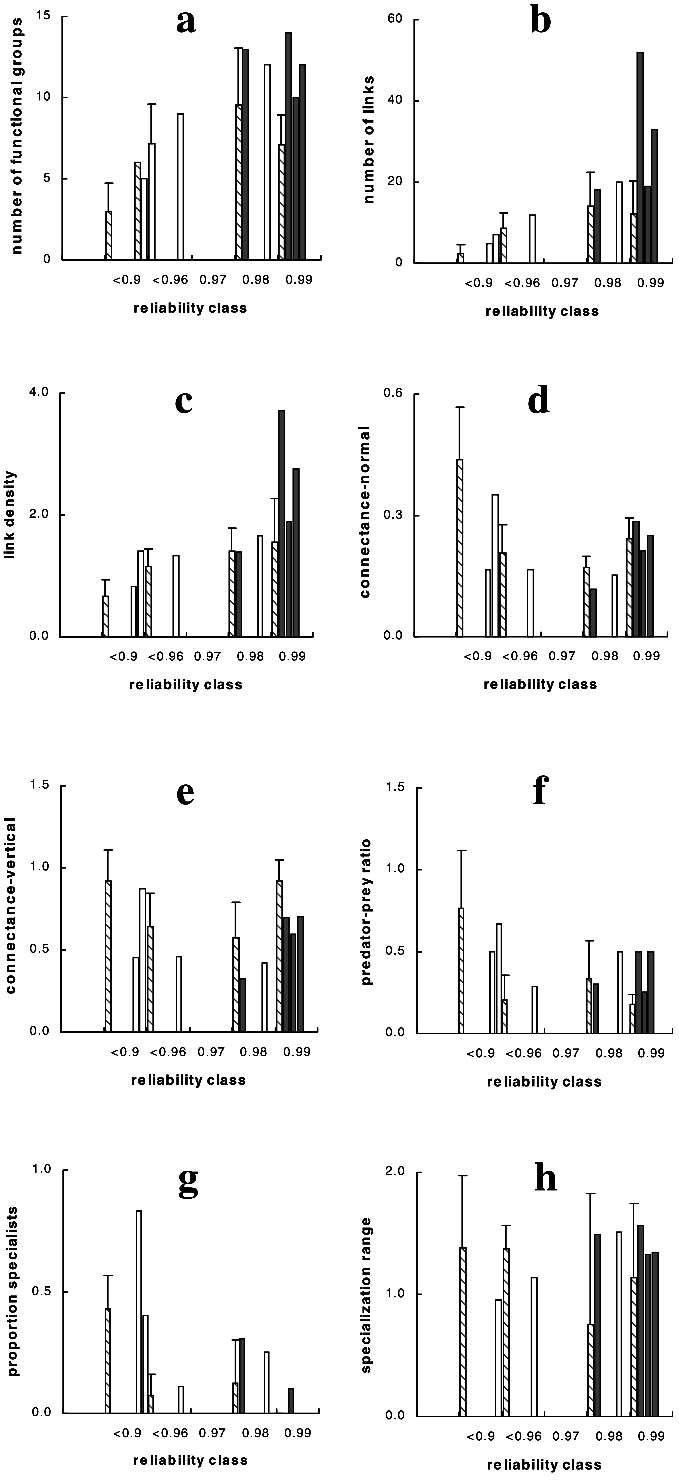


Fig. 3. All 31 sink webs derived from the four models of interaction webs from Leutratal and the four from Steudnitz. (Detailed derivations are provided in the text.) Codes: l = Leutratal, s = Steudnitz, m1 = model 1, m2 = model 2, m4 = model 4, c = complete web. Sink functional groups indicated by the three letter codes in Table 1.



a
number of functional groups
0
5
10
15
b
number of links
0
20
40
60
c
link density
0.0
2.0
4.0
d
connectance-normal
0.0
0.3
0.6
e
connectance-vertical
0.0
0.5
1.0
1.5
f
predator-prey ratio
0.0
0.5
1.0
1.5
g
proportion specialists
0.0
0.5
1.0
h
specialization range
0.0
1.0
2.0
<0.9
<0.96
0.97
0.98
0.99
reliability class

Sink webs with the highest reliabilities tended to contain more functional groups. The large webs from the Leutratal complete model occurred in the higher reliability classes (Fig. 4a). There was a similar positive relationship between the total number of links in webs and reliability class (Fig. 4b). It remained even after removing the high value of 52 links for the Leutratal complete web. High reliabilities were also associated with high link densities (Fig. 4c). There was no pattern, however, in the relationship between connectance and reliability class, despite the first column (Fig. 4d). Vertical connectance and class were also unrelated (Fig. 4e). The ratio of top groups (sinks) to others appeared least for webs in high reliability classes (Fig. 4f). This suggests a negative relationship between this ratio and reliability. However, high reliability classes had lower proportions of specialist groups (those with in-degrees of one) (Fig. 4g). Two of the Leutratal models falling in the highest reliability classes had no specialist groups at all. There was no discernible relationship of reliability class and specialization range (standard deviation of the number of in-degrees per group) (Fig. 4h). Leutratal models clustered together. They tended to occur in the higher reliability classes. Steudnitz models, however, did not cluster. They occurred across the entire range of classes.

There were highly significant Kendal rank correlations of reliability with most web characteristics. Strong positive correlations occurred with the number of functional groups, the number of links, and with link density. Strong negative correlations existed with proportion of specialists and predator–prey ratio (Table 3). Reliability did not correlate with range of specialization, or with either of the connectance values.

The first two PCA axes together explained 83.7% of all the variance in web characteristics. The remaining axes explained little additional variance. Loadings of the web characteristics on the first axis (PCA1) were all high, whether positive or negative. Only link density and vertical connectance had loadings greater than 0.500 on the second axis (PCA2) (Table 4). PCA1 thus tends to represent web size. PCA2 reflects structural aspects. Reliability correlated strongly (0.756) with the first PCA axis. But it did not correlate strongly with the second (0.260).

The quantities total number of groups, number of links and link density all correlate (Fig. 5). The ordination also indicates the correlation of proportion of specialists, predator–prey ratio and normal connectance. However, these correlate in the opposite sense. Vertical connectance, however, did not correlate closely with either of these groups of variables. Reliability plots nearly parallel to the axis of the other variables except vertical connectance. This indicates its correlation with them. The majority of Leutratal sink webs lay in the right half of the plot. They thus associate with high values on PCA1. However, they spread over the whole range of PCA2. Most Steudnitz webs, in contrast, associate with low, negative, values on PCA2. However, they extend over the range of PCA1. Sink webs from some models clustered together but others did not.

Fig. 4. The relationships between reliability classes and the other characteristics of model and sink functional group interaction webs for Leutratal and Steudnitz. Solid bars indicate Leutratal models. Open bars indicate Steudnitz models. Shaded bars are the means (± 1 standard deviation) for sink webs from all models. Plot a, number of functional groups; b, number of links; and c, link densities. Plot d, connectance – normal; e, connectance – vertical; and f, predator–prey ratio (ratio of top groups to others). Plot g, proportion of specialist groups (those with in-degrees of one). Two Leutratal complete webs in the highest reliability classes have no specialist groups. They, therefore, do not appear). Plot h, range of specialization (standard deviation of the number of in-degrees per group).

Table 3. Kendall rank correlations between reliabilities and other web characteristics for interaction webs of sink functional groups for Leutratal and Steudnitz

Characteristic	Kendall's τ	p-value
number of functional groups	0.537	<0.001
number of links	0.609	<0.001
link density	0.625	<0.001
connectance – normal	−0.130	0.280
connectance – vertical	−0.050	0.680
predator–prey ratio	−0.467	<0.001
specialist proportion	−0.681	<0.001
specialization range	0.048	0.739

Table 4. The loadings on the first two axes of a principal components analysis of the web characteristics for interaction webs of sink functional groups for Leutratal and Steudnitz

Characteristic	PCA1	PCA2
number of functional groups	0.9756	0.0754
number of links	0.8329	0.4921
link density	0.7984	0.5669
connectance – normal	−0.8139	0.3372
connectance – vertical	−0.6129	0.7335
predator–prey ratio	−0.9354	0.0069
specialist proportion	−0.8010	−0.1300
specialization range	−0.8168	−0.2156

Reliabilities of sink webs differ significantly between web types ($F_{6,23} = 2.64$, $p = 0.04$) by nested ANOVA corrected for web relationships. Nevertheless, the overall ANOVA was not significant ($F_{7,23} = 2.27$, $p = 0.65$). There were no significant differences between sites ($F_{1,23} = 0.13$, $p = 0.72$).

DISCUSSION

Our natural interaction webs are broadly as reliable as natural food-webs (Jordán and Molnár, 1999). This is true even though we used a higher failure probability. Reliabilities for interaction webs are very high using the same small failure probability of 0.01 as used for food-web studies. The most stable class contained all reliabilities. Reliabilities for our interaction webs might have been expected to be lower than for food-webs in general. This is because we omitted horizontal links, those representing competition or facilitation. However, reliabilities for our interaction webs are not lower. This suggests that adding horizontal interactions to interaction webs will make their reliabilities greater than those for food-webs. This is probable since full interaction webs include more links than food-webs.

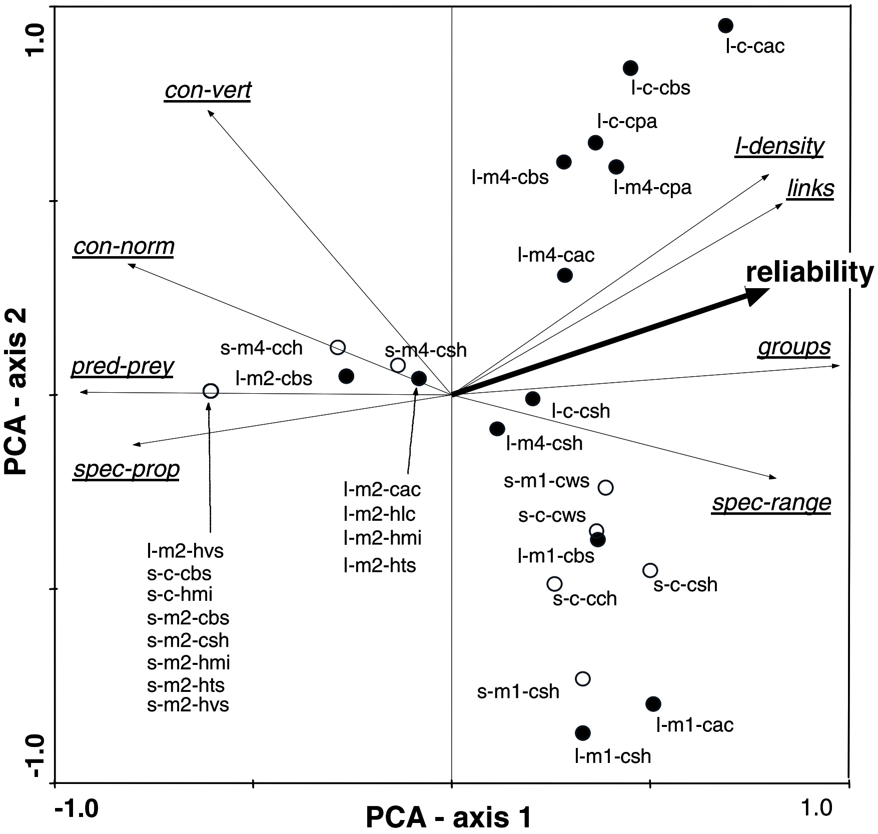


Fig. 5. PCA ordination diagram showing the relationship of reliability to the first two PCA axes and to other web characteristics. Groups = number of functional groups in the web. Links = number of links. L-density = link density. Pred-prey = predator–prey (the ratio of groups with only in-degrees to those with out-degrees). Spec-prop = proportion of specialist groups (those with only one in-degree). Spec-range = range of specialization (standard deviation of in-degree number per group). Also plotted relative to the two PCA axes are the positions of individual sink webs for Leutratal and Steudnitz. Codes: l = Leutratal, s = Steudnitz, m1 = model 1, m2 = model 2, m4 = model 4, c = complete web. Sink functional groups indicated by the three letter codes in Table 1.

They include all the trophic links of food-webs together with all the non-trophic interactions. Thus, for a given number of groups or species, interaction webs will usually contain more interactions than food-webs. Having more links, they will be more reliable.

We can exclude the possibility that our webs are unusual because they derive from a limited number of taxa. The webs derive from data on a large number and variety of plant and arthropod species. These species represent a substantial part of the whole grassland community.

Putting species in the ‘wrong’ functional group could change the orientation of links. This would affect the web and possibly alter reliability. It is unlikely that this is a systematic problem in our webs. The presence of several species in functional groups buffers against the effect of putting a single species in the wrong functional group. However, wrongly placing particularly variable species might affect reliability. This possibility thus requires theoretical examination.

Interaction webs show similar relationships between reliability and other web characteristics as small food-webs (Jordán and Molnár, 1999). It is possible to compare these patterns. However, direct comparison of the frequency histograms for interaction and food-webs is invalid. This is because we calculated reliability classes using a higher failure probability. Our data derive from a wider range of web sizes but do not show the relationships across a complete range of reliabilities. This is because we analysed only those webs represented in the field data. We did not generate numerous webs of similar sizes but varied reliabilities.

In our interaction webs, the total number of nodes strongly influences reliability. Jordán and Molnár (1999) did not see this in food-webs. The difference is probably due to the fact that the number of nodes (or functional groups) and the proportion of linked nodes positively correlate in our webs. The relationship of reliability with link density shows this. Of course, larger webs must also have larger numbers of links. However, an increase in the proportion of links derives from the particular characteristics of natural interaction webs for Leutratal and Steudnitz. Testing the generality of this relationship requires reliability analysis of more webs from ecosystems.

There is a very clear difference between food and interaction webs. There is no relationship between reliability and connectance in interaction webs. This may be illusory. The data for food-webs include all possible connectance values for the five-node webs generated (Jordán and Molnár, 1999). In contrast, our interaction webs have different sizes. Their connectances are thus not the full range of values for webs of these sizes. The data for Leutratal and Steudnitz unfortunately yielded too few webs to control for the effect of different web sizes. Such a control might have revealed a relationship with reliability similar to that for food-webs.

We found the same relationships between reliability and the number of specialists and with the predator–prey ratio as in food-webs (Jordán and Molnár, 1999). However, the relationship with degree of specialization found at high, but not at low, connectances for food-webs is absent. This arises because the connectances for interaction webs lay in the lower part of their possible range.

There may be a simple reason for the differences we describe between food-webs and interaction webs. They may arise mainly because the interaction webs derive from field data. They are not all possible webs of a given size (Jordán and Molnár, 1999). They are those possible in nature. They are a selection of those structurally conceivable (Maynard Smith *et al.*, 1985). We found broad similarities between food-webs and interaction webs. We imagine, therefore, that reliabilities for ecological webs will relate similarly to other web characteristics. Reliabilities for interaction webs should have the same relationships to trophic chain length, compartmentalization and omnivory as food-webs (Jordán and Molnár, 1999). However, we could not test these contentions. We examined the interrelations of functional groups unambiguously assigned to discrete trophic levels. Such levels may or may not exist in species-specific food-webs (Oksanen *et al.*, 1981; Polis and Strong, 1996). Nevertheless, defining such levels is intrinsic to the definition of functional groups. It unavoidably affects the analysis of their group interactions. The levels in our webs constrain chain lengths to either one or two. We did not divide functional groups of carnivores into grades (primary, secondary or higher-grade carnivores). Not dividing functional groups into grades also restricts the identification of omnivory.

Omission of horizontal links within trophic levels prevented reliable estimation of compartmentalization.

In food-webs, connectance influences relationships between reliability and other characteristics (Jordán and Molnár, 1999). The relationship is not linear, however. In our webs, the relationship is different, although not significant. It is linear and negative. Reliability decreases as connectance increases. This is surprising, since high connectance should mean high reliability. High connectance means more links between available groups. More groups must then fail to cause disconnectedness. Part of the reason for the difference is that the number of nodes and the number of links strongly influence connectance. Connectance will fall if the number of links falls but the number of nodes does not. Differences in web structure also affect the relationship, however. Different reliabilities of interrelated models and webs show this. Connectance also has a weak effect on how resistant webs are to the removal of species (Pimm, 1991). Webs with high connectance are not less likely to lose additional species after a species removal than those with low connectance. However, this deletion stability (Pimm, 1979) is a dynamic quality of webs but reliability is not. The relationship between stability, connectance, reliability and other web characteristics thus remains to be fully explored.

The close association of group number and reliability in ordination also reveals a strong effect of web size on the reliability of our natural interaction webs. Many of the other web characteristics align similarly with the number of groups. Web structure is also important, since low reliability is associated with small numbers of upward links – that is, with high predator–prey ratios and high proportions of specialists. Without differences in structure between models, their reliabilities would be similar because of their interrelationships. Models also differ because their sink webs have different ranges of characteristics. Sink webs from the same models ordinate separately. This arises predominantly because of structural differences within models. The separation is greatest in relation to the second, structural, PCA axis. Differences in the sizes of sink webs also contribute, particularly for Steudnitz models. Here the separation is in relation to PCA1. The ANOVA shows the importance of structural differences. If models were random selections from all the links possible, there would be no differences between their reliabilities. They differ between models, however. These differences are independent of web relationships. Reliabilities are also more different between models than they are between sites. The same models exist at both sites.

The assessment of reliability for ecological webs is in its infancy. Ways of improving the technique are thus not difficult to find. Among other things, failure probability of a group is not a web-wide constant as we have had to assume. Failure probabilities, in fact, will relate to the strengths of interactions. They will vary between pairs of species and with time. In conventional food-webs, the average value of pair-wise interaction strengths of nodes (D_{ij}) could estimate failure probabilities. In our interaction webs, the average value of $\boldsymbol{r}_{\mathrm{M}}$ might be appropriate. It is not clear, however, whether these values and failure probability should correlate positively or negatively. Large effects might result from weak interactions (Berlow, 1999). The variance of interaction strength might thus be a more suitable measure of failure probability. In addition, species turnover rates might indicate realistic failure probabilities. Web reliabilities would then relate to stated time intervals.

Analysis of interaction webs is also a recent development (Price, 2002). Nevertheless, its use will contribute greatly to understanding the stability and resilience of ecosystems. This is because interaction webs encapsulate more of the links in a system than do food-webs. Interaction webs are less easily detected than the trophic interactions portrayed in food-webs, however. Many interactions do not involve matter transfer and so they cannot always be observed directly. Painstakingly detailed research reveals them (e.g. Fukui, 2001; Nozawa and Ohgushi, 2002a,b). However, such studies are logistically limited to small parts of systems. Our statistical technique detects interactions in much larger systems. It therefore provides a good overall view based on abundance data. Time-series autocorrelation analysis (Turchin, 2003) might also produce similar overall views.

Reliabilities of the interaction webs of functional groups resemble those available for food-webs. They have similar sizes and relationships to other web characteristics. Using our methodology, they can assess and compare the interactions of functional groups in large, species-rich, systems. They are important measures because both web structure and web size influence them. They thus reveal topological differences between otherwise similar webs. Reliabilities are therefore one measure, among others, for assessing differences in the linkage properties of different systems. The possibility of differences in reliability between models indicates that reliabilities for the interaction webs of functional groups will depend on the proportions of links of different types they contain. In consequence, how functional groups affect the relationship between species and ecosystems will relate to web reliability. Reliability analysis is thus an important component of our understanding of the relationship between biodiversity and the functioning of ecosystems.

AUTHOR NOTE

The order of authors for this article is alphabetical and does not indicate the authors' status or the size of their contributions. A.J.D. proposed the idea originally, brought the team together, calculated web characteristics, analysed the data and wrote the paper. W.C.L. wrote the software and calculated all reliabilities. J.P. and W.V. assembled the abundances database, sorted species into functional groups, constructed the base webs and performed the principal components analysis.

ACKNOWLEDGEMENTS

We are grateful to all those who collected and identified organisms over the years and provided the base data for this study. Data were collected under several programs funded by the University of Jena and by the UFZ Halle-Leipzig GmbH. We also thank the owners and controllers of Leutratal and Steudnitz for long-term access and cooperation. Ferenc Jordán, Ian Hardy, Takayuki Ohgushi, Stuart Pimm, Matt Potts, John Sloggett and Masanori Toda made useful comments. Figures 1 and 2 incorporate web diagrams reproduced with permission of Island Press, Washington, DC. The Wellcome Trust International Partnership Research Award in Veterinary Epidemiology (IPRAVE) project supports W.C.L. A DAAD visiting lectureship funded A.J.D. in Jena.

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