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Trophic fields

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Abstract: In complex, modern food webs, the analysis of pairwise interactions gives weak predictions of the behaviour of either single species or the whole community. Indirect effects call for explicit study and quantification. However, just as focusing only on pairwise interactions is incorrect, overemphasising the role of long, indirect pathways also seems to be unrealistic. Thus, a reasonable range of indirect trophic effects spreading through the food web is to be defined and quantified. I suggest a graph theoretical measure for quantifying this range, considering only network position (topology). I call this the *trophic field* of a species (or trophic group), recalling the idea that field theory could be a fruitful research programme in biology. Further, I propose a measure for the quantification of the indirect component of the trophic field. Finally, the use of introduced concepts and indices is illustrated by analysing the trophic flow network of the Schlei Fjord ecosystem (N. Germany).

Introduction

A well-known problem in both community ecology and systems ecology is how to trace various effects spreading through the rich network of ecological interactions. For example, how the cull of marine top-predators (Yodzis 2000, 2001) may affect other species? Some people prefer to focus mainly on pairwise species interactions and to consider indirect effects less important (cf. Kareiva 1994). Others tend to emphasise the power of indirect effects, underline that practically everything is connected to everything else, and study longer pathways of effects as a possible key to understanding ecosystems behaviour (Patten 1991, Yodzis 2000). The complexity of large food webs is a property calling for explicit investigation in itself, for example focusing on indirect pathways or scaling behaviour (see Bersier and Sugihara 1997).

Since both of the two extremities (only pairwise & indirect dominance) have shortcomings, a theory of the effective range of indirect effects is strongly needed. Here, my aim is to offer a conceptual background for defining this range, and a method for quantifying indirect effects. I also present a network analysis of the Schlei Fjord trophic flow network (Christensen and Pauly 1992). Thus, the first part of the paper will be of conceptual and methodical, while the second one will be of illustrative nature.

Conceptual background

A species (or a trophic group) is always a member of an ecological community. Thus, its behaviour affects and is affected by other species. Various effects spread through the network of interactions, and both the global properties of the whole network and the local position of a particular component strongly influence what happens in the ecosystem (Higashi and Burns 1991). Of course, the neighbours (directly interacting partners) of a given species do canalise the spread of its effects (by determining the next steps of indirect pathways). So the network structure constrains who can affect whom, and to what extent, since it is very reasonable to assume that, neglecting interesting exceptions, the strength of an effect is roughly inversely related to the length of the indirect pathway of sequential effects.

Goodwin proposed *biological field theory* as a research programme (Goodwin 1989, 1994, and see also Thom 1975, p.152) for developmental biology: "*...the relational order between molecular constituents, the way they are organized in space and interact with one another in time, which requires a description in terms of fields and their properties.*" [Goodwin 1994]. This is in concert with some theories of ecosystem development emphasising that a dynamic view on ecological interactions or flows can be even more important than looking at species or nutrient stocks themselves (Ulanowicz 1986). I suggest that ecological field theory is an interesting and possibly useful view on community organisation. Each species (or trophic group) has some trophic field, defined by its feeding habits, the feeding habits of its prey and predatory species, and, ultimately, by the entire food web. It has been suggested that a topological view on ecological relationships may help in understanding the connection between local and global events in the community. Coevolutionary relationships (see Thompson 1982) are suggested to be relevant only between topologically closely related species, and it is possible to give some quantification of this effective field. The field can be understood both in a narrow (only trophic effects) and in a broad (also non-trophic effects, e.g., facilitation) sense. However, I am interested only in the narrower definition, for there is no hope of finding any data base describing a whole trophic and non-trophic community network. Here, the field of a species is analysed in a topological sense: the trophic flow network gives structural information about the range of its effects. Former quantitative studies on indirect effects (Hannon 1973, Ulanowicz and Puccia 1990) calculated the strength of indirect effects between pairs of trophic groups, while I quantify the indirect regulatory power of a certain group, i.e. I characterise nodes instead of links. Doing so, I try to offer an approach to the problem of keystone species: estimating the relative importance of species within communities is still a highly subjective and qualitative branch of ecology. Trophodynamical considerations (Jordán 2000, 2001) may help in increasing the reality of these topological studies, by considering weights on trophic links, too. Finally, I note that in quantifying the trophic field of a species, I give some information about its environ (Patten 1981).

Methods

After Harary (1961), we have proposed a slightly modified graph theoretical index (*keystone index*, Jordán et al. 1999) for characterising the importance of species (trophic components) in ecosystems, based on their position in the food web (see Margalef 1991). This index, in principle, gives the (not necessarily integer) number of species going to secondary extinction after removing a certain species from the network (recall the concept of species deletion stability, as a dynamical counterpart of this structural model; Pimm 1980). Our index takes into account direct and indirect interactions in both directions i.e. bottom-up and top-down). The keystone index of the x^{th} species is:

$$K_x = \sum_{c=1}^{n} \frac{1}{d_c}(1 + K_{bc}) + \sum_{e=1}^{m} \frac{1}{f_e}(1 + K_{te}),$$

where n is the number of predators eating species x, d_c is the number of prey of its c^{th} predator, K_{bc} is the bottom-up keystone index of the c^{th} predator, and symmetrically: m is the number of prey eaten by species x, f_e is the number of predators of its e^{th} prey, and K_{te} is the top-down keystone index of the e^{th} prey. Within this index, the first $(\Sigma 1/d_c(1+K_{bc}))$ and second $(\Sigma 1/f_e(1+K_{te}))$ sums quantify bottom-up (K_{bu}) and top-down (K_{td}) effects, respectively. Products containing K values $(\Sigma K_{bc}/d_c + \Sigma K_{te}/f_e)$ refer to indirect effects (K_{indir}), while products not containing K values $(\Sigma 1/d_c + \Sigma 1/f_e)$ refer to direct ones (K_{dir}). Both $K_{bu} + K_{td}$ and $K_{indir} + K_{dir}$ equal K. The degree of a point in a network (D) characterises only the number of its connected (neighbour) points, while the keystone index gives information also on how these neighbours are connected to *their neighbours*. For example, consider species “A” feeding on a single prey “B”, which eats many others, indirectly affected by “A”. In this case, the trophic field of species “A” includes the prey species of “B”, and even if “A” has only a single prey ($D = 1$), its trophic field still can be strong (its K keystone index refers to an important role in community regulation, cf. Paine 1969). This simple “network algebra” can contribute to assessing the importance of species and mapping the pathways of indirect interactions between them. It has been shown that points in particular network positions may be characterised by similar extinction risk (Jordán et al., *submitted*).

An illustrative network analysis

The strongly aggregated trophic flow network of the Schlei Fjord ecosystem (N. Germany) was published by Nauen (1984) and analysed by Christensen and Pauly (1992). The original food web contained 10 trophic groups, 17 “grazing” links and 9 links cycling back to detritus. I analysed a slightly different web, modified as follows. However, I appreciate the holistic view of systems ecology, focusing mainly on energetics and nutrient fluxes, also try to consider the general community ecological view, studying primarily biotic interactions between living populations. Thus, I excluded “detritus” as a trophic group, erasing the nine cycling links feeding back to that group, and two “grazing” links coming from that. My network contains only 9 nodes and 15 links (Figure 1). I study and quantify the trophic fields of trophic components, especially that of a commercially important trophic group, “small fish” (node #7).

Trophic fields

While small fish (#7) have the largest number of direct trophic links in the network ($D = 5$, see Table 1), several other trophic groups have stronger effects on the com-

Table 1. Network indices characterising the network position of trophic groups by quantifying the strength of their trophic field (*K*, keystone index) and giving its bottom-up (K_{bu}), top-down (K_{td}), indirect (K_{indir}), and direct (K_{dir}) components. *D* gives the degree of points, i.e., the number of directly connected neighbours.

Group	K_{bu}	K_{td}	K_{dir}	K_{indir}	K	D
1	8	0	2	6	8	2
2	2.77	0.5	2.5	0.77	3.27	4
3	3.23	0.5	2.33	1.4	3.73	4
4	0.25	1.17	0.92	0.5	1.42	3
5	0	0.5	0.33	0.17	0.5	1
6	0.66	0.5	0.92	0.25	1.16	3
7	1.29	1	1.75	0.54	2.29	5
8	0.25	1.92	1.42	0.75	2.17	4
9	0	6.5	2.83	3.66	6.5	4

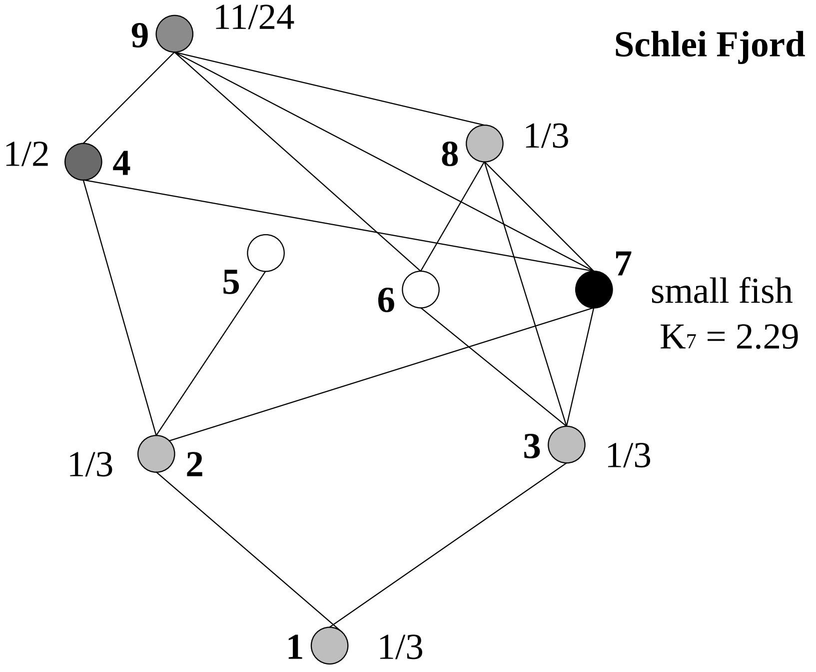

Figure 1. The trophic flow network of the Schlei Fjord ecosystem (N. Germany; modified after Christensen and Pauly 1992: carbon flux magnitudes are available here). Codes for trophic groups, given in bold, are: 1, Phytoplankton; 2, Zooplankton; 3, Zoobenthos; 4, Planktivores; 5, Temporary planktivores; 6, Whitefish; 7, Small fish; 8, Medium predators; 9, Apex predators. The quantified trophic effects of small fish (#7) on other components are also given, calculated as follows (shading tries to express the strength of the trophic field): $K_7 = K_{bu} + K_{td} = K_{dir} + K_{indir} = 2.29$, where $K_{bu} = 1/2_{\mathbf{(4)}} + 1/3_{\mathbf{(8)}} + 1/4_{\mathbf{(9)}} + 1/2 * 1/4_{\mathbf{(9)}} + 1/3 * 1/4_{\mathbf{(9)}} = 1.29$, $K_{td} = 1/3 * 1/2_{\mathbf{(1)}} + 1/3 * 1/2_{\mathbf{(1)}} + 1/3_{\mathbf{(2)}} + 1/3_{\mathbf{(3)}} = 1$, $K_{dir} = 1/3_{\mathbf{(2)}} + 1/3_{\mathbf{(3)}} + 1/2_{\mathbf{(4)}} + 1/3_{\mathbf{(8)}} + 1/4_{\mathbf{(9)}} = 1.75$, and $K_{indir} = 1/3 * 1/2_{\mathbf{(1)}} + 1/3 * 1/2_{\mathbf{(1)}} + 1/2 * 1.4_{\mathbf{(9)}} + 1/3 * 1/4_{\mathbf{(9)}} = 0.54$. Bold subscripts in parentheses give the code of the affected trophic group. See text, for further explanation. Note that the graph is directed if we consider nutrient flows but this is not shown for simplicity.

munity, viewed from a network perspective. These components (phytoplankton, $K_1 = 8$, apex predators, $K_9 = 6.5$, zoobenthos, $K_3 = 3.73$, and zooplankton, $K_2 = 3.27$) have stronger trophic fields (i.e., higher topological keystone indices) than $K_7 = 2.29$, because of their indirect effects. Table 1 shows also that, for example, the trophic field of small fish is stronger in bottom-up direction (compare K_{bu} and K_{td} for group #7, and see Figure 1 for illustration and detailed calculations), or that the direct component of the trophic field is the largest for apex predators (#9, $K_{dir} = 2.83$), and only intermediate for small fish (#7, $K_{dir} = 1.75$), even if they have the largest number of direct links (K_{dir} takes into account the exploitative and apparent competitors of trophic neighbours, i.e., predatory and prey species). Further, neither K_{dir} nor K_{indir} can predict alone the strength of the trophic field: medium predators (#8) have a higher indirect index but smaller K_{dir} and weaker trophic field (K) than small fish (#7), but phytoplankton (#1) has smaller K_{dir} but a higher indirect index and stronger trophic field than apex predators (#9). Of course, either high K_{bu} or high K_{td} can result in stronger trophic field. I suggest that the strength and directionality of the trophic field may give information on the role of a species played in community organisation. Thus, I think that in the Schlei Fjord ecosystem, small fish (#7, $K = 2.29$) plays a larger role, than, for example, whitefish (#6, $K = 1.16$), and a smaller role, than, for example, zooplankton (#2, $K = 3.27$). Of course, these results depend strongly on the actual network structure, but it is believed that the identification of trophic components in the original flow network was based on solid field experience (cf. Nauen 1984). Based on our index quantifying indirect effects (K_{indir}), phytoplankton (#1) has the strongest structural indirect effects on others (Table 1).

Discussion

I have presented a conceptual background (trophic field theory) and a graph theoretical method (keystone index) for quantifying positional importance and the effective range of indirect regulation in ecosystem flow networks. However, these are crucial problems in keystone studies (Power et al. 1996), we only have poor possibilities for expressing quantitatively the relative importance of species and their effects. As experimental data bases on species interactions are growing (for rocky shores, see Menge 1995, Abrams et al. 1996), both methodical and conceptual advances are needed for their better understanding.

I argue that aggressive invaders (e.g., Genghis Khan species, Pimm 1991) may be characterised by strong trophic fields, having richly spreading effects through their feeding links, and therefore playing a large role in community organisation (Zaret and Paine 1973, and an example for a native species: Paine 1969). However, early keystone studies considered only top-predators, a species with many prey and a number of predators can also have a strong trophic field, especially with only a few competitors: an example is the wasp-waist control in marine ecosystems (see Cury et al. 2000), and in the case of the Schlei Fjord, phytoplankton, a basal group has been shown to have the largest trophic field.

As useful quantitative indices are always badly needed in conservation biology (cf. Power et al. 1996), I hope that the concept and the measurement of trophic fields can be helpful in evaluating species importance and important indirect effects. For example, the problem of systematically changing marine food webs (Pauly et al. 1998, 2000) also calls for a quantitative network perspective in studying the changing dynamics of multispecies interactions (cf. May et al. 1979).

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