



Quantifying the importance of species and their interactions in a host-parasitoid community

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Abstract: We present a new method to assess the strength of indirect interactions and to identify candidate keystone species in quantitative food webs. We apply this method to the structural analysis of a host-parasitoid community. The strength and symmetry of indirect interactions between 12 leaf-miner hosts and their 27 hymenopteran parasitoids are quantified. It is shown that (1) quantifying longer pathways helps in determining which species have more important direct or indirect effects on others, (2) a keystone pattern of relative species importance, based on positionality in the interaction network, seems to characterize this community, (3) considering longer pathways results in a characteristic 'few strong - many weak' distribution of interaction strength, and (4) between the majority of species pairs the interaction is weakly asymmetrical. We emphasise that a very simple network algebra approach may offer important predictions on both species- and community-level patterns.

Introduction

Indirect interactions were mentioned as early as 1927 (Elton 2001, p. 122), and emphasised again by Abrams (1983). However, it is only very recently that we have begun to recognise their significance (see Kareiva 1994 and subsequent papers). The explicit analysis of indirect interactions is also important in an applied context (cf. biological control, see Godfray and Shimada 1999), in helping conservation efforts (for example, assessing the impact of the possible cull of fur seals, Yodzis 2001), in understanding macroecological patterns (comparing tropical versus temperate interaction patterns, Morris and Lewis 2002) and it is challenging theoretically, too (see Patten 1991). Following the categorisation of their basic types (Menge 1995, Abrams et al. 1996), and detailed studies on some specific ones (e.g., apparent competition, Bonsall and Hassell 1999), we now begin to understand their significance in the context of a whole community (Yodzis 2000, 2001). Since the study of indirect effects is difficult in the field, the role of laboratory and theoretical approaches seems to be relatively large.

A related, major challenge in current ecology is how to quantify the importance of species in communities, i.e., how to mathematically define keystone species (Paine 1969, cf. Power et al. 1996). Presently, only qualitative and anecdotal descriptions exist (but see Mills et al. 1993). The network perspective has been suggested as a possibly useful approach in solving these problems (Jordán et al. 1999, Solé and Montoya 2001), since most of the definitions of keystones are somehow related to how, and to what extent, do dynamical effects spread from a disturbed species to others. A web of biotic interactions can well help in tracing these spreading pathways. Here, we link the keystone problem to the quantitative analysis of indirect effects within a network context.

Recent years have seen the publication of a growing number of quantitative host-parasitoid food webs (Memmott et al. 1994, Müller et al. 1999, Müller and Godfray 1999, Godfray et al. 1999, Lewis et al. 2002). Thanks to their common methodology, species level resolution and fully quantified trophic links, these webs are ideally suited for a comparative study of community structure. Here, our purpose is to propose some methodical devel-

opments that may be helpful in understanding the structural organisation of these communities, with focus on quantifying indirect interactions and keystone species. Presently, there is no consensus on precisely how to measure the strength of direct or indirect interspecific interactions; both theoretical and experimental problems exist (cf. Laska and Wootton 1998, Berlow et al. 1999). We apply our methodology to a leaf miner-parasitoid community that was formerly analysed by quantifying apparent competition between hosts (Rott and Godfray 2000). In the present work, our purpose is (1) to quantify the strength and symmetry of interaction chain effects up to ten steps, (2) to quantify the positional importance of species within this interaction network, and (3) to identify the possible effects of considering long interaction chains on some species- and community-level patterns.

Data

Interactions between 12 *Phyllonorycter* leafminer hosts and their 27 *Hymenopteran* parasitoids have been described in a boggy woodland at the Silwood Park, Berkshire, South-England (Rott and Godfray 2000, see Figure 1d, and see the Appendix for species names). Parasitoid links were quantified, based on the frequency of parasitoids found in leafminer pupae (Table 1). Data represent the summary of four subsequent moth generations in 1992 and 1993 (summer and fall). In this former analysis, emphasis was put on estimating the strength and symmetry of apparent competition between *Phyllonorycter* host species by means of parasitoid overlap diagrams (Rott and Godfray 2000).

Methods

The strength of apparent competition between hosts in host-parasitoid communities was quantified as

$$d_{i,j} = \sum_{k=1}^n \frac{\alpha_{k,j}}{\sum_{l=1}^m \alpha_{k,l}} \cdot \frac{\alpha_{i,k}}{\sum_{k=1}^n \alpha_{i,k}},$$

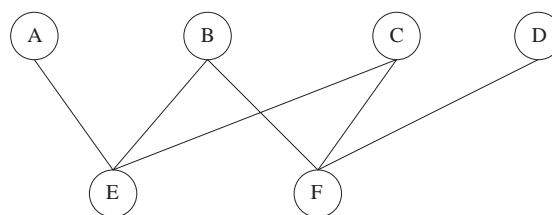
where $d_{i,j}$ is the strength of the indirect effect (apparent competition) of host j on host i , n and m are the number of parasitoid and host species, respectively, $\alpha_{x,y}$ is the frequency of the parasitoid link between species x and y , while k and l are appropriate parasitoids and hosts, respectively (Rott and Godfray 2000). In this expression, the strength of the indirect interaction is given by the product of the strengths of two direct interactions. The strength of a single, direct interaction is quantified as the ratio of parasitism frequency values measured in the field. Thus, these indices characterise a weighted food web. Apart from apparent competition, other kinds of indirect rela-

tionships can also be characterised based on the structure of these quantitative host-parasitoid webs.

We combined this index with a former one quantifying effects mediated through longer pathways (but based only on topology, Jordán et al. 1999, Jordán 2001). Here, the strength and symmetry of indirect interactions mediated through interaction chains of length n ($n < 11$) are quantified. For the n steps case, all indirect effects mediated by interaction chains of length i ($0 < i < n + 1$) are summed up. We consider every theoretically possible density-mediated interaction chain effects (see Wootton 1994), including apparent and exploitative competition. The importance of each host species is quantified as the sum of its effects on each other species of the community, divided by the density given in Table 2 (*sensu* one of the most widespread definitions of keystone species given by Tilman, see Mills et al. 1993).

Our assumptions are as follows: (1) there is no *a priori* asymmetry in trophic links, i.e., effects can spread equally in both directions; (2) interaction strength (d) can be reasonably assessed from parasitism frequency data (α); (3) interaction chain effects can be quantified as the products of direct interactions; and (4) indirect effects between two particular species i and j , mediated by different species (k, l, m, \dots), can be summed up, i.e., they are additive in this sense. If these assumptions are realistic, we believe that this approach can be informative and might help in mapping and quantifying indirect pathways. (The computer programme calculating interaction strengths and symmetries up to ten steps is available on request from WCL: weichung.liu@btinternet.com)

An hypothetical example helps understanding (for simplicity we do not include quantitative information on trophic links here):



In this graph, species A, B, C and D represent the parasitoids of two host species (E and F). The direct effect of E on C equals 1/2, because C has two direct (pairwise) interacting partners. The matrix of direct effects is as follows:

| Direct | A | B | C | D | E | F |
|--------|---|---|---|---|-----|-----|
| A | 0 | 0 | 0 | 0 | 1/3 | 0 |
| B | 0 | 0 | 0 | 0 | 1/3 | 1/3 |
| C | 0 | 0 | 0 | 0 | 1/3 | 1/3 |
| D | 0 | 0 | 0 | 0 | 0 | 1/3 |
| E | 1 | ½ | ½ | 0 | 0 | 0 |
| F | 0 | ½ | ½ | 1 | 0 | 0 |

Here, the effect of species in row i on the species in column j is given by the d_{ji} values (indexing follows the traditions of population dynamics: the species marked by the second index corresponding to row number affects the species marked by the first index corresponding to column number). The sum of each column equals 1 meaning that a unit effect reaching each species is divided among its interactive partners (affecting species); sums of rows corresponding to outgoing effects of species are not equal. In other words, we focus on the output environ of species (see Patten 1981), while input environs do not differ quantitatively.

The strength of an indirect effect mediated through a two-steps pathway between species A and C is assumed to equal the product of the two direct effects involved ($d_{CA}^2 = d_{EA} * d_{CE} = 1/3 * 1/2 = 1/6$, where the upper index refers to the two steps case). Each species affects itself through a loop of even steps (in a bipartite graph), e.g., the two-steps effect of D on itself equals

$$d_{DD}^2 = d_{FD} * d_{DF} = 1/3 * 1 = 1/3,$$

meaning that considering two steps effects, one third of any influence to D comes from itself. The two steps effect of species i on species j is assumed to be the sum of the strengths of the two steps pathways from i to j : the two steps effect of B on C equals

$$d_{CB}^2 = d_{EB} * d_{CE} + d_{FB} * d_{CF} = 1/3 * 1/2 + 1/3 * 1/2 = 1/3.$$

We note that both multiplicativity within and additivity between pathways can be strong assumptions. It is not easy to decide how realistic is our method; some authors emphasize the possibility that nonlinearity is typical in ecological systems. Here, experimental approaches can provide a solid basis for decisions (see Bender et al. 1984), but it is unclear whether there is any hope for finding general rules. We decided to choose these limits to our approach for the sake of simplicity and regard it as a rational starting point for further methodical developments. The matrix of two steps effects is as follows:

| 2 steps | A | B | C | D | E | F |
|---------|-----|-----|-----|-----|-----|-----|
| A | 1/3 | 1/6 | 1/6 | 0 | 0 | 0 |
| B | 1/3 | 1/3 | 1/3 | 1/3 | 0 | 0 |
| C | 1/3 | 1/3 | 1/3 | 1/3 | 0 | 0 |
| D | 0 | 1/6 | 1/6 | 1/3 | 0 | 0 |
| E | 0 | 0 | 0 | 0 | 2/3 | 1/3 |
| F | 0 | 0 | 0 | 0 | 1/3 | 2/3 |

Column sums give the unit effect, again. Considering n steps as the maximal length of indirect pathways mediating the effects of species i on j , we have to add the d_{ji}^n , $i=1 \dots n$ values of the n matrices. Note that d_{ji}^n is not necessarily equal to d_{ij}^n (asymmetry is inherent in topology). The sums of rows indicate how important is the position of a species in the interaction network. For example, species B can be considered as a stronger interactor than species A ($\sum d_{j,B}^2 = 4/3 > \sum d_{j,A}^2 = 2/3$). Beyond this short example, we analysed longer pathways and considered weighted webs with quantified trophic links (not only network topology).

A real example follows for additional illustration. *Cirrospilus diallus* (species #1, Figure 1a) is one out of ten parasitoids reared from the pupae of the host *Phyllonorycter kleemanella* (species #37). Table 1 lists the parasitism frequency values ($\alpha_{37;i}$) of these ten parasitoids on *P. kleemanella*. $d_{37;1}$ can be calculated as $28.42/38.05 = 0.7468$. *Cirrospilus diallus* affects indirectly, through *P. kleemanella*, *Pnigalio pectinicornis* (species #5, see Figure 1b). Since eight other hosts also affect *P. pectinicornis*, the $d_{5;37}$ effect can be calculated as previously, and $d_{5;1}$ equals $d_{37;1} * d_{5;37} = 0.7468 * 0.1834 = 0.137$. This is the strength of exploitative competition between species #1 and #5. But the effects of *C. diallus* on *P. pectinicornis* are also mediated by *Phyllonorycter froelichiella* (species #36), *P. rajella* (species #38), and *P. stettinensis* (species #39, see Figure 1c). This means that the correct value of $d_{5;1}$ results from summing up these multiple effects ($d_{5;1} = 0.2415$). Similarly, interaction strengths can be calculated for each species pair, up to ten steps length. For comparing the relative importance of short and long interaction pathways, the strength of an n -step interaction must be divided by n ("per step effect"). This is because of additivity: otherwise, longer pathways seem to be automatically more relevant. Since d_{ij} does not necessarily equal d_{ji} , the asymmetry of any relationship can be characterised by $|d_{ij} - d_{ji}|$. The importance of a particular host species h is quantified by d_{ih} divided by the host's density (Table 2), where i refers to each species of the community. Note that many possible aspects of species importance may remain out of consideration (e.g., possible engineering effects, Jones et al. 1994).

Table 1. Frequency of parasitism data measured in the field (Rott and Godfray 2000). Numbers indicate the frequency of parasitoids (#1-#27) reared on particular hosts (#28-#39). These data are referred as α_{xy} in the text.

| | Host species | | | | | | | | | | | |
|-----------|--------------|------|------|------|------|------|------|------|------|-------|------|-------|
| | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 |
| 1 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.76 | 28.42 | 4.56 | 1.51 |
| 2 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.64 | 0.11 | 0.00 | 0.00 | 0.00 | 0.00 |
| 3 | 0.00 | 0.00 | 1.51 | 7.19 | 2.75 | 1.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 4 | 25.47 | 1.69 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 5 | 0.00 | 0.00 | 0.05 | 0.01 | 0.02 | 0.00 | 0.06 | 0.03 | 0.46 | 0.75 | 2.03 | 0.69 |
| 6 | 3.87 | 0.18 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 7 | 1.35 | 0.12 | 0.09 | 0.23 | 0.13 | 0.14 | 0.03 | 0.00 | 0.15 | 0.97 | 4.00 | 34.23 |
| 8 | 0.42 | 0.03 | 0.00 | 0.04 | 0.00 | 0.01 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 9 | 0.00 | 0.00 | 0.00 | 0.01 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 10 | 0.00 | 0.03 | 0.17 | 1.11 | 0.21 | 0.14 | 0.00 | 0.00 | 0.00 | 0.00 | 0.64 | 0.00 |
| 11 | 0.77 | 0.18 | 0.09 | 0.29 | 0.01 | 0.08 | 0.00 | 0.00 | 0.00 | 0.00 | 0.72 | 0.00 |
| 12 | 1.52 | 0.14 | 0.74 | 1.21 | 0.15 | 0.71 | 0.04 | 0.04 | 0.41 | 0.84 | 2.30 | 6.35 |
| 13 | 0.00 | 0.00 | 0.00 | 0.04 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.56 |
| 14 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 2.83 | 2.03 | 0.00 |
| 15 | 0.28 | 0.00 | 0.09 | 0.01 | 0.00 | 0.08 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 16 | 0.07 | 0.00 | 0.08 | 0.30 | 0.28 | 0.20 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 17 | 0.35 | 0.00 | 0.03 | 0.20 | 0.06 | 0.31 | 0.03 | 0.01 | 1.36 | 2.25 | 6.86 | 4.52 |
| 18 | 0.15 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.40 | 1.08 | 18.23 |
| 19 | 0.00 | 0.00 | 0.00 | 0.04 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.04 |
| 20 | 0.10 | 0.00 | 0.00 | 0.05 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.56 | 0.00 | 2.36 |
| 21 | 0.06 | 0.00 | 0.00 | 0.04 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.04 |
| 22 | 1.20 | 0.09 | 0.08 | 0.35 | 0.31 | 0.17 | 0.04 | 0.02 | 0.15 | 0.90 | 4.50 | 16.41 |
| 23 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.82 | 2.94 |
| 24 | 1.51 | 0.15 | 0.01 | 0.09 | 0.07 | 0.01 | 0.00 | 0.01 | 0.00 | 0.12 | 0.08 | 0.55 |
| 25 | 0.03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.00 | 0.00 | 0.00 | 0.18 | 0.00 |
| 26 | 0.05 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| 27 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.03 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |

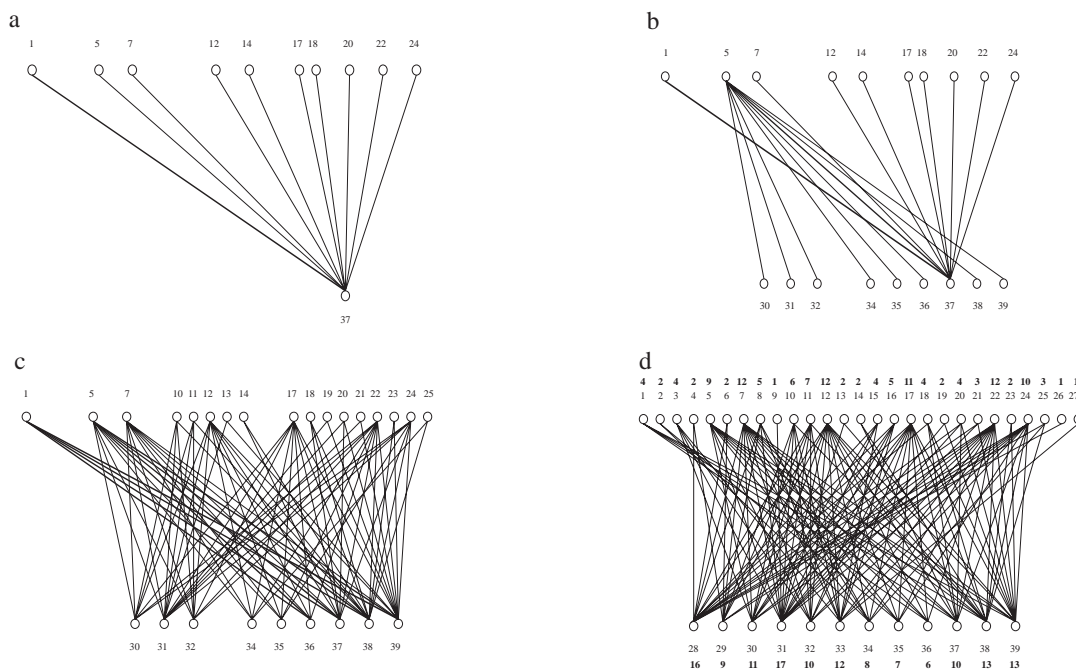


Figure 1. **a:** A graph showing how many and exactly which parasitoid species directly affect the host #37. The effect of species #1 on species #37 can be calculated from the parasitism frequency data given at Table 1 (considered with these numbers, the graph is a quantitative food web). **b:** a graph illustrating how the parasitoid species #1 affects species #5, another parasitoid, through species #37 (a host). This is an interaction chain effect mediated through a pathway of length two. For calculating the strength of this indirect effect, we need the frequency data of every links shown. **c:** a graph presenting all of the four interaction chains of length two from species #1 to species #5, together with all of the links whose weight is needed for quantifying how strongly species #1 affects species #5. This is a multiple effect, mediated by four hosts (#36, #37, #38, #39). Note that 26 out of 39 species of the whole subcommunity are involved in characterising an indirect interaction of only length two (exploitative competition). Of course, apparent competitive effects are quantified similarly. The quantification of longer pathways follows the logic of calculating the products of direct interactions constituting the interaction chain. **d:** the whole interaction network of the studied subcommunity. Twelve leaf-miner hosts (#28-#39) are parasitized by twenty-seven parasitoids (#1-#27). Species codes are given in Appendix. Bold numbers indicate the number of directly interacting species (hosts for parasitoids and parasitoids for hosts).

Results

We quantified the strength and symmetry of indirect interactions (of length up to ten), as well as the relative importance of particular species within a host-parasitoid community, based on their position in the interaction network. Our approach followed the logic of how to quantify the relevance of apparent competition between host species (Rott and Godfray 2000).

Some species have more important direct effects, while others turn out to have relatively more significant indirect interactions. Figure 2 shows the comparison of the per step effects of each species. The effects of *Phyllosorycter quercifoliella* (species #33) are mediated typically directly: considering two and ten steps effects, its relative importance continuously decreases. The reverse is true for *Sympiesis gordius* (species #7): here, if long pathways are taken into account, the per step effect increases indicating that *S. gordius* is a typically indirectly interacting species (i.e., its output environ is harder to be mapped, cf. Patten 1981). Direct and indirect effects are more characteristic to hosts and parasitoids, respectively, with exceptions. There are species showing the highest per step effect if only two steps are considered. Figure 3 illustrates the difference how considering long pathways of indirect interactions may influence our view on the relative importance of species within this community.

Table 2. The density of host species (#28–#39) measured in the field and expressed in the same units (Godfray, unpublished).

| host | density |
|------|---------|
| 28 | 74.83 |
| 29 | 6.81 |
| 30 | 11.18 |
| 31 | 27.95 |
| 32 | 7.79 |
| 33 | 9.28 |
| 34 | 2.29 |
| 35 | 0.45 |
| 36 | 21.79 |
| 37 | 154.13 |
| 38 | 94.75 |
| 39 | 346.39 |

The strength of per step effects of species #7 and #33 shows the opposite tendency of change as pathway length increases.

The shape of the importance-rank curve for species is a community-level pattern (Mills et al. 1993). For understanding biological control problems, it is a central question which leaf-miner hosts are of key importance in structuring the community. The rank shows a clear keystone pattern (Figure 4), which is the strongest if only indirect pathways of length one and two are considered ($n = 2$, see Figure 5 for the variance of importance values).

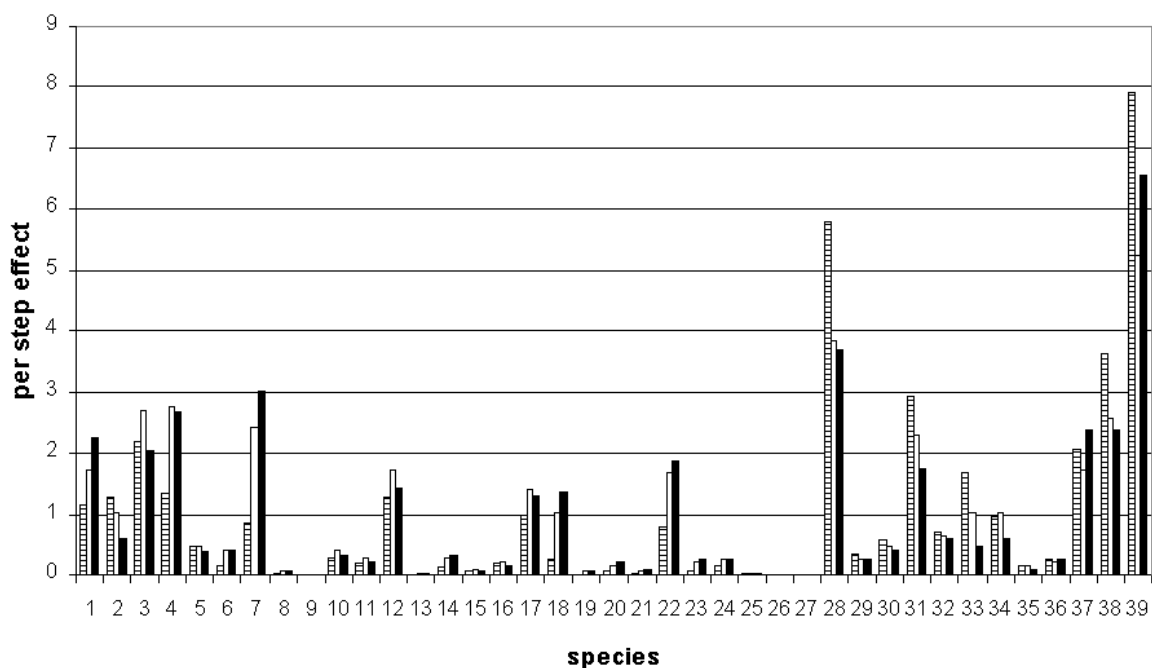


Figure 2. The summed effects of each species, considering only direct (stripped), one plus two steps (white) and up to ten steps (black) interaction pathways. Effects are normalised by step number, to make the comparison of lengths of various pathways possible (i.e., calculated ten steps effects are divided by ten, because interaction strength increases automatically with pathway length). These ‘per step effects’ show that some species (e.g., #7) have relatively stronger indirect effects, while others (e.g., #33) have relatively more important direct interactions.

Figure 4 suggests two species to be of outstanding importance (disproportionately to their density, *P. ulmifoliella*, species #34, and *P. cavella*, species #35). Interestingly, they would not seem to be keystones looking only at the interaction network given at Figure 1d, because the

number of neighbours (i.e., direct interactions) is relatively low.

Including self-regulation links (main diagonal elements), 1521 effects can be quantified among 39 species

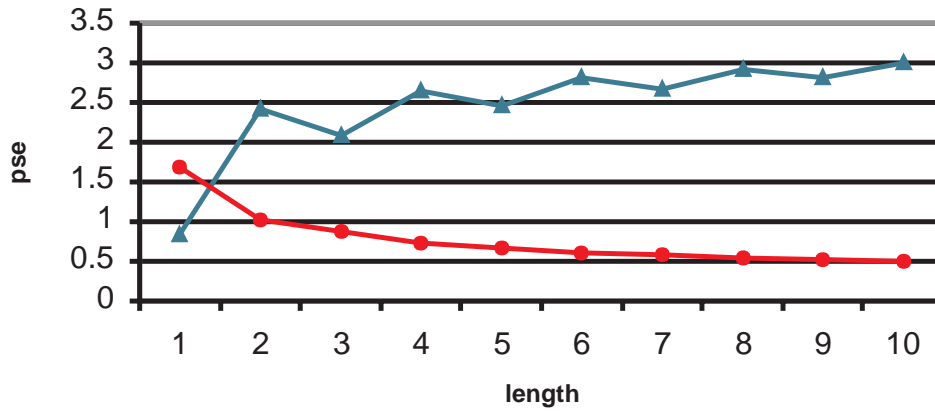


Figure 3. A graph showing how the per step effects (pse) of species #7 (triangle) and #33 (circle) changes with pathway length. Considering only direct, pairwise interactions, species #33 seems to have much larger role in structuring the community (quantified by the sum of its effects on others). If we take into account longer and longer interaction pathways, the reverse situation holds and the difference increases between the species' importance. The explicit study of indirect interactions helps to reveal the real significance of these species.

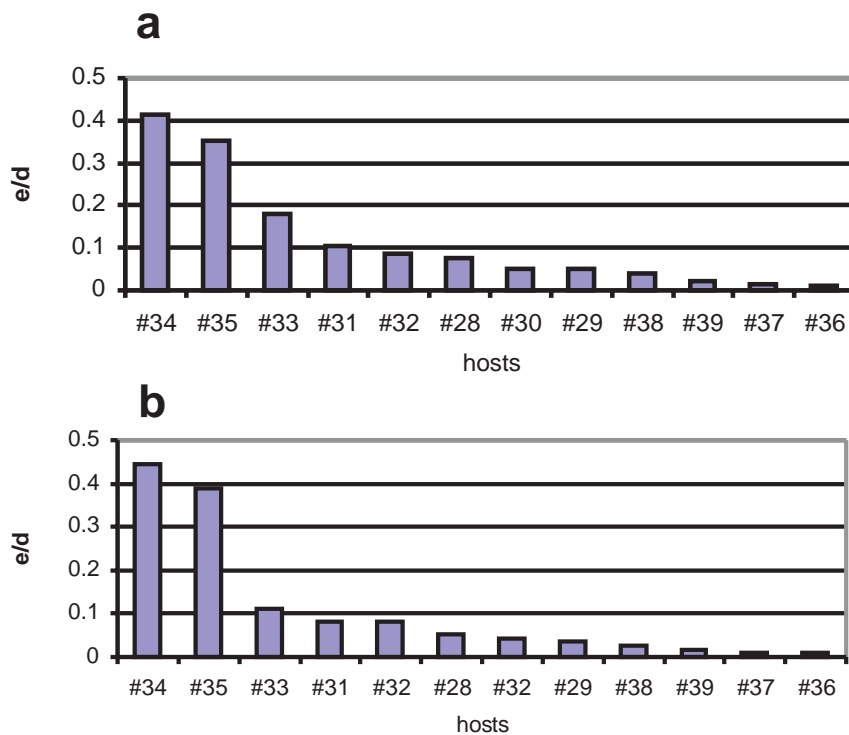


Figure 4. The importance of the 12 host species is quantified by the sum of the per step strength of their interactions divided by their density (effect / density = e/d , following Tilman, see Mills et al. 1993). Species importance ranks are given for the cases when only direct interactions are considered (a), and indirect pathways of length up to ten steps are taken into account (b). In both cases we see a keystone pattern (with species *P. ulmifoliella*, #34, and *P. cavella*, #35 as two keystones), and this pattern is stronger for the second case (b).

(39^2). The strength of these effects are calculated and the rank is compared for $n=1$ and $n=10$ (Figure 6). The strength of many effects is (or is very close to) zero, and non-zero effects are generally very weak. The recently found “few strong - many weak” pattern (Berlow 1999) is more typical as longer pathways are taken into account.

Note that the shaded areas below the curves at Figure 6a and 6b are equal.

Excluding self-regulation links and the half of the 39 by 39 interaction matrix, 741 values characterise the interaction symmetry between species pairs in the community. We only show the most typical rank-distribution

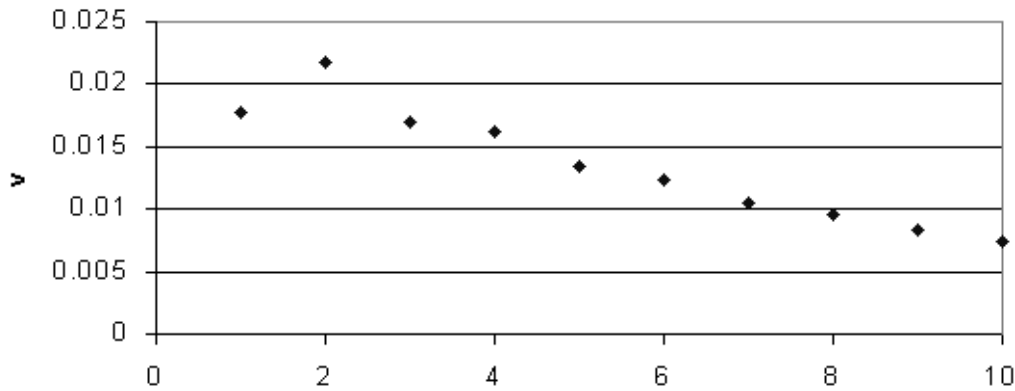


Figure 5. The variance (v) of the importance of host species is plotted against the length of pathways considered. The keystone pattern is the strongest if only one and two steps chains are considered. Taking long interaction pathways into account homogenises the importance of species.

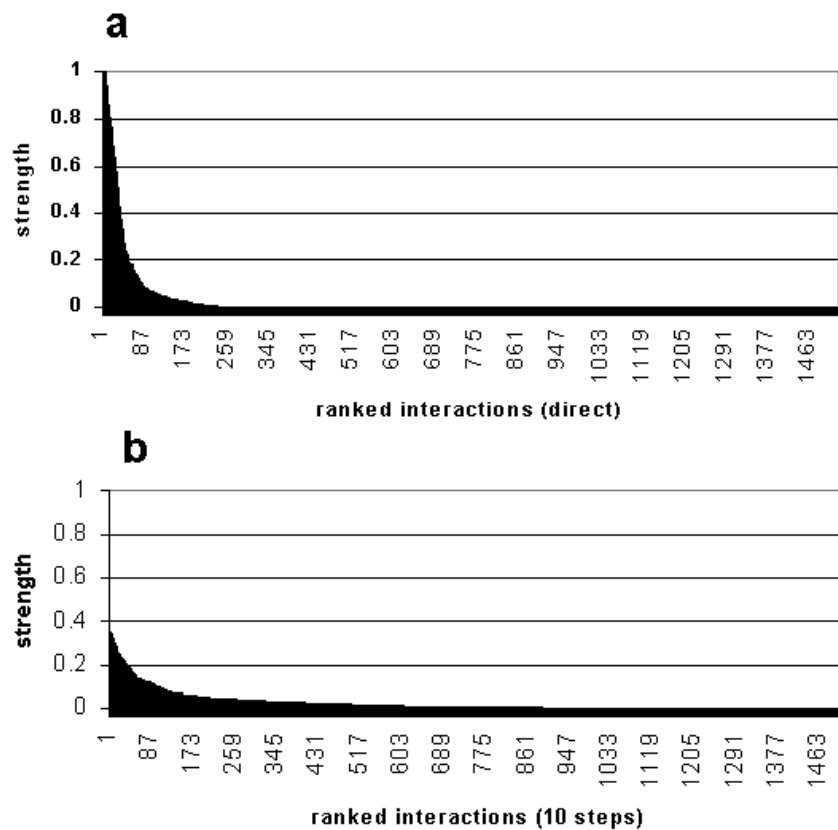


Figure 6. The rank of 1521 interaction strengths (d_{ij}) calculated for the 39 by 39 matrix (including d_{ii} self-control links). Per step effects are considered for comparison. The shaded areas under the curves are equal but their distribution differ: if only direct interactions are taken into account, nearly half of the interactions are strong (a), while if much longer interaction chains are also considered, the ‘few strong - many weak’ pattern appears (b).

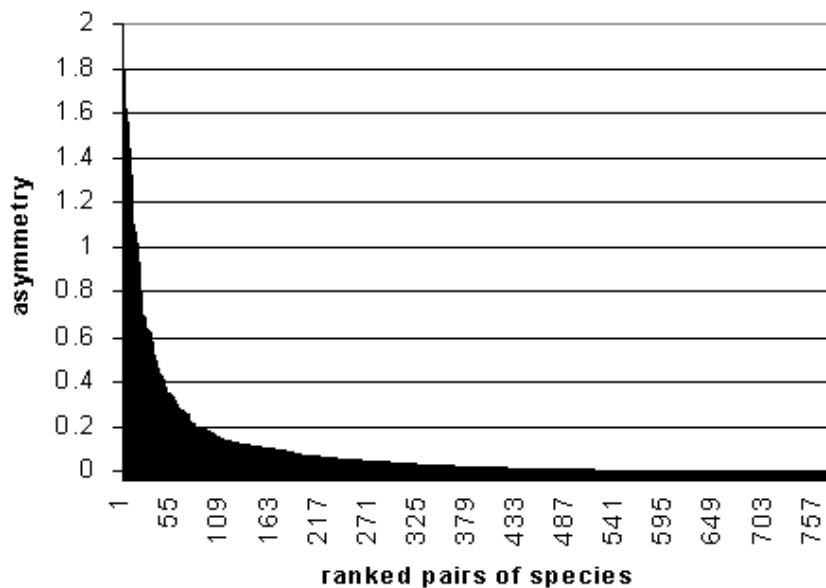


Figure 7. The rank of 741 pairs of species, based on the asymmetry of their interactions ($|d_{ij} - d_{ji}|$). Here, a typical case is shown when one, two, and three steps' length interaction pathways are considered. There is a weak asymmetry between the majority of species pairs, while both symmetry and strong asymmetry are much rarer. Note that interaction symmetry is quantified here by considering only web topology and parasitism frequency data.

curve for interaction asymmetry values (for three steps, Figure 7). The majority of asymmetrical relationships is only slightly asymmetrical (practically symmetrical), thus, strong asymmetry is rare. Strictly symmetrical relationships are not typical, in concert with Müller et al. (1999) and Chanton and Bonsall (2000). However, we do not know at which value asymmetry is significantly different from symmetry.

Conclusions

We believe that as the number of published quantitative host-parasitoid webs increases it is essential that a tailor-made methodology is developed to allow a meaningful comparison of key attributes of these communities. Further, by combining a theoretical approach with field data on real communities it will be possible to generate testable hypotheses on interaction chains and the community wide effects of keystone species. These hypotheses can be tested for example through species removal experiments in host-parasitoid communities (Memmott 1999).

We have illustrated that considering longer pathways of indirect effects may influence both community-level (the keystone pattern of importance rank) and species-level (the relative role of direct vs indirect effects) patterns. Considering only pairwise interactions is misleading. Some effective range of indirect effects have been determined by a 'network algebra' -like approach (*sensu* Higashi and Burns 1991). If longer pathways of indirect interactions are considered (Yodzis 2000, 2001), the

number of possible interaction chains increases, while the effects mediated by these long pathways may well decrease with path length (high connectance of the interaction network enhances this effect). The net outcome was studied and we found that taking into account longer pathways can be sometimes unavoidable and may help identifying keystones.

This case study is of phenomenological and descriptive nature and serves primarily to introduce our methodology. As important future goals, statistical approaches and mechanistical models could make it predictive and increase its applicability. Field experiments could test the predictions of these results (cf. Memmott 1999).

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Appendix: Species codes

Parasitoids:

- 1 *Cirrospilus diallus*
- 2 *C. lynceus*
- 3 *Elachertus inunctus*
- 4 *Pnigalio longulus*
- 5 *P. pectinicornis*
- 6 *P. soemius*
- 7 *Sympiesis gordius*
- 8 *S. grahami*
- 9 *S. sericeicornis*
- 10 *Achrysocharoides splendens*
- 11 *A. niveipes*
- 12 *A. latreillii*
- 13 *A. zwoelferi*
- 14 *Chrysocharis laomedon*
- 15 *C. nephereus*
- 16 *C. phryne*
- 17 *Pediobius alboeus*
- 18 *P. saulius*
- 19 *Minotetrastichus ecus*
- 20 *Holocothorax nepticulae*
- 21 *H. testaceipes*
- 22 *Colastes braconius*
- 23 *Apanteles* sp.
- 24 *Apanteles circumscriptus*
- 25 *Hormiinae* sp.
- 26 *Scambus* sp.
- 27 *Campopleginae* sp.

Hosts:

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|--|-----------------------------|
| 28 <i>Phyllonorycter salicicolella</i> | 33 <i>P. quercifoliella</i> |
| 29 <i>P. dubitella</i> | 34 <i>P. ulmifoliella</i> |
| 30 <i>P. harrisella</i> | 35 <i>P. cavella</i> |
| 31 <i>P. heegeriella</i> | 36 <i>P. froelichiella</i> |
| 32 <i>P. lautella</i> | 37 <i>P. kleemanella</i> |
| | 38 <i>P. rajella</i> |
| | 39 <i>P. stettinensis</i> |