

Food web structure and the strength of transient indirect effects

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The relative importance of direct and indirect effects in ecological communities remains unresolved. Indirect effects may diminish as they propagate through highly reticulate food webs. We tested this hypothesis by assembling replicate food webs of different complexity in laboratory microcosms, and comparing the transmission of indirect effects through these webs. By providing the top predator (*Didinium*) with either one (*Paramecium*) or two (*Paramecium* and *Colpidium*) species of protists as prey, we created linear or reticulate food webs where we could examine the transient response of predators to an indirect effect. Addition of *Chlamydomonas*, a small alga consumed by *Paramecium*, but not by *Colpidium*, perturbed the system and generated an indirect effect on *Didinium*. We expected the proportional response of *Didinium* to *Chlamydomonas* addition would be smaller in the reticulate web containing alternative, unperturbed prey (*Colpidium*). We measured predator response as predator yield, the maximum number of predators produced prior to overexploitation of prey and subsequent predator decline. The ratio of yield in perturbed bottles to yield in unperturbed bottles measures the proportional response of *Didinium* to *Chlamydomonas* addition. We expected this ratio to be smaller with *Colpidium* present. Contrary to expectations, alternative prey enhanced rather than diminished predator response to the perturbation. This resulted from competition between the prey species, a factor ignored in some simple verbal arguments. Food web complexity may have unanticipated consequences for the strength of indirect effects.

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The relative importance of direct and indirect effects is an important issue in community ecology (Yodzis 1988, 1998, Schoener 1993, Menge 1995, 1997, Abrams et al. 1996). Species are connected by chains of interactions, so that changes in the abundance of one species may propagate through intermediaries to species many links away (“indirect chain effects” sensu Wootton [1994]). If so, predicting the response of one species to a change in the abundance of another species will be extremely difficult (Bender et al. 1984, Yodzis 1988, 1998, Schoener 1993). Theoretical arguments on the relative importance of direct and indirect effects cut both ways (Yodzis 1988, Schoener 1993, Berryman 1993), and empirical data are scarce for all but a few experimentally tractable systems such as the rocky intertidal (Schoener 1993, Menge 1995, 1997).

Here we experimentally evaluate whether more reticulate food webs tend to dampen indirect chain effects. Consider the proportional change of a species’ density in response to a perturbation in the density of another species. Will adding species and connections to a food web reduce such changes? The reason it might is presented in Fig. 1, which contrasts a linear food web with a more reticulate web. The indirect effect on species C of a perturbation in species A (transmitted through species B) is reduced in the reticulate web because species C has alternative, unperturbed prey D available. Species B is only a fraction of C’s diet, and C’s response to the perturbation of B is correspondingly reduced. A similar argument could be made for the effects of perturbations in predator abundance on prey populations (see also Schoener 1993).

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This food web buffering hypothesis (FWBH) has appealed to many ecologists, although various presentations differ in detail. Pimm (1979, 1980) found that removing a prey species from a food web was less likely to lead to consumer extinctions when consumers were generalists instead of specialists. MacArthur (1955) suggested that a prey population crash will have minimum effect on its predators if the predators are generalists. This implies that generalists will exhibit less variable population dynamics than specialists, because generalists can switch between prey species and fluctuations in abundance of different prey species should tend to cancel out, stabilizing total food supply (Pimm 1991). Since fluctuations may involve propagation of indirect effects, this argument also implies food web buffering of indirect effects. Redfearn and Pimm (1988, 1992) and Pimm (1991) reviewed data relating number of food or predator species to variability in population dynamics. The relationship varies between datasets, but this may be due to the poor quality of much of the data (Pimm 1991).

The effect of species diversity within trophic levels on trophic cascades has received significant attention. Both theory and observations indicate the potential for diversity to weaken trophic cascades (McQueen et al. 1986, Jager and Gardner 1988, Leibold 1989, 1996, Strong 1992, Abrams 1993, Holt et al. 1994, Brett and Gold-

man 1997, Leibold et al. 1997, Watson et al. 1997). However, experiments frequently find strong trophic cascades despite heterogeneity within intermediate trophic levels (Carpenter et al. 1987, Wootton and Power 1993, Marquis and Whelan 1994, Spiller and Schoener 1996, Leibold et al. 1997). Interspecific competition within trophic levels weakens cascades because changes in the abundance of one species lead to compensatory changes in its competitors and total abundance is stabilized (Frost et al. 1995, Leibold 1996). The FWBH does not require competition within trophic levels, although competition can further buffer species against cascading effects originating on higher or lower trophic levels (MacArthur 1955, Schoener 1993).

The FWBH appears general. It makes no strong assumptions about the form of predator functional and numerical responses, prey growth functions, or environmental heterogeneity. In particular, a switching functional response is not assumed, although such a functional response might be an additional source of buffering (Elton 1927, Murdoch and Oaten 1975). Other things being equal, feeding on more prey species (or being preyed on by more predator species) should simply make a predator (prey) population less sensitive to changes in the abundance of any single prey (predator).

The FWBH does not require equilibrium dynamics, unlike much of the mathematical theory of indirect effects (Yodzis 1988, 1998, Schoener 1993). Abundances resulting from perturbations need not represent equilibrium values. Natural communities are probably rarely at equilibrium, due to internal non-equilibrium dynamics and external perturbations (Andrewartha and Birch 1954, Connell and Sousa 1983, Wiens 1984, Hastings et al. 1993, Hastings 1996).

The FWBH does assume a food web configuration which prevents the perturbation from traveling via multiple paths to an affected species (Schoener 1993). If this is not the case, then the net effect of the perturbation must be summed across all pathways. Even with multiple paths, however, reticulate food webs can still reduce the magnitude of individual indirect pathways relative to direct pathways by buffering species against changes in the abundance of any one of the species with which they interact.

The FWBH only considers how food web structure changes the strength of a perturbation as the perturbation propagates through the food web. Food web structure will also affect the number of perturbations transmitted to a species. A generalist predator might be subject to more indirect effects than a specialist because a generalist consumes more prey through which indirect effects can be transmitted.

Theoretical work indicates that the FWBH is sensitive to food web structure and the position of the perturbed species within the web (Pimm 1979, 1980, 1991). The hypothesis is consistent with observations of

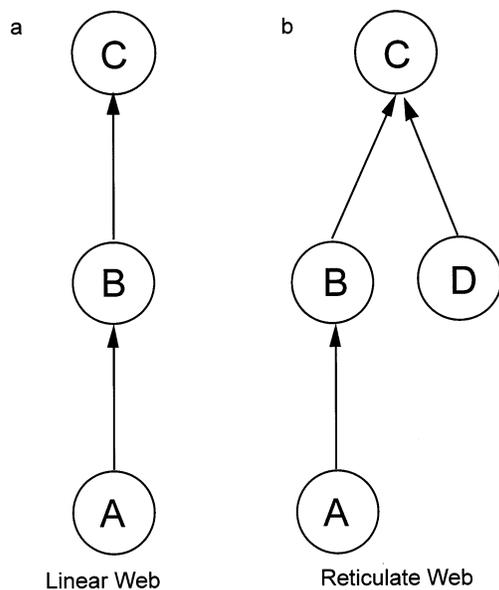


Fig. 1. Hypothetical food webs illustrating food web buffering. Each lettered circle represents a species. Arrows point from prey to predator. (a) Linear web. Perturbation of the basal species A is transmitted undiminished through intermediate species B to the top predator C, since species B is predator C's only prey. (b) Reticulate web. Perturbation of the basal species A has a smaller indirect effect on predator C, compared to a linear web. Because species C has alternative, unperturbed prey D, the perturbed species B constitutes only a fraction of C's diet.

trophic cascades, but experimental studies of heterogeneous food webs frequently find cascades and other indirect effects, and direct tests of the hypothesis are few (Davidson et al. 1984, Pimm 1991, Menge 1995, 1997, Leibold et al. 1997). A direct test requires experimental manipulation of the number of “buffer” species protecting a focal species against the indirect effect of a perturbation. Such manipulation requires replicated food webs of specified structure.

We tested the FWBH by assembling communities of aquatic protists in laboratory microcosms. Such communities are especially useful when population dynamic data are required, and serve as a way station between theory and nature (Lawler 1998, Morin 1998). Microcosms permit complete specification of food web structure together with extensive replication. Our approach examined the dynamics of the ciliate predator *Didinium nasutum* Muller (hereafter, *Didinium*) when growing on either one or two species of prey, to see whether the presence of a second prey species buffered the predator’s response to an indirect effect transmitted by the first prey species.

Materials and methods

Main experiment

We provided the predatory ciliate *Didinium* with either one (*Paramecium tetraurelia* Sonneborn, mating type VII; hereafter *Paramecium*) or two (*Paramecium* and *Colpidium striatum* Stein; hereafter *Colpidium*) species of ciliates as prey, to create linear or slightly more reticulate food webs (Fig. 2). *Didinium* readily consumes both *Paramecium* and *Colpidium*, although the predation rates on each species will vary somewhat with *Didinium* cell size (Hewett 1980, 1987). Half of the replicates of each food web treatment received a perturbation. Addition of the autotrophic flagellate *Chlamydomonas reinhardtii* Dangeard, mating type + (hereafter, *Chlamydomonas*) enhanced *Paramecium* growth rate and density. *Chlamydomonas* is readily consumed by *Paramecium*, but not by *Colpidium* or *Didinium*. Both *Paramecium* and *Colpidium*, but not *Didinium*, consume bacteria. Morphology prevents *Paramecium* and *Colpidium* from consuming one another. The indirect effect of *Chlamydomonas* addition should thus be able to travel only one path (through *Paramecium*) to *Didinium*. Unperturbed microcosms received no *Chlamydomonas*. There were four replicates/treatment combination for a total of 16 microcosms.

Microcosm assembly followed standard protocols (Lawler and Morin 1993). We used 260-ml screw-capped glass bottles containing 100 ml of nutrient medium. The medium consisted of 0.55 g of protozoan pellets (Carolina Biological Supply, Burlington, NC) and 100 mg of Herpetivite powdered vitamin supple-

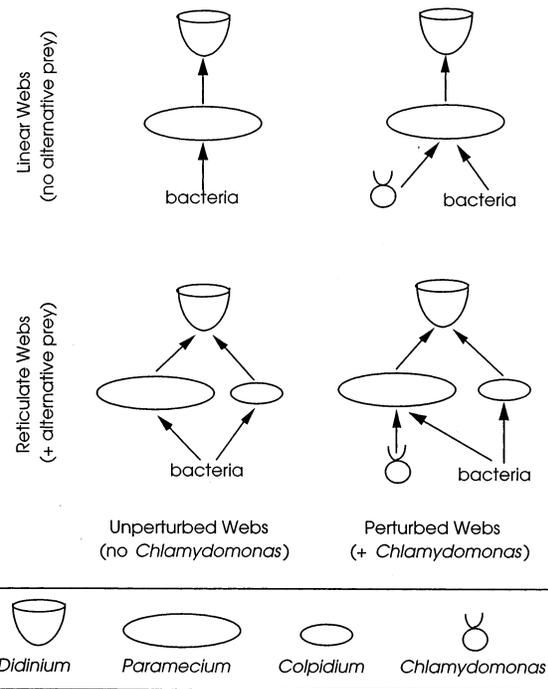


Fig. 2. Main experiment design. A 2×2 factorial design containing all combinations of a food web structure treatment and a perturbation treatment. Linear and reticulate webs provide one or two prey species to the top predator, respectively. Perturbation is by addition of *Chlamydomonas* as a food supplement for *Paramecium*. The FWBH predicts that the reticulate food web will reduce the indirect effect of the perturbation on the top predator.

ment (Rep-Cal Research Labs, Los Gatos, CA) in 1 L of autoclaved well water. Twenty-four h prior to use, we inoculated the medium with bacteria (*Serratia marcescens*, *Bacillus cereus*, and *Bacillus subtilis*) that supported the growth of *Colpidium* and *Paramecium*. The protozoan pellets provided energy and nutrients for the bacteria. We added three sterile wheat seeds to each bottle as an additional, slow-release carbon source. Loose-fitting caps minimized contamination while permitting gas exchange.

We randomly assigned treatments to bottles. All bottles received a small number of *Colpidium* and/or *Paramecium*. Both grew to carrying capacity before addition of *Didinium* (Lawler and Morin 1993). We added six to ten *Didinium* to each bottle from a stock culture maintained on *Colpidium*. In perturbed bottles, we added an inoculum of *Chlamydomonas* immediately following *Didinium*. We prepared the *Chlamydomonas* inoculum for each bottle by centrifuging 100 ml of liquid from a stock culture containing a high density of *Chlamydomonas*. After pipetting off and discarding the supernatant, we added the pellet of *Chlamydomonas* to the experimental culture. Jars not receiving *Chlamydomonas* received a 2-ml inoculum of liquid from a protist-free stock culture, to control for the small

amount of liquid added with *Chlamydomonas*. We assigned bottles to random locations on an incubator shelf (L:D 16:8, 20°C) and rotated every 2 d.

Sampling at 2–3 d intervals after the addition of bacterivores quantified the density of each protist species. This timescale is appropriate for protists having generation times < 48 h. We counted *Chlamydomonas* using a hemacytometer, and other protists using the method of Lawler and Morin (1993). We converted counts to numbers per ml before analysis. The experiment lasted until all *Didinium* populations went extinct (14–43 d after predator addition, about 17–52 *Didinium* generations).

Our main experiment used a 2 × 2 factorial design, crossing a perturbation (presence or absence of *Chlamydomonas*) with food web configurations (presence or absence of *Colpidium*) (Fig. 2). One statistical signature of food web buffering would be a proportionally smaller effect of *Chlamydomonas* addition on *Didinium* when *Colpidium* is present (Fig. 3a). Different measures of *Didinium* dynamics could be used in the analysis. Since the FWBH does not depend on equilibrium assumptions, short-term responses of *Didinium* to the perturbation may be as relevant as long-term responses. We could not measure a long-term response since *Didinium* often drove *Paramecium* extinct within 10 d (see Results). We therefore chose a measure of short-term *Didinium* response based on consideration of typical *Didinium* population dynamics.

Following introduction *Didinium* increases from low density to a level set by prey abundance and productivity. This initial increase generally reduces prey to extremely low levels, and many predators subsequently starve (Luckinbill 1973, Veilleux 1979, Holyoak and Lawler 1996, Morin and Lawler 1996). Maximum *Didinium* abundance before this crash may be thought of as *Didinium* yield. At this point nearly all prey present at the time of *Didinium* addition, or produced during the *Didinium* increase phase, have been converted into *Didinium*. We chose predator yield as our response variable. Yield represents a transient dynamical state and transient dynamics are infamously unpredictable (Hastings 1996). However, the following argument, in the spirit of other food web buffering arguments, shows that *Didinium* yield should respond to the perturbation in the predicted manner – a proportionally smaller response with alternative unperturbed prey present.

We assume that *Didinium* are introduced at near-zero abundance, subsequently consume essentially all prey individuals, and that *Didinium* yield is proportional to the number of prey consumed with a proportionality constant depending on the prey species (Fenchel 1987). We also assume that prey species do not directly affect one another's abundance or productivity. With these assumptions, *Didinium* yield from *Paramecium* may be represented as

$$x(P_i + P_n) \quad (1)$$

where P_i denotes *Paramecium* abundance at the time of *Didinium* addition, P_n denotes the number of new *Paramecium* produced from the time of *Didinium* introduction until the predator achieves maximum abundance, and x is a positive constant converting *Paramecium* into *Didinium*. *Chlamydomonas* addition will enhance P_n but not affect P_i .

Without *Colpidium*, the proportional response of *Didinium* yield to the perturbation ($R_{no\ Co}$) is

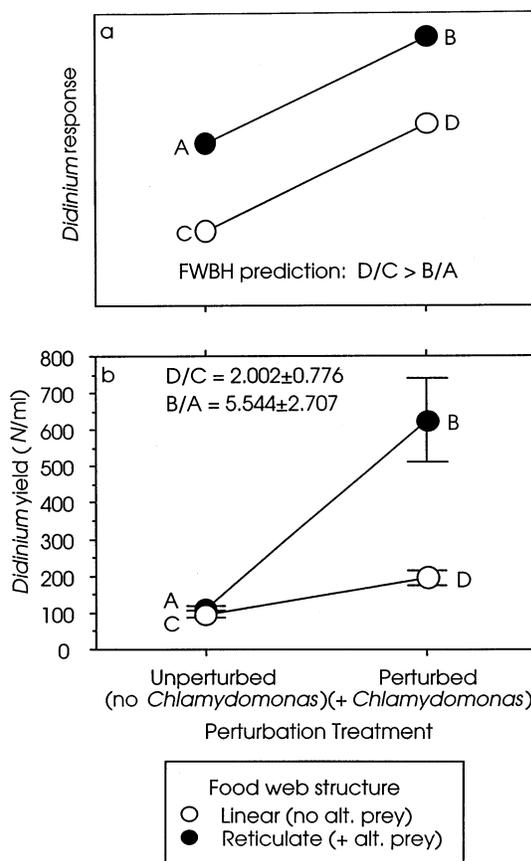


Fig. 3. (a) Predicted result of the main experiment. Hypothetical interaction plot showing the results predicted by the FWBH. The experiment is a 2 × 2 factorial design. The two treatments are a perturbation treatment (absence or presence of *Chlamydomonas* addition) and a food web structure treatment (absence or presence of alternative prey [*Colpidium*]). Letters A–D denote mean *Didinium* response to each treatment combination. The FWBH predicts a proportionally larger *Didinium* response to the perturbation in the absence of *Colpidium* ($D/C > B/A$). (b) Result of the main experiment. Interaction plot showing treatment means (± 1 SE) of the maximum density attained by *Didinium* during its initial numerical response (the *Didinium* yield). Ratios D/C and B/A are given as ± 2.36 SE, defining a 95% c.i. based on a Student- t distribution with seven degrees of freedom (see text for details of SE calculation). Contrary to the prediction, $D/C < B/A$.

$$R_{no\ c_o} = \frac{x(P_i + P_{nC})}{x(P_i + P_n)} \quad (2)$$

where P_{nC} denotes new *Paramecium* produced with *Chlamydomonas* added ($P_{nC} > P_n$). With *Colpidium*, the proportional response of *Didinium* yield to the perturbation (R_{+c_o}) is

$$R_{+c_o} = \frac{x(P_i + P_{nC}) + y(C_i + C_n)}{x(P_i + P_n) + y(C_i + C_n)} \quad (3)$$

where the *Colpidium* terms y , C_i and C_n are analogous to the corresponding *Paramecium* terms. R_{+c_o} is simply $R_{no\ c_o}$ with the same positive term $y(C_i + C_n)$ added to both the numerator and the denominator. Because $R_{no\ c_o} > 1$, this addition means $R_{+c_o} < R_{no\ c_o}$. We therefore divided average *Didinium* yield with *Chlamydomonas* by average yield without *Chlamydomonas*, calculating this ratio separately for bottles with and without *Colpidium*. We predicted that the ratio should be smaller with *Colpidium*.

We calculated approximate 95% c.i. for these two ratios by jackknifing (Arvensen 1969, Kotz and Johnson 1983, Buonaccorsi and Liebhold 1988). We converted jackknife estimates of standard error to 95% c.i. based on the Student- t distribution. Although lacking theoretical justification, these limits are more conservative than those based on the normal distribution (Hinkley 1974, Kotz and Johnson 1983, Buonaccorsi and Liebhold 1988).

Supplementary experiment

To aid in interpretation of the results of the main experiment, we conducted a supplementary experiment to test for competitive interactions between *Paramecium* and *Colpidium*, as both species consume bacteria. Assembly and sampling of microcosms followed the procedures outlined above. The experiment consisted of six treatments: each species growing either alone or together, in the presence and absence of *Chlamydomonas*. We replicated each treatment twice, except for the treatment containing both species growing together without *Chlamydomonas* (four replicates). Counts were converted to $\log_{10}((N/ml) + 1)$ before analysis to reduce heteroscedasticity. The response variables were the mean log-transformed densities of each prey species, averaged within replicates and across sampling dates. We excluded data from the transient early exponential growth phase in order to focus on the portion of the experiment when populations were dense enough to compete. The experiment lasted 28 d. Our design allowed us to test for competition in the presence and absence of *Chlamydomonas*, using two-way ANOVAs (Type III sums of squares).

We performed ANOVAs with SuperANOVA 1.1 for Macintosh (Abacus Concepts, Berkeley, CA) and jackknifing with Mathcad Plus 6.0 for Macintosh (MathSoft, Cambridge, MA).

Results

Main experiment

As expected, adding *Chlamydomonas* indirectly enhanced *Didinium* yield (Fig. 3b). However, *Colpidium* further increased the *Didinium* response to *Chlamydomonas* (Fig. 3b). The ratio R of mean *Didinium* yield with *Chlamydomonas* to mean yield without was 2.002 without *Colpidium* ($R_{no\ c_o}$) and 5.544 with *Colpidium* (R_{+c_o}).

Jackknifing yields 95% c.i. of (1.226, 2.778) for $R_{no\ c_o}$ and (2.837, 8.251) for R_{+c_o} . The 95% c.i. do not overlap, indicating that *Colpidium* significantly enhanced *Didinium* response to the perturbation ($P < 0.05$).

Fig. 4 shows population dynamics from representative replicates. *Paramecium* and *Didinium* persisted for variable lengths of time in bottles containing *Chlamydomonas*, but lacking *Colpidium*. The three replicates shown span the range of observed dynamics in this treatment (Fig. 4b–d).

Supplementary experiment

The interactions between *Colpidium* and *Paramecium* depend on whether *Chlamydomonas* is present. In two-way ANOVAs on the mean density of each prey species, both main effects (of the other species and of *Chlamydomonas*) and their interactions were statistically significant (Table 1). For *Colpidium*, *Paramecium* and *Chlamydomonas* together reduce mean density (Fig. 5a). *Colpidium* densities in the other three treatment combinations were similar. For *Paramecium*, *Chlamydomonas* enhances mean density, while *Colpidium* reduces mean density, but only in the absence of *Chlamydomonas* (Fig. 5b). No extinctions occurred.

Discussion

Theories linking number of prey species to predator dynamics hinge on whether or not prey compete, and thus on the food web structure in which predators and prey are embedded (Holt 1997). We found that alternative prey enhanced, rather than diminished, the initial response of *Didinium* to a perturbation in prey abundance (compare Fig. 3a and b). Apparently, the presence of a second prey species enhanced the initial numerical response of *Didinium* only in the presence of

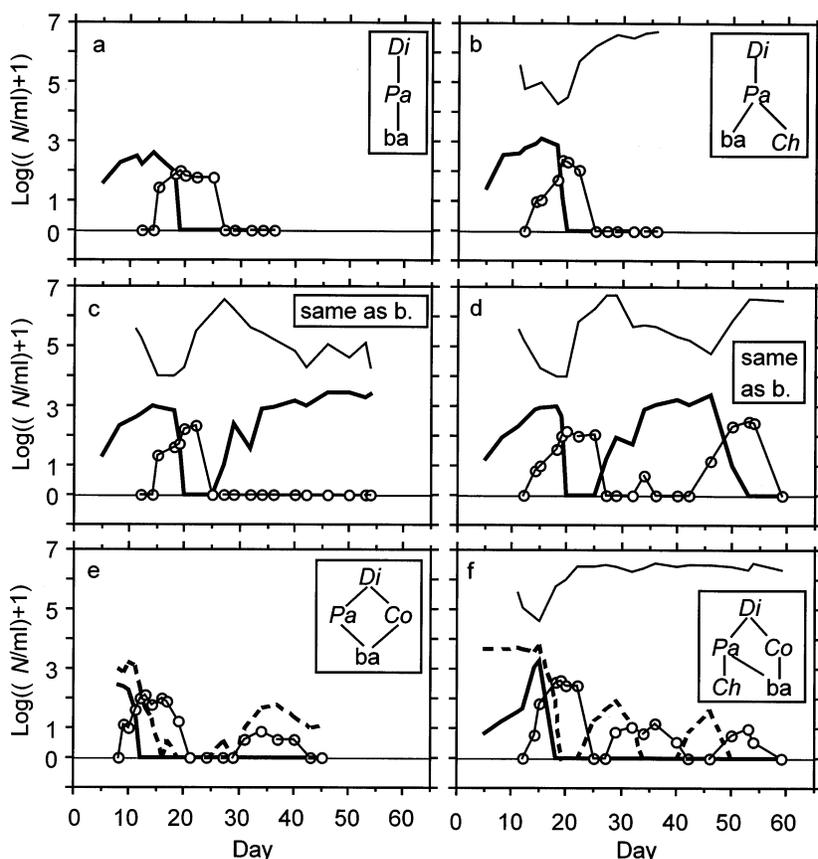


Fig. 4. Population dynamics from representative replicates of the main experiment. Bold lines = *Paramecium*, thin lines = *Chlamydomonas*, dashed lines = *Colpidium*, circles = *Didinium*. Insets show the initial food web structure of the replicates. Protists are identified by the first two letters of their genus; ba = bacteria. (a) Unperturbed/alternative prey absent. (b–d) Perturbed/alternative prey absent. (e) Unperturbed/alternative prey present. (f) Perturbed/alternative prey present.

Chlamydomonas (Fig. 3b). The most likely explanation is that *Colpidium* competes with *Paramecium*, but only in the absence of *Chlamydomonas* (Table 1, Fig. 5b). Without *Chlamydomonas*, competition from *Colpidium* reduces *Paramecium* productivity (reducing P_n in the denominator of Eq. 3). Instead of serving as additional prey, *Colpidium* serves as “substitute” prey, and would not be expected to enhance *Didinium* yield as much as would additional prey (Holt et al. 1994, Leibold 1996). Addition of *Chlamydomonas* releases *Paramecium* from competition, allowing alternative prey to enhance *Didinium* yield.

Other explanations are less likely. The density of prey at the time of *Didinium* introduction should affect predator yield (Eq. 2), and initial prey densities did vary between treatments (Fig. 4). However, this variation in initial conditions only makes our results more surprising. *Paramecium* was initially rarest in bottles with both *Colpidium* and *Chlamydomonas*, but *Didinium* exhibited its highest yield in these bottles (Fig. 3b, 4).

The results cannot be ascribed to the paradox of enrichment (Rosenzweig 1971). Addition of a second prey species and enhancement of one prey’s resources should both enhance predator-prey cycle amplitude, thereby increasing maximum *Didinium* density. However, addition of a second prey species failed to enhance predator density in the absence of *Chlamydomonas*.

Addition of *Chlamydomonas* also allows *Paramecium* to reach high enough densities to compete with *Colpidium* (Table 1, Fig. 5a). However, this competitive effect is proportionally small compared to the effect of *Colpidium* on *Paramecium* in the absence of *Chlamydomonas* (Fig. 5b), and probably did not substantially affect *Didinium* dynamics.

Table 1. ANOVA results for the supplementary experiment. For each dependent variable (the mean log-transformed densities of each prey species over time), the experiment is a 2×2 factorial design, where the two factors are *Chlamydomonas* (absent or present) and the other prey species (absent or present). A. Effects on *Colpidium*. B. Effects on *Paramecium*.

A. <i>Colpidium</i>				
Source	SS	MS	$F_{1,6}$	P
<i>Chlamydomonas</i>	0.059	0.059	17.745	0.0056
<i>Paramecium</i>	0.059	0.059	17.771	0.0056
$Ch \times Pa$	0.028	0.028	8.499	0.0268
Error	0.020	0.003		
B. <i>Paramecium</i>				
Source	SS	MS	$F_{1,6}$	P
<i>Chlamydomonas</i>	10.729	10.729	444.204	<0.0001
<i>Colpidium</i>	0.418	0.418	17.288	0.0060
$Ch \times Co$	0.652	0.652	26.988	0.0020
Error	0.145	0.024		

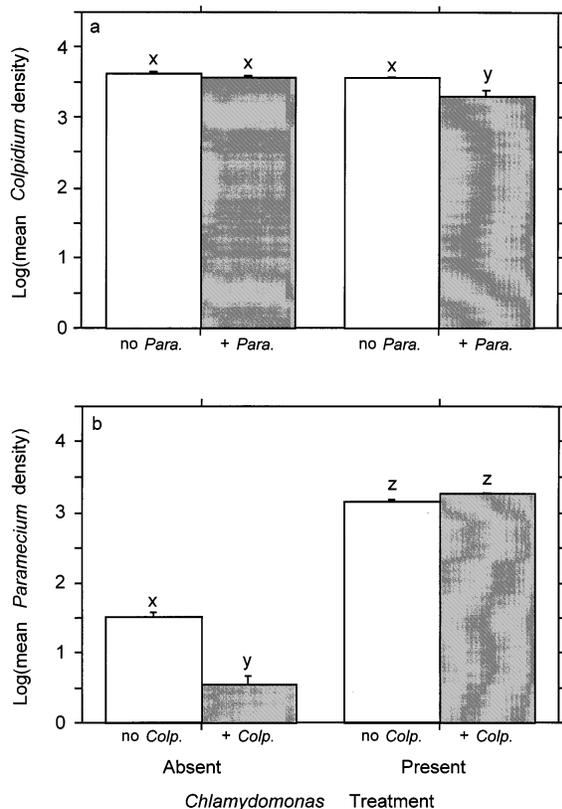


Fig. 5. Interaction plots showing treatment means (± 1 SE) of the average densities over time of (a) *Colpidium* and (b) *Paramecium* in the supplementary experiment. Treatment combinations (presence/absence of *Chlamydomonas*, and presence/absence of [a] *Paramecium* or [b] *Colpidium*) are listed below each bar. In each panel, treatments sharing a letter do not differ significantly in a Fisher's protected LSD test ($P > 0.05$).

Competition within trophic levels may act in concert with food web buffering (within-trophic level diversity) to inhibit transmission of perturbations across levels, assuming the perturbation itself does not alter the strength of competition (Abrams 1993, Leibold 1996). Our experimental design is useful generally for separating buffering due to within-trophic level diversity from additional buffering due to competition. Food web buffering reduces the proportional, not absolute, response of a species to a perturbation. Competition (density compensation) reduces the total change in abundance at one trophic level, and thus the absolute size of the response of a species on the next trophic level. The FWBH predicted a proportionally smaller response of *Didinium* to the perturbation in a more reticulate food web ($D/C > B/A$, Fig. 3a). Additional buffering from competition would be indicated by a smaller absolute response to the perturbation ($D-C > B-A$). However, our results emphasize the sensitivity of these predictions to the assumption that the perturbation does not affect the strength of competition.

In summary, the FWBH depends on the way in which the buffering species interact, and thus on the food web context in which buffering is supposed to occur. Our perturbation directly altered the density of only one species, *Paramecium*, but also reduced the effect of *Colpidium* on *Paramecium*. *Chlamydomonas* addition is analogous to a species invasion or the rapid increase of a previously rare species. Such perturbations are common in natural systems (e.g., Carlton and Geller 1993, Cronk and Fuller 1995, Ferriere and Cazelles 1999) and may frequently have effects similar to those observed here. The theoretical work of Pimm (1979, 1980) and Yodzis (1988) emphasizes that the strength of an indirect effect is sensitive to details of food web structure, and the mixed empirical results reviewed by Redfearn and Pimm (1988, 1992); see also Pimm 1991) may be due in part to varying details of food web structure in different communities. The FWBH is likely to hold in more restricted circumstances than common intuition suggests.

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