

Emergent facilitation promotes biological diversity in pelagic food webs



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ABSTRACT

Studies on the role of species interactions in community dynamics and diversity have mostly focused on competition and predator–prey interactions, but the possible role of positive interactions between species, i.e. facilitation, is increasingly recognised. A type of facilitation that received little attention is the one that arises indirectly via pathways of direct trophic and competitive interactions. Here we show that in pelagic food webs the positive effects from such ‘emergent’ facilitation can be sufficiently strong to dominate over direct negative effects, prevent competitive exclusion, promote co-existence and preserve biodiversity. We carried out a press perturbation experiment using a pelagic algae–ciliate food web model whose realism is based on extensive observations on the algae–ciliate community in Lake Constance. The model incorporated trait gradients regarding algal edibility and growth rate and ciliate selectivity and prey attack rate as commonly observed in pelagic food webs. Results of the press perturbation exercise showed that some ciliate groups did not persist alone, or only at very low biomass values, while they reached realistic biomass values in the presence of competing groups of ciliates. The mechanism behind this facilitation is that grazing by less selective ciliates protected the more edible and preferred prey for the selective ciliates. We argue that such emergent facilitation, and the positive consequences for co-existence and biodiversity, is likely to occur in real pelagic food webs. In this way, the present study revealed a potentially important mechanism in the preservation of biological diversity in pelagic food webs.

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1. Introduction

Understanding biodiversity and species richness in ecosystems is one of the most fundamental issues in biology. It has been approached by looking at niche-differentiation, e.g. due to spatial and temporal heterogeneity in habitats, or by looking at species interactions, and how these interactions influence population and community dynamics, persistence and stability. Studies on the role of species interactions have mostly focused on competition and predator–prey interactions, but the possible role of positive interactions between species, i.e. facilitation, is increasingly recognised (Bertness and Callaway, 1994; Stachowicz, 2001; Bruno et al., 2003; Altieri et al., 2007; Kéfi et al., 2012; McCoy et al., 2012). Facilitation can imply direct positive mutual effects between two species promoting their coexistence and thus diversity. Examples are symbiotic effects between plants and mycorrhizal fungi, or between plants and pollinators, both having strong effects on plant species diversity (Van der Heijden et al., 1998) and community organisation (Thébault and Fontaine, 2010). Facilitation can also result from indirect effects, for example by ecosystem engineering organisms, such as

beavers, termites or earthworms, that create or preserve habitats for other species (Jones et al., 1994; Dangerfield et al., 1998; Wright et al., 2002; Eisenhauer, 2010). The increasing recognition of facilitation as one of the driving forces in community organisation and stability has also initiated several approaches to explicitly incorporate facilitation in ecological networks (Kéfi et al., 2012; Kéfi et al., 2015).

A special mode of facilitation is the one acting between species that in fact only affect each other through competition and predator–prey interactions. Such facilitation ‘emerges’ indirectly through pathways of trophic and competitive interactions, and becomes visible when the indirect positive facilitation effects become strong enough to rule out the direct negative effects. The idea that this may happen, and even may be quite common, has first been suggested in a theoretical study on the effects of press perturbations on food web structure and stability (Yodzis, 1988). This study showed that pathways of trophic interactions in food webs may create counter-intuitive indirect effects among species, e.g. an increase in the abundance of a predator species leading to an increase in some of its prey species. Another example of indirect, or emerging facilitation has been shown by means of an age-structured predator–prey model where competing predators promoted each other by feeding selectively on different life history stages of the prey (de Roos et al., 2008).

Recently, an experimental study manipulated the presence of ciliates in an algae–ciliate food web (Filip et al., 2014). The results of this

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experiment indicated that facilitation may also have occurred, as in some experimental treatments ciliates competing for the same resources seemed to benefit from the presence of each other. However, under these experimental conditions the algae reached unrealistically high population densities, which made it difficult to conclude that such facilitation may also occur under natural field conditions (Filip et al., 2014).

In the present study we further investigated whether and how facilitation may occur in algae-ciliate communities in pelagic food webs. We used a generalized algae-ciliate food web model whose realism, in terms of food web structure, species traits and parametrization, is based on the well-studied food web dynamics in Lake Constance (Gaedke and Wickham, 2004; Tirok and Gaedke, 2007; Tirok and Gaedke, 2010). The modelled food web structure considered trait gradients at the algae and ciliate trophic levels as commonly found in pelagic food webs (Fig. 1). These trait gradients regarded edibility for the algae and prey selectivity for the ciliate consumers, and were captured by the

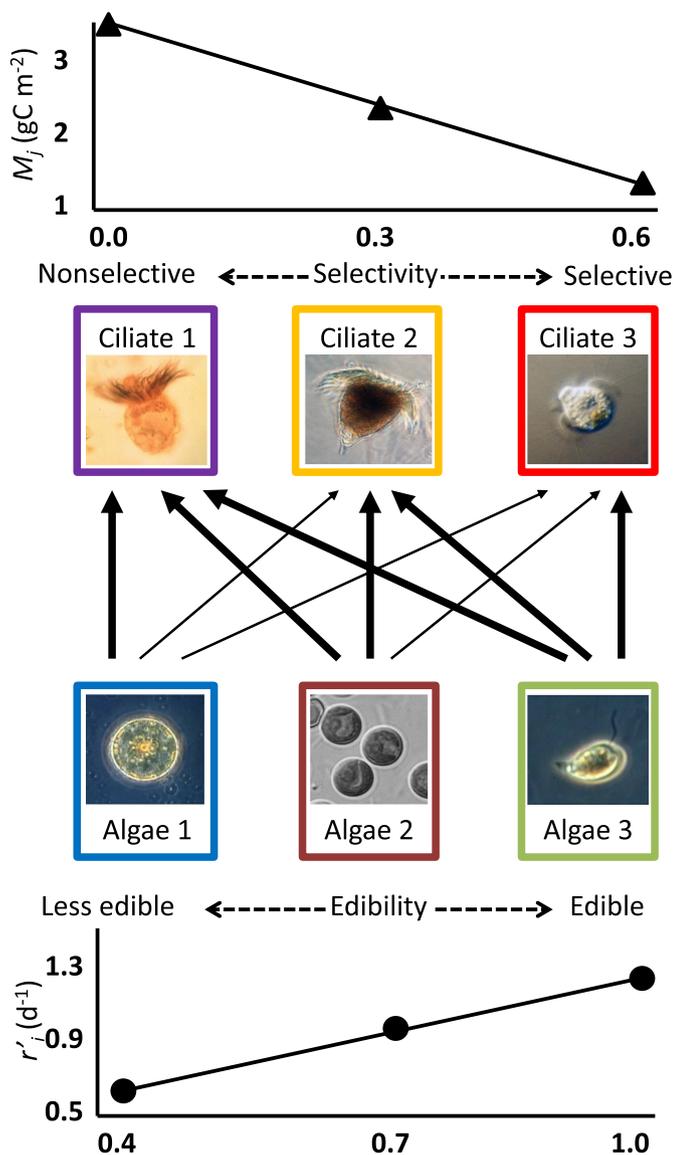


Fig. 1. Graphical representation of the modelled planktonic-ciliate food web. The thickness of the arrows refers to the different feeding preferences of the ciliate groups. The two graphs above and below the food web diagram picture the two trade-offs between algae edibility and growth rate and ciliate selectivity and the functional response half-saturation constant (Tirok and Gaedke, 2010) (see also Methods).

model by defining three functional groups of algae, based on edibility, and three functional groups of ciliates, based on selectivity (Fig. 1). Despite preferences, all ciliate groups fed on all algae groups, albeit to a different degree, and all algae competed equally well for the same resource. Furthermore, the model incorporated two trade-offs. The first is between algal edibility and maximum growth rate, i.e. the highly edible algae grow faster. The second is between ciliate selectivity and prey attack rates, implying that selective ciliates are more competitive at low food concentrations. Such trade-offs between maximum growth rates and defence, and between the degree of specialization and minimum food demand are frequently found in food webs (Yoshida et al., 2004; Litchman and Klausmeier, 2008; Tirok and Gaedke, 2010; Straub et al., 2011; van Velzen and Etienne, 2015). By taking three functional groups for each trophic level, the model captured the diversity in traits; at the same time it remained relatively simple which allowed to track the effects of population interactions (Tirok and Gaedke, 2010; Bauer et al., 2014). Because of its realism, the model was earlier found to adequately mimic the dynamics and alternations in relative importance of different functional groups at both trophic levels in Lake Constance (Tirok and Gaedke, 2010).

Using this model, a press perturbation experiment was carried out by altering the initial presence of the various ciliate groups, or combinations of ciliate groups. We analysed the model results focusing on (i) the 'success' of the ciliate groups, in terms of biomasses and persistence, depending on the presence of the other competing groups, and (ii) the resulting diversity in the algae and ciliate community. In this way we aimed to answer the following questions:

1. Can facilitation emerge in pelagic food webs purely from predator-prey interactions and competition?
2. If so, what influence has such emergent facilitation on coexistence and biodiversity of algae and ciliates in pelagic food webs?

2. Methods

2.1. Lake Constance

Monomictic Lake Constance is a large (472 km²), deep ($z_{\text{mean}} = 101$ m), mesotrophic lake situated north of the European Alps. Given its small littoral zone, large water volume (almost 50 km³) and moderate nutrient concentrations, its plankton food web has often served as a model system for large open freshwater and marine water bodies. During spring in the period 1979–1998, the cryptomonads *Rhodomonas* spp. and *Cryptomonas* spp., some green algae and small centric diatoms such as *Stephanodiscus parvus* and *Cyclotella* spp. dominated the small phytoplankton (Sommer et al., 1993; Gaedke, 1998). All algal species compete for the same resources (light and phosphorus) as silicate concentrations rarely dropped to a potentially limiting level. There is a trade-off among the different algal groups as less edible diatoms are non-motile in contrast to cryptomonads. Motility increases the resource availability and thus the growth rate, but also the likelihood of predator encounter and thus grazing susceptibility (Reynolds, 1997). Furthermore, diatoms build a hard silicate frustule which likely reduces or prevents utilization by some but not all ciliate species (Skogstad et al., 1987; Müller and Schlegel, 1999).

The spring ciliate community (1987–1998) was dominated by rather small species known to feed selectively on small plankton (Fenchel, 1987; Verity, 1991; Gaedke and Wickham, 2004; Hamels et al., 2004). These ciliate species exhibit different feeding modes. Interception feeders such as *Strobilidium* capture and process single prey particles and are thus supposed to be selective, whereas filter feeders such as *Askenasia* strain suspended food particles from surrounding water and thus feed less selectively (Fenchel, 1987). In Lake Constance, the generalist filter feeders dominated when the less edible non-cryptomonads prevailed, and selective interception feeders prevailed during periods with a dominance of highly edible cryptomonads independent of the seasonal progression (Tirok and Gaedke, 2007). In accordance,

experiments at Lake Constance revealed a strong negative selection for small diatoms by one of the dominant interception feeders but not in a filter feeder (Müller and Schlegel, 1999). These different feeding types may represent different strategies to meet the trade-off between food quantity and quality. Despite the differences in selectivity all ciliates are thought to feed on all small algae, hence they compete with each other for the same resources.

2.2. Model equations

We used a model based on comprehensive observations on species abundances, composition and ecological functioning in Lake Constance, that captures the population dynamics and interactions among three ciliate consumer groups feeding on three groups of small algae (Tirok and Gaedke, 2010).

The model was defined in terms of differential equations describing the population dynamics of the three prey groups and three consumer groups (Rosenzweig and MacArthur, 1963; Tirok and Gaedke, 2010):

$$\frac{dA_i}{dt} = r_i A_i - \sum_{j=1}^3 g_{ij} C_j \quad (1)$$

$$\frac{dC_j}{dt} = (e \sum_{i=1}^3 g_{ij} - d) C_j \quad (2)$$

$$r_i = r'_i \left(1 - \frac{\sum_{k=1}^3 A_k}{K} \right) \quad (3)$$

$$g_{ij} = g' \frac{q_{ij} A_i f_i}{(F_j + M_j)} \quad (4)$$

$$F_j = \sum_{i=1}^3 q_{ij} A_i f_i \quad (5)$$

$$f_i = \frac{A_i}{A_i + A_0} \quad (6)$$

Here A_i denotes prey species i and C_j denotes consumer species j . The parameter r'_i represents the maximum growth rate of prey species i and K is the common carrying capacity for all prey. Consumers feed according to a hyperbolic type II functional response with a maximum grazing rate of g' and a half-saturation constant M_j . The parameter q_{ij} is the feeding preference of consumer j for prey i , F_j is the total food availability and f_i is the prey density function which reduces grazing at a very low density defined by A_0 . The parameters e and d represent the consumer growth efficiency and consumer death rate, respectively. The parameter values with their description and units are summarized in the Table 1.

2.3. Press perturbations

The press perturbation treatments regarded the initial composition of the ciliate consumer community: Each ciliate species alone, the three different pairs of ciliate species, and all three ciliate species together. Total initial ciliate biomass was the same for all treatments. The mean biomass values were recorded over the 40.000 time-step period for all algal and ciliate populations per treatment. The 40.000 time steps were chosen to cancel out effects of initial population sizes on mean biomass values.

2.4. Sensitivity analysis.

To test the robustness of the model results against variation in parameter values, a sensitivity analysis was carried out in which the following parameters were varied (Table 1).

Table 1

Names, descriptions, units, default parameter values and parameters values as taken for the sensitivity analysis. For further explanation, see main text.

Name	Description	Unit	Default value	Sensitivity analysis
r'_i	Maximum prey growth rate	d^{-1}	0.37/0.77/1.17	0.57/0.77/0.97
K	Carrying capacity		$g \text{ C m}^{-2}$	8
g'	Maximum grazing rate	d^{-1}	1.7	
M_j	Half-saturation rate		$g \text{ C m}^{-2}$	3/2/1
e	Consumer growth efficiency		0.2	
d	Consumer death rate	d^{-1}	0.15	
A_0	Critical prey density		$g \text{ C m}^{-2}$	0.02
q_{i1}	Feeding preference of consumer C_1 for A_i		1/1/1	1/1/1
q_{i2}	Feeding preference of consumer C_2 for A_i		0.1/1/1	0.2,0.25/1/1
q_{i3}	Feeding preference of consumer C_3 for A_i		0.1/0.1/1	0.2,0.25/0.2,0.25/1

1. The strength of the trade-off between edibility and maximum prey growth rate (r'_i),
2. The strength of the trade-off between prey selectivity and half-saturation rate (M_j) and
3. The strength of prey selectivity of the two selective consumers, C2 for A1 (q_{12}) and of C3 for A1 and A2 (q_{13}, q_{23}).

These parameters were chosen because they quantify the strength of the model assumptions regarding prey edibility and associated trade-offs for prey and predators. We tested the sensitivity of the model results to variation in each parameter (r'_i , M_j and q_{ij}) separately, and for all possible combinations of parameter values (Appendix 1).

3. Results

3.1. Press perturbation analysis

The first three model runs started with only one of the ciliate groups initially present (Fig. 2a). These runs consistently resulted in the dominance of only one algal group. Starting with only the generalist ciliates (C_1 , cf. Fig. 1) led to the dominance of the most edible algae (A_3), because this algal group is most productive, while it is not preferentially eaten in the absence of the more selective ciliates. Starting with the intermediately selective ciliates (C_2) led to dominance of the least edible, and also least productive algae (A_1). This is because despite its low productivity, it is much less eaten than the other algal groups. Starting with the most selective ciliates (C_3) led to dominance of the intermediately edible algae (A_2), because this algal group is much less eaten than the most edible group A_3 , and has a higher growth rate than the least edible group A_1 . Regarding the ciliates, we saw that only the generalist ciliates (C_1) survived at a realistic biomass level, because the biomass of A_3 ensured its persistence (Fig. 2b). C_2 did not survive, because the biomass of A_1 was insufficient for its persistence. C_3 did persist alone, but only at a very low biomass level (Fig. 2b). These observations can be generalized as follows: Which algae dominate is primarily determined by the grazing pressure: algae that cannot be consumed efficiently will dominate. Secondly, if multiple algal species are under the same grazing pressure, the species with the highest growth rate will dominate.

The outcome for the treatments starting with pairs of ciliate groups can only partly be understood from the outcome of the single consumer treatments since additional effects arise showing facilitation among competing ciliates. Treatment $C_1 + C_2$ promoted A_3 and A_1 , treatment $C_1 + C_3$ promoted A_3 and A_2 , and treatment $C_2 + C_3$ promoted A_1 and A_2 (Fig. 2a). At the consumer level, the results show that ciliate C_2 , that did not persist alone, did now build up substantial biomass together

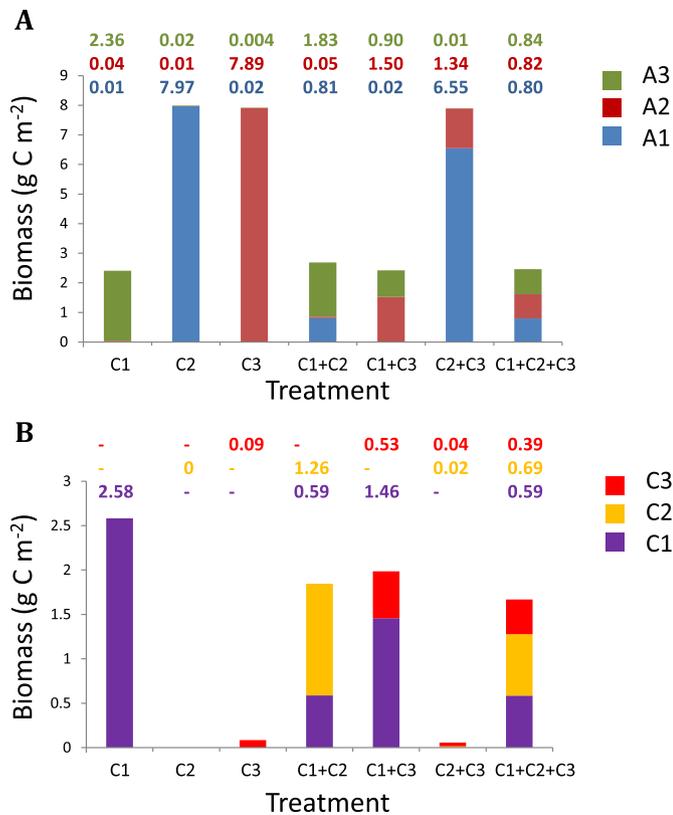


Fig. 2. Biomasses of Algae (A) and Ciliates (B) after runs of 40,000 time-steps. Numbers above bars give the reached equilibrium biomasses with the colours referring to the different algae and ciliate groups in the same way as the bars. A1 is the group of least edible algae, A2 is the group of intermediately edible algae and A3 is the group of most edible algae. C1 is the group of non-selective generalist ciliates, C2 is the group of intermediately selective ciliates and C3 is the group of most selective ciliates. Treatments are described in terms the groups of ciliates being present at the start of the model run.

with the non-selective ciliate C1 (Fig. 2b). C2 persisted together with C1 because the non-selective ciliate C1 promoted the abundance of the edible algae A3 by grazing on its competitors A1 and A2, providing enough food for C2. In turn, C2 promoted the least edible algae A1 by imposing a substantial grazing pressure on its competitors A2 and A3, hence C1 + C2 both persisted together with A1 and A3. The same mechanism applied to the outcome of the C1 + C3 treatment. The two groups of algae A2 and A3, which dominated respectively with only C3 or C1 present, did now persist together, and in this way provided enough food for both C1 and C3 to persist. The treatment with the two more selective ciliate groups C2 + C3 led to the co-existence of both ciliate groups, but at a very low biomass. Here the highly selective ciliate C3 promoted again the abundance of the intermediately edible algae A2, while C2 ensured enough biomass of A1, resulting in just enough food for both ciliate groups to survive. This treatment also showed that a very low biomass of ciliates can still have profound effects on algal composition, since the algal composition for the treatments C2 and C3 alone greatly differed from that of the treatment C2 + C3.

The treatment with all three functional groups of ciliates led to a coexistence of all three algal groups and all three ciliate groups at realistic biomass values, with a high level of evenness at both trophic levels (Fig. 2).

3.2. Sensitivity analysis

To analyse the robustness of the model to critical model assumptions, a sensitivity analysis was carried out consisting of (i) reducing the strength of the trade-off between algal edibility and maximum algal growth rate (r'_i), (ii) reducing the strength of the trade-off between prey edibility and predator half-saturation constant (M_j), and

(iii) enhancing the share of the less preferred prey the more selective ciliates take (q), i.e. altering the food web structure (Table 1).

Overall, the model results were relatively robust against changes in the values of these parameters (Fig. 3). Decreasing the strength of the trade-off between prey edibility and r'_i did not principally alter the results, i.e. C2 did not survive alone, C3 persisted only at a very low biomass level, and both C2 and C3 reached much higher biomass values in the presence of C1. The same was found for decreasing the strength of the trade-off between prey selectivity and M_j , i.e. both C2 and C3 hardly survived without the presence of C1. Decreasing the strength of prey selectivity q (i.e. enhancing q from 0.1 to 0.2) maintained the facilitation effect between C1 and C2, but the one between C1 and C3 disappeared, as now C3 reached the highest biomass when it was the only ciliate group and had not to compete with C1. Using different initial biomass values, we varied between very low (close to 0) and twice as high only affected population sizes at the beginning of the model runs but not the final equilibrium densities. Additional sensitivity analyses in which the preference was further reduced and in which values of combinations of parameters were altered gave similar results (Appendix 1).

4. Discussion

In the present study, facilitation emerged at the consumer level, via preferential consumption on the different resource species. This promoted species coexistence at both the consumer and resource species level. Earlier studies indicated that facilitation may play a role in population and community dynamics and thereby enhancing stability (see e.g. Bruno et al., 2003). For example, a theoretical approach reveals that facilitation may emerge between fish species selectively feeding on different life-history stages of the resource species (de Roos et al., 2008) enabling coexistence at the consumer level. Studies on vegetation in arid ecosystems show that facilitation via enhanced resource exploitation and habitat improvement helps plants to survive (Rietkerk et al., 2004; Kéfi et al., 2007). Furthermore, in a more general approach Kéfi and colleagues demonstrate that patterns of non-trophic interactions, including positive interactions, promotes species population sizes, persistence and stability (Kéfi et al., 2016). The present study contributes to these findings that in real ecosystems facilitation may emerge indirectly via competition and predator-prey interactions, can be strong enough to overcome the negative competition effects, and can promote coexistence at other trophic levels than the one where facilitation occurs.

Because of the relative simplicity of the modelled food web, the mechanisms behind facilitation were easily tractable: less selective ciliates altered the algae community composition in such a way that they promoted the preferred prey for the more selective ciliates. The emerging facilitation was therefore not mutualistic, as the generalist ciliates did not benefit from the more selective ones.

Second, the emerging facilitation had pronounced preserving effects on biodiversity in both the algae and ciliate community, as it prevented competitive exclusion and hence promoted coexistence. The number of algae groups equalled the number of ciliate groups initially present. At the consumer level, in two out of three cases starting with one functional group of ciliates, this group went extinct or maintained itself at a very low biomass level. In the three cases starting with two groups of ciliates, both groups survived although in one case at a very low biomass level. In the case of starting with all three groups of ciliates, all groups of ciliates persisted at a high level of biomass evenness.

We expect that the observed facilitation effects, and the consequences for biodiversity, are likely to occur in real pelagic food webs. The modelled algae-ciliate food web consisted of typical key-groups of organisms that occur in most pelagic food webs and often dominate or at least contribute substantially to food web metabolism (Breteler et al., 1999; Gaedke et al., 2002; Calbet and Landry, 2004). Also, all model parameter values had a firm empirical basis (Hansen et al., 1997; Tirok and Gaedke, 2010). Furthermore, an earlier application of

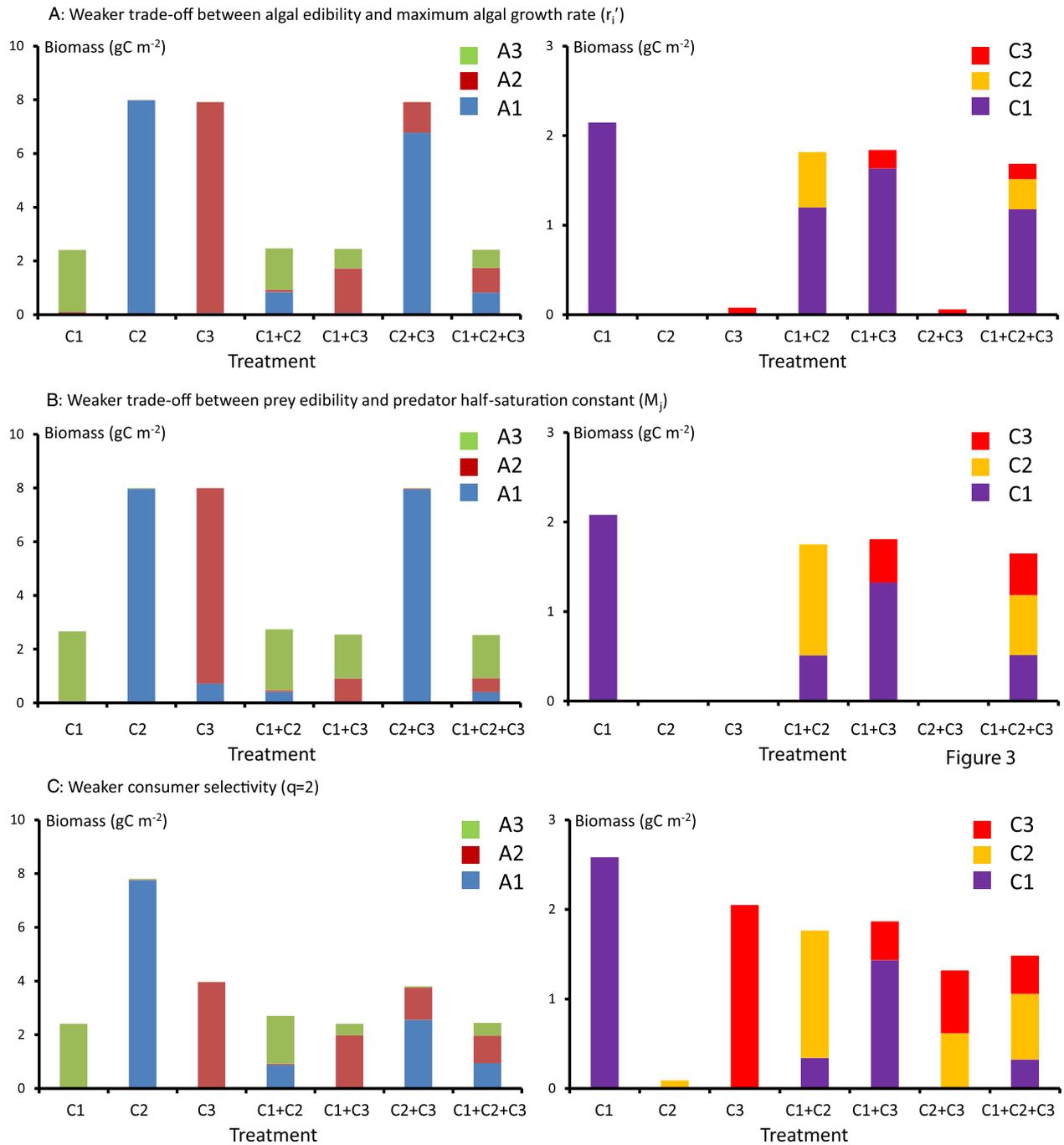


Fig. 3. Graphical representation of the results of the sensitivity analysis. Figures are constructed in the same way as Fig. 2. A: Weaker trade-off between edibility and maximum algal growth rate (r_i'). B: Weaker trade-off between prey selectivity and half-saturation rate (M_j). C: Weaker consumer selectivity (q). Values used in the sensitivity analysis are given in Table 1. Results obtained from combinations of altered parameter values are presented in Appendix 1.

the model for the analysis of the Lake Constance food web showed that the modelled biomass dynamics of the algae and ciliates were close to the observed dynamics (Tirok and Gaedke, 2010).

The mechanism underlying the emergent facilitation is simple and straightforward and was found to hold for a wide array of model parameters. Although in reality it is likely that all ciliate species will always stay present (e.g. as cysts), we expect that the facilitation still promotes the evenness within the ciliate community, which under field conditions is high compared to that of the other major plankton groups, i.e. phytoplankton, rotifers and crustaceans in Lake Constance (Vasseur and Gaedke, 2007). The present study revealed therefore a mechanism that may contribute to the intriguing biodiversity in pelagic ecosystems, and that in Lake Constance in particular. Earlier studies on the

population and community dynamics in Lake Constance indicated further mechanisms that may play a role for community structure and dynamics, and biodiversity (Boit and Gaedke, 2014). These include shared dominant frequencies and synchronization in the consumer population dynamics (Vasseur and Gaedke, 2007; Bauer et al., 2014) and food quality effects, either by stoichiometrical constraints through phosphate limitation (Gaedke et al., 2002) or morphological constraints (Weithoff et al., 2015). The emergent facilitation is linked to these mechanisms, as it likely influences the degree of synchronization and phase shifts among consumers and shows explicitly how food quality may influence the nature of interaction among resource and consumer species. By this the present finding of emergent facilitation may serve as a framework to better understand these mechanisms, and the interplay between them.

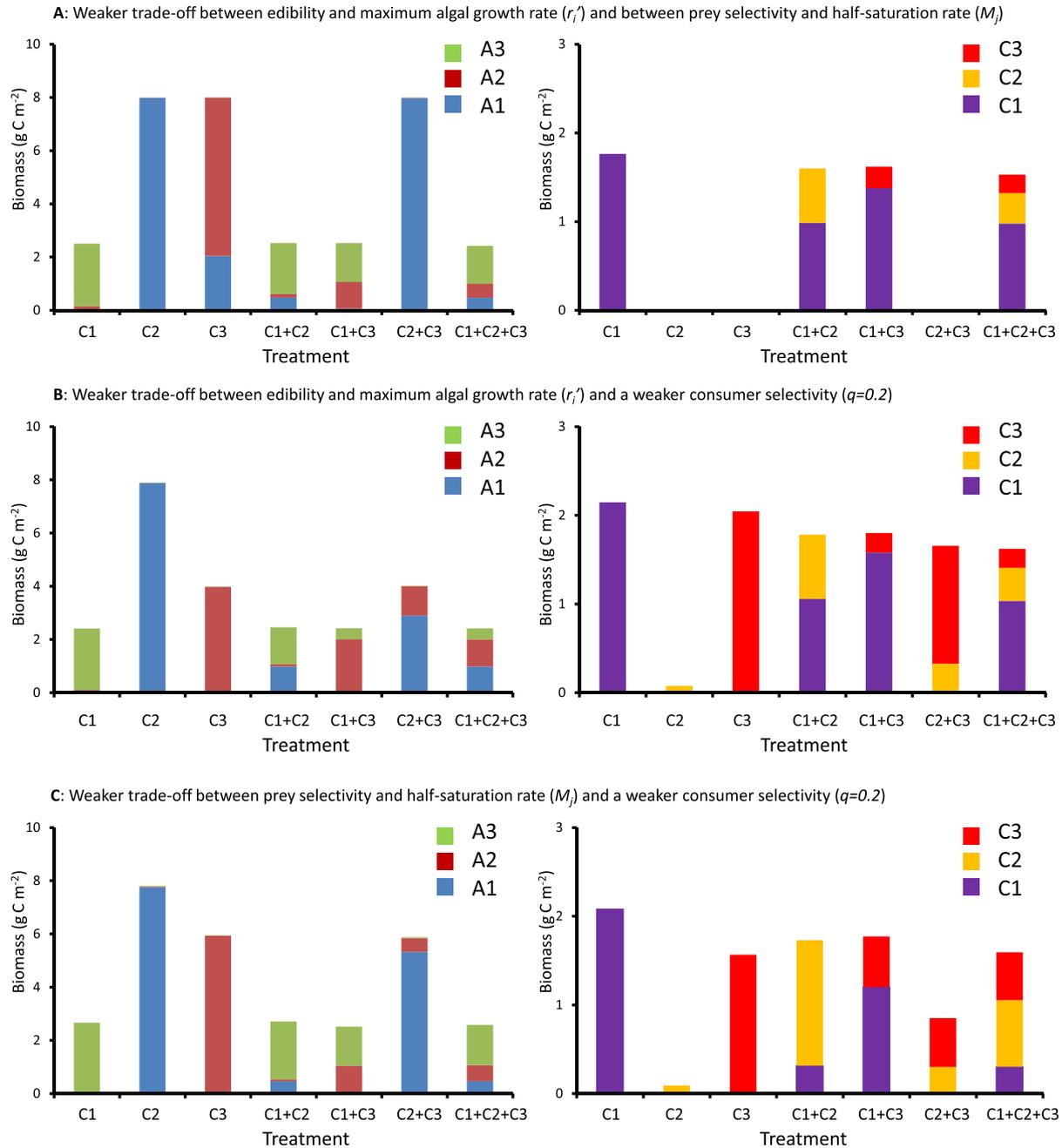
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Appendix 1. Additional sensitivity analyses

Additional sensitivity analyses were carried out in which the effects of alterations in combinations of parameters were investigated on the outcome of the modelling. These analyses also indicated a relatively high robustness of the model results (Appendix Fig. 1). Reducing the

strengths of both trade-offs simultaneously still produced a facilitation pattern similar as the default run, i.e. C2 and C3 reached much higher biomasses in the presence of C1. Reducing the strength of the trade-off between edibility and r'_i together with weakening the selectivity ($q = 0.2$) gave a similar effect as only reducing the selectivity, i.e. C1 still facilitated C2, but not C3. Reducing the strength of the trade-off between preference and (M_j) and weakening the selectivity (q) was also similar to the effect of reducing only the selectivity, i.e. C1 still facilitated C2, but not C3. When selectivity was weakened even further ($q = 0.25$) C2 did survive alone, but still it reached a higher biomass in the presence of C1. Only when the strength of both trade-offs and ciliate selectivity were all simultaneously reduced, the facilitation effects disappeared.



Appendix Fig. 1. Results of the additional sensitivity analyses. A: Weaker trade-off between edibility and maximum algal growth rate (r'_i) and between prey selectivity and half-saturation rate (M_j). B: Weaker trade-off between edibility and maximum algal growth rate (r'_i) and a weaker consumer selectivity (q). C: Weaker trade-off between prey selectivity and half-saturation rate (M_j) and a weaker consumer selectivity (q). D: Weaker trade-off between edibility and maximum algal growth rate (r'_i) and between prey selectivity and half-saturation rate (M_j) and a weaker consumer selectivity (q). E: Weaker consumer selectivity ($q = 0.25$).

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