

Emergent facilitation promotes biological diversity in pelagic food webs



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ARTICLE INFO

Article history:

Received 1 April 2016

Received in revised form 16 January 2017

Accepted 3 February 2017

Available online 7 February 2017

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

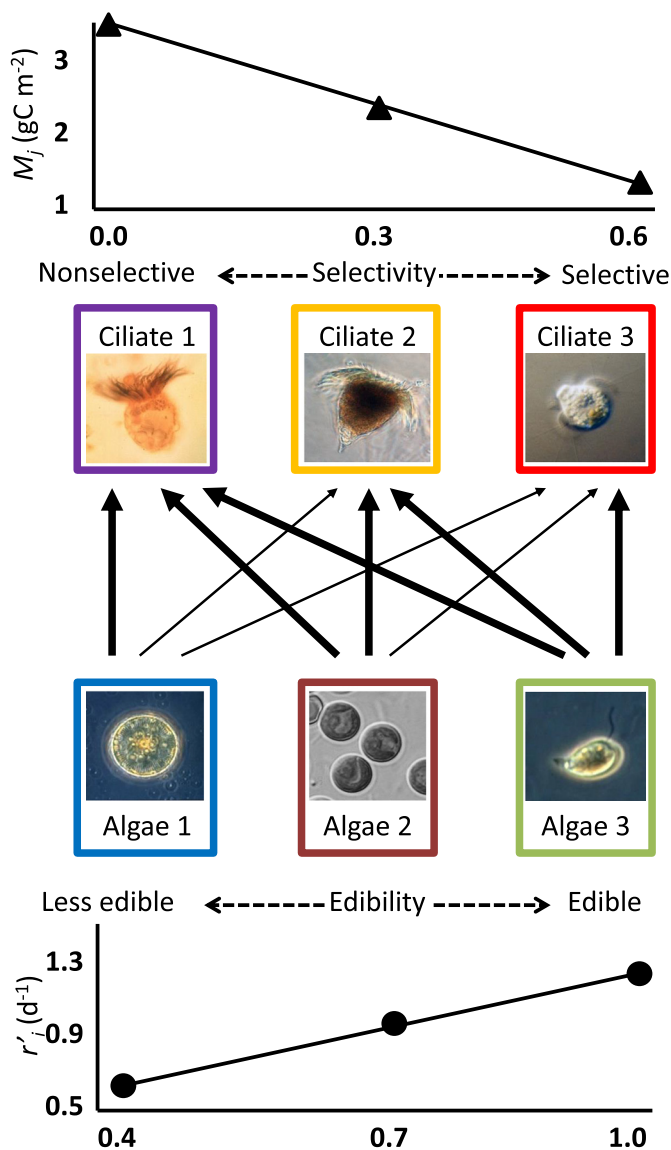


Fig. 1. Graphical representation of the modelled planktonic-ciliate food web. The thickness of the arrows refers to the different feeding preferences of the ciliate groups. The two graphs above and below the food web diagram picture the two trade-offs between algae edibility and growth rate and ciliate 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,

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