Vol. 81: 243–256, 2018
https://doi.org/10.3354/ame01866

AQUATIC MICROBIAL ECOLOGY
Aquat Microb Ecol

Published online May 16

# Inter- and intraspecific consumer trait variations determine consumer diversity effects in multispecies predator–prey systems

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ABSTRACT: This study investigated how inter- and intraspecific trait variations determine consumer diversity loss effects in a short-term microcosm experiment, using consumer and prey biovolume production and composition as the main response variables. Three levels of ciliate diversity were created, all feeding on a 3-species microalgal prey mixture. Ciliates differed in consumer specialisation, feeding on 1 (specialist, S), 2 (intermediate, I) or all 3 (generalist, G) microalgal species. Intraspecific trait variation was incorporated by including 3 different clones of I and setting up ciliate combinations with either monoclonal or polyclonal populations of I. Both increasing inter- and intraspecific consumer diversity increased total ciliate biovolume. On the species level, total ciliate biovolume was high wherever G was included, indicating a positive selection effect for a competitively superior species. Polyclonal I monocultures exceeded the biovolume of all monoclonal ones (transgressive overyielding) based on complementary differences of clone-specific feeding niches. This effect was also observed in multispecies combinations. Both inter- and intraspecific consumer diversity decreased prey evenness. Despite being able to feed on all prey species, G displayed specific grazing preferences within its dietary niche. Furthermore, G exhibited an induced offence, forming giant cells that fed on other ciliates. S responded with an inducible defence, escaping predation by the intraguild predator. Overall, our study demonstrated highly complex trophic interactions driven by consumer selectivity, grazing rates, selective feeding and phenotypic plasticity, and indicated that both inter- and intraspecific consumer trait variations determine the consequences of consumer diversity loss on ecosystem functioning.

KEY WORDS: Consumer diversity · Consumer trait variation · Intraspecific trait variation · Predator–prey system · Ciliates · Specialist · Generalist



## INTRODUCTION

Concern about unprecedented global biodiversity loss rates (Pimm et al. 1995) has triggered a paradigm shift in ecological research. Traditionally addressing biodiversity as a result of ecosystem processes, the focus of biodiversity research has shifted to examining how biodiversity affects ecosystem functioning (BDEF) over the last few decades (Gamfeldt & Hillebrand 2008). Experiments within this complex research field were initially conducted within 1 trophic level, mainly the producer level (Srivastava et al. 2009), and demonstrated that biodiversity increased ecosystem processes such as productivity (reviewed by e.g. Cardinale et al. 2011). Although these early studies provided valuable insights into BDEF relationships, they did not consider multiple trophic levels, and cross-linked trophic interactions and functions of natural food webs (Stachowicz et al. 2007).

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More recently, studies have addressed multitrophic consumer richness effects within and across trophic levels and thus expanded in realism, relevance and predictability for natural ecosystems (summarised, e.g., by Srivastava et al. 2009, Griffin et al. 2013). However, their conclusions regarding the strength and direction of consumer diversity effects within and across trophic levels were inconsistent. In a meta-analysis of consumer richness effects on prey suppression, Griffin et al. (2013) demonstrated that the strength of mean consumer richness effects increased with the taxonomic distinctness (used as a proxy of phylogenetic diversity) of the species present. This suggested that taxonomic distinctness captured aspects of functional differentiation among predators and that measures of biodiversity that go beyond species richness (e.g. the degree of trait variation) may be a better predictor for the consequences of consumer species loss. For instance, functional traits such as consumer specialisation, growth and grazing rates, as well as prey size and edibility, strongly influence consumer diversity effects across trophic levels (Steiner 2001, Straub & Snyder 2006, Finke & Snyder 2008, Worsfold et al. 2009, Filip et al. 2014, Wohlgemuth et al. 2017).

Although the potential importance of species trait variation, as opposed to mere species richness, on different trophic levels for ecosystem structure and dynamics is well recognised (e.g. Gunderson 2000, Hooper et al. 2005), it has only recently been considered to a greater extent in theoretical and empirical studies on trophic interactions. In the following, the term 'consumer specialisation' refers to the number of realized feeding links. Specialist consumers feed on 1 prey species only (1 feeding link), whereas generalist consumers feed on a variety of prey species (several feeding links). 'Grazing efficiency' refers to the impact consumers have on their prey, and is a measure of prey suppression. Analysing the influence of consumer specialisation in a plant–herbivore model, Thébault & Loreau (2003) demonstrated that generalist and specialist consumers may have very different effects within and across trophic levels. For instance, generalists had a stronger negative effect on total prey biomass in their model than specialists due to their greater prey spectrum. Filip et al. (2014) tested their model predictions in an experimental microbial food web, using ciliate consumers and microalgal prey. In their experiment, however, specialist consumers decreased prey biovolume and evenness more strongly than generalists did, thus contradicting prior model results. Filip et al. (2014) complemented their experimental study with an extended version of the model proposed by Thébault & Loreau (2003), which explicitly included prey-specific growth and consumer-specific grazing rates. This model captured the experimental results well, indicating that such species-specific traits were as important as consumer specialisation for determining multitrophic diversity effects (Filip et al. 2014). Consistent with the results of Filip et al. (2014), specialists consumers were more effective in either locating, capturing or consuming prey than generalists (e.g. Wang & Keller 2002, Norberg 2004, Egan & Funk 2006). This indicates that specialists may have a greater grazing impact on their prey than generalist, which are less efficient and have a wider prey spectrum. This trade-off between consumer specialisation and grazing efficiency has rarely been considered in empirical studies, despite its potentially far-reaching consequences for ecosystem functioning. It has, however, received some attention in recent theoretical studies that used a trait-based predator–prey modelling approach to describe species and clonal compositions of the 2 trophic levels. These studies demonstrated that processes such as predator–prey dynamics (Tirok & Gaedke 2010, Tirok et al. 2011) and biodiversity ecosystem function relationships (Bauer et al. 2014) can be modelled more accurately when trade-offs between specialisation and grazing efficiency on the consumer level, and between edibility and growth rate on the prey level are assumed. The results of these studies emphasised that an improved understanding of an ecosystem's adaptive potential (i.e. the trait variation) is of vital importance to more accurately predict its response to environmental change (Tirok & Gaedke 2010, Tirok et al. 2011, Bauer et al. 2014).

In addition to trait variation among different species, trait variation among conspecific organisms has long been recognised (Ford 1964, Roughgarden 1972). However, intraspecific trait variation has only recently received renewed attention regarding its extent and community consequences (Bolnick et al. 2003, Hughes et al. 2008). Experimental evidence suggested that intraspecific diversity increases the stability of consumer populations (Agashe 2009), species coexistence (Fridley & Grime 2010) and ecosystem processes, such as primary and secondary production (Crutsinger et al. 2006), demonstrating that intraspecific trait variation can have large ecological effects (see also Hughes et al. 2008, Becks et al. 2010).

In the present study, we investigated the effects of consumer trait variation with regard to specialisation, growth and grazing rates on consumer diversity loss,

using ciliate consumers and microalgal prey in experimental microcosms. We focussed on the trade-off specialisation versus grazing efficiency on the consumer level, and edibility versus growth rate on the prey level, as postulated in an experimental study complemented by a theoretical model by Filip et al. (2014), and explicitly included intraspecific consumer trait variation in addition to interspecific trait variation. Ciliates differed in consumer specialisation, and microalgal prey in edibility, accordingly. Three levels of ciliate species diversity were created, all feeding on a prey mixture consisting of 3 microalgae that differed in size and taxonomic classification. Intraspecific trait variation was incorporated by including monoclonal and polyclonal populations of one of the consumers. With this experimental set-up, we addressed the following hypotheses:

$H_1$: Total consumer biomass increases with increasing interspecific ($H_{1a}$) and intraspecific ($H_{1b}$) consumer diversity due to enhanced trait variation and therefore higher resource complementarity entailing enhanced secondary production.

$H_2$: Prey biomass decreases with increasing interspecific ($H_{2a}$) and intraspecific ($H_{2b}$) consumer diversity due to enhanced trait variation and therefore a more efficient use of resources, i.e. algal prey.

$H_3$: Prey evenness is affected by interspecific ($H_{3a}$) and intraspecific ($H_{3b}$) consumer trait variation, depending on consumer specialisation and specific grazing rates on particular prey. Increasing consumer specialisation (unequal grazing pressure) decreases evenness, whereas decreasing consumer specialisation (equal grazing pressure) maintains the evenness of the prey community.

## MATERIALS AND METHODS

### Organisms used, their origin and culture conditions

We used 3 freshwater ciliate consumer species — *Stylonychia* sp., *Euplotes octocarinatus*, *Coleps hirtus* — and 3 species of microalgae — *Navicula pelliculosa* (*Nav*), *Cryptomonas* sp. (*Cry*), *Tetraedron minimum* (*Tet*) — for our experiment. The ciliates differed in average cell size and in their feeding preferences, while microalgae differed in average cell size and edibility (Table 1, Fig. 1). Feeding preferences of the ciliates were investigated in feeding trials, which were performed prior to the experiment using algal monocultures. According to these trials, *Stylonychia* sp. preyed on all of the microalgal species, and was the generalist (G) in our system. The specialist (S) *E. octocarinatus* ingested only *Cry*, while *C. hirtus*, intermediate (I) in our spectrum of feeding preferences, fed and grew on *Cry* and *Nav*, but exhibited only low feeding and growth rates on *Tet*. To investigate intraspecific effects of consumer trait variation, we included 3 different clones of the intermediate consumer *C. hirtus* ($I_{mono}$, $I_2$, $I_3$).

Mineral water (Volvic) served as the culture medium for our ciliate strains, and WEES culture medium (Kies 1967) for the microalgae. Prior to the experiment, all species and clonal ciliate cultures were fed *Cry*. The present study is part of a research programme that studies short- and long-term aspects of consumer diversity effects in multispecies predator–prey systems. Previous studies have demonstrated the potential for predator–prey oscillations, when

Table 1. Abbreviations, taxonomy, average cell size and origin of algal and ciliate cultures used in the experiment. G: generalist, I: intermediate, S: specialist, mono: monoculture

| Species | Abbreviation | Class | Average cell size ($\mu m^3$) | Origin |
|---|---|---|---|---|
| **Microalgae** | | | | |
| *Cryptomonas* sp. | *Cry* | Cryptophyceae | 664 | Culture Collection of Algae at Göttingen University (SAG) |
| *Navicula pelliculosa* | *Nav* | Bacillariophyceae | 100 | SAG |
| *Tetraedron minimum* | *Tet* | Chlorophyceae | 357 | SAG |
| **Ciliates** | | | | |
| *Stylonychia* sp. | G | Stichotricha | 1004210 | Provided by Dr. K. Eisler, Eberhard Karls University Tübingen, Germany |
| *Coleps hirtus* clone 1 | $I_{mono}$ | Prostomatea | 9125 | Provided by Dr. U.G. Berninger, University of Salzburg, Austria |
| *Coleps hirtus* clone 2 | $I_2$ | Prostomatea | 9125 | Provided by Dr. M. Schweikert, University of Stuttgart, Germany |
| *Coleps hirtus* clone 3 | $I_3$ | Prostomatea | 9125 | Culture Collection of Algae and Protozoa (CCAP) |
| *Euplotes octocarinatus* | S | Stichotricha | 34444 | University of Pisa, Italy |

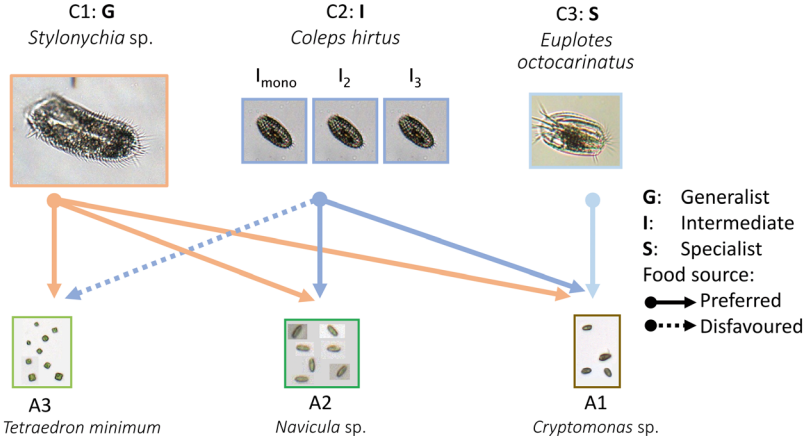


Fig. 1. Consumer–prey system, consisting of ciliate consumers (C) and algal prey (A). Different food preferences of the ciliates are indicated by arrows. Photographs are not to scale

nitrogen is the limiting factor for algal growth (e.g. Boraas 1980, Fussmann et al. 2000, Becks et al. 2012). To achieve nitrogen limitation, a modified WC medium (Guillard 1975) with the nitrogen concentration set to 70 µmol $l^{-1}$ was used to cultivate the microalgae before they were used to inoculate the experiment.

### Experimental design

Three levels of consumer species diversity were created, setting up ciliate monocultures, 2-species and 3-species mixtures with all possible combinations of ciliate species in polycultures. This resulted in 7 different consumer species combinations (Fig. 2). The ciliate species G and S were inoculated with monoclonal cultures, while for ciliate species I, 3 different clones ($I_{mono}$, $I_2$, $I_3$) were used to address the effects of intraspecific consumer trait variation. As monocultures, we set up each of the *C. hirtus* clones ($I_{mono}$, $I_2$, $I_3$) and added an additional polyclonal ($I_{poly}$) culture that consisted of all 3 *C. hirtus* clones. All ciliate species combinations were set up with monoclonal *C. hirtus* populations in 1 set of experimental units using only $I_{mono}$, and with polyclonal *C. hirtus* populations ($I_{poly}$), using all 3 of the *C. hirtus* clones in a second set. Monocultures (*Cry*, *Nav*, *Tet*) and polycultures of all 3 microalgal species without consumers were used as controls. Six ciliate monocultures, five 2-species and two 3-species combinations, all comprising a set of mono- and of polyclonal cultures of I, as well as 4 algal controls, each replicated 3-fold, resulted in 51 experimental units. Duration of the experiment was 3 wk.

Culture medium was the same N-reduced WC medium (Guillard 1975) that was used for pre-culturing the microalgae. All ciliate treatments were inoculated with equal total ciliate biovolume (9.13 × $10^5$ µm$^3$ ml$^{-1}$), i.e. in 2- and 3- species combinations, each species was inoculated with half or one-third of the total ciliate biovolume, and the 3 *C. hirtus* clones with one-third of the biovolume of other monoclonal ciliate cultures, respectively. At the beginning of the experiment (Day 0) each ciliate treatment was supplied with an equal biovolume of the 3 microalgal prey species combined (total biovolume: 65 × $10^7$ µm$^3$ ml$^{-1}$). Algal controls were inoculated with the same total biovolume. The experimental communities were grown in semi-continuous culture using Erlenmeyer flasks and a total culture volume ($V_{tot}$) of 100 ml. Every other day, 20 ml of $V_{tot}$ were replaced with new medium ($V_{new}$), resulting in a dilution rate $D$ ($D = V_{new}/V_{tot}$) of 0.1 d$^{-1}$. Prior to medium replacement, the cultures were gently shaken by

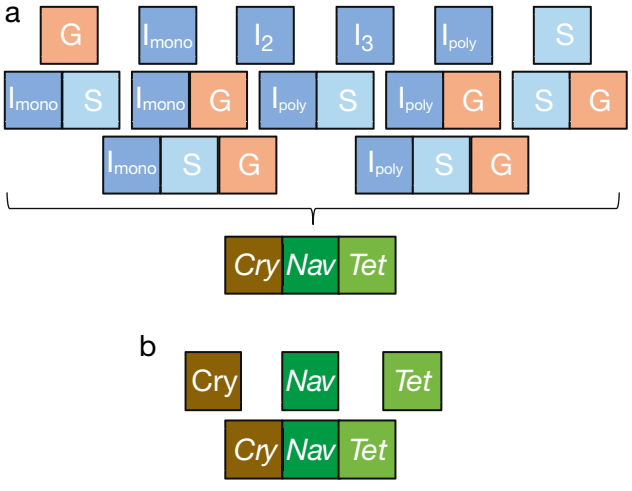


Fig. 2. Schematic representation of the experimental set-up. (a) The main experiment consisted of 3 levels of ciliate diversity. Top row: monoculture treatments of generalist (G), specialist (S) and intermediate (I) clones $I_{mono}$, $I_2$, $I_3$ plus a polyclonal I treatment ($I_{poly}$). 2nd row: 2-species combination treatments: all possible combinations of G, S, $I_{mono}$ and $I_{poly}$. 3rd row: 3-species combination treatments: all possible combinations of G, S, $I_{mono}$ and $I_{poly}$. Bottom row: microalgal food (*Cry*: *Cryptomonas*, *Nav*: *Navicula*, *Tet*: *Tetraedron*); all ciliate treatments were supplied with the same combination of all 3 species of microalgal prey. (b) Monocultures and polycultures of the microalgae *Cry*, *Nav* and *Tet* were used as algal controls

hand to ensure a homogenous distribution of (3) organisms. All culture work was done under sterile conditions. The experimental temperature (18°C) was kept constant using a culture cabinet (Rumed, Rubarth Apparate). Light intensity of 70 ± 5 µmol $m^{-2}$ $s^{-1}$ was supplied at a day:night cycle of 12:12 h. The slightly uneven light distribution was accounted for by randomly re-arranging the flasks in the light field every second day.

Samples were taken from the culture volume that was replaced by new medium every second day. Samples for microscopical analysis of ciliate and microalgal abundance (10 ml) were fixed with Lugol's solution (1% final concentration) and stored in brown glass bottles. Samples for analysis of the dissolved fraction of nutrients were taken every fourth day, filtered using syringe filters (0.2 µm, cellulose acetate, Macherey-Nagel) and stored frozen until analysis.

### Sample and data analyses

Soluble reactive fractions of nitrogen and phosphorus and silicate concentration were analysed using a Scalar analytical auto-analyser (San$^{++}$ System, Scalar Analytical), following the methods published by Grasshoff et al. (1999).

Algal abundance was analysed microscopically counting at least 400 cells per sample (Lund et al. 1958), ciliates were counted determining the total abundance in a subsample sized 1–2 ml. Prior to the experiment, the dimensions of 20 living individuals of each ciliate and algal species were determined using the digital image system program (Cell-P). These were used to calculate the average specific biovolume (Hillebrand et al. 1999). These data were then used to calculate total population and community biovolume ($B_{tot}$) and relative biovolume and the evenness index ($J$):

$$J = \frac{H_B'}{H_B'_{max}} \quad (1)$$

and

$$H_B' = -\sum p_i \ln p_i \quad (2)$$

where $H_B'$ denotes the Shannon index, $H_B'_{max}$ denotes the theoretical diversity maximum (= ln [species richness]), and $p_i$ is the relative proportional contribution of species $i$ to total biovolume (Pielou 1975). Growth rates were calculated based on biovolume according to:

$$\mu = \frac{\ln B_2 - \ln B_1}{t_2 - t_1} \quad (3)$$

where µ denotes the specific growth rate $d^{-1}$, which was calculated between Days 3 and 7 ($t_1$ and $t_2$) of the experiment, and $B_1$ and $B_2$ denote the total community biovolume at $t_1$ and $t_2$, respectively. To be able to calculate growth rates in cases when the abundance of a species was below the detection limit of our counting method (see above), we made the assumption that the abundance equalled half the detection limit.

Ciliate grazing rates, also based on biovolume, can be calculated by subtracting the growth rates of the microalgal prey species within the ciliate treatments from the growth rates these species showed in the algal controls. *Nav* did not grow well in all replicates of the controls, but grew better in the experimental treatments with consumers, where it presumably used dissolved organic matter in addition to inorganic nutrients provided with the growth medium. We therefore used the growth rate of *Nav* in the S monoculture treatment to calculate ciliate grazing rates for *Nav*. Since S fed only on *Cry*, there was no grazing pressure on the other microalgae in this treatment.

### Statistical analysis

Due to fast-developing dominances at the consumer level, experimental results were only considered up to Day 7 after inoculation. Consumer dominances were established and resources depleted beyond Day 7, so that those data were not useful for our purposes. The effects of species and clonal diversity of the ciliate consumers were tested using a 1-way analysis of variance (ANOVA), with ciliate species or clonal combination as the independent factor and total ciliate biovolume, grazing rate, total algal biovolume, evenness of the algal community and net growth rates of the algal prey species as response variables. In doing so, unequal treatment levels and incomplete nested designs could be avoided. In case of significant treatment effects, 4 planned comparisons (PCs) among different consumer treatment groups were performed: (1) monocultures versus polycultures, (2) 2-species combinations versus 3-species combinations, (3) $I_{mono}$ versus $I_{poly}$ and (4) all combinations comprising $I_{mono}$ versus combinations comprising $I_{poly}$.

One outlier was removed from the analysis. Compared to all other treatments and replicates, replicate 2 of the consumer combination $I_{mono}$+G had very low

ciliate and microalgae biomass and contained an extremely high concentration of bacteria and heterotrophic flagellates.

## RESULTS

### Consumer biovolume and growth rates

Ciliate biovolume on Day 7 showed significant differences in response to the experimental treatments (1-way ANOVA, $p < 0.001$, Table 2, Fig. 3a; for graphs showing the time course of ciliate biovolume, see Figs. S1–S3 in the Supplement at www.int-res.com/articles/suppl/a081p243_supp.pdf). The average total ciliate biovolume significantly increased with increasing ciliate diversity (PC 1: polycultures > monocultures, PC 2: 3-species combinations > 2-species combinations, $p < 0.001$, Table 2, Fig. 3a). Intraspecific ciliate diversity also increased average ciliate biovolume; biovolume in the polyclonal $I_{poly}$ monoculture exceeded the average of the monoclonal monocultures $I_{mono}$, $I_2$ and $I_3$, and biovolume in consumer combinations comprising polyclonal $I_{poly}$ were significantly higher on average than combinations containing monoclonal $I_{mono}$ (PC 3 and 4: $p < 0.001$, Table 2, Fig. 3a, see Figs. S1–S3 for differences between monoclonal and polyclonal I monocultures over time).

The generalist *Stylonychia* sp. (G) produced the highest biovolume in monoculture treatments, followed by the intermediate consumer *Coleps hirtus* (I) and then the specialist *Euplotes octocarinatus* (S), which produced the lowest biovolume (Fig. 3a). Species dominances developed fast between Day 3 and Day 7 of the experiment (Figs. S1–S3). In 2- and 3-species combinations, ciliate biovolume was high wherever G was included (Fig. 3a). These treatments were dominated by G (Fig. 3b), which was due the high growth rates G displayed in all of these treatments (Fig. 3c). The specialist consumer S was still present, but contributed little to the total ciliate biovolume in 2- and 3-species combinations (Fig. 3b). In fact, S did not grow in either of the experimental treatments (Fig. 3c). The intermediate consumer I dominated in 2-species combinations with S, but could not be detected or was close to the detection level in 2- and 3-species combinations comprising G (Fig. 3b). $I_{poly}$ showed high growth rates especially in the $I_{poly}$+S treatment. In any species combination including G, however, the growth rate of I was negative (Fig. 3c).

### Microalgal prey biovolume and evenness

Consumer species and clonal combination significantly affected total microalgal biovolume and evenness on Day 7 of the experiment (1-way ANOVA, $p < 0.001$, Table 2, Fig. 4a,c; see Figs. S1–S3 for graphs showing the time course of algal biovolume). Both inter- and intraspecific consumer diversity decreased prey evenness (PC 1: polycultures < monocultures; PC 2: 3-species combinations < 2-species combinations; PC 3: polyclonal $I_{poly}$ monoculture < monoclonal I monocultures; PC 4: polyclonal $I_{poly}$ polycultures < monoclonal $I_{mono}$, $I_2$, $I_3$ polycultures, $p < 0.05$, Table 2, Fig. 4b,c). In contrast, the effects of inter- and intraspecific consumer diversity on total microalgal biovolume differed. While algal biovolume significantly increased with ciliate species diversity (PC 1: polycultures > monocultures; PC 2: 3-species combinations > 2-species combinations, $p < 0.01$, Table 2, Fig. 4a), it was

Table 2. One-way ANOVA results and planned comparisons for total ciliate biovolume, total microalgal biovolume and evenness of the microalgal community. Data were ln-transformed to achieve homoscedasticity. Degrees of freedom in the error term were 25. I: intermediate

| | Total ciliate biovolume | | Total microalgal biovolume | | Evenness microalgae | |
|---|---|---|---|---|---|---|
| | *F* | p | *F* | p | *F* | p |
| One-way ANOVA result (df = 12) | 238.2 | <0.001 | 48.4 | <0.001 | 16.3 | <0.001 |
| Planned comparisons (df = 4) | 208.3 | <0.001 | 19.0 | <0.001 | 25.3 | <0.001 |
| (1) Mono- vs. polycultures | | <0.001 | | <0.001 | | <0.001 |
| (2) 2-species vs. 3-species combinations | | <0.001 | | <0.01 | | <0.001 |
| (3) Monoclonal *Coleps hirtus* (I) monocultures vs. polyclonal ($I_{poly}$) monocultures | | <0.001 | | <0.01 | | <0.001 |
| (4) Consumer combination comprising $I_{mono}$ vs. combinations comprising $I_{poly}$ | | <0.001 | | <0.702 | | <0.05 |

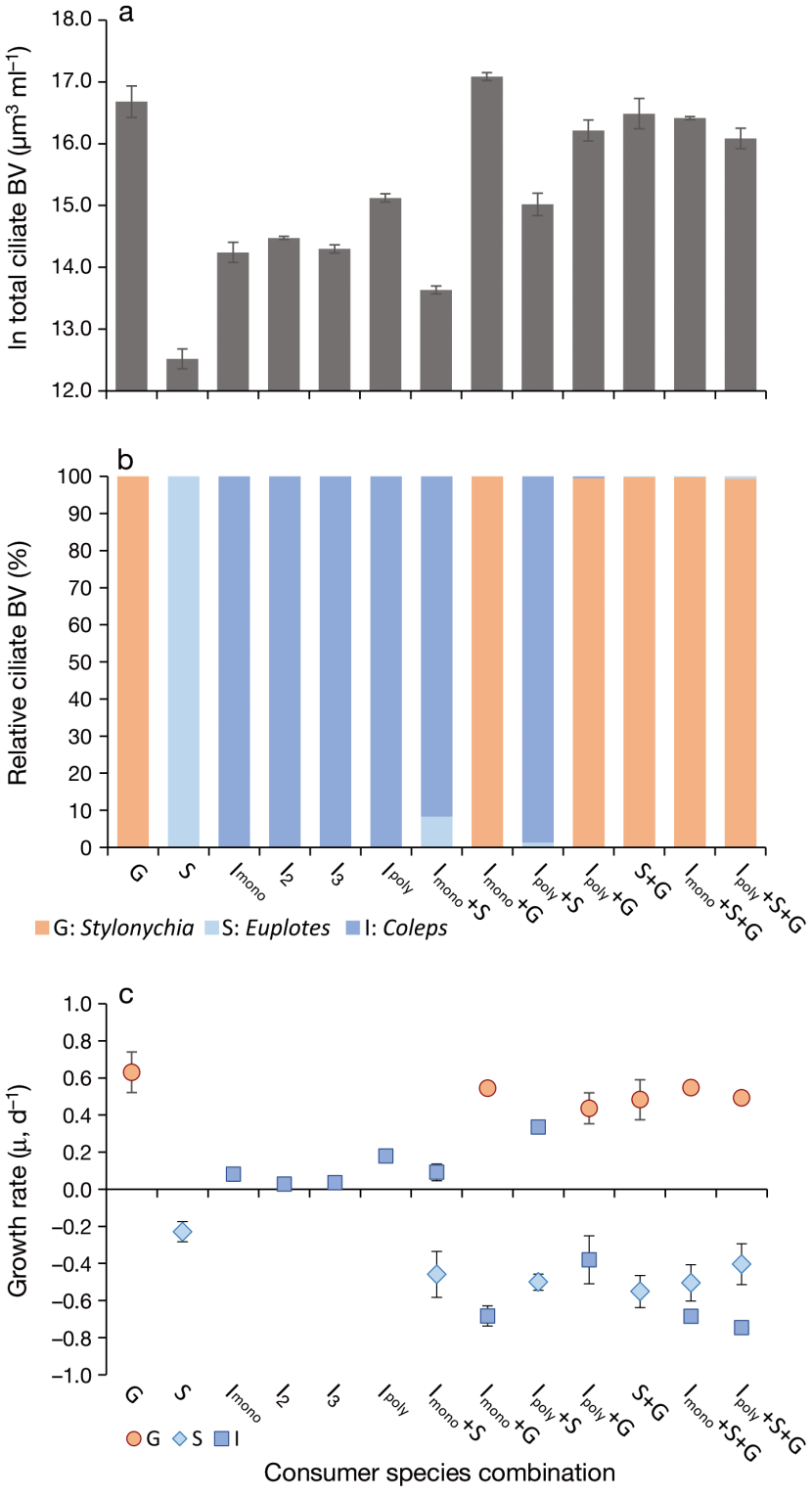


Fig. 3. Ciliate biovolume (BV), log-transformed at the end of the experiment (Day 7). (a) Total ciliate BV, error bars represent SD. (b) Percent contribution of the species *Stylonychia* sp., *Euplotes octocarinatus* and *Coleps hirtus* to the total ciliate BV. (c) Ciliate growth rates. G: generalist, I: intermediate grade of specialisation, S: specialist, $I_{mono}$: clone intermediate 1, $I_2$: clone intermediate 2, $I_3$: clone intermediate 3, $I_{poly}$: polyclonal intermediate

lower in polyclonal I monocultures compared to monoclonal ones (PC 3, $p < 0.01$, Table 2, Fig. 4a).

The highest microalgal biovolume was observed in the S monoculture, whereas it was much lower (and in the same range) in the G and I monocultures. *Tet* accounted for the majority of the microalgal biovolume and dominated in all ciliate combinations (>80%, except for treatment $I_3$, Fig. 4b). Percent *Nav* biovolume ranged from 2% in the 2-species combination $I_{mono}$+S to 20% in the G monoculture (Fig. 4b). The relative *Cry* biovolume was <1% in $I_2$, polyclonal $I_{poly}$ and 2-species combination $I_{mono}$+G. In the G monoculture treatment, the 2-species combination S+G and the 3-species combinations, this species was below the detection level. Consequently, evenness was low in these treatments (Fig. 4c).

### Consumer grazing rates, prey growth rates and resource concentrations

Consumer grazing rates and the growth rate of the prey community were also strongly affected by consumer species and clonal combination (1-way ANOVA, $p < 0.001$, Table 3, Fig. 5). Grazing rates for the most preferred algal prey *Cry* significantly increased with consumer species diversity (PC 1 and 2, $p < 0.001$, Table 3, Fig. 5), whereas average grazing rates for the less preferred algae *Nav* and *Tet* were lower in consumer mixtures compared to monocultures, and in 2-species combinations compared to 3-species combinations (PC 1 and 2, $p < 0.05$, Table 3, Fig. 5). Highly grazed upon, the growth rate of *Cry* was negative in most consumer treatments. Experiencing reduced grazing pressure in polycultures, *Nav* and *Tet* grew faster than in consumer monocultures (data not

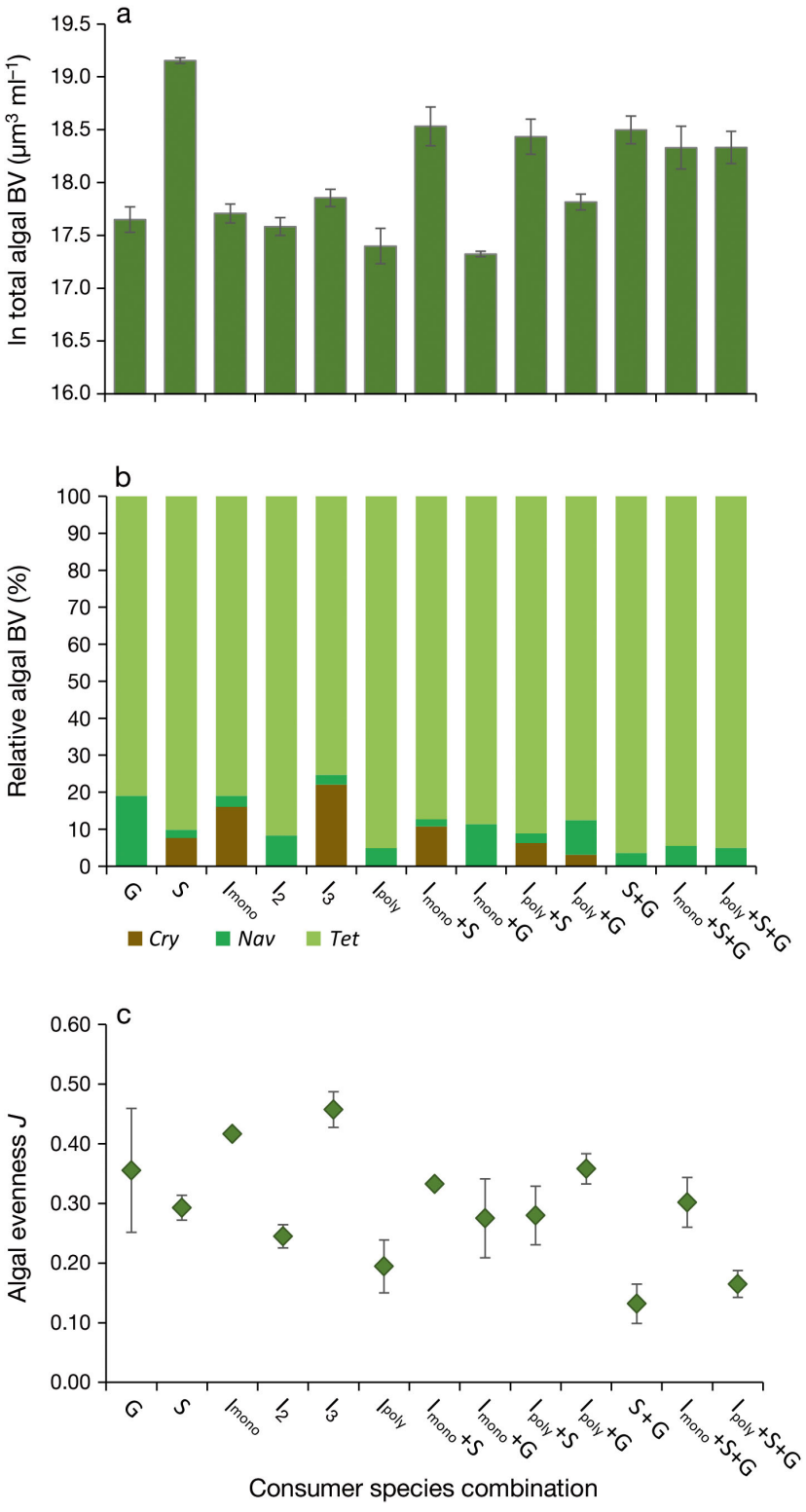


Fig. 4. Microalgal biovolume (BV), log-transformed at the end of the experiment (Day 7). (a) Total microalgal BV. (b) Percent contribution of the species *Cryptomonas* sp. (*Cry*), *Navicula pelliculosa* (*Nav*) and *Tetraedron minimum* (*Tet*) to the total microalgal BV. (c) Pielou's evenness index (*J*) based on BV. Error bars represent SD. Abbreviations as in Fig. 3

shown). Due to the growth response of *Nav* and *Tet*, the average community growth rate of the microalgal prey increased with ciliate species diversity (PC 1 and 2, $p < 0.001$, Table 3, Fig. 5).

The average grazing rate for *Cry* in monocultures containing the polyclonal $I_{poly}$ significantly exceeded the one for monocultures containing monoclonal I populations (PC 3, $p < 0.001$, Table 3). However, this effect could not be observed for multispecies combinations containing polyclonal populations of I. In contrast, average grazing rates for both *Cry* and *Tet* were lower in consumer combinations containing monoclonal I populations as opposed to monoclonal ones (PC 4, $p < 0.05$, Table 3, Fig. 5). No difference in total prey community growth rate was detected among mono- and polyclonal treatment combinations (Table 3, Fig. 5).

*Cry* was heavily consumed in all treatments except for the S monoculture, with the highest grazing rates recorded in the G monoculture, the 2-species combination S+G and the 3-species combinations (Fig. 5). *Tet* was consumed at low rates by G and the monoclonal and polyclonal I monocultures. It was also grazed upon in 2-species combinations comprising I and G, but not in 3-species combinations. *Nav* was not consumed in G and S monocultures and in 3-species combinations. The highest growth rates were recorded for *Tet*. *Nav* growth rates were positive in all treatments except in the monoclonal $I_3$ treatment.

The concentrations of silicate (Si) and soluble reactive phosphorus (SRP) decreased between Day 3 and Day 7 of the experiment to approximately 50% and 75%, respectively, while the concentration of the limiting nutrient nitrogen was getting depleted in nearly all treatments from Day 3 to Day 7, except for the monocultures G and $I_2$ (Fig. 6).

Table 3. One-way ANOVA results and planned comparisons for consumer grazing rates. Since *Cryptomonas* (*Cry*), *Navicula* (*Nav*) and *Tetraedron* (*Tet*) grazing rates were homoscedastic, untransformed data were used for the analysis. Degrees of freedom in the error term were 25. I: intermediate

| | Consumer grazing rates | | | | | | Growth rate Prey community | |
|---|---|---|---|---|---|---|---|---|
| | *Cry* | | *Nav* | | *Tet* | | | |
| | *F* | p | *F* | p | *F* | p | *F* | p |
| One-way ANOVA result (df = 12) | 1077 | <0.001 | 4.64 | <0.001 | 10.17 | <0.001 | 21.27 | <0.001 |
| Planned comparisons (df = 4) | 894.3 | <0.001 | 4.36 | <0.01 | 7.50 | <0.001 | 9.77 | <0.001 |
| (1) Mono- vs. polycultures | | <0.001 | | <0.01 | | <0.001 | | <0.001 |
| (2) 2-species vs. 3-species combinations | | <0.001 | | <0.05 | | <0.01 | | <0.001 |
| (3) Monoclonal *Coleps hirtus* (I) monocultures vs. polyclonal ($I_{poly}$) monocultures | | <0.001 | | <0.869 | | <0.631 | | <0.303 |
| (4) Consumer combinations comprising $I_{mono}$ vs. combinations comprising $I_{poly}$ | | <0.001 | | <0.416 | | <0.05 | | <0.405 |

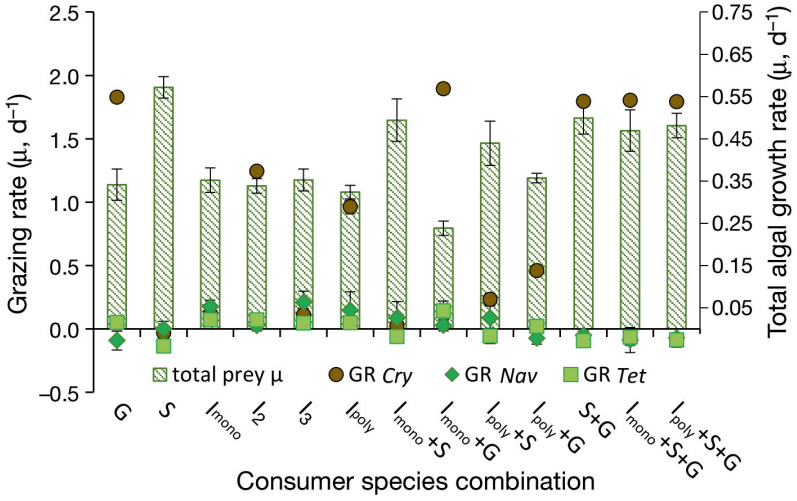


Fig. 5. Consumer grazing rates and community growth rate (GR) of the microalgal prey. Error bars represent SD. Abbreviations as in Fig. 3. *Cry*: *Cryptomonas* sp., *Nav*: *Navicula pelliculosa*, *Tet*: *Tetraedron minimum*

## DISCUSSION

Both inter- and intraspecific consumer trait variation strongly determined ciliate consumer and algal prey biovolume, as well as community composition. Total consumer biovolume increased with increasing inter- and intraspecific consumer trait variation. At the level of interspecific consumer trait variation, this positive diversity effect on consumer production was due to the presence of a very productive and competitively superior consumer species that was able to feed not only on all species of microalgal prey, but also on other ciliates, thus acting as an intraguild predator (partly supporting $H_{1a}$). At the level of intraspecific consumer trait variation, on the other hand, complementary feeding niches among different clones led to higher biovolume production based on higher resource use efficiency (supporting $H_{1b}$). Total prey biovolume increased with increasing interspecific consumer trait variation (refuting $H_{2a}$), but decreased with increasing intraspecific consumer trait variation (supporting $H_{2b}$). Both inter- and intraspecific consumer diversity decreased prey evenness. At the species level, this effect was determined by the highly selective feeding behaviour of the generalist consumer, resulting in unequal grazing pressure on the prey community (partly refuting $H_{3a}$). The effect of intraspecific consumer trait variation on prey evenness depended on clone-specific feeding preferences and grazing rates on particular prey (confirming $H_{3b}$).

### Effects of consumer trait variation on the consumer level

On average, total consumer biovolume in our experiment increased with increasing interspecific consumer trait variation. This effect, however, was not based on consumer niche complementarity, leading to a more efficient use of resources (Tilman et al. 1997). Instead, it was based on the presence of a very productive and competitively superior species (Loreau & Hector 2001), the generalist consumer *Stylonychia* sp. (G). Therefore, $H_1$ could only partly be supported in our study. The generalist consumer G displayed growth rates far above the ones of the other consumers. Also showing competitive superiority in the presence of other ciliate consumers, G was the most productive species in our study and rapidly gained

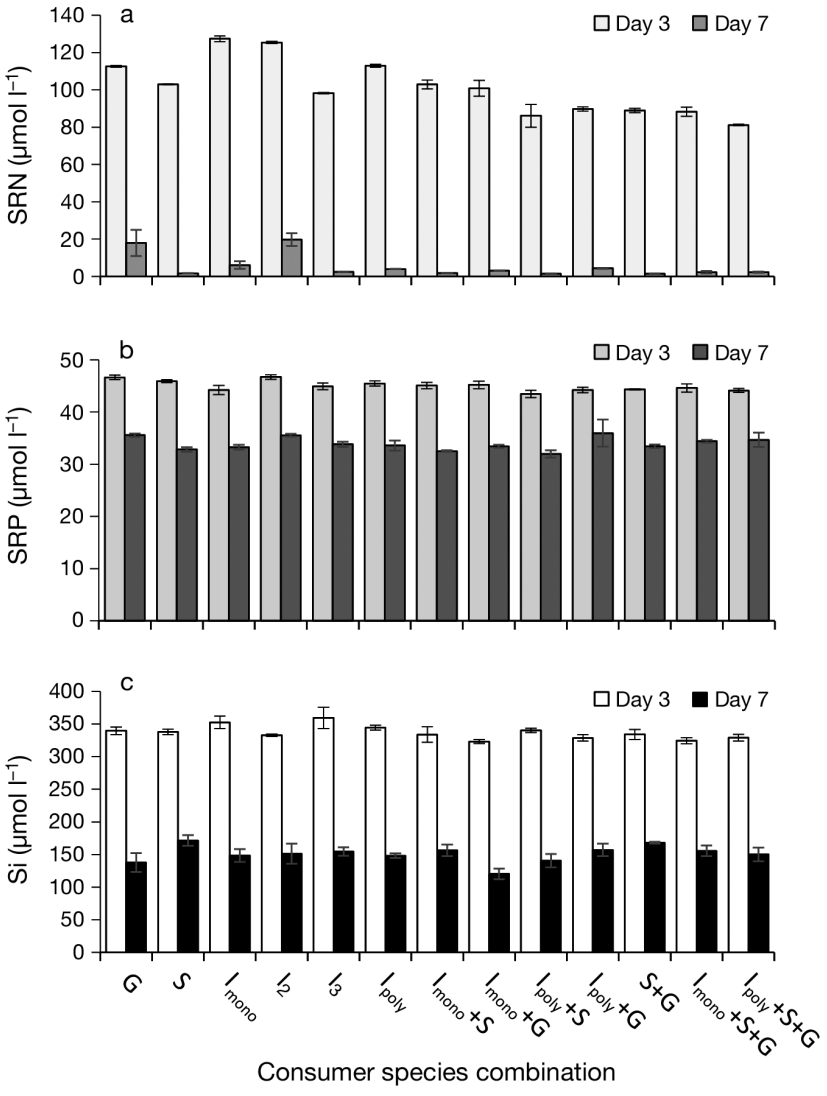


Fig. 6. Nutrient concentrations on Day 3 and at the end of the experiment (Day 7). (a) Soluble reactive nitrogen (SRN), (b) soluble reactive phosphorus (SRP), (c) silicate (Si). Error bars represent SD. Abbreviations as in Fig. 3

dominance in every treatment in which it was included. The positive consumer species diversity effect on consumer biovolume can therefore be attributed to this high performing species (Loreau & Hector 2001).

The ability of G to feed and grow on all 3 of the microalgal prey species offered in the experiment had been verified in prior feeding trials on algal monocultures. In algal mixtures, however, G showed a high degree of selectivity within its feeding niche, grazing mainly on *Cry*, ingesting only a small quantity of *Tet* and avoiding *Nav*. These results support the findings of Wohlgemuth et al. (2017), who demonstrated that not only the degree of specialisation, but also the selectivity for certain prey species within the dietary niche may play an important role in altering the consequences of diversity loss in a food web context (see below). In addition to feeding on algal prey, G formed giant morphotypes during the experiment that fed as intraguild predators (IGPs) on the other, smaller ciliates, but mainly on the intermediate consumer *Coleps hirtus* (I).

Omnivory in *Stylonychia* has previously been described (Giese & Alden 1938, Wiąckowski et al. 2004). A filter feeder with low mobility when feeding on small microalgal prey, the species becomes a raptorial feeder when feeding on ciliates (Wiąckowski et al. 2004). This type of phenotypic plasticity, resulting in morphological and behavioural changes in the consumer, has been characterised as an inducible offence (Kopp & Tollrian 2003), enabling the consumer to prey on organisms of its own trophic guild, either on different species, or on individuals of its own species by exhibiting cannibalism (Banerji & Morin 2014). In *Stylonychia*, this mechanism is related to shortages in microalgal prey (Giese & Alden 1938, Wiąckowski et al. 2004). In our experiment, however, microalgal prey was still abundant when G formed giant morphotypes and selectively fed on other ciliates. Therefore, it can be assumed that either the remaining algae (mainly *Tet* and to a lesser extent *Nav*) were not a sufficient food source for G (resulting in resource depletion), or that ciliate competitors released certain chemical cues (Banerji & Morin 2009), or mechanical cues (Wiąckowski et al. 2004) induced this morphological change, as was shown for other ciliates. The fact that G mainly fed on the intermediate consumer I can be deduced from the strong negative growth rates I showed when combined with G, and the fact that on Day 7 of the experiment, I was already below or close to the detection level in these treatments. Losses of the specialist consumer *Euplotes octocarinatus* (S) were more likely due to competitive exclusion rather than G preying on it, since this species showed similar negative growth rates in all ciliate species combinations. Furthermore, S exhibited a predator-induced defence in our experiment, a morphological

change through cell enlargement (Kuhlmann & Heckmann 1985). These larger morphotypes of S could not easily be ingested by the *Stylonychia* sp. giants, and were still present in low abundances on Day 7 of the experiment. Inducible defences have been reported for many species and across a wide range of taxa. They include changes in behaviour, morphology and life history that influence the interaction between prey and predators, and between competitors (Tollrian & Harvell 1999). In contrast to inducible defences, inducible offences of predators in response to prey limitation have received considerably less attention and remain greatly underappreciated (e.g. Kopp & Tollrian 2003, Mougi et al. 2011, Banerji & Morin 2014).

The strategy of eating its competitor (see Thingstad et al. 1996) shown by G in our experiment represents a competitive advantage for the consumer. Such intraguild predation can lead to stable coexistence only when grazing and growth rates of the IGP are low compared to the other competitors in the system (Morin 1999). In our system, however, G was the strongest competitor in its trophic guild, exhibiting the highest grazing and growth rates in combination with intraguild predation, consequently controlling other consumers and their prey, except for S, which was able to escape predation due to its own phenotypic plasticity. Overall, trophic interactions and interspecific consumer diversity effects in our system were not only determined by consumer selectivity and specific grazing rates, but by much more complex interactions, such as selective grazing within dietary niches and phenotypic plasticity, resulting in induced offence in one and induced defence in another consumer.

Increased intraspecific consumer trait variation also led to an increased consumer biovolume. The polyclonal I monoculture biovolume exceeded the biovolume of all monoclonal ones (transgressive overyielding [see Tilman et al. 1997, Fridley 2001], supporting $H_{1b}$. Here, the different clones varied in their specific feeding niches, resulting in niche complementarity (Tilman et al. 1997). The *Coleps hirtus* clone $I_2$ mainly fed on *Cry*, while $I_{mono}$ and $I_3$ both grazed on *Nav* and *Cry*; however, $I_3$ ingested more *Nav* than $I_{mono}$. Although small quantities of *Tet* were ingested by all I clones, $I_3$ had the lowest grazing rate for this species. This niche complementarity in polyclonal I populations likely resulted in a more efficient resource use than in the monoclonal populations and thus in higher biovolume production (Tilman et al. 1997). Furthermore, polyclonal I populations may have been more resistant to grazing by G due to the higher biovolume production (see Figs. S1–S3 in the Supplement for detailed information on the development of G and I populations), since the probability of individual organisms being eaten is reduced when population density is high (Molles 2002). Alternatively, differences in their feeding preferences may have resulted in altered food quality of different I clones, which might have affected the chance of being ingested by highly selective G. Another possibility is that the attack rate by G differs among clones, as the I clones show differences in swimming behaviour. The positive effect of intraspecific trait variation on consumer biovolume could also be observed in multispecies consumer combinations, as consumer biovolume in combinations including polyclonal I was significantly higher than in the same species combinations containing monoclonal populations of I. Our results are consistent with Crutsinger et al. (2006), who demonstrated the effects of intraspecific trait variation of the old-field plant species *Solidago altissima* to cascade across trophic levels. Genotypic diversity has also been shown to increase productivity in marine invertebrates (Aguirre & Marshall 2012) and honey bees (Mattila & Seeley 2007), which further emphasises the importance of intraspecific trait variation for ecosystem functioning.

Positive consumer diversity effects leading to increased secondary production based on niche complementarity have also been demonstrated on an interspecific level in various previous studies. Increased consumer species richness resulted in higher biomass production in microbial microcosms (Gamfeldt et al. 2005, Moorthi et al. 2008, Filip et al. 2012, 2014) and marine seagrass mesocosms (Duffy et al. 2003). Our study demonstrates that intraspecific consumer trait variation might be as important as interspecific trait variation in this context.

### Effects of consumer trait variation on the prey level

Total biovolume of the microalgal prey community increased with increasing consumer species richness and thus interspecific consumer trait variation, refuting $H_{2a}$. Rather than displaying a more efficient resource use due to increased trait variation, consumers in multispecies combinations fed selectively on algal mixtures. *Tet* was avoided in most consumer polycultures and experienced only small grazing losses in G and I monocultures. Grazing pressure on *Cry* was high, especially in 3-species consumer combinations. This can be attributed to the selective feeding behaviour of the highly productive G, which

dominated all species combinations where it was included (see above). *Tet* dominated in all ciliate combinations. Fast-growing species like the small coccoid green algae *Tet* are known to use phases of high resource availability for unlimited growth. These species gain dominance and continue increasing in abundance until population growth is reduced by increasing resource limitation (Reynolds et al. 1993, Flöder et al. 2006). At the end of our experiment, nitrogen was limiting and competition for resources became more important than the capacity for growth. The increased grazing pressure on *Cry* and *Nav* in ciliate polycultures released *Tet* from competition for nitrogen. Competitive release in combination with a low grazing pressure enabled *Tet* to use the available nutrients to produce a very high biovolume. As a result, total prey biovolume increased with increasing consumer trait variation. A similar increase in feeding-resistant algae with increasing consumer diversity has been reported in other studies on consumer diversity effects in aquatic systems (e.g. Steiner et al. 2005).

In contrast to interspecific consumer trait variation, intraspecific trait variation led to a decrease in prey biovolume. As detailed above, the different I clones varied in their specific feeding niches, resulting in niche complementarity among the clones and thus a more efficient resource use in the polyclonal populations of I compared to the monoclonal ones. This in turn resulted in a lower prey biovolume, supporting $H_{2b}$.

Evenness of the microalgal prey community decreased with both inter- and intraspecific consumer trait variation. Although prey evenness was clearly affected by interspecific trait variation, $H_{3a}$ has to be partly refuted. Instead of showing the expected equal grazing pressure on the prey community, the high selectivity of G exerted an unequal grazing pressure on the prey community, as did the specialists. Selective grazing decreased prey evenness, since all consumers preferred *Cry*, which led to a strong biovolume reduction of this prey species in polycultures, even to biovolumes below the detection limit (see e.g. Porter 1977, Hillebrand & Shurin 2005, Flöder & Sommer 2006). This decrease in prey evenness with increasing consumer trait variation, however, is attributed to a combination of mechanisms: presence of a competitively superior consumer species (Loreau & Hector 2001) that selectively fed on *Cry*, intraguild predation that further promoted the dominance of G, and the capacity of *Tet* for fast reproduction. This emphasises the importance of consumer-mediated growth responses of the prey (i.e. prey's capacity to grow better when released from competition and grazing pressure) in determining the strength and direction of biodiversity effects across trophic levels. Our results contrast the study of Filip et al. (2014), where specialist consumers decreased prey evenness more strongly than generalist consumers, again indicating that not only consumer selectivity, but also specific feeding preferences within dietary niches may determine consumer diversity effects in consumer–prey systems (Montagnes et al. 2008).

Increased intraspecific consumer trait variation also led to a decrease in prey evenness. Regarding consumer specialisation among the different clones of the intermediate consumer I as a spectrum ranging from generalists to specialists, $I_{mono}$ and $I_3$ were closer to the generalist end than $I_2$, which showed a strong preference for *Cry*. As a consequence of the more equal grazing pressure of $I_{mono}$ and $I_3$, prey evenness in $I_{mono}$ and $I_3$ monocultures was higher than in the $I_2$ monoculture, which supports $H_{3b}$. This pattern corroborates the results of Filip et al. (2014) on the level of intraspecific trait variation, according to which specialist consumers decrease prey evenness more strongly than generalist consumers. This result also emphasises the importance of intraspecific trait variation for BDEF research, as its impact on ecosystem functions might well be comparable to interspecific trait variation (Bolnick et al. 2003, Hughes et al. 2008).

## CONCLUSION

Overall, our study demonstrated that both inter- and intraspecific consumer trait variation affected consumer and prey biomass, as well as community composition, indicating that effects on both hierarchical levels may be equally strong in determining the consequences of consumer diversity loss on ecosystem functioning. In our study, inter- and intraspecific effects of consumer trait variation differed and were based on different mechanisms. Interspecific consumer diversity effects were driven by a strong selection effect of a competitively superior species (G) that exhibited strong feeding selectivity despite its wide dietary niche, while intraspecific consumer diversity effects were determined by niche complementarity and more efficient resource use. Our study further demonstrated that trophic interactions in our system were not only determined by selectivity and grazing rate of the consumers and corresponding edibility and growth rate of the prey. Instead, additional consumer-specific traits such as selective feed-

ing within dietary niches and phenotypic plasticity (induced offence and defence) were of at least equal importance. Although our study was conducted with a simple ciliate–microalgae model system using highly controlled laboratory microcosms, the mechanisms we observed are most likely also relevant for natural systems, as the trophic complexity inherent in our system well reflects the complexity of trophic interactions and the adaptive potential inherent in food webs of higher organisms.

*Acknowledgements.* This work was funded by the German Research Foundation (DFG, MO 1931/3-1). We thank Heike Rickels for conducting the nutrient analysis.

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*Editorial responsibility: Urania Christaki, Wimereux, France*

*Submitted: August 8, 2017; Accepted: December 29, 2017*
*Proofs received from author(s): May 1, 2018*