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Dispersal mitigates bacterial dominance over microalgal competitor in metacommunities

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Abstract

Ecological theory suggests that a combination of local and regional factors regulate biodiversity and community functioning in metacommunities. The relative importance of different factors structuring communities likely changes over successional time, but to date this concept is scarcely documented. In addition, the few studies describing successional dynamics in metacommunity regulation have only focused on a single group of organisms. Here, we report results of an experimental study testing the effect size of initial local community composition and dispersal between local patches on community dynamics of benthic microalgae and their associated bacteria over community succession. Our results show that over time dispersal outweighed initial effects of community composition on microalgal evenness and biomass, microalgal β -diversity, and the ratio of bacteria to microalgae. At the end of the experiment (ca. 20 microalgal generations), dispersal significantly decreased microalgal evenness and β -diversity by promoting one regionally superior competitor. Dispersal also decreased the ratio of bacteria to microalgae, while it significantly increased microalgal biomass. These results suggest that the dispersal-mediated establishment of a dominant and superior microalgal species prevented bacteria from gaining competitive advantage over the autotrophs in these metacommunities, ultimately maintaining the provision of autotrophic biomass. Our study emphasizes the importance of time for dispersal to be a relevant community-structuring mechanism. Moreover, we highlight the need for considering multiple competitors in complex metacommunity systems to properly pinpoint the consequences of local change in dominance through dispersal for metacommunity function.

Keywords Community composition · Ecological succession · Competition · Interaction · Microcosm

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Introduction

Community ecology has largely focused on understanding how distinct factors regulate species diversity, with direct implications for ecosystem functioning. By describing how both, local and regional factors affect local species interactions and thus regulate diversity in ecological communities, the metacommunity concept has become irreplaceable in community ecology (Gilpin and Hanski 1991; Wilson 1992; Leibold et al. 2004; Holyoak et al. 2005). Dispersal is a regional factor that can significantly influence local-scale interactions. Dispersal-limitation can facilitate competitive exclusion and thus increase the dominance of the best-adapted local competitor, thereby decreasing local diversity (Mouquet and Loreau 2003). Low to intermediate dispersal can mitigate local competitive exclusion and thus increase local and regional diversity either by exhibiting a trade-off between competitive and dispersal abilities (Levins

and Culver 1971; Cadotte et al. 2006) and/or by promoting source-sink dynamics (Mouquet and Loreau 2003). In contrast, by favoring the best regional competitor, high dispersal often enhances local and regional competitive exclusion, and in consequence decreases local and regional diversity (Mouquet and Loreau 2003; Matthiessen et al. 2010).

Another important community-structuring factor is the initial local community composition, that can determine the course of local-scale interactions and thus the structural and functional fate of the community. In experimental communities, the initial composition can have comparable effects to those of priority effects in natural systems, either due to the complete presence/absence of specific species or due to varying dominance patterns. Priority effects occur when first colonizers have a competitive advantage over later arrivals by monopolizing shared local resources (Urban and de Meester 2009; Fukami et al. 2010; de Meester et al. 2016 and references therein). This concept can be further extended to initially dominant species that have an advantage over initially rare species in experimental and simulated communities (Shurin et al. 2004; Eggers and Matthiessen 2013).

Despite extensive information on how regional factors (i.e. dispersal) and initial community composition affect local species interactions separately, their relative importance for metacommunity diversity and functioning throughout community succession remains elusive. Though other metacommunity studies have touched upon the effect of dispersal and/or initial composition on local-scale interactions (Fukami et al. 2005; Limberger and Wickham 2012; Pu and Jiang 2015; Zha et al. 2016; Sferra et al. 2017), collectively the results are, to some extent, inconclusive. In fact, the importance of dispersal for structuring communities should change with time and depend on the intensity of dispersal. Specifically, we expect that under dispersal limitation, initial community composition should remain important longer than in communities with dispersal.

Our study system consisted of benthic microalgae communities collected from an intertidal flat. In intertidal ecosystems, benthic microalgae are key organisms that provide up to 50% of the total primary production and fuel the benthic food web (Underwood and Kromkamp 1999). Benthic microalgae are characterized by relatively short generation times with up to one cell division per day under favorable conditions (Underwood and Paterson 1993) and by different degrees of attachment to the substrate (Svensson et al. 2014). On soft-bottom intertidal flats, these unicellular eukaryotic algae are often dominated by epipellic diatoms that can reposition themselves actively in biofilms (Admiraal et al. 1984; MacIntyre et al. 1996; Underwood and Smith 1998).

In nature, benthic microalgae occur in association with heterotrophic bacteria (Decho 2000), that utilize the algae's vast carbon exudates as energy sources (Bratbak and Thingstad 1985; Thingstad and Pengerud 1985; Danger

et al. 2007) and in exchange provide the algae with specific chemical compounds such as vitamins (Cole 1982; Amin et al. 2012). Associated bacteria and algae form extensive biofilms covering the sediment surface of coastal ecosystems worldwide (Decho 2000). Microalgae and bacteria in these biofilms compete for inorganic nutrients, especially phosphate (Thingstad and Pengerud 1985; Jansson 1988; Danger et al. 2007). Under replete nutrient conditions, as is the case in many temperate coastal systems, microalgae and their associated bacteria coexist (Thingstad and Pengerud 1985; Grover 2000), with the algae being the superior competitors. However, once phosphate becomes limiting, bacteria often outperform the algae as the bacterial nutrient uptake affinity is higher (Jansson 1988; Thingstad et al. 1993; Løvdal et al. 2007).

In this manuscript, we present results from a laboratory experiment aiming to resolve the question of whether initial community composition and dispersal are equally important for attenuating or promoting local and regional dominance at early compared to late successional time. We hypothesized that initial species composition determines community structure and functioning at early succession and under dispersal limitation, while dispersal increases in importance through time, determining metacommunity structure and functioning at late successional stages.

Materials and methods

Sediment sampling, extraction of microalgae, and establishment of algae cultures

We collected biofilm samples from three distinct locations (hereafter referred to as local community A, B, and C) on a mudflat off the Dutch Island of Schiermonnikoog in the Wadden Sea in September 2014. The exact locations of the sampling sites were N 53.47391, E 6.20584 (Site A); N 53.47191, E 6.21205 (Site B); and N 53.3018, E 6.1951 (Site C). Sites A and B were located South of the island on a mudflat and approximately 500 m apart, while site C is East of the island close to a salt marsh and approximately one km from the other two sites. The three sampling locations differed in sediment grain size and exposure and thus in species composition. We collected the biofilm by scraping off the top few mm of the sediment surface in a 1 m² area in each location and transported the sediment in sealed bags in cool boxes to the laboratory (< 24 h). We extracted the motile benthic diatoms (hereafter referred to as 'microalgae') and their associated bacteria from the collected sediment. To do so, we spread the sediment in shallow containers and placed lens cleaning tissue paper on top of the sediment. We then exposed the sediment to light, inducing the motile benthic diatoms to migrate upwards in the sediment into the tissue.

We then removed the tissue and rinsed the microalgae with their associated bacteria into beakers. Finally, we filtered the microalgae through a 200 µm sieve to remove grazers and stored them in sterile filtered (0.2 µm) North Sea water (NSW) at 19 °C in a climate cabinet in the dark until further processing (< 5 h).

Experimental design

We inoculated 120 cell culture flasks (Techno Plastic Products AG (TPP), 60 mL, bottom area 9 cm²), each with organisms from either local community A, B or C, resulting in 3 sets of 40 flasks with different initial community compositions. The initial microalgal biovolume was equal to approximately 10,000,000 µm³ cm⁻¹ in each flask. Prior to inoculation, we filled 40 mL medium (sterile filtered (0.2 µm) NSW enriched with nutrients in a 14:14:1 ratio, yielding final concentrations of 40 µM nitrate and silicate and 2.7 µM phosphate) into each flask. We distributed the culture flasks randomly in a climate cabinet that was equipped with artificial day light (CTS Environmental Test System Type TP 0/600 L with OSRAM Biolux L 36 W/965 lights, light level: 10.8 µmol m⁻² s⁻¹, temperature: 19 °C).

For the experiment, three culture flasks (i.e. three local communities) formed one metacommunity. Each metacommunity consisted of one local community of each A, B, and C. To create two different dispersal treatments, we simulated dispersal in half of the metacommunities (DISP) every other day by pipetting 3 mL solution (i.e. microalgae and bacteria in medium) out of each local flask (e.g. 2A, 2B, 2C) into a sterile beaker. We thoroughly mixed the three separate solutions together, before pipetting 3 mL of the new metacommunity-specific dispersal mixture back into each local flask (of the same local communities e.g. 2A, 2B, and 2C). Hence, at each dispersal event, we added 2.5% (1 mL) solution from each local flask into the respective other flasks of each metacommunity. The other half of metacommunities (NO.DISP) were not connected with each other (no dispersal was simulated). However, like the dispersal communities, at the start of the experiment, three local communities were assigned to form a metacommunity in the experiment (e.g. 1A, 1B, and 1C formed metacommunity 1, even though no dispersal was simulated between the local patches). Before applying the dispersal treatment, we turned all culture flasks carefully three times. In doing so, loosely attached species were more prone to be re-suspended in the solution and subsequently more likely to be dispersed. Thus, this approach allowed for the indirect inclusion of species-specific dispersal abilities. The no-dispersal flasks were also turned three times, but no solution was pipetted in or out of the flasks. All flasks were returned to the climate cabinet after dispersal was concluded. Turning all bottles ensured that the boundary layer around the cells in all flasks was diffused in a similar way

and thus nutrient uptake dynamics were not confounded by the dispersal treatment. For a schematic and detailed overview of the dispersal treatments see Fig. A1.1.

To avoid nutrient depletion, we replaced the medium in all flasks every third day by removing the top 20 mL of each flask and carefully adding fresh sterile medium without resuspending the microalgae. Nevertheless, phosphate was depleted quickly after addition and therefore remained low in all communities throughout the experiment (see Fig. A2.1 for average nutrient concentrations in the local communities over the course of the experiment).

The experiment ran for 21 consecutive days and we sampled destructively at four time-points (day 5, 8, 12, 21). Destructive sampling means that the complete sample was collected at predetermined days and thus entire culture flasks were removed from the experiment at each sampling day. This ensured independence of samples of the same treatment at different time points. Before sample collection, we thoroughly scraped the bottom of the culture flasks with a sterile cell scraper and subsequently homogenized the biofilm in the medium by shaking the flasks. The combination of the four sampling days, three local communities (A, B, C) per metacommunity, two dispersal treatments (DISP, NO.DISP), and five replicates per treatment combination, led to a total $n = 120$ local communities encompassing a total of 40 metacommunities.

Microalgae identification and quantification, and response variables

Immediately after sampling, we fixed the microalgae samples with Lugol's iodine solution and stored them in brown glass bottles in a dark cold room (4 °C) until further processing. To determine microalgae cell numbers and biovolume, we counted the samples using an inverted microscope after Utermöhl (1958). We identified microalgae groups microscopically (400× magnification) to the highest resolution possible (hereafter referred to as species; for species list see Table A3.1) and calculated species-specific cell biovolumes based on procedures described in Hillebrand et al. (1999), which allowed us to compute the total biovolume contribution of each species and total community biovolume. We refer to biovolume as 'biomass' throughout the manuscript. We calculated regional microalgal biomass by adding the values of the respective three local communities per metacommunity. We calculated microalgal Pielou's evenness on the local and regional scale using biomass data. To calculate microalgal β-diversity, we generated a Bray–Curtis dissimilarity matrix based on biomass data and used this matrix to calculate and average the distance between individual local communities within a metacommunity. For each time-point, β-diversity is displayed as the mean of the five replicate metacommunities per dispersal treatment.

Bacteria identification and quantification

We performed total DNA extraction on three replicates per treatment combination using the MoBio PowerSoil DNA isolation kit (MoBio Laboratories, Carlsbad, CA, USA). DNA quality and quantity were determined using PicoGreen double-stranded DNA assay (Invitrogen, Carlsbad, CA, USA). The bacterial absolute abundances were determined by quantitative PCR (qPCR; as previously described in details; see for example Dini-Andreote et al. 2014), and is expressed as the number of bacterial 16S rRNA gene copies per mL of sample. We used qPCR of bacteria as a proxy for bacterial abundance in this experiment. It is worth noting that—despite being broadly used in the literature—the quantification of the bacterial 16S rRNA gene represents a proxy, and not a precise measurement, of bacterial abundance. That is, biases can be imposed due to the fact that (1) some organisms can have more than one copy of the 16S rRNA gene (Pei et al. 2010; Sun et al. 2013); and (2) in specific environments such as soils, ‘relic’ DNA (i.e. extracellular DNA from dead cells) can persist from weeks to years (Carini et al. 2016). Due to the intrinsic dynamics of our experimental system, the latter should not have affected our measurements. The former aspect, however, requires caution, because the changes in the abundance of the 16S rRNA gene in our system could be driven by change in community composition.

We performed high-throughput sequencing of the bacterial 16S rRNA gene on a Mi-Seq 2 × 250 platform in these samples to gather information on the structure of bacterial communities, which was useful to confirm the dominance of heterotrophic bacteria living in association with the microalgae (Table A4.1). In brief, bacteria communities were dominated by Proteobacteria (at least 60% contribution to total abundance, up to 99%). Bacteroidetes were second and Planctomycetes third most abundant in the samples (contributing up to 39% and up to 7% to total abundance, respectively). Even though they were present in minimal amounts, in none of our samples the percentage of cyanobacteria (i.e. the only group of autotrophic bacteria present in our samples) exceeded 0.2% of total bacterial abundance and in 58% of the samples, cyanobacteria were completely absent. Thus, heterotrophic groups clearly dominated the bacteria and processes concerning autotrophic bacteria can be neglected in this experiment. Graphical exploration of changes in relative bacterial composition over time revealed no large differences between the dispersal treatments (see Appendix 4) and thus we feel confident using qPCR data as proxy for bacterial abundance for our analysis and the subsequent interpretation of our results.

While the absolute abundance of associated bacteria depends on the abundance and biomass of the microalgae that provide their carbon source in the system, the ratio

between the two should directly reflect the competitive state of the two mutually interacting organismal groups. For this reason, we analyzed the ratio of bacterial abundance per unit of algal biomass instead of providing the absolute bacterial abundance values. To calculate the ratio, we divided the bacterial abundance (gene copies mL⁻¹) by microalgal biomass (μm³ mL⁻¹) in each sample. Hereafter, we refer to these values as the ‘ratio of bacteria to microalgae’. For the regional scale analysis, we calculated a mean local ratio of bacteria to microalgae.

Statistical analyses

We performed all statistical analyses in R v 3.3.2 (R CoreTeam 2017). On the local scale, we used a 3-way ANOVA to test the effect of time (sampling day, categorical, four levels: 5, 8, 12, 21), local initial community composition (local, categorical, three levels: A, B, C) and dispersal treatment (dispersal, categorical, two levels: DISP, NO.DISP) in a full-factorial design on the response variables microalgal biomass, microalgal evenness, and local ratio of bacteria to microalgae. Due to interaction effects between sampling day and the other factors (dispersal and initial community composition), we also constructed GLMs for each sampling day separately. From these separate analyses, it was possible to calculate the change in effect sizes over the course of the experiment. We calculated effect sizes for all factors and combinations as ω^2 (Graham and Edwards 2001, Olejnik and Algina 2003; Eq. 1)

$$\omega^2 = \frac{(SS_{\text{treatment}}) - (df_{\text{treatment}} \cdot MS_{\text{error}})}{(SS_{\text{total}} + MS_{\text{error}})} \quad (1)$$

Since the local communities in the dispersal treatment were connected within each metacommunity and therefore strictly not independent samples, we tested the calculated *F*-values from the GLMs for significance using critical *F*-values corresponding to $\alpha = 0.05$ at a third of the original residual degrees of freedom (32 instead of 96; Hillebrand and Lehmpfuhl 2011, Eggers et al. 2012). All calculated $F_{x,96}$ for significant effects were larger than the critical $F_{x,32}$ for $\alpha = 0.05$, therefore providing reliable and significant information on local community composition effects. On the regional scale, we performed 2-way ANOVAs to test the effect of time (sampling day, categorical, four levels: 5, 8, 12, 21), dispersal treatment (dispersal, categorical, two levels: DISP, NO.DISP), and the interaction of the two factors on microalgal biomass, microalgal evenness, mean local ratio of bacteria to microalgae, and microalgal β -diversity. We also constructed separate models for each sampling day and calculated the effect size (ω^2) of dispersal.

Results

Initial microalgal species composition of the three local communities varied greatly (Bray–Curtis dissimilarity A-B: 0.81, A-C: 0.79, B-C: 0.81), which was reflected in differences in the initial species-specific dominance in the local communities A, B and C (Fig. 1a), and evenness (Fig. A8.1). Community B had the lowest initial evenness and community C the highest. *Entomoneis paludosa* (ENT) initially dominated community A, *Gyrosigma acuminatum* (GYA) dominated community B, and *Pleurosigma aestuarii* (PLE) dominated community C (Fig. 1a). Over time the different communities homogenized. While ENT was initially rare in communities B and C (Fig. 1a), by the end of the experiment (i.e. day 21—approximately 20 microalgal generations) ENT was the most dominant species in all communities subjected to dispersal (Fig. 1e). ENT also increased in the closed communities compared to the initial species composition, but in communities B and C considerably less than in their counterpart communities that were connected by dispersal (Fig. 1e). This finding suggests that community A acted as a source for dispersal of ENT (or a specific ENT strain) into all other local communities subjected to dispersal.

With time, the importance of dispersal for metacommunity dynamics increased, which was reflected in the treatment responses of local and metacommunity-wide microalgal evenness and biomass, and the ratio of bacteria to microalgae over the course of the experiment (Figs. 2, 3, Fig. A6.1). On the local scale, initial community composition largely explained all measured variables until the middle of the experiment (i.e. day 12), which equals approximately 10 microalgal generations (Fig. 2a–c, Table A6.1). At the end of the experiment (i.e. day 21), the effect size of dispersal increased for all local response variables, while the effect size of initial composition strongly declined (Fig. 2a–c, Table A6.1). At day 21, local microalgal evenness and the ratio of bacteria to microalgae were significantly lower ($F_{1,24} = 36.09$, $p < 0.01$ and $F_{1,12} = 19.94$, $p < 0.01$, respectively), and local microalgal biomass was significantly higher ($F_{1,24} = 27.28$, $p < 0.01$) in the dispersal communities compared to the no-dispersal communities (Fig. A6.1, Table A6.1).

Accordingly, on the regional scale, the effect size of dispersal increased for all measured variables at the end of the experiment (Fig. 2d–g, Table A7.1), which was reflected in divergent patterns between the dispersal treatments for all response variables from day 12 onwards (Fig. 3, Table A7.1). On day 21, dispersal decreased the average regional microalgal evenness by 44% ($F_{1,8} = 46.32$, $p < 0.01$; Fig. 3a, Table A7.1), while at the same time increasing the average regional biomass of microalgae by

Fig. 1 Relative microalgal species composition in the different treatments on sampling days **a** initial, **b** day 5, **c** day 8, **d** day 12, and **e** day 21. This figure displays the average relative biomass contribution to total community biomass of the seven most common species and groups in the experiment. These common species were *Entomoneis paludosa* (ENT, black), *Gyrosigma acuminatum* (GYA, dots), *Pleurosigma aestuarii* (PLE, diagonal stripes), *Navicula* (NAV, diamonds), *Amphora Sp. 1* (AMP, horizontal stripes), *Stauroneis* (STA, horizontal waves), and *Cylindrotheca closterium* (CYL, vertical stripes). All other species (OTH, white) are grouped in this figure. For a color version of this figure that includes all separate species see Fig. A3.1 in the Electronic Supplementary Material

Fig. 2 Effect sizes of the factors dispersal (black), local community composition (light gray), and the combination of local community composition and dispersal (dark gray) over time. These effect sizes describe the explained variation in the experimental results. Displayed are results for **a** local microalgal Pielou's evenness, **b** local microalgal biomass, **c** local ratio of bacteria to microalgae (local bacteria microalgae ratio), **d** regional microalgal Pielou's even-

ness, **e** regional microalgal biomass, **f** mean local ratio of bacteria to microalgae (mean local bacteria microalgae ratio), and **g** microalgal β -diversity. Effect size was calculated as ω^2 at the different sampling days. Bars represent the total effect size of the three factors combined, whereas the different shading displays the total effect size of each separate factor

Fig. 3 **a** Regional microalgal Pielou's evenness ("N=40"), **b** regional microalgal biomass ("N=40"), **c** mean local ratio of bacteria to microalgae (bacteria microalgae ratio, "N=24"), and **d** microalgal β -diversity ("N=40") in the different treatments on the different sampling days. Displayed are means $\pm$ standard errors. Solid circles with solid lines represent no-dispersal treatments (NO. DISP), whereas empty circles with dashed lines show dispersal treatments (DISP)

130% ($F_{1,8} = 59.74$, $p < 0.01$; Fig. 3b, Table A7.1). The positive effect of dispersal on algal biomass also greatly influenced the mean local ratio of bacteria to microalgae: On day 21, dispersal decreased the average bacteria ratio by 81% ($F_{1,16} = 10.14$, $p = 0.01$; Fig. 3c, Table A7.1).

Dispersal caused a consistent decrease in microalgal β -diversity over the course of the experiment (Fig. 3d),

indicating that metacommunities connected by dispersal were more homogeneous than the communities with no dispersal. This difference was strongest at the end of the experiment (day 21), when β -diversity was on average 39% lower in the dispersal compared to the no-dispersal treatment ($F_{1,8} = 33.27$, $p < 0.01$; Fig. 3c, Table A7.1).

Discussion

Dispersal has been shown to be a fundamental factor structuring metacommunities in numerous experimental systems and meta-analyses (Kneitel and Miller 2003; Cadotte 2006; Doi et al. 2010; Howeth and Leibold 2010; Lindström and Östman 2011; Grainger and Gilbert 2016; Lancaster and Downes 2017). In our study, dispersal overtook initial community composition as the factor with the largest effect size, but only after ca. 10 microalgae generations. After this time period, one regionally superior microalgae competitor (*Entomoneis Paludosa*) established in all local communities, with especially strong increases in communities subjected to dispersal. While the gain in dominance of *Entomoneis paludosa* (ENT) significantly decreased microalgal β -diversity and evenness, it strongly increased total microalgal biomass. At the same time, our data suggest that the estimated relative abundance of the competing microalgae-associated bacteria (based on the quantification of their 16S r RNA copy numbers) significantly decreased. Thus, dispersal facilitated the dominance of one microalgal competitor and thereby likely prevented heterotrophic bacteria from outcompeting the autotrophic component of the communities.

Moreover, the progressive dominance of ENT suggests that there was one particularly successful strain that dispersed across metacommunities. Based on the species composition and biomass results, we assume that community A acted as a source community for the competitively superior strain of ENT, because here it dominated both the dispersal and the no-dispersal treatments from the beginning to the end of the experiment.

The greater effect of dispersal towards the end of community succession shows that there can be a lag between the spread of a species from a source community and its qualitative and quantitative effect on local population sizes that can propagate to the metacommunity scale. Like other studies (e.g. Fukami et al. 2005; Zha et al. 2016) we detected a strong effect of initial species composition on diversity and functioning of communities. However, in combination with dispersal, this effect diminished over time. As such, it can be conceptualized that the time necessary for dispersal to influence community structure and function is dependent on dispersal intensity, as this strongly influences the time it takes for species to be spread and finally get established in new local habitats. In our experiment, we have applied an intermediate dispersal rate compared to other studies reported in the literature (e.g. Howeth and Leibold 2010; Matthiessen et al. 2010; Eggers et al. 2012; de Boer et al. 2014).

With intermediate to high dispersal rates, local patches in metacommunities tend to homogenize as has been

shown elsewhere (Mouquet and Loreau 2003; Matthiessen et al. 2010). In heterogeneous landscapes, such homogenization of local communities (and thus lower diversity) is expected to lower productivity and ecosystem functioning due to declined complementarity in resource use (Tilman et al. 1997; Mouquet and Loreau 2003). In homogeneous environments, however, the direction and strength of selection are constant for all local communities. This circumstance naturally prevents complementarity in resource use across the metacommunity, and thus should not affect ecosystem functioning in the same predictable way as in heterogeneous systems. Our set-up facilitated a homogenous environment across the local patches, with a general phosphorous limitation in all communities (Fig. A2.1). We observed homogenization in the local patches, and consequently in the metacommunities. This homogenization was greatly amplified by dispersal and mainly caused by the increased dominance of one species, ENT, which was most likely a strong competitor for phosphate uptake, and at the same time an efficient disperser. In our system, homogenization in local patches and across the metacommunities did not reduce ecosystem functioning (i.e. biomass), because specific local conditions stimulated the selection of a species that was best suited for the conditions in the local patches. Thus, even though overall dispersal decreased diversity over time, this resulted in a positive effect on ecosystem functioning both on the local and regional level, because a superior species successfully dispersed. In addition, our data suggest this selection effect on the autotrophs in the system likely mitigated the possibility for heterotrophic bacteria to outcompete the microalgae.

Dispersal has been shown to foster regionally superior competitors in both environmentally homogeneous and heterogeneous metacommunities (Mouquet and Loreau 2003; Matthiessen et al. 2010). However, previous studies have also shown that the dominance of one species can either have a positive or a negative impact on ecosystem functioning. Studies in grassland systems had conflicting results. In some studies, increased dominance (i.e. decreased evenness) led to higher ecosystem functioning (Mulder et al. 2004), whereas others reported higher biomass production with decreased dominance (i.e. increased evenness) (Wilsey and Potvin 2000; Mattingly et al. 2007). Likewise, in a study with lake phytoplankton, there was a negative relationship between phytoplankton resource use efficiency (RUE) and phytoplankton evenness, but a positive relationship between zooplankton RUE and phytoplankton evenness (Filstrup et al. 2014). The direction of the dominance effect on resource use or biomass mainly depends on the relative importance of selection and/or complementary effects as well as environmental differences (i.e. homogeneous/heterogeneous patches). In addition, there are many different

functions that can be measured in an ecosystem (e.g. biomass production, RUE, nutrient uptake) and depending on what function is measured, the effect of diversity on function can vary. Likewise, in a given system, biodiversity can have positive effects on one function while simultaneously having a negative effect on another function. Our results add to a growing literature showing that the biodiversity-ecosystem functioning relationship is complicated, and not always positive. We show that the biodiversity effect strongly depends on (1) the identities of the species that are present in local patches (initially or dispersal-mediated), (2) the characteristics (i.e. heterogeneity or homogeneity) of the local habitat patches allowing for resource partitioning, and (3) the particular ecosystem function measured.

Another important finding in this study was that dispersal can have varying effects in a community depending on whether the focus is on the interaction between autotrophs and heterotrophs, or solely on autotrophs (Fig. 4). Regarding the autotrophs, dispersal promoted the dominance of one species (ENT) (Fig. 4a) that was able to cope and thrive under recurrent phosphorous limiting conditions, which, when considering both groups together, controlled for bacteria dominance (Fig. 4b). Other explanations for ENT dominance in this experiment are possible. In this study, due to our controlled experimental conditions, we can exclude bacteria-consuming micro-grazers as well as specific laboratory conditions, such as variation in light levels, as possible interferences for dynamics between algae and bacteria. In

Fig. 4 Schematic representation of how dispersal influences dominance **a** within microalgae and **b** between microalgae and bacteria. Within microalgae, dispersal (DISP) leads to the dominance of one superior species. In contrast, between microalgae and bacteria, dispersal prevents the dominance of bacteria over their microalgae competitors

general, removing organisms from their natural environment and doing laboratory experiments inherently leads to problems in that the artificial conditions in the lab influence natural dynamics in sometimes unpredictable ways. As such, some unmeasured variable could have positively affected ENT which could have explained their dominance within microalgae. However, the even stronger dominance in the dispersal treatment cannot be explained by artificial conditions, because the conditions were controlled to be identical for both dispersal and no-dispersal communities. In addition, since the vast majority of bacteria present in our communities were heterotrophic, and thus not dependent on light or other external parameters, in our opinion, the most likely explanation for differential dynamics between bacteria and algae is competition for inorganic resources. As previously mentioned, bacteria are better competitors for limited inorganic nutrients, especially phosphorus, compared to most microalgae species (Jansson 1988; Thingstad et al. 1993; Løvdal et al. 2007). Since inorganic phosphorous (i.e. phosphate) concentrations were low throughout our experiment, although nutrients were constantly replenished (see Fig. A2.1), we assume that competition for this resource between microalgae and bacteria was ubiquitous. Even though bacteria have a general competitive advantage over microalgae, our results suggest that dispersal significantly mitigated the bacterial competitive superiority by favoring one specific highly competitive autotroph. Furthermore, the differential effect of dispersal on dominance, depending on comparisons within or between (auto- or heterotrophic) groups points to the importance of considering multiple organismal groups that potentially compete for the same resource to properly unravel the regulatory role of dispersal in metacommunities.

Dominance shifts from benthic microalgae to heterotrophic bacteria can potentially have severe effects for coastal systems. Benthic microalgae are responsible for much of the primary production on intertidal flats (Underwood and Kromkamp 1999) and thus oxygenate the sediment (Baillie 1986) as well as remove carbon dioxide from the system (Chen et al. 2019). They are also the main or preferred food source for many primary consumers living in intertidal habitats and therefore fuel the intertidal food web (Evrard et al. 2012). In addition, benthic microalgae play a pivotal role in sedimentary nutrient dynamics (Sundbäck et al. 2000) and are associated with increased sediment stabilization (Yallop et al. 1994, 2000). Consequently, a shift from autotrophic to heterotrophic dominance in intertidal systems can lead to habitat degradation, potential oxygen depletion, and loss of the above described critical functions due to the suppression of a key component in the system. It is worth noting that in our experiment, we limited the community to motile benthic microalgae and their associated bacteria. Community dynamics and the relationship between autotrophs and heterotrophs might differ in natural environments where

community complexity is further increased by the presence of bulk sediment heterotrophic and autotrophic microbes which are likely affected by other and more fluctuating environmental factors such as tides, salinity, temperature and consumption.

In summary, our study highlights the importance of time for understanding the role of initial community composition and dispersal on metacommunity structure and functioning. In addition, we emphasize the significance of investigating a comprehensive spectrum of competitors for a certain resource of a community in a given system (i.e. microalgae and heterotrophic bacteria that compete for phosphate) in order to better understand the role of dispersal in regulating metacommunity diversity and functioning. Lastly, we argue that greater community diversity (i.e. evenness) might not inevitably lead to higher ecosystem functioning. We show that one superior autotrophic species that dominates the communities can sustain biomass production by mitigating heterotrophic bacteria superiority. However, whether this positive effect of dominance can be sustained for longer time scales, and in the face of stressors or disturbances remains to be tested.

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Author contribution statement BKE, BM and FGE conceived and designed the experiment; FGE performed the experiment with the help of BKE and FDA; FGE and FDA conducted fieldwork; FDA, MJdLB and JFS generated sequencing data and molecular analyses for bacteria; FGE and BM analyzed the microalgae data; FGE, BM and BKE wrote the manuscript; other authors provided editorial advice.

Compliance with ethical standard

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

Conflict of interest The authors declare that they have no conflict of interest.

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