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SANTA ROSALIA 50 YEARS ON

# Diversity and community biomass depend on dispersal and disturbance in microalgal communities

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**Abstract** The evidence for species diversity effects on ecosystem functions is mainly based on studies not explicitly addressing local or regional processes regulating coexistence or the importance of community structure in terms of species evenness. In experimental communities of marine benthic microalgae, we altered the successional stages and thus the strength of local species interactions by manipulating rates of dispersal and disturbance. The treatments altered realized species richness, evenness and community biomass. For species richness, dispersal mattered only at high disturbance rates; when opening new space,

dispersal led to maximized richness at intermediate dispersal rates. Evenness, in contrast, decreased with dispersal at low or no disturbance, i.e. at late successional stages. Community biomass showed a non-linear hump-shaped response to increasing dispersal at all disturbance levels. We found a positive correlation between richness and biomass at early succession, and a strong negative correlation between evenness and biomass at late succession. In early succession both community biomass and richness depend directly on dispersal from the regional pool, whereas the late successional pattern shows that if interactions allow the most productive species to become dominant, diverting resources from this species (i.e. higher evenness) reduces production. Our study emphasizes the difference in biodiversity–function relationships over time, as different mechanisms contribute to the regulation of richness and evenness in early and late successional stages.

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## Introduction

The rapidly accelerating rates of global species extinction (Lotze et al., 2006) have encouraged ecologists to study the ecological consequences of diversity loss. To date, the majority of a large number

of experimental studies suggest that species extinction can decrease important ecosystem processes such as community biomass production (Hooper et al., 2005; Cardinale et al., 2006a, b) or stability (Tilman et al., 2006). The findings have been mechanistically explained by locally operating effects of species complementarity and selection effects (Wardle, 1999; Loreau & Hector, 2001; Loreau et al., 2002; Fox, 2005). These studies made important arguments for the conservation of biodiversity; however, the regulation of diversity has so far been rarely involved in the debate. This is important, first, because different regulating factors on coexistence can have different consequences for ecosystem functioning (reviewed in Hillebrand et al., 2008; Hillebrand & Matthiessen, 2009). There is a strong need to place local processes into a broader spatial and temporal context such as the metacommunity perspective (Leibold et al., 2004; Holyoak et al., 2005) where factors such as dispersal and disturbance can mediate locally acting processes. Second, the realized distribution of species in a community determines the distribution of functionally relevant effect traits, i.e. not only richness but dominance has to be considered when diversity is related to community functioning (Hillebrand et al., 2008; Hillebrand & Matthiessen, 2009).

The most cited perspective for species coexistence is patch dynamics, where dispersal allows the colonization of new habitat patches and prevents competitive exclusion by moderating local dominance effects in a set of identical homogeneous patches (competition–colonization trade-off; Tilman, 1994; Yu & Wilson, 2001; Calcagno et al., 2006). In empirical metacommunities driven by patch dynamics, local diversity shows a non-linear hump-shaped pattern with increasing dispersal (Kneitel & Miller, 2003; Cadotte, 2006; Matthiessen & Hillebrand, 2006) which is also predicted by theoretical models simulating competition–colonization trade-offs (Levins & Culver, 1971; Hastings, 1980; Tilman, 1994). However, it remains to be tested what this type of regulation of diversity means for the functioning of a community.

Both dispersal and disturbance determine the successional stage of a community. This has been little considered so far as a regulating factor for the relationship between local species richness and community biomass. In a patch dynamics model, Cardinale et al. (2004) combined the successional stage of a community with system openness. The

model predicts that at early successional stages, local processes alone cannot generate a positive relationship between species richness and patch biomass production. These predictions were confirmed by results of a simple experimental phytoplankton system showing that species at early successional stages grow independently from one another and thus have no influence on total community productivity (Weiss et al., 2007). By the time regional processes (dispersal) were included to the model, local patch biomass of highly disturbed patches in relation to colonization rates (early successional stages) becomes a function of regional species richness. In contrast, local communities at late successional stages (i.e. low disturbance rate in relation to colonization) produced the same positive relationship between species richness and biomass as in closed communities at late successional stages because here biomass production was primarily determined by local species interactions.

In many natural communities few but dominant species maintain community functioning (Eriksson et al., 2006; Hillebrand et al., 2008), and therefore, in such systems species richness appears to be unimportant or even unfavourable for community functioning. Amongst the rare literature on the role of evenness, Norberg et al. (2001) theoretically predict that in a stable environment a certain optimal trait allows for the highest process rate. Therefore, highest community productivity will occur in a system dominated by the most productive species, because resources consumed by less productive species will reduce total community production. However, recent conceptual advancements highlight that this might not be true when looking at multiple functions (Gamfeldt et al., 2008) or under temporally and spatially variable conditions (Hillebrand et al., 2008).

To combine the regulating effects of dispersal and disturbance on species richness and evenness with predictions for the relationships between species richness or evenness and biomass, we experimentally manipulated rates of dispersal in terms of random propagule rains from a surrounding regional species pool into physically equal local community patches of benthic marine microalgae. In addition, the local patches were differentially disturbed to simulate different stages of community succession. This experimental design allowed for testing the following predictions:

1. Local species richness, evenness and community biomass depend on both dispersal and disturbance rates.
2. The effect of dispersal on richness and evenness changes with disturbance rate, i.e. with successional time.
3. Enhanced realized local species richness is positively correlated with community biomass only at high disturbance. Here, species grow independently from each other (i.e. interactions are weak), and both richness and biomass depend on dispersal resulting in a non-causal positive correlation.
4. Owing to the dominance of one very productive species, evenness is negatively correlated to community production. This effect is predicted to be the strongest without disturbance because local competitive interactions are strong and the dominant species can outcompete inferior species.

## Methods

### Experimental design

The experiment was conducted in 18 plastic aquaria (10 l). Each aquarium comprised 16 local community patches and a large surrounding region (Matthiessen & Hillebrand, 2006) (Appendix 1—Supplementary Material, Fig. S1) which contained a species pool of 11 species. The species were isolated from periphyton assemblages in Kiel Fjord, Western Baltic Sea. The species varied in size and in attachment strength to the bottom (for a detailed species list with mean cell sizes and abbreviations used for each species see Appendix 1—Supplementary Material, Table S4).

The local community patches were situated in plastic tubes (surface area: 5.5 cm<sup>2</sup>, volume: 4.2 ml, height: 7.7 cm) which were vertically placed into the aquaria (Appendix 1—Supplementary Material; Figs. S1A, S2). The plastic tubes were permanently submerged, and thus constantly connected to the water of the surrounding region. Whilst closed at the bottom and opened on the top, for microscopic algae with an attached bottom-living lifestyle the tubes represented a barrier between the surrounding region and the local patches (Appendix 1—Supplementary Material, Fig. S2). On a very small scale (a few mm

up to a cm), however, which is hardly sufficient to overcome the barrier, the majority of species in this community are actively mobile (see Appendix 1—Supplementary Material, Table S4). To avoid shading in a biofilm or grazing in sediments the species are able to glide in a matrix of excreted photosynthetically built extracellular polymeric substances (EPS). The remaining species are not able to actively move and instead are more or less strongly attached to the bottom by growing on stalks or just floating above the ground which also enables them to get closer to the light. On a larger scale (a few cm to m) passive dispersal is possible through currents or wave actions which can detach the algae off the bottom and transport them to another place where they sediment down and attach again. For this type of mobility the individual dispersal ability is determined by size (weight) and the individual attachment strength on the bottom. Therefore, in calm conditions the local patches remain relatively isolated from the surrounding regional pool and can be colonized only by highly mobile and/or floating or very small and light species.

The experiment lasted for 56 days corresponding to 28–56 generations of microalgae. Before the experimental manipulations started the aquaria were filled with 7 l of sterile seawater (0.2 µm pore size) with added nutrients (80 µmol silicon, 90 µmol nitrogen and 6 µmol phosphorus per l). The molar ratio of dissolved N to dissolved P was 15:1 at the beginning and 3.7:1 at the end of the experiment. During the experiment 250 ml of water from each aquarium was replaced with original medium three times a week. The 11 diatom species were established in the surrounding region and colonized the bottom outside the local habitat patches (Appendix 1—Supplementary Material, Fig. S2). Initially, the local patches were empty. Each species contributed an equal amount of biovolume to the total initial inoculum of 4.3<sup>6</sup> µm<sup>3</sup> cm<sup>-2</sup>. Biovolume was calculated following Hillebrand et al. (1999).

In this experiment we manipulated (1) dispersal rate of random propagule rains from the regional pool into the local patches (six levels) and (2) disturbance rate of the communities in the local patches (three levels). Both experimental treatments' dispersal and disturbance rate were replicated three times. Whereas each dispersal level was replicated in independent aquaria, the three disturbance levels were situated within each aquarium. This design resulted in 18 aquaria each

containing three disturbance and only one dispersal level (Appendix 1—Supplementary Material, Fig. S3). Additionally each disturbance rate was fourfold pseudoreplicated within each aquarium (see statistical analyses how this was accounted for). That is within each aquarium three different disturbance levels were distributed across 12 local community patches. On top of that four more undisturbed local community patches were situated in each aquarium. These were used to observe algal growth over the course of the experiment to determine when communities reached stationary phase, i.e. when final sampling should take place (see Appendix 1—Supplementary Material, Fig. S3 for experimental design).

The propagule rains (dispersal) from the regional species pool into the local communities were created by scraping the aquarium bottom with a cell scraper and afterwards cautiously stirring the water between and around the cylinders defining the local pools. The scraping effectively detached the algae off the bottom of the regional species pool and the stirring initiated stochastic propagule input into the local pools (Appendix 1—Supplementary Material, Fig. S2). Such passive dispersal can be found in nature, e.g. when bottom-living animals, rolling stones, or wave actions mechanically detach algae off the bottom. Small-scale currents transport them up in the water column from where the individuals sink down again and randomly settle at another site. The rates of propagule rains were manipulated in six levels in a logarithmic series (0, 3, 7, 14, 28, 56 propagule rains in 56 days), which created a range from simple open communities without enhanced dispersal up to a rate of daily propagule rains during the entire experiment (Appendix 1—Supplementary Material, Fig. S3). It should be noted that the zero-dispersal treatment did not represent a closed treatment, but one without enhanced dispersal.

Disturbance in the local communities was created by eliminating the algal biofilm. Algae were simultaneously scraped and cleared off from the bottom of the plastic tubes by suction using a 10-ml pipette. Such locally complete elimination of biomass can be frequently found in nature when snails graze on these algae. For example on a feeding track behind a periwinkle, no algae are left. Disturbance was manipulated in three frequency levels (non-, low and high). The infrequent disturbance level was defined as one disturbance event per week (i.e. eight events over the course of the experiment), and the

frequent disturbance level was defined as three disturbance events per week (i.e. 24 events over the course of the experiment). In other words in the high disturbance level the algae had 2.3 days, in the low disturbance level 7 days to grow between disturbance events. The elimination of the algal biofilm opened up new space in the local communities. The walls of the plastic tubes comprising the local communities prevented the induction of dispersal in the regional pool whilst disturbing the local communities.

Due to fungal contamination, one aquarium (one replicate of dispersal level 14) was omitted from the consecutive sampling and analyses.

### Sampling and measurements

Termination of the experiment was set to the time when local algal biomass growth reached a plateau. Therefore, four undisturbed local communities in each aquarium were destined for biomass samplings conducted every second week to measure the increase of local biomass over time (Appendix 1—Supplementary Material, Figs. S1, S3). Due to this sampling design 12 local communities per aquarium remained for final sampling after 56 days. The plastic tubes (local communities) were carefully taken out of the aquaria, and the algae were scraped off the bottom. The total content of algae and water of each plastic tube (local community) were collected. From each of these samples, we microscopically determined measures of algal biomass (magnification 20-times, Zeiss AXIO Observer.A1), species richness, evenness and occupancy. Final algal biomass was measured as biovolume (Hillebrand et al., 1999). Local species richness is represented as the number of species recorded in the sample. Evenness is measured by Pielou's evenness based on biovolume proportions (Hillebrand & Sommer, 2000). Occupancy is expressed as the percentage of communities occupied by species *i*. To calculate occupancy all pseudoreplicates across the three aquaria (i. e. true replicates) have been included. In addition, species richness in the regional pool was determined at the end of the experiment.

### Statistical analysis

Addressing the first prediction that local diversity and community biomass depend on both dispersal and

disturbance, effects of dispersal and disturbance rates as continuous factors and their interaction on richness, evenness and community biomass were tested by performing multiple linear regressions. In order to allow for unimodal relationships along the dispersal gradient (six levels), both the log-transformed dispersal gradient and its squared counterpart were considered. The dependent variables did not pass the test for normality. We therefore applied robust linear regression models rather than ordinary least-square regressions (Fox, 1997). AIC selection criterion was used (Johnson & Omland, 2004) to select the most parsimonious model out of the following four models: Model 1 =  $\text{disp} + \text{disp}^2$ ; model 2 =  $\text{disp} + \text{dist}$ ; model 3 =  $\text{disp} + \text{disp}^2 + \text{dist}$ ; model 4 =  $\text{disp} + \text{disp}^2 + \text{dist} + \text{dist} \times \text{disp}$ . When comparing a linear with a quadratic model, the linear model was preferred unless the quadratic one had a clearly lower AIC value (absolute delta AIC > 2; Johnson & Omland, 2004). As each disturbance level was fourfold pseudoreplicated within each aquarium, we applied a bootstrap analysis where we drew repeatedly ( $n = 999$ ) 51 truly independent replicates (from different aquaria, i.e. without pseudoreplication) out of 204 replicates. The 51 independent replicates resulted from 17 aquaria (one out of the 18 was omitted due to fungal contamination) each with 12 local pools for final sampling. In each aquarium these 12 local pools comprised three levels of disturbance; however, each was fourfold pseudoreplicated. From this total of 204 replicates, 51 true replicates were repeatedly drawn ( $n = 999$ ). From each draw, a set of linear regressions models was calculated and their AIC values,  $R^2$ s and regression coefficients were stored. After the bootstrap, the best model was chosen applying AIC criterion as described above. Significance levels of coefficients are given by their bootstrap distribution ( $n$  deviating sign/ $n$  tot).

For testing prediction two, i.e. the effect of dispersal on diversity changes with disturbance rate, the effect of dispersal within each disturbance level was tested by comparing models with linear and quadratic dispersal terms. The same robust regression analysis was repeated with dispersal as factor within each disturbance level, implying that here 17 out of 68 replicates were analysed per draw.

Two taxa became dominant during the experiment and comprised the bulk of the biomass. In order to test whether those taxa respond similarly to the

applied treatments, we applied the regression analyses as outlined above to the absolute and relative abundances of those taxa.

We tested hypotheses 3 and 4, i.e. the signs of diversity biomass-correlations depend on the measure of diversity and on the disturbance rate, by calculating Pearson's correlation coefficients amongst local species richness, evenness and community biomass within each of the three disturbance levels. Average correlation coefficients were calculated from bootstrap samples as outlined above. Also here, significance levels of coefficients are given by their bootstrap distribution ( $n$  deviating sign/ $n$  tot).

We performed a redundancy analysis (RDA; Legendre & Legendre, 1998) on the relative, cubic-root transformed species biovolumes in order to illustrate the species' distribution along the experimental gradients. We performed this analysis on the relative rather than on the absolute biovolumes, since the relative biovolumes represent better the success of a given species under given experimental conditions.

All statistical analyses were done using *R* (R Development Core Team, 2009).

## Results

Effects of dispersal and disturbance on species richness, evenness and community biomass

The model which included the factors disturbance and the linear and quadratic terms of dispersal rate (model 3) best explained the variation of algal species richness and community biomass (Table 1). The model which included only the linear and quadratic term of dispersal rate (model 1) best explained the variation of evenness (Table 1).

Across all disturbance levels, species richness showed a significant hump-shaped response to increasing dispersal rate (Fig. 1A; Table 1) with the highest number of coexisting species at intermediate dispersal rates. Species richness also significantly decreased with increasing disturbance rate (Fig. 1A; Table 1). Evenness exhibited a significant U-shaped relationship with dispersal in the full model, with lowest evenness (i.e. highest dominance) at intermediate dispersal rate (Fig. 1B; Table 1). Also community biomass was non-linearly



**Table 1** Summary statistics of the regression analysis from the full model (both gradients)

Variable	AIC mod1	mod2	mod3	mod4	Intercept	disp	disp <sup>2</sup>	dist	R <sup>2</sup>
evenn	<b>-99.4</b>	-94.2	-98.0	-96.4	0.60**	-0.59**	0.66**		0.21
rich	184.9	175.0	<b>169.9</b>	170.4	7.95**	6.69**	-10.08**	-0.85**	0.36
log(biovol)	166.7	111.1	<b>98.6</b>	100.0	23.79**	7.2**	-7.29**	-1.22**	0.80
log(AMP abs)	155.9	103.9	<b>102.0</b>	102.6	27.28**	4.65**	-3.65**	-1.04**	0.74
AMP rel	419.4	421.7	<b>411.3</b>	412.2	34.62**	-97.01**	140.81**	6.67**	0.32
log(STA abs)	182.6	144.6	<b>128.0</b>	129.4	27.56**	10.07**	-10.92**	-1.34**	0.76
STA rel	419.6	428.2	<b>416.6</b>	417.3	46.58**	123.23**	-158.94**	-4.91*	0.31

Given are the AIC values for the different models (mod1–mod4), as well as the coefficients and the R<sup>2</sup> for the best model (AIC value in bold). Significance levels of coefficients were calculated from the bootstrap distribution. mod1 = disp + disp<sup>2</sup>; mod2 = disp + dist; mod3 = disp + disp<sup>2</sup> + dist; mod4 = disp + disp<sup>2</sup> + dist + dist × disp

Significance levels: \*\*  $P < 0.001$ , \*  $P < 0.01$ , +  $P < 0.1$

affected by dispersal rates. Biomass significantly increased with dispersal and was maximized at intermediate dispersal rate; at high dispersal rates community biomass decreased (Fig. 1C; Table 1). With increasing disturbance rate community biomass significantly decreased, i.e. in the high disturbance treatment community biomass was one order of magnitude lower compared to the undisturbed treatment (Fig. 1C; Table 1).

In general, the factors dispersal and/or disturbance explained more variance for community biomass than for richness and evenness (Table 1).

Dispersal did not affect species richness in the regional pool (Supplementary Material—Fig. S5).

#### Effects of dispersal in different disturbance levels

Despite the absence of the interaction term in the selected combined models the strength of the non-linear effects of dispersal on species richness and evenness varied amongst the disturbance regimes. That is, the non-linear hump-shaped response of species richness to dispersal remained significant in the high disturbance level only (Fig. 2A; Table 2). In the low and no disturbance regimes neither the linear nor the quadratic term of dispersal affected species richness (Fig. 2B, C; Table 2). Evenness in contrast showed a significant linear decline with increasing dispersal rate at low and no disturbance (Fig. 2E, F; Table 2). Community biomass showed a significant hump-shaped response with a maximum in biomass

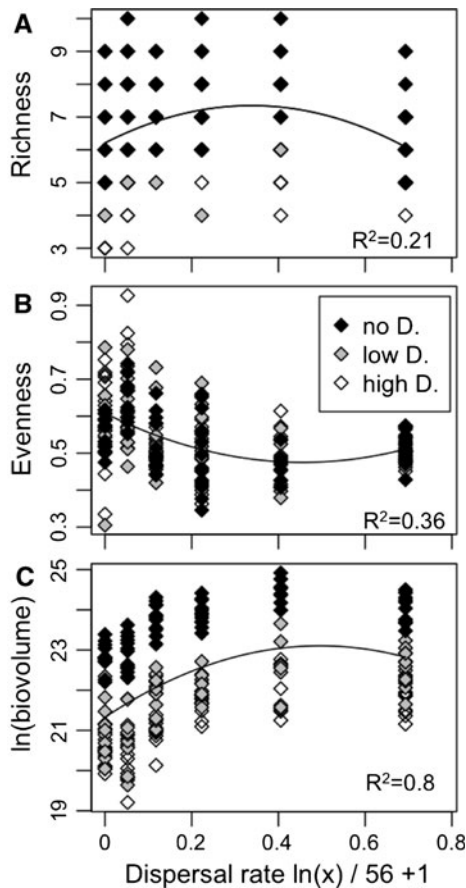
at intermediate dispersal rates in all the three disturbance levels (Fig. 2G–I; Table 2).

#### Correlations between species richness, evenness and community biomass

Correlations between species richness and community biomass, and between evenness and community biomass in the different disturbance regimes showed opposing patterns. Biomass was significantly correlated with richness in the high disturbance treatments (Fig. 3A; high disturbance: median  $r = 0.34$ ,  $P < 0.01$ ). This trend disappeared at low and no disturbance (Fig. 3B, C; low disturbance: median  $r = 0.22$ ,  $P > 0.1$ ; no disturbance: median  $r = 0.05$ ,  $P > 0.1$ ). Evenness in contrast showed a significant negative correlation with community biomass in all disturbance levels (Fig. 3D–F). The strength of the correlation, however, decreased with disturbance (no disturbance: median  $r = -0.66$ ,  $P < 0.001$ ; low disturbance: median  $r = -0.55$ ,  $P < 0.001$ ; high disturbance: median  $r = -0.46$ ,  $P < 0.01$ ).

#### Community structure

*Amphora coffaeiformes* (AMP) and *Stauroneis constricta* (STA) dominated the algal communities in the treatments, contributing on average 41 and 48% to the total biovolume, respectively (Fig. 2J–L). Without disturbance STA contributed on average 53% and thus more biomass than AMP with 34% (Fig. 2L). Conversely, at high disturbance AMP was more



**Fig. 1** Effects of dispersal rates on local **A** species richness, **B** evenness and **C** community biomass (disturbance levels pooled). *Black, grey and white diamonds* represent undisturbed, low (i.e. eight events in 56 days) and highly disturbed (i.e. 24 events in 56 days) communities, respectively. The *lines* give linear regressions with a quadratic dispersal term ( $\text{disp} + \text{disp}^2$ ) for the pooled data across all disturbance levels. *P*-values for all models and terms are highly significant ( $\ll 0.01$ ).  $R^2 = 0.09$  (A), 0.19 (B) and 0.21 (C)

dominant with on average 47% compared to 43% in STA (Fig. 2J). However, whilst both taxa generally seemed to thrive under most treatments as seen by their high proportional biomass, they exhibited inverse patterns along the dispersal gradient (Fig. 2J–L; see also coefficients for AMP and STA in Tables 1 and 2). Relative biomass of AMP was maximized at low and very high dispersal (Tables 1, 2). In contrast, relative contribution of STA was enhanced at intermediate dispersal rate (Fig. 2J–L; Tables 1, 2). The opposing patterns of AMP and STA were more pronounced in the high disturbance

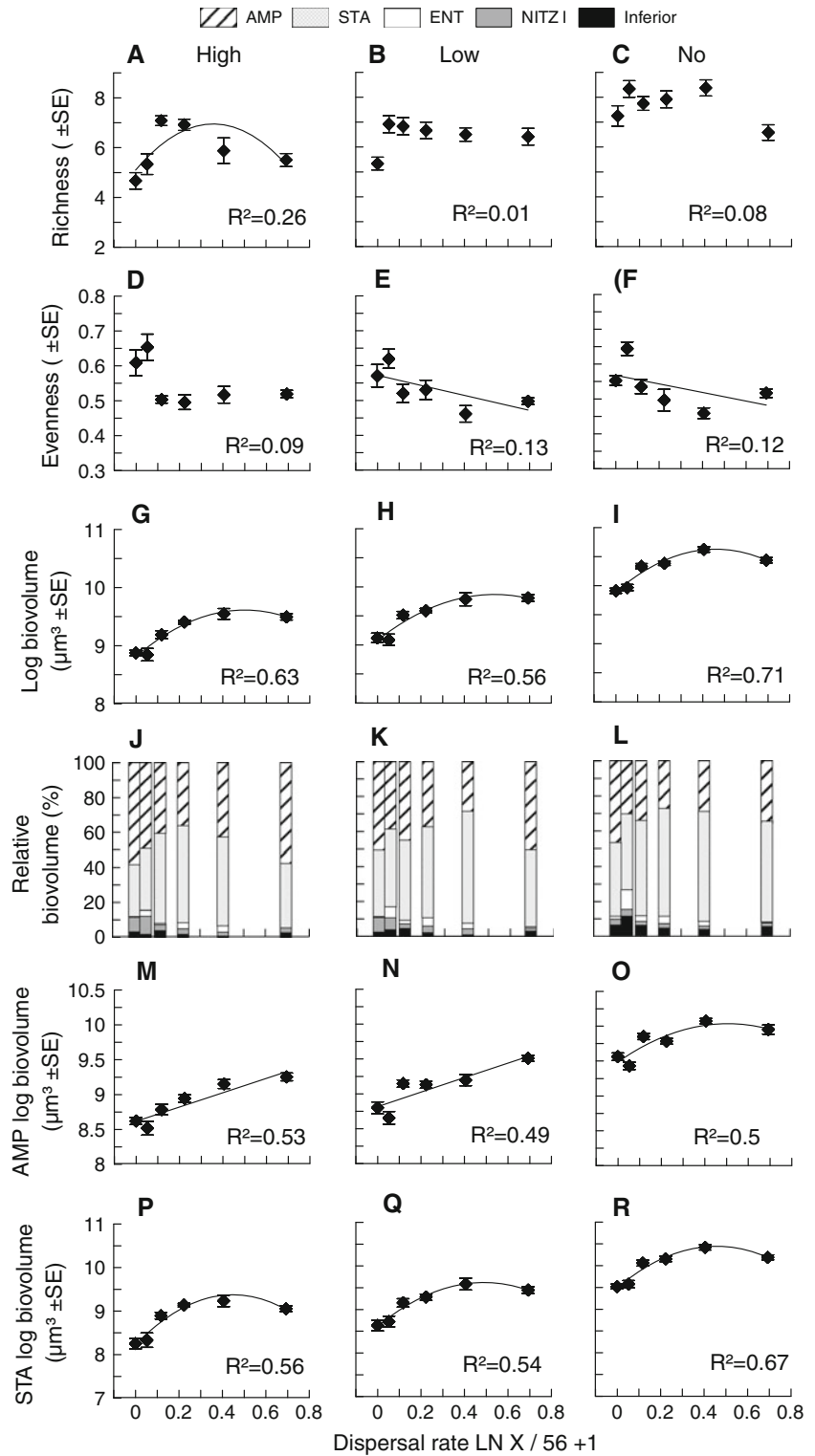
treatments (see scaling of linear and quadratic terms in Table 2), albeit the absence of a significant interaction term dispersal  $\times$  disturbance (Table 1). STA was the most productive species in this community and reached three times as much biovolume as the second productive species AMP when community productivity was highest at intermediate dispersal without disturbance rates (Fig. 2R). Total community biomass (Fig. 2I) clearly followed the non-linear relative biomass responses of the two dominants AMP and STA (Fig. 2O, R).

Several inferior species decreased in relative biomass with increasing dispersal rate (*Entomoneis paludosa* (ENT), *Nitzschia* sp. (NITZ I) and *Nitzschia oblongella* (NITZ II); Figs. 2J–L, 4; Supplementary Material—Fig. S6). Amongst these ENT and NITZ II and other species (*Achnanthes brevipes* (ACH), *Cocconeis* sp. (COC), *Navicula ramosissima* (NAV) and *Nitzschia sigma* (NITZ III)) were present in a greater proportion of patches when dispersal rate was intermediate or high (Supplementary Material—Fig. S7). Only two inferior species (ENT and NITZ I) contributed up to 10% to total community biovolume at low dispersal rate (Fig. 2J–L). The remaining species on average did not contribute more than 4% (NAV, NITZ II), and 1% (ACH, COC, *Melosira varians* (MEL), NITZ III) to total local biomass, respectively. See also Fig. 4 and Supplementary Material—Fig. S6 for relative and total biovolume of all species in response to treatments.

## Discussion

In our experimental communities local coexistence and community biomass strongly depended on the rates of dispersal and disturbance (prediction 1). The treatments, however, explained a much higher proportion of variance for community biomass than for richness and evenness. The effects of dispersal on diversity depended on the rate of disturbance (prediction 2), and varied amongst the measures of diversity. That is, for richness, dispersal mattered only in very early successional stages, i.e. when new space was opened up by high rates of disturbance. In contrast, for evenness, dispersal was important when communities were more established at low or no disturbance. We found a positive correlation between species richness and community biomass at high

**Fig. 2** Effects of dispersal and disturbance rates on local species richness (A–C), evenness (D–F) local community biomass as biovolume (G–I), relative biomass of AMP, STA, ENT, NITZ I and pooled inferior species (J–L), and total biomass contribution of the two dominant species AMP (M–O) and STA (P–R) at high and low disturbance rate, and without disturbance. High disturbance treatments represent 24, low disturbance eight events in 56 days. The following abbreviations were used for species names: *Amphora coffaeiformes* (AMP), *Entomoneis paludosa* (ENT), *Melosira varians* (MEL), *Nitzschia* sp. (NITZ I) and *Stauroneis constricta* (STA)



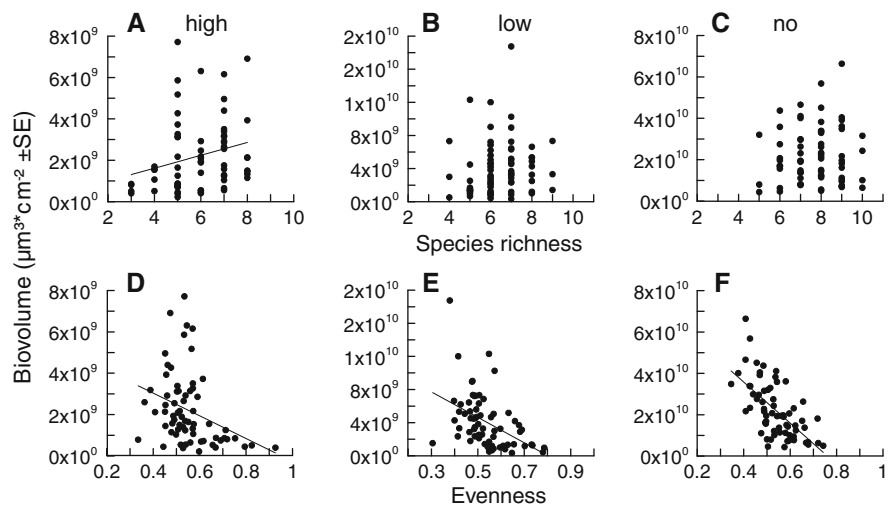


**Table 2** Summary statistics of the regression analysis from the reduced model (split by disturbance level)

Variable	dist	AIC mod 1	mod 2	Intercept	disp	disp <sup>2</sup>	R <sup>2</sup>
evenn	0	<b>-31.7</b>	-32.7	0.56**	-0.11*		0.12
	1	<b>-28.5</b>	-28.1	0.56**	-0.12*		0.13
	2	<b>-25.3</b>	-26.9	0.56**	-0.1 <sup>+</sup>		0.09
rich	0	<b>59.0</b>	58.3	8.05**	-1.61 <sup>+</sup>		0.08
	1	<b>57.8</b>	58.1	6.32**	0.3 ns		0.01
	2	64.0	<b>60.4</b>	5.1**	11.12*	-15.66*	0.26
log(biovol)	0	<b>31.0</b>	20.5	22.79**	7.21**	-7.8**	0.71
	1	<b>38.7</b>	36.5	20.92**	6.84**	-6.38*	0.56
	2	<b>37.6</b>	32.6	20.27**	7.37**	-7.39**	0.63
STA rel	0	<b>141.2</b>	139.1	41.12**	113.59**	-131.4*	0.33
	1	<b>145.6</b>	142.8	36.96**	113.08**	-150.07**	0.24
	2	<b>148.3</b>	143.3	32.46**	142.79*	-200.87**	0.33
log(STA abs)	0	<b>41.9</b>	32.5	26.5**	9.53**	-10.5**	0.67
	1	<b>49.7</b>	46.3	24.45**	9.33**	-9.57*	0.54
	2	<b>53.5</b>	47.2	23.65**	11.46**	-12.82**	0.56
AMP rel	0	<b>138.1</b>	136.4	34.94 (2.9)	-6.4 ns		0.02
	1	<b>145.3</b>	143.4	40.66 (3.28)	6.66 ns		0.00
	2	146.0	<b>141.2</b>	54.25 (6.36)	-117.09*	176.99*	0.31
log(AMP abs)	0	29.7	<b>27.1</b>	26.44**	4.91**	-4.7**	0.50
	1	<b>36.1</b>	37.0	24.93**	2.38**		0.49
	2	<b>33.1</b>	32.7	24.42**	2.36**		0.53

Given are the AIC values for the linear and for the quadratic model (mod1, mod2), as well as the coefficients and the R<sup>2</sup> for the best model (AIC value in bold). Significance levels of coefficients were calculated from the bootstrap distribution  
 Significance levels:  
 \*\*  $P < 0.001$ , \*  $P < 0.01$ ,  
 +  $P < 0.1$

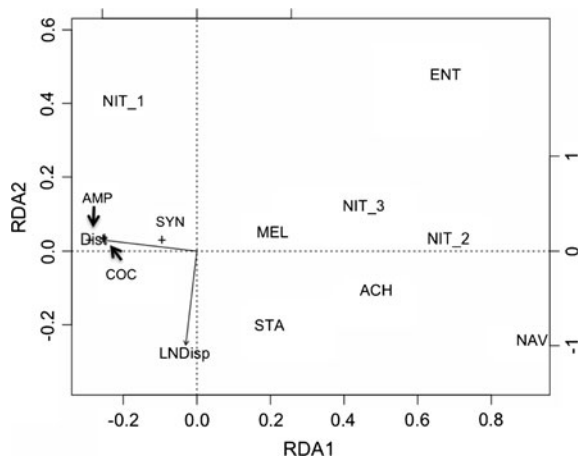
**Fig. 3** Realized species richness plotted versus community biomass at **A** high disturbance, **B** low disturbance and **C** without disturbance. Realized evenness plotted versus community biomass at **D** high disturbance, **E** low disturbance and **F** without disturbance. The fits indicate whether a correlation is significant



disturbance (prediction 3), and a negative correlation between evenness and biomass at low and no disturbance (prediction 4). We suggest the first correlation to be a non-causal relationship because both species richness and biomass strongly depend on dispersal. The second derives from competitive interactions and the resulting dominance structure.

Effects of disturbance and dispersal on species richness and evenness

The overall strong negative effect of disturbance on species richness in our experiment is because removal of biomass at the same time also means removal of species (especially the rare ones).



**Fig. 4** Redundancy analysis (RDA), grouping species corresponding to their occurrence in the experimental communities. The first two canonical axes are largely identical to the two experimental manipulations (disturbance and dispersal, see arrows) and explain 13 and 3% of the total variation seen in the community data. The following abbreviations were used for species names: *Achnanthes brevipes* (ACH), *Amphora coffaeiformes* (AMP), *Cocconeis* sp. (COC), *Entomoneis paludosa* (ENT), *Melosira varians* (MEL), *Navicula ramosissima* (NAV), *Nitzschia* sp. (NITZ I), *Nitzschia oblongella* (NITZ II), *Nitzschia sigma* (NITZ III), *Stauroneis constricta* (STA) and *Synedra* sp. (SYN)

Maximized species richness at intermediate dispersal rates appears to be a general response to increasing connectivity in experimental metacommunities with homogeneous patches (see also Kneitel & Miller, 2003; Cadotte, 2006; Matthiessen & Hillebrand, 2006). Because in this experiment the same species (AMP) showed highest relative biomass contribution at low and at very high dispersal rates; however, we do not see a trade-off between good colonizers and good competitors (Hastings, 1980; Tilman, 1994; Cadotte et al., 2006). One possible explanation can be that in this system which is characterized by frequent disturbance (e.g. by grazing) dispersal ability in general means a competitive advantage. Another possibility is that AMP and STA also dominate the surrounding region and thus had an advantage from the beginning because they colonized the local pools with proportionally higher biomass. However, because we have no data about the community structure in the regional pool we can only speculate about these possible explanations. Nevertheless, our data show that this community is also regulated by dispersal limitation at high disturbance and low dispersal rates, and in contrast by

competitive interactions at low disturbance and high dispersal rates.

Without enhanced dispersal, most likely only good dispersers were able to colonize, and high disturbance shortened the time for successfully colonized species to grow. In total, only three species (AMP, NITZ I and STA) occupied all patches in the high disturbance regime (Supplementary Material—Fig. S7). Amongst these only two relatively small species (AMP and NITZ I, Fig. 2J) showed enhanced relative biomass contribution at low compared to enhanced dispersal conditions. Another study showed that, these two species (especially NITZ I) as well as STA show significantly higher growth rates compared to some other species (NAV and NITZ II) in this community (Matthiessen et al., 2010). Growth rates potentially allowed NITZ I to divide 3.8 times, and AMP and STA three times between two disturbance events in the high disturbance treatment. Thus, both high dispersal ability via small cell size and/or high growth rates might have allowed NITZ I, AMP and STA to establish even at very low dispersal rates and within the short time to the next disturbance event.

With increasing dispersal increasing species richness can be explained by alleviated dispersal limitation. More (also inferior) species (ACH, COC, ENT, NAV, NITZ II and NITZ III) were able to occupy more habitat patches. Regarding the benthic microalgal species used in this system, it has been shown that dispersal rate alone could alter species-specific colonization success (Matthiessen & Hillebrand, 2006). Due to size and life-form, the algal species varied in their intrinsic dispersal abilities, and the individual colonization success of species depended on the frequency of induced dispersal (for cell sizes and life-forms of algae used in this study, see Appendix 1—Supplementary Material, Table S4). Alleviated dispersal limitation was also observed by Östman et al. (2006) who showed that local richness was decreased in isolated (i.e. no enhanced dispersal) and disturbed regions. Östman et al. (2006) suggested that dispersal might allow the maintenance of disturbance-sensitive species which can migrate from undisturbed neighbour patches. In our experiment the surrounding regional species pool was undisturbed and thus served as a propagule source.

Because with sufficient dispersal all species had the chance to reach all local patches, species richness

was now regulated by competition. Exclusion of three inferior species (ACH, ENT and NITZ III) explains the drop in species richness at high dispersal rates. Due to probably higher density of AMP and STA also in the regional pool, however, it is likely that these species had a competitive advantage from the beginning when colonizing, i.e. in all dispersal treatments they colonized the local patches with proportionally higher biomass than the inferior species and thus had competitive advantage. Why exactly STA and AMP dominate this community cannot be answered because we do not know which resource amongst dissolved inorganic carbon, nitrogen, phosphorous, silicate or light was limiting. Moreover, we do not know resource-use efficiencies of the single species.

That competitive interactions became more important with increasing dispersal rate at no and low disturbance is also reflected in the increase of dominance of STA and AMP. In total both species gained in total biomass but alternated in their relative contribution. From low to intermediate dispersal rates the relative contribution of STA increased. Conversely, biomass contribution of the other dominant species (AMP) and three inferior species (ENT, NITZ I and NITZ II; Fig. 2J–L) decreased along this gradient. Why STA relatively performed better at intermediate and AMP better at very high dispersal can be only speculated. One possible mechanism is that increased dispersal can substitute growth rates and thus change competitive abilities as shown for species in this community in Matthiessen et al. (2010). Unfortunately, we cannot finally prove that local community structure was not confounded by changed regional pool community structure through dispersal. Whereas regional pool richness was not affected by dispersal, we do not have data showing that the regional pool community structure was unaffected from the dispersal treatments.

In contrast to our experiment, in other studies, evenness in competitive producer communities increased when mortality increases (Cardinale et al., 2006a, b; Hillebrand et al., 2007). Cardinale et al. (2006a, b) showed that disturbance effects on evenness of algal assemblages depend on local productivity, whereas Hillebrand et al. (2007) showed that herbivory effects on producer evenness tended to be more positive at low species richness. We did not observe a significant effect of disturbance on evenness. This might be due to the fact that mortality rates

were not density-dependent, as we removed biomass completely.

#### Relationship between realized richness, evenness and community biomass

Besides species richness and evenness, community biomass was also non-linearly affected by increasing dispersal. Moreover, the explained variance for biomass by the manipulated factors was much higher than for richness and evenness. This shows that besides possible indirect effects via changing community structure, community biomass was strongly directly affected by the manipulated factors, that is, direct removal of biomass via disturbance, and direct addition of biomass via dispersal.

For the counteracting correlations between richness and biomass, and evenness and biomass we suggest different mechanisms depending on the successional stage of the communities. At high disturbance, and from low to intermediate dispersal rate, it is most likely that community biomass is exclusively related to dispersal rate but not to richness. Increased propagule input in such a system which is permanently set back to an early successional stage means both at the same time, more species and more biomass, but unrelated to each other. Such disturbance scenarios are highly realistic in benthic microalgae communities, e.g. by frequent resuspension of sediment microalgae or spatially highly heterogeneous grazing on hard substrata. Cardinale et al. (2004) showed in their model that a relationship between richness and biomass can be found in highly disturbed systems without species interactions. Such non-causal relationships occur if both species richness and biomass is strongly dependent on dispersal rates. Thus dispersal from the region is the only possible factor explaining community properties in such a highly disturbed system.

In turn, with less or no disturbance, and at high dispersal rates, the communities are in later successional stages and as discussed above the influence of competition increases. We suggest that at this successional stage besides direct quantitative effects of dispersal, indirect effects via changing community structure also affect community biomass. From exclusively direct effects of dispersal we would have expected a linear increase in community biomass with increasing dispersal (i.e. more dispersal intensity

means more biomass input). Biomass, however, declined at very high dispersal rates when the less productive AMP again contributes more to total community biomass [information on species productivity from Matthiessen et al. (2010)]. Therefore, the negative correlation between evenness and community biomass is likely a translation of productivity of the relative dominant species into community biomass, i.e. a consequence of competition. The correlation was strongest in the treatments without disturbance because competitive interactions were not alleviated by removing biomass.

The suggested non-causal richness biomass-correlation coincides with model predictions by Cardinale et al. (2004). The model predicts that in highly disturbed closed communities a positive relationship between richness and biomass caused by complementarity or selection effects *sensu* Loreau & Hector (2001) is not possible. Here, the species grow independently from each other and thus do not interact. However, as the simulation allowed for regional processes (dispersal), local patch biomass of communities in early successional stages (i.e. highly disturbed patches in relation to colonization rates) becomes a function of regional species richness. In our experiment the regional pool was undisturbed, thus with increasing dispersal local richness reflected the regional pool richness. Experimentally, Weiss et al. (2007) were able to confirm the model predictions with a simple additive experimental design with three species of phytoplankton. The authors showed that species at early successional stages grow independently from one another and have no influence on total community productivity.

Contrary to our results, in the model by Cardinale et al. (2004), which differs from our system because it allowed for niche complementarity, communities at late successional stages (i.e. low disturbance rate in relation to colonization) produced the same positive relationship between species richness and biomass as in closed communities at late successional stages. In our experiment, community biomass was also primarily determined by local species interactions which, however, selected for the most productive species (STA) and produced the negative correlation between evenness and biomass.

Literature on the consequences of evenness for community productivity show inconsistent pattern (reviewed in Hillebrand et al., 2008). As suggested by

Norberg et al. (2001), in a stable environment a negative effect of evenness on community productivity is regulated by the most productive species (i.e. sampling effect of a certain trait) which without disturbance can dominate the community and thus drive community processes (Cardinale & Palmer, 2002). A positive effect of evenness can be explained by complementarity in resource use. Norberg et al. (2001) suggest that across larger time scales which include temporary environmental variability, evenness can have a positive effect on ecosystem functioning because higher trait availability allows quicker adaptation to new abiotic conditions and thus can maintain community productivity over time. In our system resource partitioning was not possible because all patches had the same environmental conditions which did not vary over time. Thus, regional dispersal and local conditions allowed competitive interactions to select for one species which appeared to drive community biomass in established communities.

Our experiment adds to the evidence that components of diversity such as richness (Cardinale et al., 2006a, b) or evenness (Hillebrand et al., 2008) can affect important ecosystem processes. However, only few studies have explicitly included mechanisms for changes in diversity into the consideration, although the actual mechanism of species coexistence might affect the way how diversity affects ecosystem processes (Mouquet et al., 2002).

We are aware that the negative relationship between evenness and biomass is correlative and that we do not have a causal proof for selection effects in resource use (i.e. we did not explicitly manipulate diversity). Furthermore, we were not able to distinguish between how much biomass derived from local community production or from regional input. However, the strong negative correlation between evenness and community biomass strongly suggests that local competitive interactions become more important with increasing dispersal and without disturbance which in turn can have resulted in increased biomass via decreased evenness (i.e. increased dominance). To our knowledge only three experimental studies addressed system openness and the relationship of diversity and ecosystem functioning. In a similar microalgal system (Matthiessen & Hillebrand, 2006), we showed that local diversity and community biomass were maximized at intermediate

dispersal rate. However, compared to this study the experimental duration was shorter and we did not manipulate disturbance. Therefore it was not possible to distinguish between regionally and locally driven processes. For actively migrating grazers we showed that in an open system of connected rock pools it is initial grazer identity rather than grazer diversity which sustains grazing over time (Matthiessen et al., 2007). Further, France & Duffy (2006) showed that both grazer diversity in a metacommunity and dispersal interactively affect the predictability of ecosystem functioning in an eelgrass system.

This study is to our knowledge amongst the first experiments which explicitly consider drivers of species richness and evenness in open communities in early and late successional stages. Furthermore, we show that the relative importance of species interactions driving diversity ecosystem functioning relationships depends on community successional stage. Thus, to achieve generality and predictability on the importance of diversity, it is crucial to take real-world scenarios such as different regulation of diversity in early and late successional stages into account. In the future, this approach might allow to assess the relative importance of diversity compared to direct drivers of ecosystem properties.

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