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Dispersal decreases diversity in heterogeneous metacommunities by enhancing regional competition

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Abstract. Experiments and models reveal that moderate dispersal rates between local communities can increase diversity by alleviating local competitive exclusion; in contrast, high dispersal rates can decrease diversity by amplifying regional competition. However, hitherto experimental tests on how dispersal affects diversity in the presence and absence of environmental heterogeneity are largely missing, although it is known that environmental heterogeneity influences diversity. For the first time we experimentally show that the interaction between dispersal rate and the presence of an environmental gradient with on-average lower resource availability than the homogeneous control treatment affects diversity. In metacommunities of nine co-occurring species of marine benthic microalgae we factorially manipulated dispersal rate and the presence and absence of a light intensity gradient across local patches to test effects on local, regional, and beta diversity and to compare results to predictions from monoculture experiments. Although species in this experiment did not show resource partitioning along the light gradient as assumed by source–sink models, dispersal limitation maintained diversity in metacommunities with light gradients but not without. Local diversity and evenness were high under low light intensities when dispersal was limited and decreased with both increasing light intensities and dispersal rates. These diversity changes can be explained by the reduction of growth of the regional superior competitor at low light intensities alleviating its competitive strength. Increasing dispersal rate in turn compensated for the superior competitor's slow growth in those local patches with rather unfavorable light conditions and thus led to decreasing diversity and evenness. In contrast, diversity in the metacommunities without a light gradient was constantly low. Here, the superior competitor contributed 90% to total community biomass in all patches. High dominance, however, likely resulted from on-average higher resource availability (i.e., higher light intensities) compared to metacommunities with light gradient and not from patch homogeneity in itself.

Key words: benthic microalgae; competition; dispersal; diversity; environmental heterogeneity; evenness; metacommunity; resource availability.

Introduction

Rapid global loss of native species and increasing community homogenization through species invasions urges the need to understand factors maintaining species diversity. Ecologists try to understand regulating factors of diversity in spatially structured habitats by combining local processes such as competition for limiting resources with regional factors such as spatially distributed environmental heterogeneity and dispersal of species among local communities. This view has been conceptualized as the metacommunity concept (Leibold et al. 2004, Holyoak et al. 2005). Despite the substantial theoretical background on this topic, however, experimental studies are largely lacking testing how dispersal affects local and regional diversity in the presence and absence of environmental heterogeneity.

Locally diversity can be maintained by resource partitioning when different species are limited by different resources (Tilman 1977). Here, the number of limiting resources defines the maximum number of coexisting species. This concept has been applied to regional scales such that spatial differences in resource availability shape regional and among patch diversity (beta diversity); with sufficient dispersal species sort along environmental gradients according to their resource use efficiency (Leibold 1998, Shurin et al. 2004). Observational studies confirm that beta diversity depends on heterogeneous resource availability across a region (Cottenie et al. 2003, Cottenie 2005) which allows for regional resource partitioning. However, often more species appear to coexist locally than predicted by the number of limiting resources (Hutchinson 1961). Metacommunity models and experimental studies have shown that more species can co-occur locally if dispersal between communities leads to added diversity beyond the level maintained by resource partitioning. Moderate to intermediate dispersal rates between local communities can weaken local competitive exclusion either by a

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colonization–competition trade-off (Hastings 1980, Tilman 1994, Cadotte 2006, Cadotte et al. 2006, Calcagno et al. 2006) and/or by source–sink dynamics when resource availability is spatially distributed (Amarasekare and Nisbet 2001, Mouquet and Loreau 2003). Models further reveal that high dispersal rates among communities homogenize communities and can lead to regional competitive exclusion by the regional superior competitor (Mouquet and Loreau 2003, Mouquet et al. 2006).

We set out to experimentally test these theoretical predictions whether diversity in metacommunities shows a positive, a negative or a hump-shaped response to dispersal and whether the presence of an environmental gradient increases diversity. In particular, we tested whether these two factors interact. We used metacommunities with naturally co-occurring marine benthic microalgae from the western Baltic Sea. Environmental conditions for hard-bottom microphytobenthos communities are characterized by steep light gradients due to water depth, shading by canopy forming macroalgae, phytoplankton blooms, and on a smaller scale by shading from the microalgal community. Thus, competition for light is crucial and species vary in life-form along a trade-off between growth towards the light (i.e., non-mobile chain-forming and stalked cells which can form canopies) and avoidance of grazers and wave actions (i.e., mobile more or less attached flat solitary cells) (Kawamura et al. 2006). On a small scale, mobile microphytobenthos species disperse by "crawling" on excreted extracellular polymeric substances. On a larger scale, wave actions can detach the algae from the bottom and they sink down and reattach at some other location. Over the course of the succession the different life-forms build a three-dimensional biofilm initially consisting of randomly assembled fast growing small single-cell species, later on dominated by larger and upwards growing forms (Hillebrand and Sommer 2000). In this experimental model system, we manipulated dispersal rates between local patches as well as presence/absence of a light gradient. The treatments with light gradient present showed on-average lower light availability than treatments without light gradient. Because in this community we expect some species to be more tolerant than others to low light conditions (i.e., growth rates of some but not all species are negatively affected by decreasing light intensity) we hypothesize (1) that dispersal differentially affects diversity depending on the presence or absence of the light gradient, (2) that in the presence of the light gradient, low to intermediate dispersal rates increase local diversity and evenness by maintaining inferior species in adverse light conditions, and (3) that absence of the light gradient, and/or high dispersal rates in the presence of the light gradient cause a homogenization of the whole metacommunity which favors the best regional competitor leading to a decline in local and regional diversity and evenness and beta diversity.

METHODS

Community and monoculture experiments

The community experiment comprised of 48 metacommunities with marine benthic microalgae (i.e., diatoms). Each metacommunity was located in a cell culture plate with six wells, i.e., each well (9.08 cm^2 bottom area) represented one local community and all six wells together represented the metacommunity. Each metacommunity contained nine species: *Achnanthes brevipes* (ACH), *Amphora coffaeiformes* (AMP), *Cocconeis* spec. (COC), *Entomoneis paludosa* (ENT), *Melosira varians* (MEL), *Navicula ramosissima* (NAV), *Nitzschia* sp. (NITZ I), *Nitzschia sigma* (NITZ II), and *Stauroneis constricta* (STA). These nine species cover a wide range of life-forms from chain-forming and stalked to solitary more or less mobile flat cells that we expect different competitive abilities concerning light limitation. (For sizes and life-forms of individual species, see Appendix A. Photos of the species are given in Appendix B). These nine species naturally co-occur in the western Baltic Sea and are fairly abundant in Kiel Fjord, from which they were isolated. The experimental duration was 30 days, which corresponds to 15–30 algae generations.

Presence and absence of the light gradient and dispersal rate were manipulated in a full-factorial design. Presence and absence of the light gradient was manipulated in two levels by spatially varying and non-varying light intensities across a metacommunity. Therefore, in half of the metacommunities ($N = 24$), light intensities were altered by attaching printer foil on the top lid above and on the bottom below each local patch. By varying the strength of print on the foils, six levels of shading were created resulting in different light intensities (5, 10, 15, 20, 30, and 40 $\mu mol \cdot m^{-2} \cdot s^{-2}$) among the patches of metacommunities with the light gradient present. In the metacommunities without the light gradient, light intensities were kept constant at 40 $\mu mol \cdot m^{-2} \cdot s^{-2}$. Please note that this design resulted in lower average light intensity in the metacommunities with light gradient compared to metacommunities without light gradient.

Dispersal was manipulated using a 5-mL plastic pipette to punch a small circle (diameter 2 mm) out of the biofilm of each local community in one metacommunity. After punching the pipette tip was carefully filled with 2 mL of supernatant water of the respective local community and the water was transferred to an autoclaved glass jar. In the jar, the samples from all patches within one metacommunity were pooled and carefully mixed by agitating. Afterward, 2 mL of the algae mix was carefully retransferred to each of the local communities. Assuming 100% cover, the punched circles comprised 0.35% of total algal biomass in one local patch. In practice, more biomass was sucked into the pipette when filling it up with supernatant water because at the edges of the punched circles algae were mechanically detached and thus also withdrawn by suction. Therefore, approximately 1% of total algal biomass of each local community was moved around by dispersal. The holes which were punched in the biofilm were overgrown within 24 hours. This design provided each species with the same chance to reach each local community independent of distance or species specific dispersal ability, i.e., resulted in a spatial implicit design. The dispersal gradient was manipulated in six levels in a logarithmic series (0, 1, 2, 4, 15, 30 dispersal events in 30 days). This created a gradient from isolated local communities without dispersal to dispersal treatments with only one dispersal event in 30 days up to a dispersal rate of daily dispersal. The experimental treatments, i.e., two levels of light gradient present or absent and six levels of dispersal were replicated four times, which resulted in 48 metacommunities comprising 288 local patches (144 with and without light gradient, respectively). Please note that one out of the six local patches in metacommunities without a light gradient was used to roughly estimate when community growth during experimental runtime reached stationary phase and therefore was already sampled before termination (i.e., final sampling of the experiment took place after communities reached stationary phase, but see *Sampling and measurements*). That means that, from the metacommunities without light gradient, 120 local communities remained for final sampling and analyses. From the metacommunities with light gradient, one sample of one local community got lost (light intensity, 10 μmol·cm^2·s^{-1} and dispersal rate, 15 events in 30 days). Thus 143 samples remained for final analyses from metacommunities with light gradient.

At the onset of the experiment each local patch was filled with 7 mL media which consisted of sterile filtered (pore size 0.2 μm) seawater with added nutrients in a concentration of 105 μmol/L nitrate and 7 μmol phosphate (i.e., a molar ratio of N:P of 15:1). The available space for the algae in each well was 7000 mm^3. Initially each local community was inoculated with all nine species comprising an initial total local biovolume of 8 000 000 μm^3/cm^2. This means that the initial inocula occupied only 0.001% of total available space in a well. Please note, however, that benthic algae grow on the bottom and that the community reaches a three dimensional structure either by erect growth of cells and/or by growing on each other. Such a biofilm will approximately not exceed 0.5 mm in height and therefore the algae will not use the total available space in the well. At the beginning all species equally contributed to total biomass and thus had equal chances to colonize the bottom of the well. The initial contributed aliquot of the biggest species (NITZ II) was 131 and of the smallest species (NITZ I) 6999 individuals per cm^2 which we considered as enough to take off. The initial inocula comprised on average 1% of final biomass which the communities reached at the end of the experiment. During the entire experimental time 4 mL of supernatant water in the local communities were carefully exchanged with new medium every third day to prevent nutrient depletion. By doing this, we did not remove biomass because without stirring or wave actions the cells stay attached at the bottom of the well.

In an additional experiment, the effect of differing light intensities was tested on growth rates and carrying capacities of all nine species in monoculture. The experimental set-up, duration and final sampling (see *Sampling and measurements*) were identical to the metacommunities with a light gradient present in the community experiment, however, without dispersal. Each monoculture culture plate was replicated four times, which resulted in 36 culture plates comprising 216 local populations. Because the monoculture experiment was carried out after the community experiment it allows only for qualitative comparisons.

Sampling and measurements

After 30 days all local communities were sampled by carefully scraping the algae off the bottom. The total amount of algal material and water of each local community was sampled and analyzed by inverted microscopy at 400-fold magnification. From these samples, local and regional species richness, Shannon diversity, Pielou's evenness, as well as beta diversity were calculated. Local diversity within a metacommunity was expressed by the mean values of the calculated diversity measures of the six local communities. Measures of regional diversity were calculated additively according to total species richness or distribution across the whole metacommunity. Beta diversity was expressed as Bray-Curtis dissimilarity (Bray and Curtis 1957) which reflects changes in relative species proportions. Here, the mean value of all possible pair wise calculations of Bray-Curtis dissimilarities gives the beta diversity for one metacommunity. To avoid confounding measurements of diversity with abundance data of largely differing cell sizes among species (Appendix A) Shannon diversity, Pielou's evenness and Bray-Curtis dissimilarity were determined according to individual species biomass calculated as biovolume (Hillebrand et al. 1999).

Population growth in all 216 local monoculture populations was recorded directly in the cell wells by inverted microscopy and image analyses every second day during experimental runtime. All populations had reached their carrying capacity after 30 days, i.e., cell growth was in the stationary phase when sampling took place (Appendix C). All data were log transformed and growth rates and carrying capacities for each replicated local population were derived by fitting a density dependent logistic growth model. However, due to the high number of local populations we had to compromise the number of counted individuals per population per day. This in parts led to high variability of the data; especially of those from larger species with lower cell numbers such as NITZ II and NAV. Therefore, not all recorded growth data of each replicated population significantly fit the model (significance level $P < 0.05$).

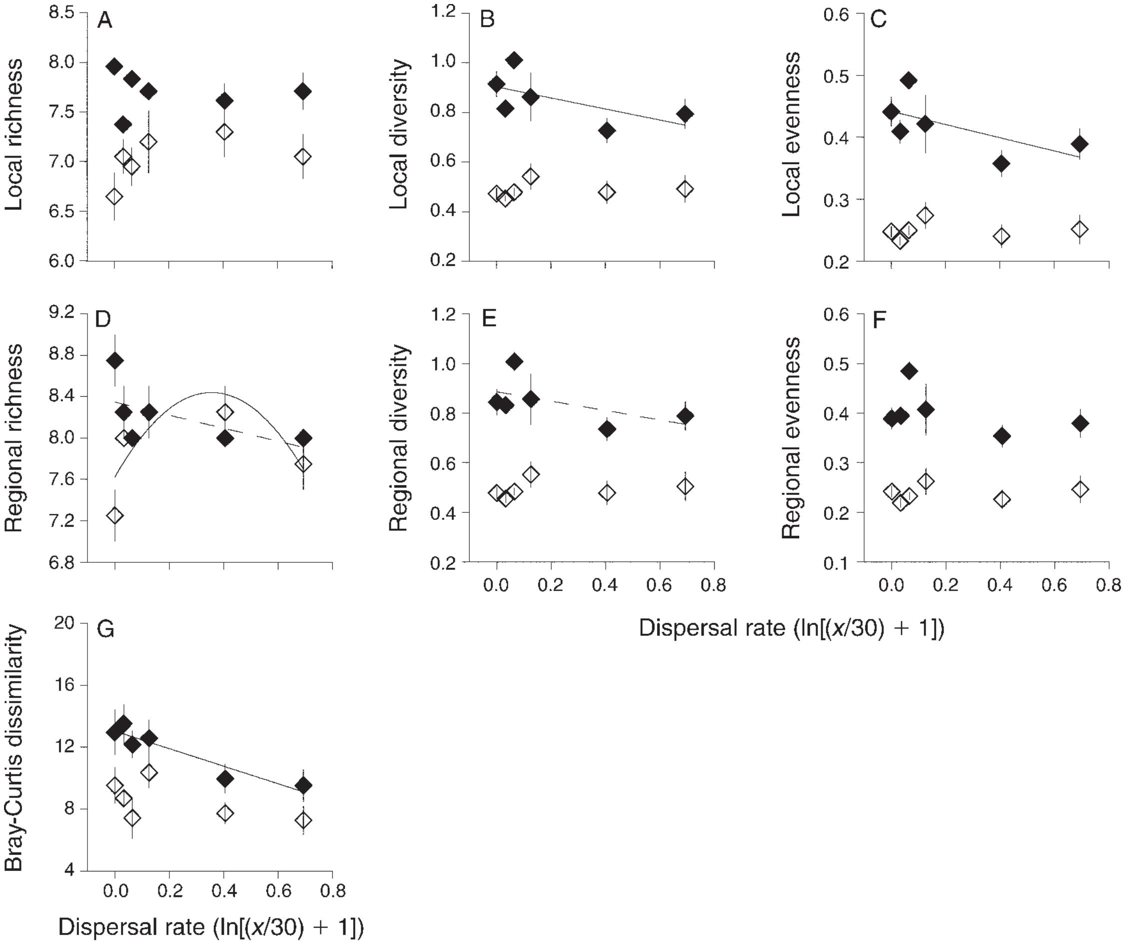

FIG. 1. The figure gives (A–C) local and (D–F) regional species richness, Shannon diversity, and Pielou's evenness as well as (G) beta diversity expressed as Bray-Curtis dissimilarity in metacommunities with a light gradient (solid diamonds) and without (open diamonds). Error bars represent SE. The regression lines refer to separate analyses of metacommunities with or without light gradient and indicate a significant (solid line) or marginally significant (dashed line) decline of diversity measures with increasing dispersal rate, where x is the number of dispersal events in 30 days.

In such cases, growth rates and carrying capacities of a population could not exactly be identified and the respective replicate was omitted from the consecutive analyses (please note degrees of freedom in the regression analyses).

Statistical analyses

Prior to statistical analyses data were tested for homogeneity of variances. If variances were not homogeneous data were log transformed. Addressing hypothesis 1, effects of the factors dispersal rate, presence and absence of the light gradient, and their interaction were tested on mean local and regional richness, evenness, diversity, and on beta diversity by calculating all possible factor combinations of a general linear model. Presence and absence of the light gradient was used as a categorical and dispersal rate as a continuous factor. To test for potential nonlinear effects of dispersal, also the quadratic term for dispersal was included in the model. If more than one model was significant, weighted Akaike selection criteria (wAIC; Johnson and Omland 2004) were used to select the best model.

Addressing hypotheses 2 and 3, in the metacommunities with light gradient linear and nonlinear effects of the factors dispersal rate and light intensity and their interaction were tested on all measures of mean local diversity. All possible factor combinations of the general linear model were tested. To take into account potential nonlinear effects of dispersal rate and light intensity for both factors, the quadratic terms were included in the model. The most parsimonious model was selected by wAIC.

In the metacommunities without light gradient potential linear and non-linear effects of dispersal rate on all measures of mean local and regional diversity were tested by linear and quadratic regression. In case both models were significant, wAIC were used to choose the best model. The same analysis was applied in order

TABLE 1. Results of selected models from the full general linear model (GLM) that best explained the treatment effects of light gradient absent/present as a categorical factor and the linear and quadratic term of dispersal rate as continuous factors and their interactions on local and regional diversity measures (Rich, H), evenness (Even), and beta diversity (Beta) across all metacommunities.

Response variable	Selected model	wAIC	Whole model				Contributing factors				Regression slope
			df	r^2	F	P	df	MS	F	P	
Mean local											
Rich	het	0.29	1, 46	0.43	35.88	<0.0001	1, 46	5.33	35.88	<0.0001	
H	het	0.26	3, 44	0.76	51.27	<0.0001	1, 44	1.19	108.2	<0.0001	
	disp						1, 44	0.03	2.9	0.1	−0.1
	het × disp						1, 44	0.04	3.87	0.06	
Even	het	0.28	3, 44	0.77	52.9	<0.0001	1, 44	0.25	110.72	<0.0001	
	disp						1, 44	0.01	3.69	0.06	−0.05†
	het × disp						1, 44	0.01	3.9	0.06	
Regional											
Rich	het	0.25	2, 45	0.1	3.67	<0.05	1, 45	1.5	7.25	<0.01	
	het × disp						1, 45	0.5	2.41	0.13	
H	het	0.23	3, 44	0.74	46.33	<0.0001	1, 44	1.12	93.34	<0.0001	
	disp						1, 44	0.03	2.38	0.13	−0.1
	het × disp						1, 44	0.04	3.31	0.08	
Even	het	0.17	2, 45	0.72	61.11	<0.0001	1, 45	0.23	84.79	<0.0001	
	het × disp						1, 45	0.01	2.24	0.14	
Beta	het	0.28	2, 45	0.46	21.04	<0.0001	1, 45	128.6	30.04	<0.0001	
	disp						1, 45	51.59	12.05	0.001	−4.15**

Notes: The table gives the weighted Akaike information criterion (wAIC), the results for the whole selected model, individual results for each contributing factor in the model, and regression slopes for continuous factors. Abbreviations are: het, heterogeneity; disp, dispersal rate.

* $P < 0.05$; ** $P < 0.01$; † $P < 0.1$.

to test for dispersal effects on all measures of regional and beta diversity in the metacommunities with the light gradient present.

To show which species were competitively superior and inferior in response to treatments (addressing hypothesis 2 and 3) and thus responsible for changes in diversity, effects of the factors dispersal rate and light intensity (in case the light gradient was present) were also tested on the relative local biomass of species in the metacommunities with and without light gradient present. The analyses were performed as described for tests on all measures of diversity and biomass in the previous paragraph. Since some species in the communities remained extremely rare, for clarity we show only species that contributed more than 4% to total community biomass in at least one of the treatment combinations.

In order to show species specific responses to decreasing light intensities, first one-factorial ANOVA was used to compare individual growth rates and carrying capacities of species in the monocultures across all light levels. Second, potential linear and nonlinear effects of light intensity on individual growth rates and carrying capacities were tested by linear and quadratic regressions. Please note that for clarity we show only those species which contributed more than 4% to total community biomass in at least one of the treatment combinations.

RESULTS

Main effects of light gradient being present/absent

All measures of mean local and regional diversity (i.e., richness, diversity, and evenness) and beta diversity were significantly higher in the metacommunities with than without light gradient present (Fig. 1A–G; Table 1).

Effects of dispersal rate in the presence and absence of the light gradient

Mean local diversity and evenness were differentially affected by dispersal depending on the presence or absence of the light gradient (Fig. 1B, C; Table 1). Both variables significantly decreased with increasing dispersal in the presence but not in the absence of the light gradient (Table 2). Beta diversity overall decreased with increasing dispersal rate (Fig. 1G, Table 1), though showed a decline only in the metacommunities with light gradient present when analyzed separately (Table 2). Mean local species richness (Fig. 1A) and all measures of regional diversity (Fig. 1D–F) were neither affected by the interaction between dispersal rate and the light gradient being present or absent nor by dispersal as main effect (Table 1). Among these variables, however, regional richness and diversity marginal significantly decreased with dispersal in the presence of the light gradient. In the absence of the light gradient regional richness in contrast showed a non-linear hump-shaped response to increasing dispersal rates (Fig. 1D; Table 2), whereas regional diversity was not affected by dispersal.

Effects of dispersal and light intensity

In the metacommunities with the light gradient present, local diversity and evenness significantly decreased with both increasing dispersal rate and light intensity (Fig. 2B, C; Table 2). The decline of local diversity and evenness at low light intensities with

TABLE 2. The table gives results of selected models from the full GLM that best explained the treatment effects of the linear and quadratic terms of light intensity and dispersal rate and their interaction on local measures of diversity (Rich, H) and evenness (Even) in the metacommunities with light gradient present and results of the GLM with the linear and quadratic term of dispersal rate on mean local and regional measures of diversity, evenness, and beta diversity (Beta) in metacommunities with and without the light gradient.

Response variable	Selected model	wAIC	Whole model				Contributing factors				Regression slope
			df	r^2	F	P	df	MS	F	P	
With light gradient											
Local											
Rich	light		2, 140	0.002	1.13	0.33	1, 140	0.75	2.04	0.16	0.03
	light^2						1, 140	0.82	2.24	0.14	−0.001
H	light	0.31	4, 138	0.26	13.34	<0.0001	1, 138	1.51	35.37	<0.0001	−0.01***
	disp						1, 138	0.4	9.36	<0.01	−0.97**
	disp^2						1, 138	0.12	2.91	0.09	0.71
	light × disp						1, 138	0.22	5.19	<0.05	0.01*
Even	light	0.32	4, 138	0.27	13.85	<0.0001	1, 138	0.35	36.92	<0.0001	−0.01***
	disp						1, 138	0.09	9.41	<0.01	−0.46**
	disp^2						1, 138	0.03	2.83	0.09	0.33
	light × disp						1, 138	0.05	5.42	<0.05	0.01*
Mean local											
Rich	disp		1, 22	0.04	0.12	0.74	1, 22	0.01	0.12	0.74	−0.08
H	disp		1, 22	0.13	4.45	<0.05	1, 22	0.07	4.45	<0.05	−0.22*
Even	disp		1, 22	0.14	4.84	<0.05	1, 22	0.02	4.84	<0.05	−0.12*
Regional											
Rich	disp		1, 22	0.11	3.88	0.06	1, 22	0.59	3.88	0.06	−0.73†
H	disp		1, 22	0.11	3.85	0.06	1, 22	0.06	3.85	0.06	−0.31†
Even	disp		1, 22	0.07	2.71	0.12	1, 22	0.01	2.71	0.11	−0.09
Beta	disp		1, 22	0.3	10.72	<0.01	1, 22	47.72	10.72	<0.01	−5.64**
Without light gradient											
Mean local											
Rich	disp		2, 21	0.07	1.89	0.18	1, 21	0.7	3.47	0.08	2.89
	disp^2						1, 21	0.57	2.82	0.11	−3.72
log H	disp		1, 22	0.04	0.16	0.9	1, 22	0.0003	0.02	0.9	0.01
log(even)	disp		1, 22	0.05	0.01	0.93	1, 22	0.0001	0.01	0.93	−0.01
Regional											
Rich	disp		2, 21	0.24	4.65	<0.05	1, 22	1.78	9.25	<0.01	4.61**
	disp^2						1, 22	1.74	9.03	<0.01	−6.49**
log H	disp		1, 22	0.04	0.01	0.92	1, 22	0.0002	0.01	0.92	0.01
log(even)	disp		1, 22	0.05	0.001	0.99	1, 22	0.0001	0.001	0.99	0.001
beta	disp		1, 22	0.07	2.64	0.12	1, 22	10.56	2.64	0.12	−2.65

Notes: The table gives the weighed Akaike Information Criterion (wAIC), the results for the whole selected model, individual results for each contributing factor in the model, and regression slopes. Abbreviations are: disp, dispersal rate; light, light intensity gradient.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$; † $P < 0.1$.

increasing dispersal rates explains the significant interaction between light intensity and dispersal rate (Fig. 2B, C; Table 2). Local richness was not affected by dispersal rate and light intensity and thus could not be explained by any of the linear and nonlinear factor combinations ($P > 0.33$ in all models; Fig. 2A, Table 2). However, the linear and quadratic term of light intensity were selected to best explain the response of local richness and thus used to show statistical results (Table 2).

Species biomass contribution

Both the metacommunities with and without the light gradient present were dominated by a single species (STA, Fig. 3A, F). In the metacommunities without the light gradient 90% of total community biomass was contributed by the dominant species. This dominance was not affected by dispersal (Fig. 3F; Table 3). For the results of regression analyses of subdominant species without light gradient see also Table 3. In contrast, in the metacommunities with light gradient the dominance of STA and the relative biomass contributions of the subdominant species significantly changed with dispersal rate and/or light intensity (Fig. 3A–E; Table 3). Relative biomass of the dominant STA significantly increased with increasing light intensity and dispersal rate (Fig. 3A; Table 3). With a minimum relative biomass of 62% STA was lowest at low light treatments when dispersal was low and significantly increased up to 84% with increasing light intensity and up to 80% with increasing dispersal rate (Fig. 3A; Table 3). The response of the subdominant species to increasing light intensity was contrary to the dominant species. Relative biomass of all subdominant species significantly decreased with increasing light intensity (Fig. 3B–E; Table 3). Relative biomass of two subdominant species (NITZ I, NITZ II) also significantly decreased with increasing dispersal rates (Fig. 3D, E). With 8% relative biomass of NITZ I was highest at low light with low dispersal rates and

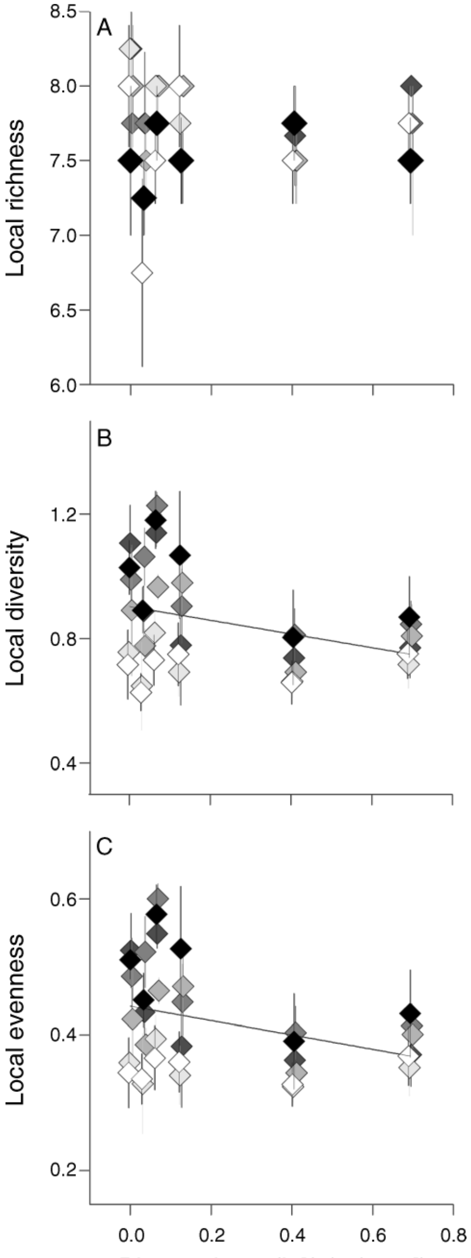

FIG. 2. (A) Local richness, (B) Shannon diversity, and (C) Pielou's evenness in the metacommunities with the light gradient. The light gradient is described with shades of gray from white diamonds (40 μmol·cm^{-2}·s^{-1}) toward black diamonds (5 μmol·cm^{-2}·s^{-1}). Error bars represent ±SE. Regression lines show significant decline with dispersal rate.

decreased down to 2% with increasing light intensity and dispersal rate (Fig. 3D; Table 3). Maximum relative biomass of NITZ II was 6% at low light intensities and low dispersal rates and decreased below 1% with increasing light and dispersal (Fig. 3E; Table 3). One species (NAV) showed a significant U-shaped response to increasing dispersal rates. Relative biomass of NAV dropped from 6% at low light down to 1% at high light intensities and significantly interacted with dispersal (Fig. 3C; Table 3). Relative biomass of AMP was not affected by dispersal (Fig. 3B, Table 3). AMP showed a maximum in relative biomass of 18% at low light and decreased down to 8% with increasing light intensity (Fig. 3B; Table 3).

Please note, that we consider only species which contribute at least four percent to total biomass in at least one of the treatment combinations, i.e., AMP, NAV, NITZ I, NITZ II.

Individual species growth rates and carrying capacities

Species in the monocultures reached their carrying capacities between 11 and 24 days of experimental runtime (for results and regression analyses for individual species, see Appendix C). Species significantly differed in average individual growth rates ($F_{4,91}$ = 72.02; $P < 0.0001$) and carrying capacities ($F_{4,91} = 31.91$; $P < 0.0001$; Fig. 4A, B). NITZ I showed significantly highest growth rate compared to the other species (Tukey's hsd test, $P < 0.001$; Fig. 4A). STA (the dominant species) and AMP showed intermediate growth rates and were significantly lower than NITZ I and significantly higher compared to NAV and NITZ II (Tukey's hsd test, $P \leq 0.05$; Fig. 4A). With increasing light intensity, two species, the dominant STA and NAV, significantly increased in growth rates (Fig. 4A; STA, $r^2 = 0.16$, $F_{1,21} = 5.04$, $P < 0.05$, regression slope = 0.02; NAV, $r^2 = 0.3$, $F_{1,16} = 8.29$, $P < 0.05$, regression slope = 0.001). Only STA reached carrying capacity marginal significantly earlier in higher compared to lower light intensities (i.e., after 18 days in 30 and 40 μmol·s^{-1}·cm^{-1} and after 22 days in 5 μmol·s^{-1}·cm^{-1}; for regression analyses, see Appendix C).

NAV showed highest carrying capacity and significantly differed from AMP, NITZ I, and STA (Tukey's hsd test, $P < 0.01$; Fig. 4B). NITZ I had lowest carrying capacity and significantly differed from NAV, NITZ II, and STA (Tukey's hsd test, $P < 0.01$; Fig. 4B). Carrying capacities of species did not significantly change with increasing light intensity (P values of all tested models > 0.05; Fig. 4B). Carrying capacity of STA, however, marginal significantly decreased with increasing light intensity (Fig. 4B; $r^2 = 0.12$, $F_{1,2} = 3.99$, $P = 0.06$, regression slope = –0.02).

DISCUSSION

Our results show that dispersal differentially affects diversity depending on the absence and presence of the light gradient. Increasing dispersal rates led to a decline of local diversity and evenness, regional richness, and diversity, and beta diversity in the presence of the light gradient. In metacommunities without the light gradient, i.e., with homogeneous distributed high light availability, diversity, and evenness remained low at all dispersal levels due to dominance of one good competitor in all local communities. Thus, both uniform high

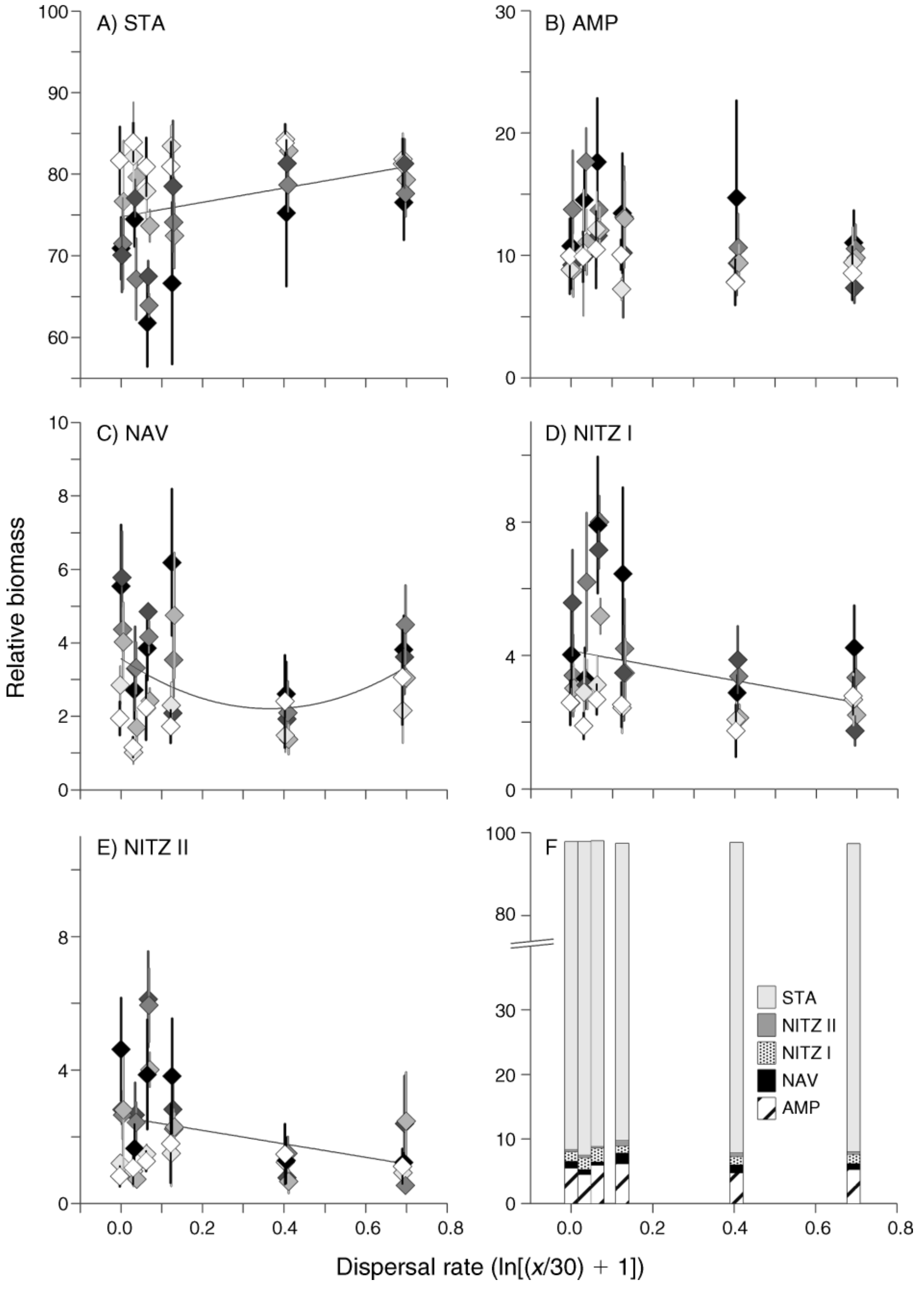

FIG. 3. (A–E) Relative biomass of species that contributed more than 4% to total biomass in metacommunities with the light gradient and (F) without. The light gradient in the heterogeneous metacommunities (A–E) is described with shades of gray from white diamonds (40 $\mu mol \cdot cm^{-2} \cdot s^{-1}$) to black diamonds (5 $\mu mol \cdot cm^{-2} \cdot s^{-1}$). Error bars represent ±SE. Abbreviations are: STA, *Stauroneis constricta*; AMP, *Amphora coffaeiformes*; NAV, *Navicula ramosissima*; NITZ I, *Nitzschia* sp.; NITZ II, *Nitzschia sigma*. Regression lines show significant responses to increasing dispersal rate.

resource availability across a metacommunity and high dispersal rates homogenize the whole metacommunity by benefitting the superior competitor.

To our knowledge in this controlled experiment we show for the first time that the presence of an environmental gradient with on-average lower light intensity compared to the treatments without a light gradient was strong enough to enhance diversity and evenness by reducing dominance and maintaining inferior species in certain local patches when dispersal was limited. The interaction effect of dispersal and the presence/absence of the light gradient on mean local diversity and evenness can be explained by the weakened competitive strength of the superior competitor (STA) in low light conditions due to its relatively slower growth compared to high light conditions. In contrast, except

TABLE 3. Results of selected models from the full GLM that best explained the treatment effects of the linear and quadratic terms of light intensity and dispersal rate and their interaction on relative biomass of species in the metacommunities with the light gradient, and the linear and quadratic terms for the effect of dispersal rate on relative biomass of species in the metacommunities without the light gradient.

Response variable	Selected model	wAIC	Whole model				Contributing factors				Regression slope
			df	r^2	*F*	*P*	df	MS	*F*	*P*	
With light gradient											
STA	light	0.23	3, 139	0.22	14.19	<0.0001	1, 139	2104.14	28.55	<0.0001	0.43***
	disp						1, 139	742.02	10.7	<0.01	17.81**
	light × disp						1, 139	263.24	3.57	0.06	−0.46†
log(AMP)	light	0.2	2, 140	0.03	3.25	<0.05	1, 140	0.13	4.02	<0.05	−0.01*
	disp						1, 140	0.69	2.45	0.12	−0.28
log(NAV)	light	0.29	3, 139	0.23	15.41	<0.0001	1, 139	13.46	30.69	<0.0001	−0.03***
	disp						1, 139	6.67	15.21	<0.01	−3.69**
	disp^2						1, 139	6.25	14.26	<0.01	5.1**
log(NITZ I)	light	0.14	2, 140	0.12	11.01	<0.0001	1, 140	6.92	15.99	<0.0001	−0.02***
	disp						1, 140	2.59	5.97	<0.05	−0.54*
log(NITZ II)	light	0.41	3, 139	0.25	15.83	<0.0001	1, 139	18.18	22.8	<0.0001	−0.04***
	disp						1, 139	13.02	22.82	<0.0001	−0.25***
	light × disp						1, 139	5.67	9.29	<0.01	0.07**
Without light gradient											
STA	disp		1, 22	0.04	0.02	0.9	1, 22	0.1	0.02	0.9	−0.23
AMP	disp		1, 22	0.03	0.15	0.7	1, 22	0.25	0.15	0.7	−0.4
NAV	disp		1, 22	0.03	0.18	0.67	1, 22	0.08	0.18	0.67	0.23
NITZ I	disp		1, 22	0.004	1.1	0.3	1, 22	0.36	1.1	0.3	−0.49
NITZ II	disp		2, 21	0.03	1.35	0.28	1, 21	0.29	2.7	0.12	1.8
	disp^2						1, 21	0.27	2.5	0.13	−2.5

Notes: The table gives the weighed Akaike Information Criterion (wAIC), the results for the whole selected model, individual results for each contributing factor in the model, and regression slopes. Abbreviations are: STA, *Stauroneis constricta*; AMP, *Amphora coffaeiformes*; NAV, *Navicula ramosissima*; NITZ I, *Nitzschia* sp.; NITZ II, *Nitzschia sigma*; disp, dispersal rate; light, light intensity gradient.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$; † $P < 0.1$.

for one subdominant species (NAV), growth rates of the other inferior species did not change with light intensities. This shade tolerance allowed the inferior species to gain in relative biomass when the dominant species was competitively weaker in low light conditions. Dispersal rates in turn subsidized the relatively weaker but still superior competitor in unfavored low light conditions which compensated for its slower growth and led to high local dominance and low diversity and evenness in the same way as in conditions in its favored high light conditions. We can only speculate why STA was the best competitor in these communities although it did not show fastest growth rate, highest carrying capacity or largest cell size. One likely explanation is that light intensity is not the only limiting factor for the species used in this experiment. Hence, STA might be a weak competitor for light but the best competitor for another limiting resource such as dissolved inorganic carbon, nitrogen, phosphorous or silicate. This can be indirectly inferred by the fact that biomass of STA did not proportionally increased with light availability.

Although the competitive structure/hierarchy from high towards low light conditions was not completely reversed in terms of a dominance shift, i.e., we did not observe regional niche partitioning (species sorting after Leibold 1998, Leibold et al. 2004), this relatively small alteration of competitive hierarchy was strong enough to maintain diversity even at the regional scale when dispersal was limited. The absence of an interaction effect between dispersal rate and the light gradient being present or not on local species richness can be explained by the relatively longer response time to actually lose a species by complete competitive exclusion compared to observe changes in dominance and diversity (cf. Hillebrand et al. 2008).

Due to the lack of regional niche partitioning, our results do not confirm the prediction that low to intermediate dispersal rates enhance local diversity by maintaining inferior species in adverse environmental conditions. Instead, by subsidizing the relatively weaker but still superior competitor in unfavored low-light conditions, increased dispersal rates in this system homogenized the metacommunities, which is reflected in decreasing regional and beta diversity. To successfully test for the intermediate dispersal prediction, however, the difference between local environmental conditions across a metacommunity must be sufficient to lead to regional niche partitioning (sensu Leibold 1998). This assumption was made for a source–sink model by Mouquet and Loreau (2003) which shows that with increasing dispersal more species can coexist by rescuing locally inferior species. Our results, however, show that already minor changes in local competitive structure/hierarchy due to resource heterogeneity across a region can have major effects on the maintenance of local

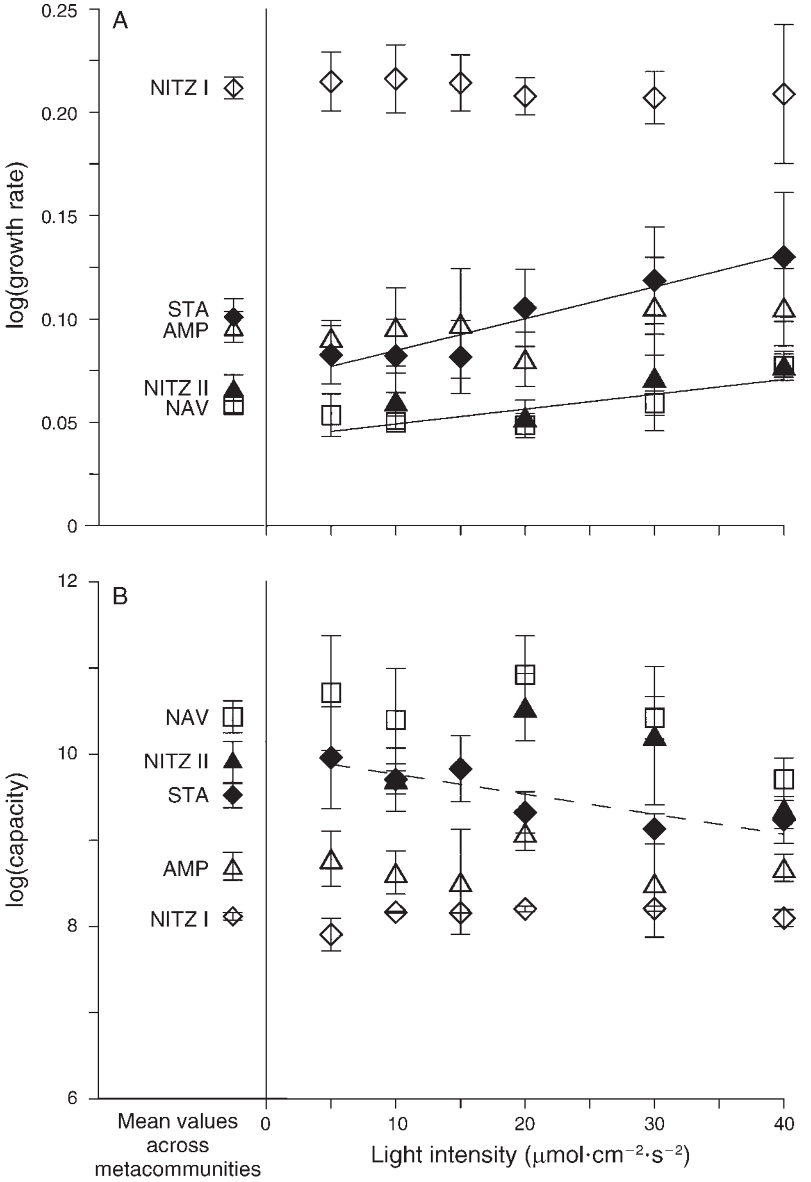

FIG. 4. (A) Growth rate and (B) carrying capacity of species in monocultures. The tagged values are mean values across all light levels across a metacommunity. Regression lines show significant (solid lines) and marginally significant (dashed line) responses to increasing light intensity. Error bars represent ±SE.

diversity and evenness and regional diversity when dispersal is limited.

The absence of dispersal effects on local diversity in the homogeneous system with uniformly distributed high light conditions could be explained in two ways. First, dispersal was manipulated in an artificial way. All species had equal chances to reach each local patch in a metacommunity, which did not allow for species-specific dispersal abilities. Therefore, trade-offs between dispersal and competitive abilities (Cadotte et al. 2006, Calcagno et al. 2006, Cadotte 2007) could not maintain diversity in our system. We chose this method because it corresponds to the way dispersal has been simulated in theoretical source–sink metacommunity models (Loreau et al. 2003, Mouquet and Loreau 2003) and thus our data are more directly comparable to these models. Moreover, passive dispersal can be relevant when complete pieces of a biofilm are detached from the bottom and disperse due to wave actions. For future experiments, however, less artificial dispersal methods will allow for potential life history trade-offs as shown experimentally in (Cadotte et al. 2006, Cadotte 2007). Second, the high dominance of STA also means that this species had the highest propagule transfer to the other patches. As a consequence of the dominance, the low supply of the inferior species was probably not sufficient to sustain populations (Hillebrand et al. 2008). However, the maintenance of one more species present in the region at intermediate dispersal rates might point to the fact that even this highly artificial and spatial implicit dispersal method led to the maintenance of one more rare species (though at very low abundances) in the metacommunity.

Although the light gradient was sufficient to sustain diversity in some local patches when dispersal was limited, it is likely that the strong main effect of the light gradient present on local and regional diversity does not result from patch heterogeneity alone but is confounded with overall light availability. The average light intensity in the metacommunities with gradient was 20 $\mu mol \cdot cm^{-2} \cdot s^{-1}$ whereas light intensity in the homogeneous system was constantly high with 40 $\mu mol \cdot cm^{-2} \cdot s^{-1}$. Competitive exclusion is known to get stronger with both, patch homogeneity and resource availability (Tilman 1982). Therefore, in this experiment we are not able to disentangle these two possible sources leading to high dominance.

We show that both uniformly distributed habitat patches with high resource availability and high dispersal rates of species among habitat patches with heterogeneously distributed and on-average lower resource availability led towards homogenization of the whole metacommunity by favoring the already best competitor. It has been shown that habitat loss and hence environmental homogenization such as by intensive farming is the main factor decreasing global biodiversity (Balmford and Bond 2005, Millenium Ecosystem Assessment 2005). In addition, increasing rates of human-mediated species introductions are on the rise (Millenium Ecosystem Assessment 2005). In the same way as dispersal, this can additionally lead to homogenization of communities by favoring opportunistic species which are often well adapted to high resource availability and high disturbance regimes (reviewed in McKinney and Lockwood 1999). These observations are in line with our experimental results. STA's dominance is strongest under high resource availability and increases everywhere in the region as soon as the local patches were highly connected. Thus, similar to the real world in our controlled experiment an already dominant competitor in some areas of a region becomes dominant everywhere when either dispersal rates are high or the environment provides a uniform, high resource level.

Due to the absence of regional resource partitioning, i.e., all patches were more or less dominated by the same species (STA), it was impossible that another regionally best adapted species to mean environmental conditions became dominant at high dispersal as shown in Loreau et al. (2003) and Mouquet and Loreau (2003). In contrast to the Loreau et al. and the Mouquet and Loreau (2003) models where each species in the regional pool is best adapted to a certain local condition, our experimental system describes a different organization of a metacommunity. The species are subject to a gradient from good to bad conditions. Species that are inferior competitors in the good conditions appear to be good stress tolerators in the bad conditions and vice versa. Thus, the community organization on the regional scale is not a consequence of niche partitioning due to different resource use traits as in Loreau et al. (2003) and Mouquet and Loreau (2003) but a result from differing performance under high (good conditions) vs. low resource availability (bad conditions). This kind of community organization has often been shown in the literature about intertidal ecosystems (Schonbeck and Norton 1980, Keddy 1989). Therefore, our experimental results might provide an alternative perspective how diversity in metacommunities is regulated by the interacting effects of differing stress tolerance, competition, and dispersal.

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APPENDIX A

Species list and life-forms (*Ecological Archives* E091-139-A1).

APPENDIX B

Photographs of species, communities, and experimental setup (*Ecological Archives* E091-139-A2).

APPENDIX C

Duration of each species to reach carrying capacity (*Ecological Archives* E091-139-A3).