Stressor fluxes alter the relationship between beta-diversity and regional productivity

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Abstract

Dispersal of organisms can influence the relationship between beta-diversity and regional productivity in heterogeneous environments. However, many ecosystems are also linked by fluxes of stressors, with an unknown influence on this relationship. In this study, we assess the relationship between beta-diversity (measured as Bray-Curtis dissimilarity) and regional productivity (measured as biovolume) under various levels of a stressor flux in meta-ecosystems that were composed of two marine micro-algae communities. We created heterogeneity by exposing one of the two communities to a herbicide and manipulated regional diversity by applying a dispersal gradient, which decreased beta-diversity. We applied four stressor flux levels, which homogenized the herbicide concentration between the communities over time. The stressor flux changed the relationship between beta-diversity and regional productivity by changing the effect of dispersal on regional productivity. In absence of the stressor flux, the relationship between beta-diversity and regional productivity was mostly not significant, but positive at the end of the experiment. This positive relationship was generated by a negative effect of dispersal on regional productivity, probably because dispersal disrupted local dynamics by removing organisms from the most-productive unstressed community. In presence of the stressor flux, the relationship between beta-diversity and regional productivity was often negative as dispersal now increased regional productivity. Dispersal increased regional productivity by increasing the productivity of the stressed community. This positive effect was stronger in the presence than in the absence of the stressor flux because the stressor flux reduced the concentration of the herbicide in the stressed community, where it facilitated recovery. Our study shows that stressor fluxes can strongly interact with the effects of dispersal on productivity and thus influence diversity-productivity relationships.

Keywords

diversity-productivity relationships, meta-ecosystems, stressor flux, dispersal, spatial insurance effect

Introduction

Stressors such as global warming, habitat fragmentation or the release of chemical stressors are changing global biodiversity (Vörösmarty et al. 2010, Malaj et al. 2014, Pimm et al. 2014). To date, both theoretical and field studies have provided ample evidence that biodiversity changes affect ecosystem provisioning in closed systems, and that the consequences of biodiversity changes are altered by stressors (Cardinale et al. 2012, Hooper et al. 2012, Tilman et al. 2014, De Laender et al. 2016, Baert et al. 2018). However, a major open challenge is to unravel how biodiversity and ecosystem functioning are related at a regional scale. Meta-ecosystems are ecosystems in which spatial fluxes of organisms (dispersal), energy and materials are explicitly considered (Loreau et al. 2003a, Massol et al. 2011). Those fluxes can change regional and local diversity, ecosystem functioning (e.g. productivity) and the relationship between both (Loreau et al. 2003a, Haegeman and Loreau 2014, Leibold et al. 2017, Massol et al. 2017).

The dispersal of organisms, which is currently the most studied flux, is often demonstrated to influence the diversity and productivity of communities. A well-known component of diversity is beta-diversity, which quantifies the difference in community composition (Whittaker 1960). In heterogeneous environments, differences in composition among communities are mainly generated by local competitive processes (Cottenie 2005, Myers et al. 2015). Dispersal may disrupt these local processes, homogenizing community composition and decreasing beta-diversity. First, dispersal can decrease the differences in species densities among communities (Baselga 2013, Gianuca et al. 2016). Second, dispersal can introduce new species from other communities or maintain species in communities where they would otherwise be excluded through competition (Mouquet and Loreau 2003, Baselga 2013). The latter occurs in source-sink communities in which organisms disperse from communities where they are strong competitors (the source), to communities where they are weak competitors (the sink) (Leibold et al. 2004). Dispersal is predicted to reduce regional productivity in source-sink communities (Mouquet and Loreau 2003, Leibold et al. 2017) because dispersal can move organisms from communities where they are locally adapted (and therefore highly productive) to communities were they are less adapted (and therefore less productive) (Mouquet and Loreau 2003). Negative dispersal effects on productivity mostly appear at high dispersal rates (Howeth and Leibold 2010, Lindström and Östman 2011), but have also been found at low dispersal rates in micro-algae communities (Eggers et al. 2012, de Boer et al. 2014). Furthermore, dispersal is shown to increase regional productivity by maintaining diversity under changing environmental conditions, also referred to as the spatial insurance effect (Loreau et al. 2003b, Steiner et al. 2011, Symons and Arnott 2013, de Boer et al. 2014).

Fluxes of materials, such as resources and chemical stressors, generate spatiotemporal changes of environmental conditions that can interfere with the effect of dispersal on diversity and productivity on a regional scale (Loreau et al. 2003a, Massol et al. 2011, Haegeman and Loreau 2014). However, empirical studies that combine dispersal and material fluxes are generally lacking (Massol et al. 2017). Moreover, to test how dispersal and material fluxes interact, there is a need for studies that manipulate dispersal and material fluxes independently (Massol et al. 2017). To our knowledge, so far only one study has done so, finding dispersal and a resource flux to increase ecosystem functioning (Harvey et al. 2016). However, it is unsure to what extent these results apply to other kinds of material fluxes. Indeed, organisms can produce or consume resources (Staddon et al. 2010, Harvey et al. 2016), while they are generally not able to impact environmental stressors such as pesticides (Chase and Leibold 2003).

This study independently manipulates dispersal and the flux of a chemical stressor to investigate how both factors combine in affecting the relationship between beta-diversity and regional productivity. We used heterogeneous two-patch meta-ecosystems, in which both patches initially contained an identical micro-algae community. Within each meta-ecosystem, heterogeneity was created by initially exposing only one community to the photosynthesis inhibiting pesticide atrazine. This stressor reduced the growth of the micro-algae in a species-specific way and therefore induced a different composition in the unstressed (no stressor present on day 0) than in the stressed (stressor present on day 0) community. We manipulated dispersal over the two-patch meta-ecosystems, to homogenize the composition and to install a gradient in beta-diversity. Next, we simulated a stressor flux (four levels) within the meta-ecosystems. Because of this stressor flux, the stressor concentration increased in the unstressed community and decreased in the stressed community.

Regardless of the stressor flux level, we expected that dispersal would reduce beta-diversity (Mouquet and Loreau 2003), creating a beta-diversity gradient. In the absence of the stressor flux we expected that dispersal would decrease regional productivity by disrupting local processes, as theoretically predicted by Mouquet and Loreau (2003) and experimentally found in other marine micro-algae communities (Eggers et al. 2012, de Boer et al. 2014). Thus, in the absence of the stressor flux, we predicted a positive relationship between beta-diversity and regional productivity (Fig. 1). Conversely, in the presence of the stressor flux, we predicted that dispersal would increase regional productivity by introducing better-adapted organisms in communities where the stressor concentration was changed by the stressor flux, generating a negative relationship between beta-diversity and regional productivity (Fig. 1). Thus, overall, we expected the stressor flux to change the relationship between beta-diversity and regional productivity from positive (without flux) to negative (with flux).

We performed additional analyses to investigate how the stressor flux influenced the relationship between beta-diversity and regional productivity. First, we investigated the effect of dispersal on beta-diversity and on community composition (the density of the dominant algae strains). Second, we examined how dispersal changed regional and local productivity for the various stressor flux levels. Last, we also assessed the sensitivity of the dominant algae strains towards the stressor.

Materials and methods

Algae strains

Marine diatoms (*Bacillariophyceae*) were collected from the Belgian part of the Southern Bight of the North Sea with a 10 µm mesh size phytoplankton net. We isolated individual algae cells following the protocol of Andersen and Kawachi (2005). Each algae cell thus gave rise to a monoclonal algae culture, indicated as *strain*. The algae strains were identified to the genus level using a light microscope and cell volumes were calculated according Hillebrand et al. (1999) (Supplementary Material Appendix A1, Table A1). They were grown in f/2 medium (Guillard and Ryther 1962) composed of artificial seawater (Instant Ocean®, Aquarium Systems) supplemented with 30 $mg\ l^{-1}$ silicon and kept in a climate room (20 ± 1°C) with a 16h photoperiod at 35 ± 5 μmol photons $m^{-2}s^{-1}$ light intensity (Lumilux® Coolwhite, Osram). New cultures were inoculated every week to keep the cultures in the exponential or early stationary growth phase. From the available stock cultures, six strains (*Navicula* sp., *Thalasiossira* sp., *Odontella* sp., *Asterionellopsis* sp., *Asterionella* sp., *Melosira* sp.) were randomly selected for the experiment.

Experimental design

Each experimental meta-ecosystem consisted of two local patches that contained micro-algae grown in individual Erlenmeyer flasks at two different concentrations of the chemical stressor atrazine (unstressed: 0 $\mu g\ l^{-1}$ and stressed: 250 $\mu g\ l^{-1}$) to create stressor heterogeneity. At the start of the experiment, the six algae strains were added together in f/2 medium at an equal abundance of $5x\ 10^7\ \mu m^3$ per strain to achieve a final culture volume of 30 ml per flask. We used a full factorial design with 4 stressor flux levels (0%, 5%, 10% and 15%, see below) and 5 dispersal levels (0%, 5%, 10%, 15% and 20%, see below). The stressor flux and dispersal were manipulated on the same day, every 4 days. All treatments were replicated 3 times, obtaining 60 two-patch meta-ecosystems. The experiment ran for 24 days.

At a stressor flux of x%, we simulated every four days the exchange of x% of medium containing the stressor between the unstressed and stressed community. Hence, the concentration of the stressor in the unstressed community increased and the concentration of the stressor in the stressed community decreased, while the total amount and the mean concentration of the stressor across the meta-ecosystem remained constant (Supplementary Material Appendix A, Fig. A1). We simulated the exchange of the stressor by removing old and adding new medium, manipulating the stressor concentration. To manipulate the stressor concentration, 10 ml of culture was centrifuged (Supplementary Material Appendix A, Fig. A2) and 9 ml of supernatant was removed and stored for nutrient and atrazine analysis. The residue, containing the algae, was added back to the culture. Next, 10 ml of new medium was added to the flask. The atrazine concentration of the added medium depended on the stressor flux rate. The added medium had the appropriate atrazine concentration to obtain the same concentration as if the medium would have been directly exchanged between flasks (Supplementary Material Appendix A, Table A2a-A2c). By adding new medium, we made sure that only the stressor was manipulated but no other compounds in the water, such as nutrients. Supplementary Material Appendix A, Table A2a, A2b, A2c provides the values of theoretical concentration of the stressor in the medium after a stressor flux, the concentration of stressor in the added medium, and the measurements of the stressor concentrations at the end of the experiment (mean concentration of the three replicates within the no-dispersal treatment). Our measurements show small deviations between the predicted and measured concentrations and confirmed that a higher stressor flux increased the concentration in the unexposed communities, while reducing the concentration in the exposed communities. However, the flux did not completely homogenize the stressor concentration by the end of the experiment. The mean concentration per stressor flux level was always close to 125 $\mu g\ l^{-1}$. The added medium was not added directly to the flasks because the medium was used to rinse the centrifuge tubes to avoid any algae loss. 5 ml was used to rinse the centrifuge tube during the stressor flux phase, and 5 ml was used to rinse the centrifuge tube during the dispersal phase (see below).

Next to the replacement of medium during the stressor flux, we also renewed medium two days after the manipulation of the stressor flux (days 2, 6, 10, 14, 18 and 22). Medium replacement was done for two reasons. First, atrazine had to be replaced regularly because it is degraded by light (half-life value between 90-120 days (Solomon et al. 1996)). By replacing the medium, the atrazine concentration mostly changed because of the simulated stressor flux rather than because of degradation. Second, medium replacement delayed nutrient depletion. Medium replacement was done by removing 10 ml from the upper layer of the culture (diatoms tend to sink to the bottom of the flask), followed by the addition of 10 ml of clean medium at the original atrazine concentration and manual shaking of the flasks.

Dispersal was manipulated together with the stressor flux by moving a fixed proportion of the algae between the two patches of each meta-ecosystem. First, a flask was shaken to homogenize the algae cultures. Next, we pipetted 0%, 5%, 10%, 15% or 20% of each culture into a 8 ml centrifuge tube. After centrifugation, the supernatant was added back to the original flask, after which only 0.2 ml of the residue remained in the centrifuge tube. Because the algae and medium cannot be completely separated, we rinsed the algae with new medium that had the same concentration as the flask where the algae dispersed to. To remove the rinsing medium, the tube was centrifuged again, after which the supernatant was removed until 0.2 ml of residue remained. After adding the residue to the target flask, the centrifuge tube was rinsed with 5 ml of medium, which had the appropriate concentration to reach the target concentration, to avoid any algae loss (see above). This rinsing medium was then also added to the target flask.

All cultures were grown in a climate room (20±1 °C) under 35 ± 5 μmol photons $m^{-2}s^{-1}$ light intensity at a 16h photoperiod. Erlenmeyer flasks were repositioned every 2 days to eliminate potential differential light effects in the climate room. Every 4 days, just before manipulating the stressor flux and dispersal, we took 1 ml samples for algae counting. The samples thus show the state of the communities 4 days after the most recent manipulation of the stressor flux and dispersal. The samples were conserved with 0.2 ml of formaldehyde (35%) and stored at 4°C in 24 multiwell-plates for conservation. From each sample, a subsample was counted using an inverse microscope and Whipple grid. The size of the subsample depended on the cell density, but was sufficient to always include more than 100 cells of the most dominant strain. Nutrient samples were stored at 4°C and analyzed by Spectroquant® spectrophotometry (Supplementary Material Appendix A1, Table A3). Atrazine concentrations were determined using HPLC (Supplementary Material Appendix A1, Table A2a, A2b, A2c).

Before the meta-ecosystem experiment, we determined the algae growth parameters and sensitivity to the chemical stressor in monoculture at 5 different concentrations of the chemical stressor atrazine (Sigma Aldrich) (0, 50, 100, 250, 500 $\mu g\, l^{-1}$). Algae were grown during 14 days in Erlenmeyer flasks under the same conditions as the two-patch experiment. Cell densities were determined at day 4, 7, 9, 11, and 14 from 1 ml samples using a Whipple Grid.

Data analysis

We quantified beta-diversity by measuring Bray-Curtis dissimilarity, using the betapart package in R (Baselga et al. 2013). Because of the variability in cell sizes among strains, Bray-Curtis dissimilarity was determined using the individual strains' biomass calculated as biovolume (Hillebrand et al. 1999). As a measure of productivity, we used total biovolume. For the statistical analyses, biovolumes were log transformed to obtain normality of the residuals. All analyses were performed for each sampling day and stressor flux level separately. To test for the effect of beta-diversity on regional productivity, we fitted a linear model with Bray-Curtis dissimilarity as the predictor variable and the log-transformed regional productivity as the response variable. To test for the effect of dispersal on beta-diversity, we fitted a beta-regression model, which is used when the dependent variable is a proportion between 0 and 1. We used dispersal as the predictor variable and the Bray-Curtis dissimilarity as the response variable by using the betareg package in R (Cribari-neto and Zeileis 2010). To measure the significance of the predictor variables, the betareg package uses the zstatistic, which is the regression coefficient divided by its standard error. To test for the effect of dispersal on the densities of (the most abundant) strains, regional productivity and local productivity, we fitted a linear model with dispersal as the predictor variable and the log-transformed strain density, regional productivity or local productivity as the response variable respectively.

The growth rate (μ) and carrying capacity (K) of the six strains were determined by fitting a logistic growth curve to the monoculture data. The best model fit was calculated by minimizing the sum of squared errors with a simulated annealing algorithm using the GenSA package in R (Xiang et al. 2013). A log-logistic dose-response curve (equation 1) was fitted to model the effect of atrazine on the per-capita growth rate and carrying capacity using the drc package in R (Ritz et al. 2015)

$$f(conc) = \left(\frac{max}{1 + e^{s(ln(conc) - ln(EC_{50}))}} \right) \tag{1}$$

With $f(conc)$ the growth rate (μ) or carrying capacity (K) as a function of the concentration of the chemical stressor $conc$ ($\mu g\ l^{-1}$), max ($\mu g\ l^{-1}$) the maximum value of the logistic function, s the slope of the dose respons curve and EC_{50} ($\mu g\ l^{-1}$) the concentration at which the growth rate or carrying capacity is reduced with 50%. All calculations were performed in R (R. Core Team 2016).

Results

The relationship between beta-diversity and regional productivity

The stressor flux changed the relationship between beta-diversity (Bray-Curtis dissimilarity) and regional productivity (Fig. 2, Table 1). In the absence of the stressor flux, the relationship between beta-diversity and regional productivity was mostly non-significant, but became positive at the end of the experiment (day 24) (Fig. 2, Table 1). At a low stressor flux, the relationship between beta-diversity and regional productivity was positive on day 8, negative on day 20 and not significant on the other days (Fig. 2, Table 1). At a medium stressor flux, the relationship between beta-diversity and regional productivity was positive on day 8, not significant on day 12 and negative afterwards

(Fig. 2, Table 1). Last, at a high stressor flux the relationship between beta-diversity and regional productivity was not significant on day 8, negative on days 12, 16 and 20, but not significant on day 24 (Fig. 2, Table 1).

The effect of dispersal on beta-diversity and strain abundances

The presence of the stressor strongly decreased the density of *Asterionellopsis* sp. and *Navicula* sp. in the stressed community (i.e. the community where the stressor was initially present) (Fig. 3), generating a high beta-diversity in the meta-ecosystems without dispersal. Dispersal reduced beta-diversity across all stressor flux levels (Fig. 2, Supplementary Material Appendix A, Table A4) by decreasing the difference in density of the strains between the unstressed and stressed community (Fig. 3). In the unstressed community (i.e. the community where the stressor was initially absent), dispersal decreased the density of *Navicula* sp. on day 24 in the absence of the stressor flux (Fig. 3, Supplementary Material Appendix A, Table A6). In the stressed community, dispersal increased the density of *Asterionellopsis* sp. and *Navicula* sp. at all stressor flux levels (Fig. 3, Supplementary Material Appendix A, Table A7-A8). Positive effects of dispersal on density were generally stronger in the presence than in the absence of the stressor flux and appeared earlier for *Asterionellopsis* sp. than for *Navicula* sp.

The effect of dispersal on regional and local productivity

Dispersal affected productivity at a regional and local scale. In the absence of the stressor flux, dispersal increased (on day 20) and decreased regional productivity (on day 24; Fig. 4, Supplementary Material Appendix A, Table A9). In presence of the stressor flux, the effect of dispersal on regional productivity was initially not significant or negative, but positive afterwards (Fig. 4).

In the absence of the stressor flux, dispersal effects on the productivity of the unstressed community were non-significant at early and intermediate time steps, but negative at the end of the experiment (Fig. 4, Table 2). Dispersal increased the productivity of the stressed community during almost the entire experiment (Table 3). In the presence of the stressor flux, dispersal decreased the productivity of the unstressed community in the medium stressor flux treatment during the first weeks of the experiment (Fig. 4, Table 2). Dispersal increased the productivity of the stressed community during the entire experiment and its effect was generally stronger than in the absence of the stressor flux (Fig. 4, Table 3).

Stain sensitivities

Asterionellopsis sp. and *Navicula* sp. greatly influenced community dynamics, as they together accounted for more than 90% of the total biovolume in the unstressed and stressed community (day 24 - no stressor flux, no dispersal treatment) (Fig. 3, Supplementary Material Appendix A, Fig. A3). A monoculture bioassay showed that the growth rate of these two dominant strains had a similar sensitivity to the chemical stressor, while the carrying capacity of *Asterionellopsis* sp. was less sensitive than that of *Navicula* sp. (Fig. 4, Supplementary Material Appendix A, Table A1).

Discussion

The obtained results empirically demonstrate that stressor fluxes can change the relationship between beta-diversity and regional productivity and offer insight into the underlying mechanisms. In our study system, this change was the result of dispersal affecting regional and local productivity differently in the presence of the stressor flux, compared to when no flux was present. In contrast, we did not find the stressor flux to alter dispersal effects on beta-diversity as these were negative across all stressor flux levels.

The relationship between beta-diversity and regional productivity in the absence of the stressor flux.

In the absence of the stressor flux, we predicted a positive relationship between beta-diversity and regional productivity, because dispersal would decrease both beta-diversity and regional productivity. Dispersal was expected to reduce regional productivity by disrupting local dynamics when exporting well-adapted (and therefore highly productive) organisms while importing less well-adapted, and thus less-productive, organisms (Mouquet and Loreau 2003). Contrary to this expectation, we found a positive relationship between beta-diversity and regional productivity on day 24 only, while the relationship was not significant before. At first, this seems surprising because dispersal disrupted local dynamics in the unstressed community by moving organisms of *Asterionellopsis* sp. and *Navicula* sp. from the unstressed to the stressed community. This movement was due to higher density in the unstressed than in the stressed community in absence of dispersal, which reflects the negative effects of the chemical stressor on growth. Although a reduction of the density of the best-adapted strains in the unstressed community is expected to decrease productivity, dispersal did not induce a regional productivity decrease, except on day 24. A main reason for this is that the negative effect of dispersal in the unstressed community (essentially, the withdrawal of biomass) was compensated by a positive effect of dispersal in the stressed community. Moreover, negative dispersal effects on the productivity of the unstressed community were often low or absent. Indeed, dispersal-induced productivity decreases are generally found at dispersal rates that are high compared to the reproduction rate (40%-100%) (Leibold et al. 2017). In the present study, the highest dispersal rate was approximately only 5% of the exponential growth rate of *Asterionellopsis* sp. without the stressor.

Only on day 24, we found a positive relationship between beta-diversity and regional productivity (Fig. 2). On day 24, dispersal reduced regional productivity by reducing the productivity of the unstressed community (Fig. 3). It is not clear why dispersal reduced the productivity in the unstressed community only on day 24 and not on earlier days. Moreover, the negative effect of dispersal on productivity in the unstressed community was unexpectedly high (80%), given that the highest dispersal rate was only 20%. A part of the negative effect of dispersal on productivity was probably due the dispersal-induced removal of organisms of *Navicula* sp. from the unstressed community on day 20, limiting biovolume production between day 20 and 24. However, the reduction in productivity was also the result of cell lysis in the communities at a high dispersal rate.

Cell lysis may occur when nutrients are limited, or waste products are accumulating (Brussaard et al. 1997, Brussaard and Riegman 1998, Andersen and Kawachi 2005). However, it is not clear why cell lysis occurred first in the highest dispersal treatments. A possible explanation is that dispersal altered interactions between algae strains or interactions between algae and other organisms such as bacteria, which are shown to influence algae growth through facilitation or competition (Cole 1982, Grossart 1999). Our results thus indicate that an increasing homogenization through dispersal can reduce regional productivity in the absence of a stressor flux, as was found before in other marine micro-algae communities (Eggers et al. 2012, de Boer et al. 2014). However, this reduction may be caused by more complex interactions than predicted by theory in Mouquet and Loreau (2003).

In absence of the stressor flux, dispersal increased the productivity of the stressed community, but this effect was initially too weak to increase regional productivity because the high stressor concentration disabled the growth of the introduced organisms (Fig. 5). Only on day 20, the recurrent dispersal events increased the productivity of the stressed community enough to increase regional productivity (Fig. 4). However, on that day, dispersal did not induce a significant relationship between beta-diversity and regional productivity, because the difference in beta-diversity among the meta-ecosystems under dispersal was too small (Fig. 2).

The relationship between beta-diversity and regional productivity in the presence of the stressor flux.

In the presence of the stressor flux, we predicted a negative relationship between beta-diversity and regional productivity because dispersal would decrease beta-diversity but increase regional productivity. Theory predicts that under changing environmental conditions dispersal can increase productivity by introducing strains that are better adapted (Loreau et al. 2003b). As predicted, we found negative relationships between beta-diversity and regional productivity in the presence of the stressor flux from day 12 (Fig. 2). Dispersal increased regional productivity by increasing the productivity of the stressed community, while not affecting the productivity of the unstressed community (Fig. 4).

The stressor flux reduced the stressor concentration in the stressed community, generating recovery by increasing the growth rate of the stress-tolerant strains (Fig. 5). Instead of introducing new strains to the stressed community, dispersal introduced the strains that were also most abundant in the stressed community without dispersal because the most stress-tolerant strains, *Asterionellopsis* sp. and *Navicula* sp. dominated the unstressed as well as stressed community. By introducing organisms of *Asterionellopsis* sp. and *Navicula* sp., dispersal increased recovery in the presence of the stressor flux (Fig. 3). The positive effect of dispersal on the productivity of the stressed community was stronger in the presence than in the absence of the stressor flux, because the dispersed organisms could grow in the presence of the stressor flux while their growth was suppressed in the absence of the stressor flux because of the high stressor concentration (Fig. 5).

The fact that dispersal can reinforce recovery by subsidizing population growth was also demonstrated in communities that were exposed to heat stress by de Boer et al. (2014). However, in de Boer et al. (2014), the stressor was applied synchronically across all communities, while the environmental conditions in our study were spatiotemporally varied. There are some studies that applied temporal fluctuations (Steiner et al. 2011, Guelzow et al. 2014), but they only alternated the environment between two conditions. Such rapid transitions select for the strains that persist in the extreme conditions. Instead, in the present study, the stressor flux gradually changed the stressor concentration, allowing the community composition to track this change. As such, negative relationships between beta-diversity and regional productivity initially appeared at the highest stressor flux level and only later at the low- and medium stressor flux level.

In the unstressed community, the stressor flux increased the concentration of the chemical stressor. However, dispersal did not affect productivity in the unstressed community by introducing stress-tolerant strains, because the strain which was most stress-tolerant, *Asterionellopsis* sp., dominated the unstressed community early in the experiment (Fig. 3). Because the stressor effect on the carrying capacity of *Asterionellopsis* sp. was nonlinear (Fig. 5d), the effect of the increasing stressor concentration on productivity was small in the unstressed community. When communities proceeded from the initial to the final concentration in the unstressed community (86 $\mu g\ l^{-1}$ for the highest stressor flux), the decrease of the carrying capacity in the unstressed community was therefore almost negligible.

The stressor flux generated a negative spatial covariance of the stressor concentration between the unstressed and stressed community, homogenizing the environmental conditions and decreasing the difference in productivity between the unstressed and stressed community. Hence, the effect of dispersal on beta-diversity and regional productivity decreased at the end of the experiment, which resulted in the absence of a significant relationship between beta-diversity and regional productivity on day 24 at the highest stressor flux level. Stressor fluxes may thus reduce dispersal effects on diversity and productivity in the long term.

Concluding remarks

Our study system and design are characterized by five aspects that should be bared in mind when extrapolating to other systems or scenarios. First, competitive interactions were strong, which induced the dominance of two algae strains. Planktonic microalgae systems are often subject to strong interspecific competition because of the limited spatial heterogeneity (Giller et al. 2004), and are hence in laboratory conditions generally dominated by only a few species (Mensens et al. 2015, Baert et al. 2016, 2017). Second, in the present study, the unstressed and stressed community were dominated by the same algae strains. However, how community compositions change highly depends on the correlation between competitive abilities and the sensitivity to the stressor (De Laender et al. 2016, Baert et al. 2017, Spaak et al. 2017). Third, our study design used six algae strains that were initially present in each community, and we did not allow dispersal from the regional species pool (Lessard et al. 2012). Dispersal from the region could have introduced more stress-tolerant or more competitively dominant species, leading to a stronger positive effect of dispersal on productivity. Fourth, in this study, the stressor flux and dispersal were enforced by moving organisms between the patches. In reality, stressor fluxes are caused by agents such as water currents and diffusion. When organisms move passively, stressor fluxes and dispersal are often linked. Our results indicate that in such cases, regional productivity can be positively affected by dispersal. When organisms move actively, avoidance of less appropriate patches can occur, e.g. because of the presence of a chemical stressor (Araújo et al. 2016), or because of a lower nutrient availability (Byers 2000, Kennedy and Ward 2003). Such avoidance behavior precludes positive dispersal effects under stressor fluxes. Last, in the present study, we applied symmetric dispersal (dispersal probability in both directions is equal) and equal per capita dispersal rates, which have been shown to favor competitive dominant species (Salomon et al. 2010). Many habitats are characterized by asymmetric dispersal, e.g. planktonic organisms follow the water current, and plant seeds disperse according to the wind direction. Moreover, organisms show different per capita dispersal rates (Edelaar and Bolnick 2012, Bonte and Dahirel 2017). Therefore, our study is only a first step to understand beta-diversity – productivity relationships and studies that use other dispersal mechanisms and properties are required.

Previous studies have shown that the relationship between beta-diversity and productivity is often positive (Chase and Leibold 2002, Chalcraft et al. 2004, Chase and Ryberg 2004, Harrison et al. 2006). While this study found a positive relationship in the absence of the stressor flux, this relationship shifted to negative in the presence of the stressor flux. Dispersal and a stressor flux may thus interact in regulating the relationship between beta-diversity and productivity. This interaction can have consequences when managing ecosystem functioning of landscapes in which some local communities are exposed to growth-affecting agents, such as the chemical stressors that were used in this study. The concentration at which we applied atrazine can usually only be found in agricultural areas after application (Graymore et al. 2001). Although background concentrations are generally much lower (Nödler et al. 2013), chemical stressors are abundant in many marine waters (Halpern et al. 2008, Abessa et al. 2018) and the present experiment helps to gain mechanistic insight how the flux of chemical stressors may affect the relationship between diversity and productivity. Based on our study, we recommend further investigating how these fluxes affect communities and interact with the dispersal of organisms.

Acknowledgement

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Declarations

The authors declare that they have no conflict of interest.

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Figure captions

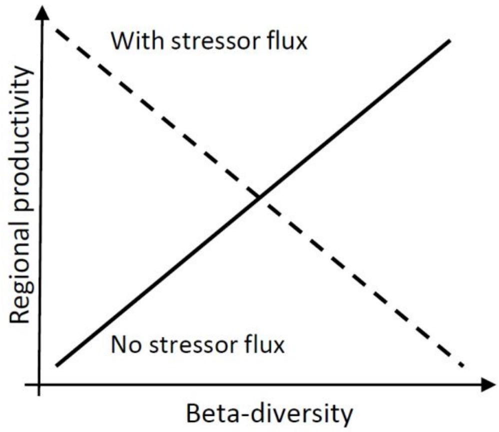
Fig. 1. Hypothesized relationship between beta-diversity and regional productivity in the absence or the presence of the stressor flux.

Fig. 2. The log transformed regional productivity in function of beta-diversity between days 8 and 24, for the four stressor flux treatments. Symbols represent the data, lines depict the regression lines based on linear models. Regression lines are only depicted if significant ($p < 0.05$). Samples were taken just before the stressor flux and dispersal were manipulated.

Fig. 3. The log transformed local density of *Asterionellopsis* sp. and *Navicula* sp. in function of dispersal between days 8 and 24, for the four stressor flux treatments. Symbols represent the data, lines depict the regression lines based on linear models. The green symbols and lines represent the unstressed community (i.e. the community were the stressor was initially absent), and the red symbols and lines represent the stressed community (i.e. the community were the stressor was initially present). Regression lines are only depicted if significant ($p < 0.05$).

Fig. 4. Local and regional productivity in function of dispersal between days 8 and 24, for the four stressor flux treatments. Symbols represent the data, lines depict the regression lines based on linear models. The full lines represent local productivity and the dotted lines represent regional productivity. Regression lines are only depicted if dispersal is a significant predictor of log transformed productivity ($p < 0.05$). Data of regional productivity are not shown.

Fig. 5. The growth rate of (a) *Navicula* sp. and (b) *Asterionellopsis* sp. and the carrying capacity of (c) *Navicula* sp. and (d) *Asterionellopsis* sp. in function of the stressor (atrazine) concentration. The dots represent the data, the curve represents the fitted logistic dose-response relationship (eq. 4). The dotted line represents the EC_{50} i.e. concentration at which the growth rate and carrying capacity are reduced with 50%.



570

571 Fig. 1. Hypothesized relationship between beta-diversity and regional productivity in the absence or the presence of the stressor flux.

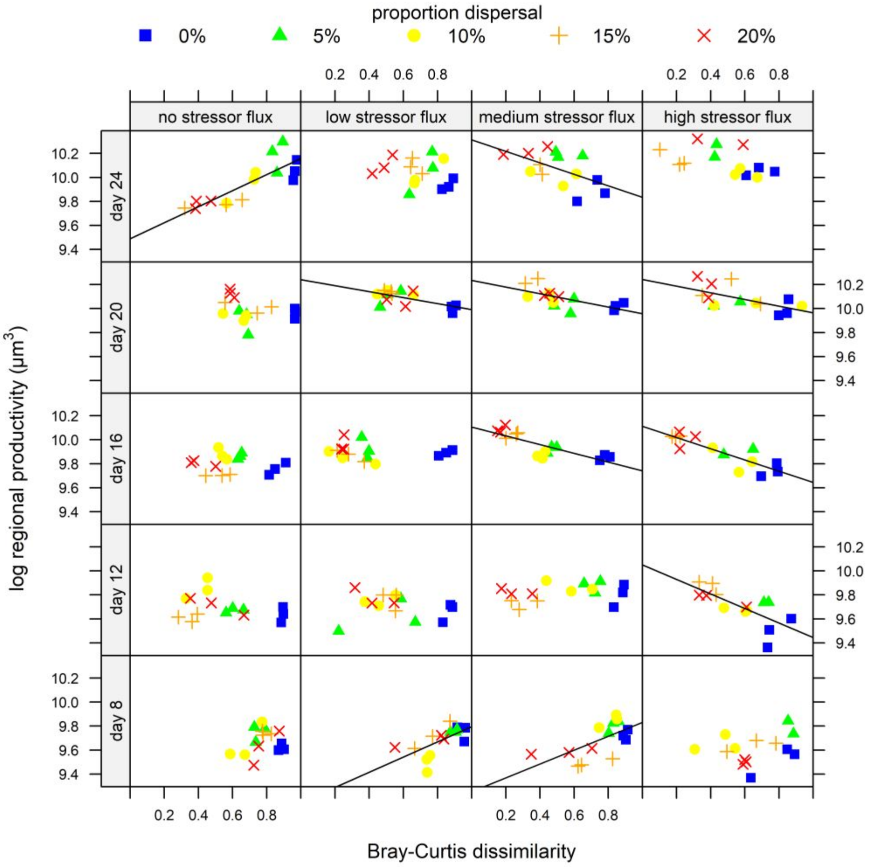


Fig. 2. The log transformed regional productivity in function of beta-diversity between days 8 and 24, for the four stressor flux levels. Symbols represent the data, lines depict the regression lines based on linear models. Regression lines are only depicted if significant ($p < 0.05$). Samples were taken just before the stressor flux and dispersal were manipulated.

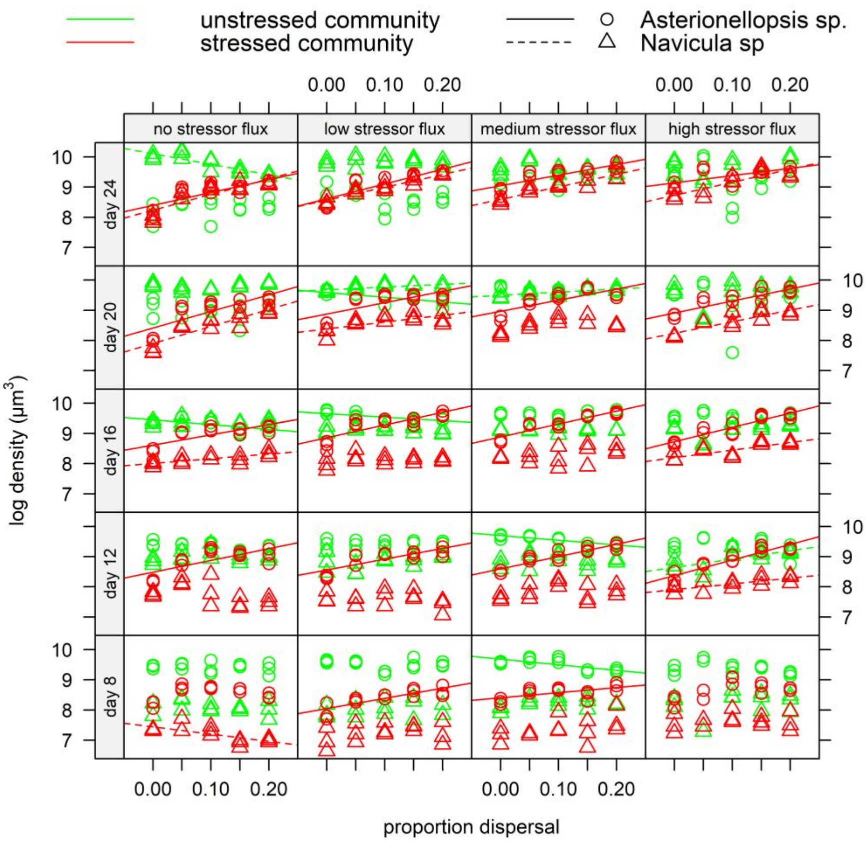


Fig. 3. The log transformed local density of *Asterionellopsis* sp. and *Navicula* sp. in function of dispersal between days 8 and 24, for the four stressor flux treatments. Symbols represent the data, lines depict the regression lines based on linear models. The green symbols and lines represent the unstressed community (i.e. the community were the stressor was initially absent), and the red symbols and lines represent the stressed community (i.e. the community were the stressor was initially present). Regression lines are only depicted if significant ($p < 0.05$).

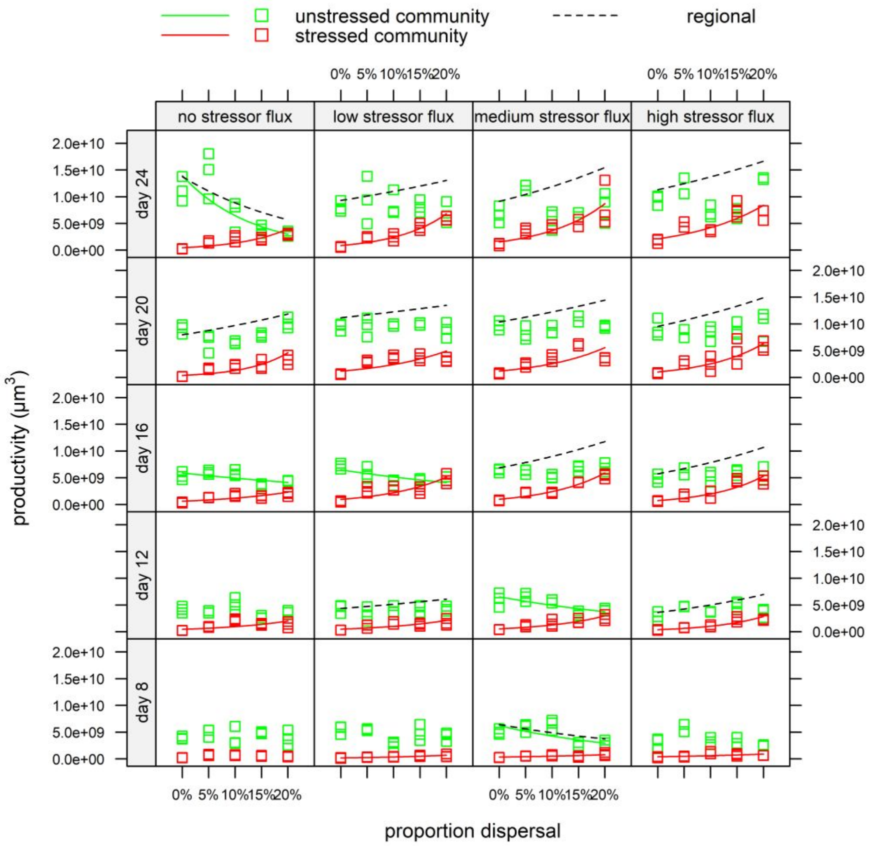


Fig. 4. Local and regional productivity in function of dispersal between days 8 and 24, for the four stressor flux treatments. Symbols represent the data, lines depict the regression lines based on linear models. The full lines represent local productivity and the dotted lines represent regional productivity. Regression lines are only depicted if dispersal is a significant predictor of log transformed productivity ($p < 0.05$). Data of regional productivity are not shown.

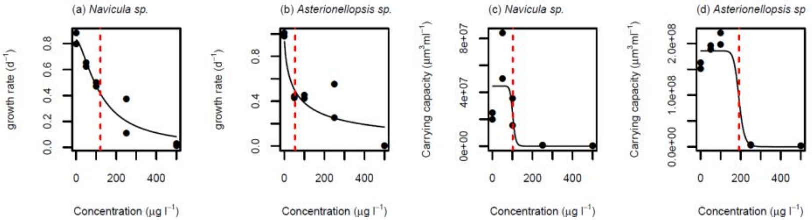


Fig. 5. The growth rate of (a) *Navicula* sp. and (b) *Asterionellopsis* sp. and the carrying capacity of (c) *Navicula* sp. and (d) *Asterionellopsis* sp. in function of the stressor (atrazine) concentration. The dots represent the data, the curve represents the fitted logistic dose-response relationship (eq. 1). The dotted line represents the EC_{50} i.e. concentration at which the growth rate and carrying capacity are reduced with 50%.

Table 1. Results of the generalized linear model with the Bray-Curtis dissimilarity index (BC diss) as a measure of beta-diversity as the predictor variable and the log transformed regional productivity as the response variable. *mean±sd*. Significance levels: * 0.05, ** 0.01, *** 0.001

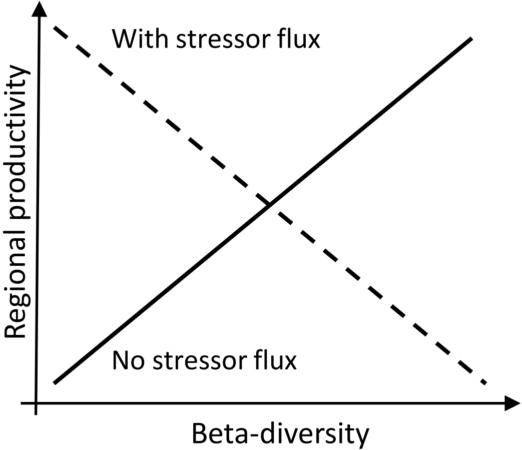
Day	Factor	No stressor flux	Low stressor flux	Medium stressor flux	High stressor flux
8	Intercept	9.435 ± 0.250***	9.163 ± 0.179***	9.253 ± 0.154***	9.475 ± 0.129***
	BC diss	0.311 ± 0.319	0.633 ± 0.216*	0.577 ± 0.199*	0.194 ± 0.327
12	Intercept	9.753 ± 0.069***	9.816 ± 0.109****	9.775 ± 0.046***	10.084 ± 0.097***
	BC diss	-0.317 ± 0.128*	-0.234 ± 0.190	0.079 ± 0.077	-0.670 ± 0.163**
16	Intercept	9.831 ± 0.078***	9.918 ± 9.918***	10.106 ± 0.033***	10.112 ± 0.040***
	BC diss	-0.049 ± 0.126	-0.046 ± 0.074	-0.366 ± 0.072***	-0.468 ± 0.079***
20	Intercept	10.124 ± 0.123***	10.240 ± 0.055***	10.236 ± 0.053***	10.242 ± 0.067***
	BC diss	-0.191 ± 0.169	-0.249 ± 0.088*	-0.278 ± 0.094*	-0.278 ± 0.108*
24	Intercept	9.482 ± 0.083***	10.147 ± 0.153***	10.313 ± 0.107***	10.265 ± 0.071***
	BC diss	0.686 ± 0.115***	-0.155 ± 0.217	-0.480 ± 0.202*	-0.274 ± 0.138

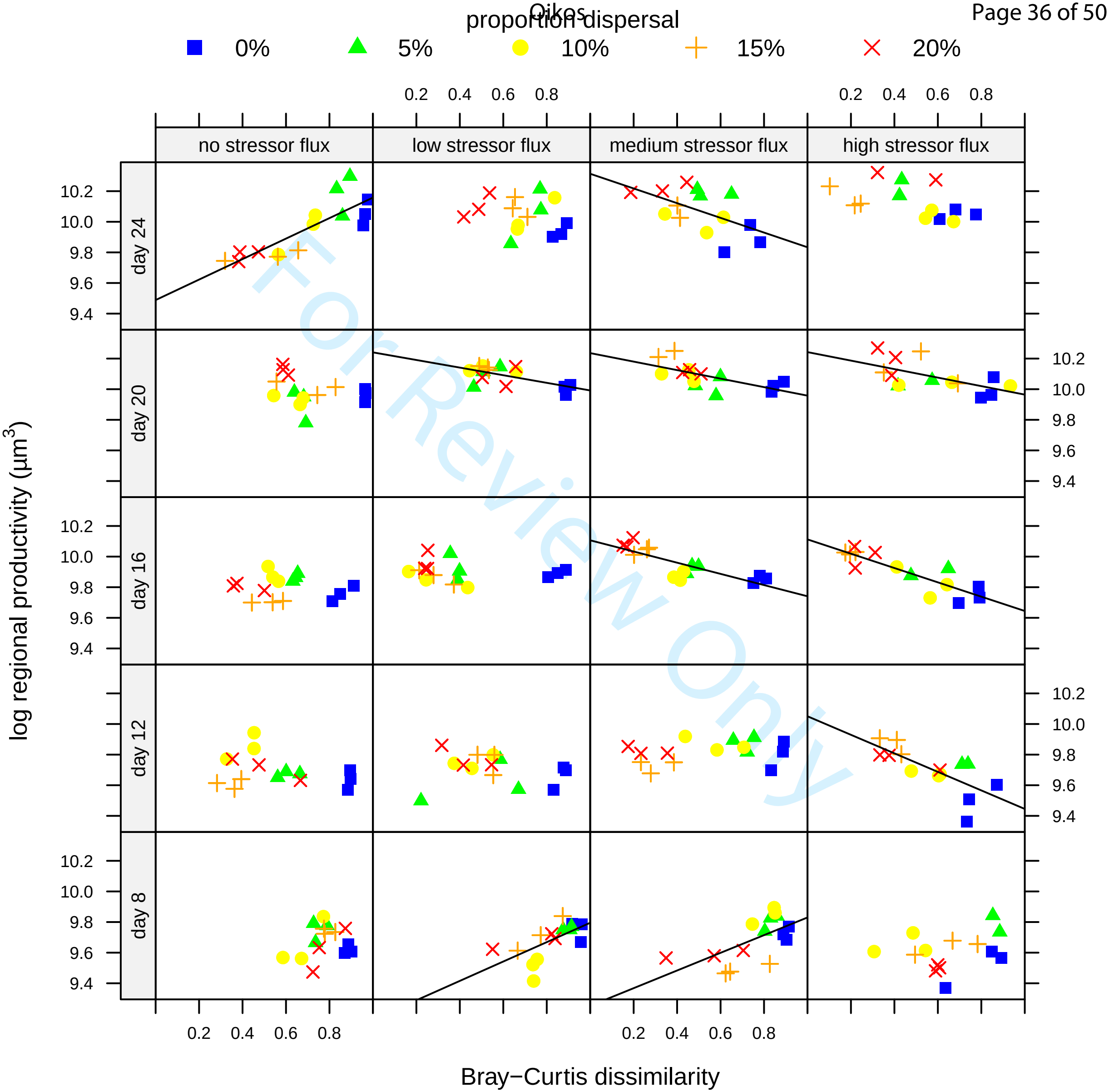
Table 2. Results of the generalized linear model with dispersal as the predictor variable and the log transformed local productivity in the unstressed community as the response variable. *mean±sd*. Significance levels: * 0.05, ** 0.01, *** 0.001

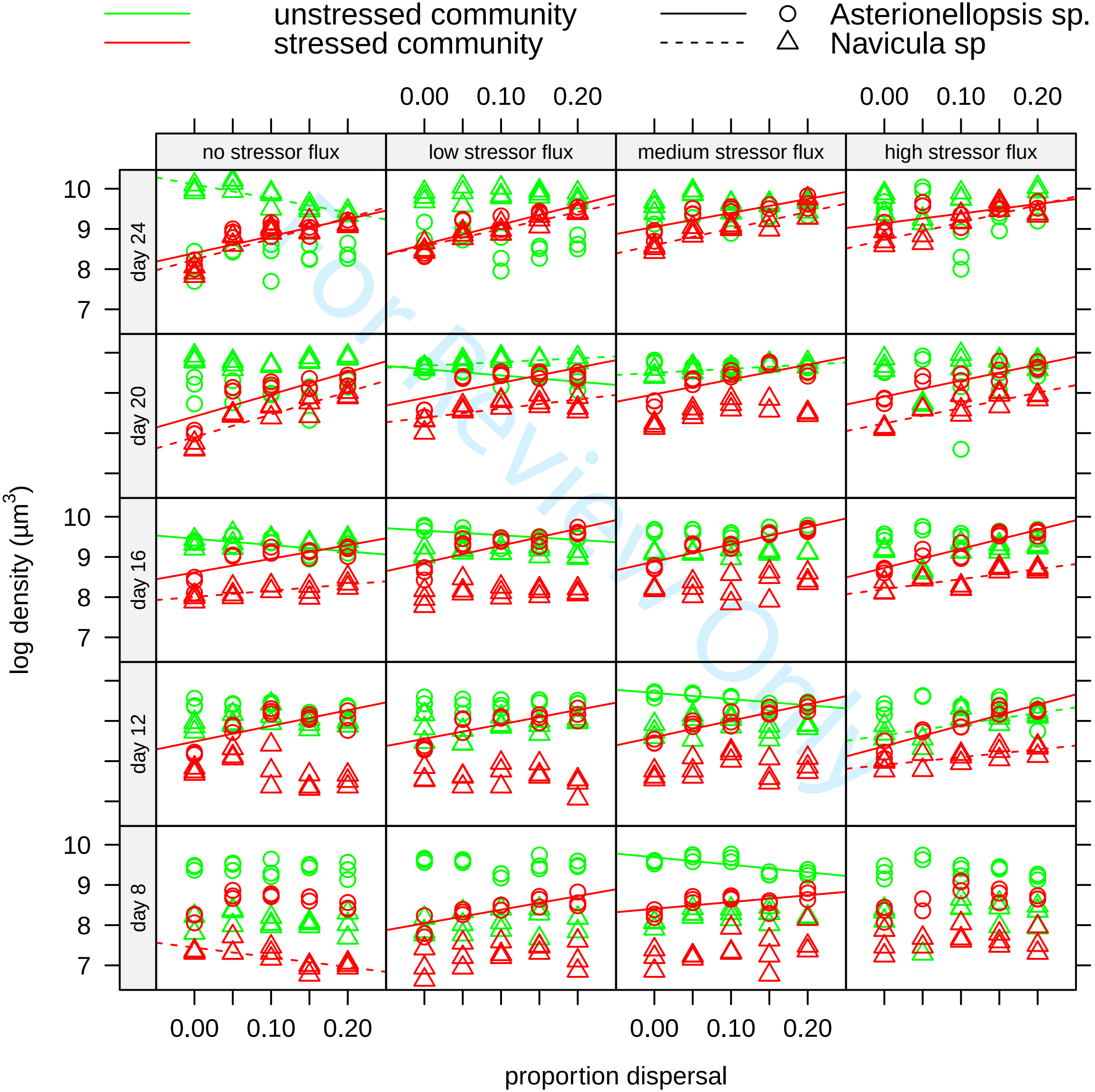
Day	Factor	No stressor flux	Low stressor flux	Medium stressor flux	High stressor flux
8	Intercept	9.633 ± 0.051***	9.700 ± 0.059***	9.794 ± 0.057***	9.575 ± 0.066***
	dispersal	-0.084 ± 0.051	-0.610 ± 0.484	-1.620 ± 0.469**	-0.510 ± 0.347
12	Intercept	9.620 ± 0.046***	9.491 ± 0.052***	9.816 ± 0.040***	9.514 ± 0.057***
	dispersal	-0.400 ± 0.304	0.813 ± 0.425	-1.210 ± 0.328**	0.626 ± 0.456
16	Intercept	9.771 ± 0.035***	9.813 ± 0.032***	9.773 ± 0.024***	9.714 ± 0.034***
	dispersal	-0.774 ± 0.285*	-0.996 ± 0.265**	0.226 ± 0.198	0.255 ± 0.270
20	Intercept	9.982 ± 0.023***	9.858 ± 0.044***	9.949 ± 0.025***	9.928 ± 0.038***
	dispersal	-0.068 ± 0.187	0.375 ± 0.356	0.174 ± 0.204	0.155 ± 0.300
24	Intercept	10.155 ± 0.065***	9.932 ± 0.053***	9.888 ± 0.072***	9.956 ± 0.064***
	dispersal	-3.404 ± 0.527***	-0.340 ± 0.435	-0.154 ± 0.599	-0.049 ± 0.538

Table 3. Results of the generalized linear model with dispersal as the predictor variable and the log transformed local productivity in the stressed community as the response variable. *mean±sd*. Significance levels: * 0.05, ** 0.01, *** 0.001

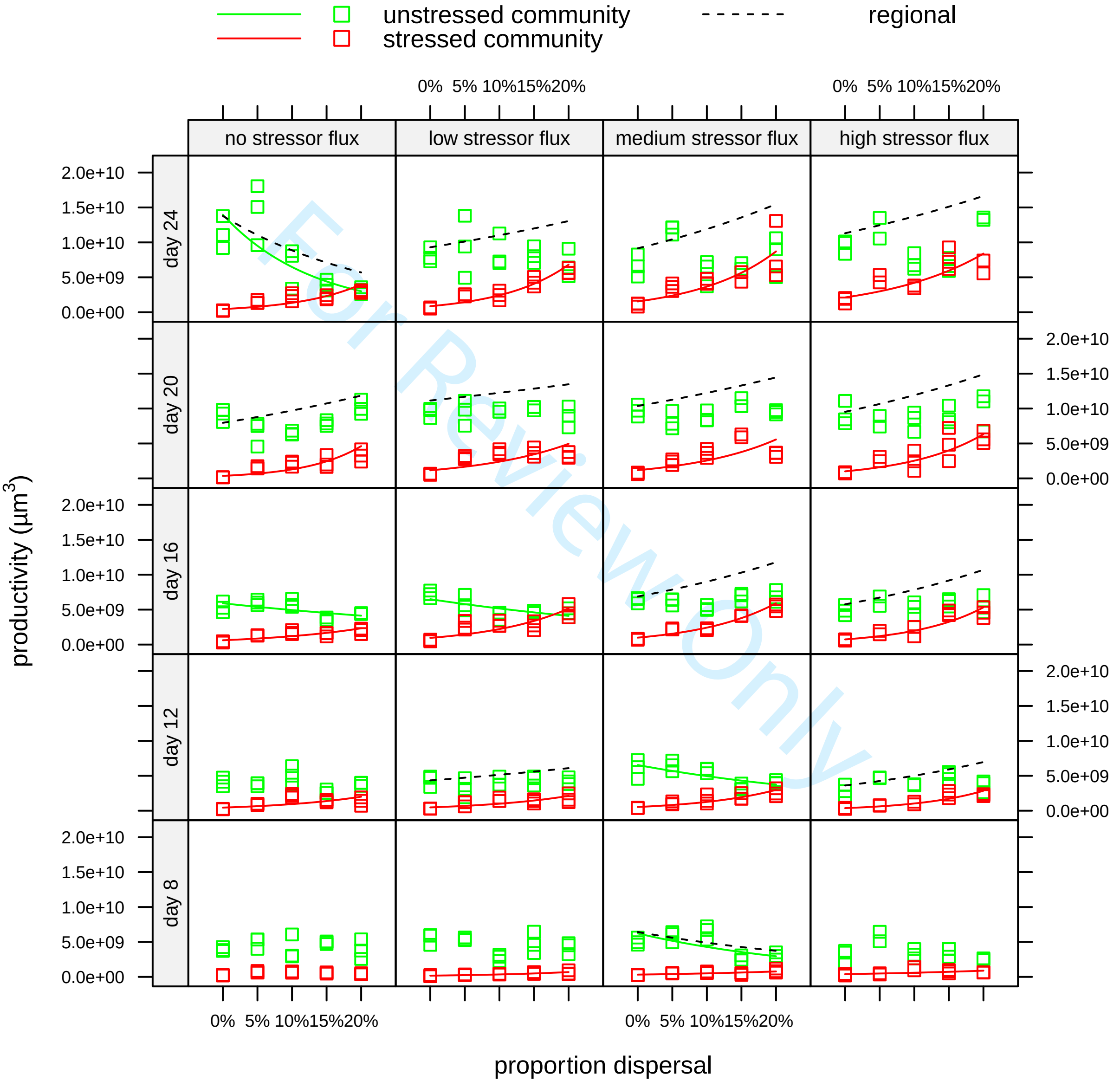
Day	Factor	No stressor flux	Low stressor flux	Medium stressor flux	High stressor flux
8	Intercept	8.603 ± 0.084***	8.248 ± 0.068***	8.513 ± 0.066***	8.584 ± 0.103***
	dispersal	0.863 ± 0.689	2.947 ± 0.553***	1.886 ± 0.542**	1.826 ± 0.820*
12	Intercept	8.612 ± 0.097***	8.678 ± 0.084***	8.729 ± 0.056***	8.573 ± 0.055***
	dispersal	3.260 ± 0.791**	3.242 ± 0.685***	3.729 ± 0.490***	4.413 ± 0.434***
16	Intercept	8.791 ± 0.079***	8.980 ± 0.088***	8.996 ± 0.045***	8.869 ± 0.070***
	dispersal	2.883 ± 0.643***	3.658 ± 0.718***	3.882 ± 0.365***	4.289 ± 0.558***
20	Intercept	8.559 ± 0.128***	9.065 ± 0.103***	9.071 ± 0.090***	9.006 ± 0.091***
	dispersal	5.529 ± 1.048***	3.147 ± 0.837**	3.377 ± 0.749***	3.982 ± 0.724***
24	Intercept	8.658 ± 0.106***	8.938 ± 0.069***	9.189 ± 0.074***	9.326 ± 0.069***
	dispersal	4.714 ± 0.866***	4.478 ± 0.567***	3.756 ± 0.612***	2.987 ± 0.583***

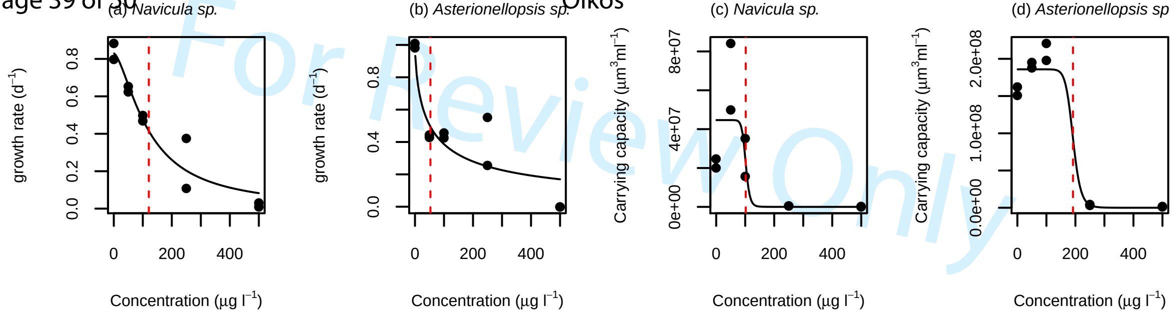

With stressor flux
No stressor flux
Regional productivity
Beta-diversity


proportion dispersal
■ 0%
▲ 5%
● 10%
+ 15%
× 20%
no stressor flux
low stressor flux
medium stressor flux
high stressor flux
day 24
day 20
day 16
day 12
day 8
log regional productivity (µm³)
Bray−Curtis dissimilarity
0.2
0.4
0.6
0.8
9.4
9.6
9.8
10.0
10.2



unstressed community
stressed community
Asterionellopsis sp.
Navicula sp
no stressor flux
low stressor flux
medium stressor flux
high stressor flux
day 24
day 20
day 16
day 12
day 8
0.00
0.10
0.20
7
8
9
10
log density (µm^3)
proportion dispersal


unstressed community
stressed community
regional
no stressor flux
low stressor flux
medium stressor flux
high stressor flux
day 24
day 20
day 16
day 12
day 8
0.0e+00
5.0e+09
1.0e+10
1.5e+10
2.0e+10
0%
5%
10%
15%
20%
productivity (μm^3)
proportion dispersal


(a) *Navicula sp.*
growth rate (d^{-1})
0.0
0.2
0.4
0.6
0.8
0
200
400
Concentration (μg l^{-1})
(b) *Asterionellopsis sp.*
growth rate (d^{-1})
0.0
0.4
0.8
0
200
400
Concentration (μg l^{-1})
(c) *Navicula sp.*
Carrying capacity ($\mu m^3 ml^{-1}$)
0e+00
4e+07
8e+07
0
200
400
Concentration (μg l^{-1})
(d) *Asterionellopsis sp*
Carrying capacity ($\mu m^3 ml^{-1}$)
0.0e+00
1.0e+08
2.0e+08
0
200
400
Concentration (μg l^{-1})

Supplementary Material. Appendix A. Tables and Figures.

Table A1. Algae strains with their respective volume, mean growth rate μ, mean carrying capacity K, EC_{50} $and\ slope$ (s) for the growth rate and carrying capacity. Mean growth rate and mean carrying capacity were determined by using a logistic growth curve. EC_{50} and s are the turning point and slope of the log-logistic dose-response relationship (eq. 4).

Genus name	Volume (μm^3)	Growth rate at 0 $\mu g\ l^{-1}$ (d^{-1})	Carrying capacity at 0 $\mu g\ l^{-1}$ (μm^3)	$EC_{50,\mu}$ $(\mu g\ l^{-1})$	s_μ	$EC_{50,K}$ $(\mu g\ l^{-1})$	s_K
Thalasiossira	27784	0.35	5.1×10^8	95	16.7	74	55.4
Odontella	72804	0.70	3.2×10^9	480	13.8	88	16.6
Melosira	24980	0.75	2.4×10^8	137	1.0	209	15.2
Asterionella	1116	0.81	1.8×10^8	64	2.2	85	18.2
Navicula	563	0.84	2.2×10^7	121	1.5	102	14.9
Asterionellopsis	482	0.99	1.6×10^8	53	0.7	192	14.5

Table A2a. The concentration (conc) of atrazine in the added medium, theoretical concentration of atrazine in the community after medium renewal and measured concentration of atrazine in the unstressed and stressed community at a low stressor flux.

Date (day)	Conc to add in unstressed $(\mu g\ l^{-1})$	Conc to add in stressed $(\mu g\ l^{-1})$	Conc unstressed $(\mu g\ l^{-1})$	Conc stressed $(\mu g\ l^{-1})$	Measured conc unstressed $(\mu g\ l^{-1})$	Measured conc stressed $(\mu g\ l^{-1})$
4	38	213	13	238		
8	46	204	24	226		
12	54	196	34	216		
16	61	189	43	207		
20	68	182	51	199	46	220

Table A2b. The concentration (conc) of atrazine in the added medium, theoretical concentration of atrazine in the community after medium renewal and measured concentration of atrazine in the unstressed and stressed community at a medium stressor flux.

Date (day)	Conc to add in unstressed $(\mu g\ l^{-1})$	Conc to add in stressed $(\mu g\ l^{-1})$	Conc unstressed $(\mu g\ l^{-1})$	Conc stressed $(\mu g\ l^{-1})$	Measured conc unstressed $(\mu g\ l^{-1})$	Measured conc stressed $(\mu g\ l^{-1})$
4	75	175	25	225		
8	85	165	45	205		
12	93	157	61	189		
16	99	151	74	176		
20	105	145	84	166	71	174

Table A2c. The concentration (conc) of atrazine in the added medium, theoretical concentration of atrazine in the community after medium renewal and measured concentration of atrazine in the unstressed and stressed community at a high stressor flux.

Time (day)	Conc to add in unstressed $(\mu g\ l^{-1})$	Conc to add in stressed $(\mu g\ l^{-1})$	Conc unstressed $(\mu g\ l^{-1})$	Conc stressed $(\mu g\ l^{-1})$	Measured conc unstressed $(\mu g\ l^{-1})$	Measured conc stressed $(\mu g\ l^{-1})$
4	113	138	38	213		
8	116	134	64	186		
12	119	131	82	168		
16	121	129	95	155		
20	122	128	104	146	86	151

Table A3. Nutrient concentrations. rep: replicate, ns: unstressed, s: stressed, NA: not measured.

time (d)	Environ-mental flux	dispersal	community	rep	Nitrate-N $(mg\ l^{-1})$	Silicate-Si $(mg\ l^{-1})$	Phosphate-P $(mg\ l^{-1})$
8	0	0	ns	1	7.8958	1.0774	NA
8	0	0.05	ns	1	7.229	1.5498	NA
8	0	0.1	ns	1	6.9406	1.5069	NA
8	0	0.15	ns	1	7.3994	0.8437	NA
8	0	0.2	ns	1	6.9607	0.6401	NA
8	0.05	0	ns	1	7.01	14.5686	NA
8	0.05	0.05	ns	1	6.601	1.6588	NA
8	0.05	0.1	ns	1	6.8595	0.939	NA
8	0.05	0.15	ns	1	6.0714	1.5444	NA
8	0.05	0.2	ns	1	7.2589	0.8918	NA
8	0.1	0	ns	1	7.6041	1.0654	NA
8	0.1	0.05	ns	1	7.3086	0.5366	NA
8	0.1	0.1	ns	1	7.6359	1.1502	NA
8	0.1	0.15	ns	1	7.3346	0.7612	NA
8	0.1	0.2	ns	1	7.76	1.4583	NA
8	0.15	0	ns	1	7.6298	0.2043	NA
8	0.15	0.05	ns	1	7.1377	1.6047	NA
8	0.15	0.1	ns	1	5.7851	0.0835	NA
8	0.15	0.15	ns	1	8.9798	0.6369	NA
8	0.15	0.2	ns	1	7.8581	0.5435	NA
8	0	0	ns	2	NA	NA	0.1814
8	0	0.05	ns	2	NA	NA	0.1718
8	0	0.1	ns	2	NA	NA	0.2112
8	0	0.15	ns	2	NA	NA	0.1864
8	0	0.2	ns	2	NA	NA	0.1763
8	0.05	0	ns	2	NA	NA	0.2249
8	0.05	0.05	ns	2	NA	NA	0.1455
8	0.05	0.1	ns	2	NA	NA	0.1708
8	0.05	0.15	ns	2	NA	NA	0.1329
8	0.05	0.2	ns	2	NA	NA	0.0905
8	0.1	0	ns	2	NA	NA	0.1966
8	0.1	0.05	ns	2	NA	NA	0.2345
8	0.1	0.1	ns	2	NA	NA	0.1742
8	0.1	0.15	ns	2	NA	NA	0.2062
8	0.1	0.2	ns	2	NA	NA	0.1556
8	0.15	0	ns	2	NA	NA	0.1339
8	0.15	0.05	ns	2	NA	NA	0.1733
8	0.15	0.1	ns	2	NA	NA	0.0582
8	0.15	0.15	ns	2	NA	NA	0.1779
8	0.15	0.2	ns	2	NA	NA	0.0189

16	0	0	ns	2	3.2066	NA	<0.05
16	0	0.05	ns	2	4.1204	NA	0.0653
16	0	0.1	ns	2	3.5374	NA	0.0658
16	0	0.15	ns	2	NA	NA	NA
16	0	0.2	ns	2	NA	NA	NA
16	0.05	0	ns	2	2.26936	NA	<0.05
16	0.05	0.05	ns	2	2.5404	NA	0.0749
16	0.05	0.1	ns	2	2.4126	NA	<0.05
16	0.05	0.15	ns	2	2.4003	NA	<0.05
16	0.05	0.2	ns	2	2.509	NA	0.1031
16	0.1	0	ns	2	2.2605	NA	<0.05
16	0.1	0.05	ns	2	2.2014	NA	<0.05
16	0.1	0.1	ns	2	2.4415	NA	<0.05
16	0.1	0.15	ns	2	2.0004	NA	<0.05
16	0.1	0.2	ns	2	1.9213	NA	<0.05
16	0.15	0	ns	2	2.2535	NA	<0.05
16	0.15	0.05	ns	2	2.7182	NA	0.0567
16	0.15	0.1	ns	2	1.8491	NA	<0.05
16	0.15	0.15	ns	2	1.8509	NA	0.0577
16	0.15	0.2	ns	2	2.0331	NA	0.0648
16	0	0	ns	3	NA	0.302	NA
16	0	0.05	ns	3	NA	0.2748	NA
16	0	0.1	ns	3	NA	0.1917	NA
16	0	0.15	ns	3	NA	NA	NA
16	0	0.2	ns	3	NA	NA	NA
16	0.05	0	ns	3	NA	0.1212	NA
16	0.05	0.05	ns	3	NA	0.2617	NA
16	0.05	0.1	ns	3	NA	0.3543	NA
16	0.05	0.15	ns	3	NA	0.2712	NA
16	0.05	0.2	ns	3	NA	0.0934	NA
16	0.1	0	ns	3	NA	0.2916	NA
16	0.1	0.05	ns	3	NA	0.7589	NA
16	0.1	0.1	ns	3	NA	0.4447	NA
16	0.1	0.15	ns	3	NA	0.3452	NA
16	0.1	0.2	ns	3	NA	0.2048	NA
16	0.15	0	ns	3	NA	<0.1	NA
16	0.15	0.05	ns	3	NA	0.118	NA
16	0.15	0.1	ns	3	NA	0.1841	NA
16	0.15	0.15	ns	3	NA	NA	NA
16	0.15	0.2	ns	3	NA	0.1787	NA
24	0	0	ns	1	0.9516	0.3479	NA
24	0	0.05	ns	1	0.7842	0.2717	NA
24	0	0.1	ns	1	0.9553	0.3048	NA
24	0	0.15	ns	1	0.7196	0.1841	NA
24	0	0.2	ns	1	1.1328	0.1028	NA
24	0.05	0	ns	1	4.0076	0.1728	NA

24	0.05	0.05	ns	1	3.7665	0.3712	NA
24	0.05	0.1	ns	1	2.7859	0.1616	NA
24	0.05	0.15	ns	1	1.8366	0.1512	NA
24	0.05	0.2	ns	1	3.5738	0.3125	NA
24	0.1	0	ns	1	4.2411	0.189	NA
24	0.1	0.05	ns	1	4.971	0.531	NA
24	0.1	0.1	ns	1	4.5919	0.1575	NA
24	0.1	0.15	ns	1	5.1635	NA	NA
24	0.1	0.2	ns	1	5.2576	0.1589	NA
24	0.15	0	ns	1	5.0149	0.1239	NA
24	0.15	0.05	ns	1	2.1148	1.2591	NA
24	0.15	0.1	ns	1	4.9669	<0.1	NA
24	0.15	0.15	ns	1	<0.2	0.9505	NA
24	0.15	0.2	ns	1	0.2354	0.3402	NA
24	0	0	s	1	11.441	>5	NA
24	0	0.05	s	1	11.246	>5	NA
24	0	0.1	s	1	10.259	>5	NA
24	0	0.15	s	1	10.405	>5	NA
24	0	0.2	s	1	10.539	>5	NA
24	0.05	0	s	1	11.206	>5	NA
24	0.05	0.05	s	1	9.8305	>5	NA
24	0.05	0.1	s	1	9.5413	>5	NA
24	0.05	0.15	s	1	9.8979	>5	NA
24	0.05	0.2	s	1	9.1202	>5	NA
24	0.1	0	s	1	10.88	>5	NA
24	0.1	0.05	s	1	9.6177	>5	NA
24	0.1	0.1	s	1	9.22	>5	NA
24	0.1	0.15	s	1	9.495	>5	NA
24	0.1	0.2	s	1	8.8331	>5	NA
24	0.15	0	s	1	10.526	>5	NA
24	0.15	0.05	s	1	9.8427	>5	NA
24	0.15	0.1	s	1	8.5868	>5	NA
24	0.15	0.15	s	1	9.3523	>5	NA
24	0.15	0.2	s	1	9.295	>5	NA
24	0	0	ns	2	NA	NA	<0.05
24	0	0.05	ns	2	NA	NA	<0.05
24	0	0.1	ns	2	NA	NA	<0.05
24	0	0.15	ns	2	NA	NA	<0.05
24	0	0.2	ns	2	NA	NA	<0.05
24	0.05	0	ns	2	NA	NA	<0.05
24	0.05	0.05	ns	2	NA	NA	<0.05
24	0.05	0.1	ns	2	NA	NA	<0.05
24	0.05	0.15	ns	2	NA	NA	<0.05
24	0.05	0.2	ns	2	NA	NA	<0.05
24	0.1	0	ns	2	NA	NA	<0.05
24	0.1	0.05	ns	2	NA	NA	0.0956

24	0.1	0.1	ns	2	NA	NA	<0.05
24	0.1	0.15	ns	2	NA	NA	0.1381
24	0.1	0.2	ns	2	NA	NA	<0.05
24	0.15	0	ns	2	NA	NA	<0.05
24	0.15	0.05	ns	2	NA	NA	<0.05
24	0.15	0.1	ns	2	NA	NA	<0.05
24	0.15	0.15	ns	2	NA	NA	<0.05
24	0.15	0.2	ns	2	NA	NA	<0.05
24	0	0	s	2	NA	NA	0.7811
24	0	0.05	s	2	NA	NA	0.5788
24	0	0.1	s	2	NA	NA	0.2968
24	0	0.15	s	2	NA	NA	<0.05
24	0	0.2	s	2	NA	NA	0.0718
24	0.05	0	s	2	NA	NA	0.9179
24	0.05	0.05	s	2	NA	NA	0.4851
24	0.05	0.1	s	2	NA	NA	0.4465
24	0.05	0.15	s	2	NA	NA	<0.05
24	0.05	0.2	s	2	NA	NA	<0.05
24	0.1	0	s	2	NA	NA	0.6844
24	0.1	0.05	s	2	NA	NA	0.4627
24	0.1	0.1	s	2	NA	NA	0.1885
24	0.1	0.15	s	2	NA	NA	0.0597
24	0.1	0.2	s	2	NA	NA	<0.05
24	0.15	0	s	2	NA	NA	<0.6135
24	0.15	0.05	s	2	NA	NA	0.4104
24	0.15	0.1	s	2	NA	NA	<0.05
24	0.15	0.15	s	2	NA	NA	0.0557
24	0.15	0.2	s	2	NA	NA	<0.05

Table A4. Result of the beta regression models with dispersal as the predictor variable and BC dissimilarity as the response variable. *mean±sd*. Significance levels: * 0.05, ** 0.01, *** 0.001

Day	Factor	No stressor flux	Low stressor flux	Medium stressor flux	High stressor flux
8	Intercept	1.453 ± 0.209***	2.274 ± 0.276***	2.155 ± 0.233***	1.195 ± 0.324***
	BC diss	1.947 ± 0.235	-6.979 ± 1.977***	-9.317 ± 1.674***	-5.115 ± 2.455*
12	Intercept	1.140 ± 0.289***	0.942 ± 0.294***	1.718 ± 0.190***	1.199 ± 0.196***
	BC diss	-9.086 ± 2.327***	-7.001 ± 2.364**	-15.140 ± 1.537***	8.628 ± 1.510***
16	Intercept	1.338 ± 0.162***	0.767 ± 0.278**	0.923 ± 0.121***	1.044 ± 0.210***
	BC diss	-9.059 ± 1.267***	-11.433 ± 2.445***	-13.251 ± 1.084***	-12.215 ± 1.746***
20	Intercept	1.832 ± 0.316***	1.066 ± 0.272 ***	0.982 ± 0.244***	1.206 ± 0.341***
	BC diss	8.178 ± 2.343***	-5.739 ± 2.141**	-8.224 ± 2.011***	-7.725 ± 2.611**
24	Intercept	2.536 ± 0.258***	1.672 ± 0.169***	0.758 ± 0.172***	0.548 ± 0.312
	BC diss	-15.555 ± 1.850 ***	-7.998 ± 1.263***	-7.743 ± 1.450***	-7.138 ± 2.683**

Table A5. Result of the linear model with dispersal as the predictor variable and the log transformed local density of *Asterionellopsis sp.* in the unstressed community as the response variable. *mean±sd*. Significance levels: * 0.05, ** 0.01, *** 0.001

Day	Factor	No stressor flux	Low stressor flux	Medium stressor flux	High stressor flux
8	Intercept	9.456 ± 0.063***	9.554 ± 0.072***	9.687 ± 0.063***	9.461 ± 0.082***
	dispersal	-0.304 ± 0.512	-0.524 ± 0.591	-1.851 ± 0.513**	-0.787 ± 0.648
12	Intercept	9.421 ± 0.053***	9.425 ± 0.113***	9.698 ± 0.039***	9.425 ± 0.113***
	dispersal	0.689 ± 0.436	-0.822 ± 0.898	-1.538 ± 0.320***	-0.822 ± 0.898
16	Intercept	9.453 ± 0.065***	9.655 ± 0.056***	9.619 ± 0.036***	9.542 ± 0.071***
	dispersal	-1.578 ± 0.528*	-1.158 ± 0.459*	0.357 ± 0.293	0.000 ± 0.562
20	Intercept	9.045 ± 0.134***	9.591 ± 0.057***	9.715 ± 0.037***	9.421 ± 0.272***
	dispersal	0.084 ± 1.093	1.563 ± 0.462**	-0.549 ± 0.304	-0.521 ± 2.159
24	Intercept	8.234 ± 0.152***	8.755 ± 0.135***	9.302 ± 0.105***	9.438 ± 0.285***
	dispersal	1.048 ± 0.152	-1.369 ± 1.103	0.510 ± 0.871	1.965 ± 2.408

Table A6. Result of the linear model with dispersal as the predictor variable and the log transformed local density of *Navicula sp.* in the unstressed community as the response variable. *mean±sd*. Significance levels: * 0.05, ** 0.01, *** 0.001

Day	Factor	No stressor flux	Low stressor flux	Medium stressor flux	High stressor flux
8	Intercept	8.077 ± 0.095***	7.984 ± 0.113***	8.149 ± 0.067***	8.067 ± 0.193***
	dispersal	-0.186 ± 0.778	0.707 ± 0.925	0.622 ± 0.549	1.305 ± 1.530
12	Intercept	8.953 ± 0.078***	8.697 ± 0.100***	8.837 ± 0.092***	8.643 ± 0.102***
	dispersal	0.236 ± 0.637	1.365 ± 0.816	0.124 ± 0.751	2.770 ± 0.808**
16	Intercept	9.360 ± 0.049***	9.137 ± 0.043***	9.100 ± 0.025***	9.014 ± 0.102***
	dispersal	0.136 ± 0.401	-0.229 ± 0.349	0.055 ± 0.205	1.277 ± 0.808
20	Intercept	9.745 ± 0.044***	9.675 ± 0.034***	9.497 ± 0.039***	9.426 ± 0.180***
	dispersal	0.387 ± 0.358	0.928 ± 0.277**	1.037 ± 0.324**	1.643 ± 1.426
24	Intercept	10.106 ± 0.069***	9.839 ± 0.061***	9.674 ± 0.079***	9.514 ± 0.120***
	dispersal	-3.486 ± 0.565***	-0.048 ± 0.500	-0.324 ± 0.658	1.700 ± 1.009

Table A7. Result of the linear model with dispersal as the predictor variable and the log transformed local density of *Asterionellopsis sp.* in the stressed community as the response variable. *mean±sd*. Significance levels: * 0.05, ** 0.01, *** 0.001

Day	Factor	No stressor flux	Low stressor flux	Medium stressor flux	High stressor flux
8	Intercept	8.474 ± 0.103***	8.045 ± 0.081***	8.406 ± 0.076***	8.453 ± 0.120***
	dispersal	0.909 ± 0.840	3.386 ± 0.662***	1.686 ± 0.619*	1.989 ± 0.951
12	Intercept	8.487 ± 0.127***	8.556 ± 0.093***	8.596 ± 0.056***	8.372 ± 0.077***
	dispersal	3.899 ± 1.035**	3.595 ± 0.759***	4.081 ± 0.487***	5.152 ± 0.611***
16	Intercept	8.615 ± 0.108***	4.858 ± 0.101***	8.883 ± 0.059***	8.727 ± 0.072***
	dispersal	3.392 ± 0.880**	4.229 ± 0.828***	4.294 ± 0.480***	4.741 ± 0.573***
20	Intercept	8.413 ± 0.142***	8.875 ± 0.126***	8.964 ± 0.095***	8.908 ± 0.097***
	dispersal	5.493 ± 0.158***	3.759 ± 1.027**	3.700 ± 0.787***	3.976 ± 0.773***
24	Intercept	8.400 ± 0.112***	8.616 ± 0.109***	9.048 ± 0.081***	9.142 ± 0.099***
	dispersal	4.225 ± 0.915***	4.892 ± 0.886***	3.490 ± 0.676***	2.396 ± 0.834*

Table A8. Result of the linear model with dispersal as the predictor variable and the log transformed local density of *Navicula sp.* in the stressed community as the response variable. *mean±sd*. Significance levels: *0.05, **0.01, ***0.001

Day	Factor	No stressor flux	Low stressor flux	Medium stressor flux	High stressor flux
8	Intercept	7.442 ± 0.080***	7.125 ± 0.131***	7.149 ± 0.149***	7.585 ± 0.114***
	dispersal	-2.416 ± 0.651**	1.154 ± 1.068	2.059 ± 1.217	0.343 ± 0.907
12	Intercept	7.985 ± 0.140***	7.665 ± 0.106***	7.765 ± 0.117***	7.906 ± 0.068***
	dispersal	-2.407 ± 1.145	-0.723 ± 0.862	0.761 ± 0.954	1.921 ± 0.538**
16	Intercept	8.005 ± 0.057***	8.073 ± 0.070***	8.149 ± 0.106***	8.198 ± 0.074***
	dispersal	1.552 ± 0.462**	0.420 ± 0.576	1.274 ± 0.865	2.502 ± 0.586**
20	Intercept	7.901 ± 0.103***	8.383 ± 0.085***	8.359 ± 0.089***	8.241 ± 0.079***
	dispersal	5.621 ± 0.839***	2.266 ± 0.697**	1.542 ± 0.737†	3.818 ± 0.631***
24	Intercept	8.234 ± 0.114***	8.572 ± 0.047***	8.596 ± 0.074***	8.727 ± 0.099***
	dispersal	5.196 ± 0.931***	4.238 ± 0.383***	4.135 ± 0.614***	4.323 ± 0.833***

Table A9. Result of the linear model with dispersal as the predictor variable and the log transformed regional productivity as the response variable. *mean±sd*. Significance levels: *0.05, **0.01, ***0.001

Day	Factor	No stressor flux	Low stressor flux	Medium stressor flux	High stressor flux
8	Intercept	9.677 ± 0.048***	9.716 ± 0.052***	9.808 ± 0.053***	9.631 ± 0.058***
	dispersal	-0.007 ± 0.388	-0.347 ± 0.428	-1.180 ± 0.433*	-0.232 ± 0.461
12	Intercept	9.679 ± 0.047***	9.638 ± 0.038***	9.839 ± 0.033***	9.557 ± 0.048***
	dispersal	0.176 ± 0.381	0.735 ± 0.314*	-0.204 ± 0.272	1.429 ± 0.384**
16	Intercept	9.816 ± 0.034***	9.882 ± 0.030***	9.838 ± 0.023***	9.761 ± 0.037***
	dispersal	-0.136 ± 0.280	0.176 ± 0.243	1.170 ± 0.186***	1.344 ± 0.296***
20	Intercept	9.901 ± 0.033***	10.047 ± 0.026***	10.016 ± 0.028***	9.979 ± 0.033***
	dispersal	0.865 ± 0.027**	0.411 ± 0.214	0.722 ± 0.231**	0.969 ± 0.260**
24	Intercept	10.139 ± 0.054***	9.969 ± 0.044***	9.961 ± 0.052***	10.054 ± 0.045***
	dispersal	-1.919 ± 0.441***	0.0736 ± 0.360	1.141 ± 0.432*	0.838 ± 0.382

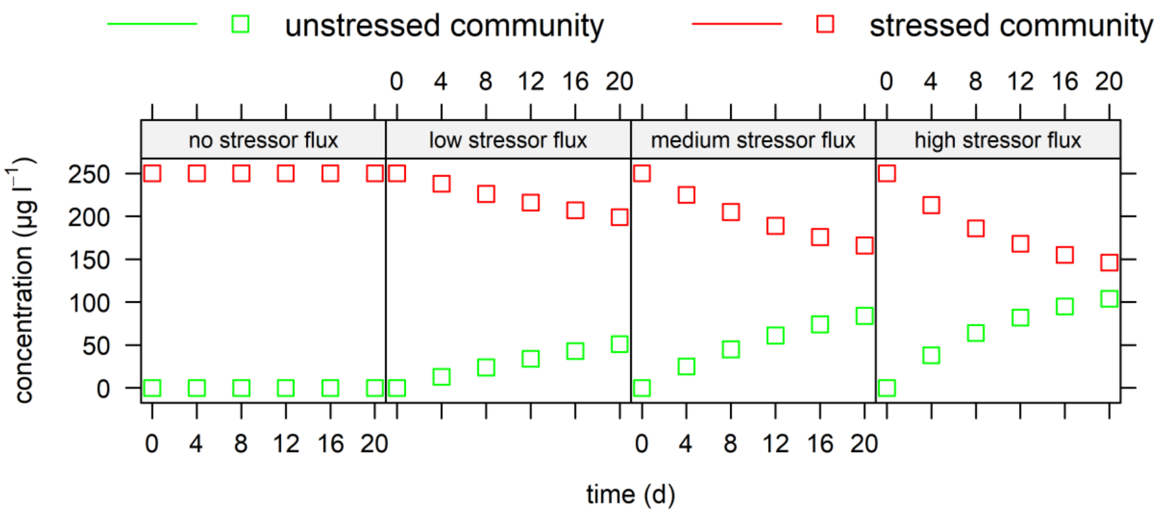


Fig. A1. Target concentration of atrazine in function of time for the unstressed and stressed community and for the different stressor flux levels. The symbols represent the concentration after the manipulation of the stressor flux on that day (see also table A2a-A2c).

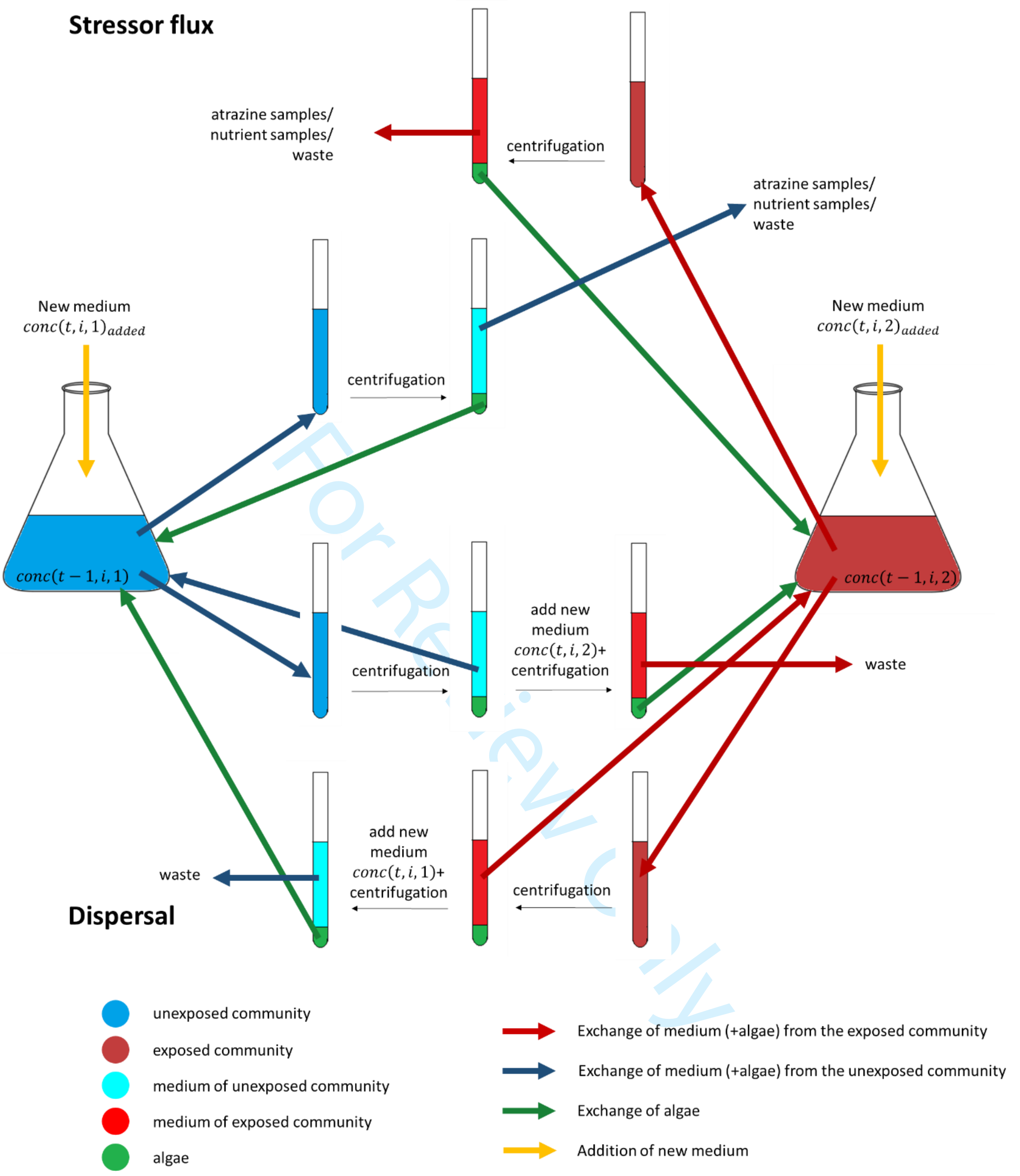


Fig. A2. Manipulation of the stressor flux and dispersal between an unexposed (blue) and exposed community (red). The stressor flux and dispersal were performed on days 4, 8, 12, 16 and 20. Thick arrows represent a manipulation that was performed by pipetting algae and/or medium. For $conc(t,i,j)_{added}$ and $conc(t,i,j)$, see main text and equations 1-3. For clarity, the rinsing of the centrifuge tubes is not shown in the figure.

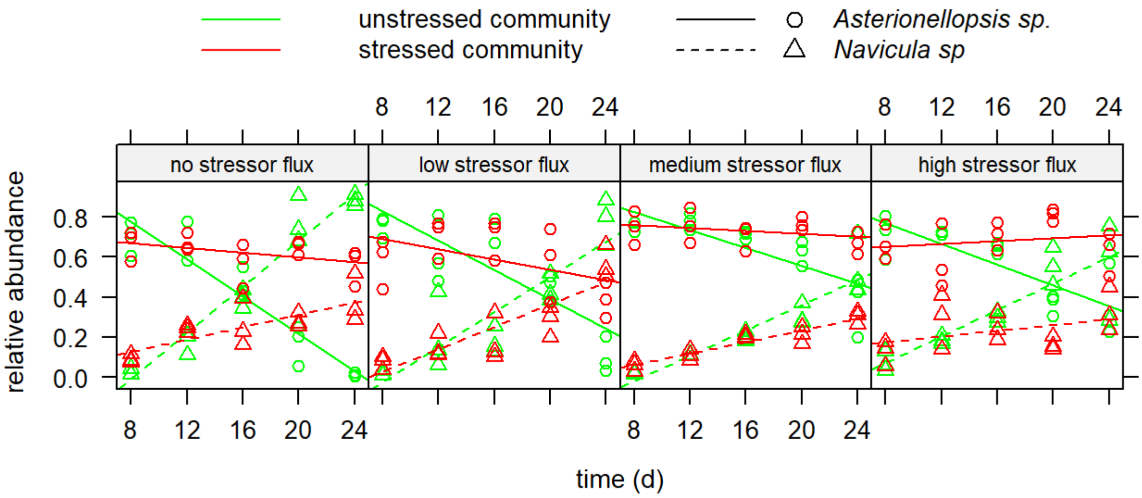


Fig. A3. The relative abundance of *Asterionellopsis sp.* and *Navicula sp.* in function of time in the no - dispersal treatments for the 4 stressor flux treatments. Symbols represent the data, the lines depict the best fit using a generalized linear model.