Dispersal restricts local biomass but promotes the recovery of metacommunities after temperature stress

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Landscape connectivity can increase the capacity of communities to maintain their function when environments change by promoting the immigration of species or populations with adapted traits. However, high immigration may also restrict fine tuning of species compositions to local environmental conditions by homogenizing the community. Here we demonstrate that dispersal generates such a tradeoff between maximizing local biomass and the capacity of model periphyton metacommunities to recover after a simulated heat wave. In non-disturbed metacommunities, dispersal decreased the total biomass by preventing differentiation in species composition between the local patches making up the metacommunity. On the contrary, in metacommunities exposed to a realistic summer heat wave, dispersal promoted recovery by increasing the biomass of heat tolerant species in all local patches. Thus, the heat wave reorganized the species composition of the metacommunities and after an initial decrease in total biomass by 38.7%, dispersal fueled a full recovery of biomass in the restructured metacommunities. Although dispersal may decrease equilibrium biomass, our results highlight that connectivity is a key requirement for the response diversity that allows ecological communities to adapt to climate change through species sorting.

Human driven changes in climate conditions are becoming an increasingly important driver of community dynamics that will influence the functioning of valuable ecosystems for generations to come (Millennium Ecosystem Assessment Report 2005). Although much effort has been made to predict effects of gradual climatic changes on species communities (Walther et al. 2002, Parmesan and Yohe 2003, Perry et al. 2005), global and regional climate models forecast an even stronger increase in the frequency and intensity of extreme climatic events (IPCC 2007). The capacity of local communities to maintain their function when subjected either to gradual changes in the environment or disturbances depends on connectivity, because dispersal allows favorable species traits to enter communities through immigration (Loeuille and Leibold 2008, Urban et al. 2008, Venail et al. 2008). This emphasises that one of the key steps towards realistically testing consequences of climate change on the functioning of ecosystems is to include the interplay between short term extreme climatic disturbances, and regional factors maintaining diversity and ecosystem functioning, i.e. dispersal.

Here we focus on how dispersal influences the capacity of local communities to respond to climate change through species sorting (Folke et al. 2002, Norberg 2004). Under environmental stress, biodiversity can protect against declines in ecosystem functioning by providing opportunities to keep or regenerate functions through reorganisation of community structure (Peterson et al. 1998, Yachi and Loreau 1999, Elmqvist et al. 2003, Gonzalez and Loreau 2009). Thus, species sorting processes provide local communities with an ecological capacity to maintain their functions when conditions change (Norberg 2004). At the same time, loss of species or biomass on a local scale can be compensated by immigration (Mouquet and Loreau 2003). Here, the degree of dispersal is critical. Dispersal limitation would prevent species sorting, i.e. the match between trait and environment, because potentially well adapted species never reach a site. Immigration rate should be just high enough to supply best adapted species but not as high to sustain maladapted species in sink populations through mass effects. The latter would create a regionally best adapted species that is not locally optimal (Leibold et al. 2004). Consequently, under stable conditions, high dispersal rates may homogenize local communities and reduce local adaptation by not allowing fine-tuning of the composition of species and populations to the specific local environmental conditions (Urban et al. 2008). Thus, too high or too low connectivity may generate a tradeoff between functional optimisation and recovery potential, making it difficult to optimize long-term

carrying capacity of systems subjected to climate change. Still, experiments testing local effects of warming almost never set the experiments in a relevant spatial context with immigration from other heated patches or actively manipulate dispersal. We close this gap in the present study by using the concept of metacommunities, which offers relatively simple models to explain species coexistence and diversity patterns in sets of connected habitat patches (Leibold et al. 2004, Holyoak et al. 2005, Gonzalez 2009).

We experimentally test if high dispersal generates a tradeoff between biomass accumulation during times of stable environmental conditions, and recovery potential after an environmental disturbance in the form of a realistically simulated heatwave. We used spatially heterogeneous metacommunities of nine marine diatom species that coexist naturally in a rocky shore periphyton community common in the Baltic Sea. Periphyton communities consist of a complex mixture of different benthic microalgae, mostly of diatoms. Each experimental metacommunity comprised a gradient of light intensity to introduce environmental heterogeneity among local communities (Matthiessen et al. 2010a). Steep light gradients naturally characterize the environmental conditions for periphyton due to shading caused either by their three dimensional community architecture and/or by macroalgae. Periphyton species have developed different types of life forms not only to enhance their competitive advantage for light absorption but also to prevent grazing and being flushed away through currents and wave actions. Non-mobile chain-forming and stalked cells form canopies and thus are good competitors for light but are prone to grazers and wave actions. In contrast mobile and more or less attached solitary species are able to avoid grazing but are inferior competitors for light (Supplementary material Appendix 1 Table A1, A2, Matthiessen et al. 2010a, Eggers et al. 2012). We hypothesized: 1) that dispersal decreases regional biomass accumulation of heterogeneous metacommunities in stable conditions by homogenizing the composition of species between the local patches in the metacommunity and thereby holding back the fine-tuning of species compositions to the specific local environmental conditions (different light levels in our experiment), but 2) that dispersal promotes regional recovery of metacommunities after an environmental disturbance (heat-wave in our experiment) by spreading species with traits that match local environments and thereby enhancing the reorganization of community structure.

Material and methods

Study organisms

Nine diatom species were isolated from the Kiel Fjord, western Baltic Sea, and kept as monocultures prior to the experiment (54°20′N, 10°09′E; Supplementary material Appendix 1 Table A1). These cultures were non axenic and were kept in medium that consisted of sterile filtered natural seawater from the Kiel Fjord at a salinity of 17.5, with nutrients added to achieve a molar ratio of Si:N:P of 15:15:1 (40 μM Si (silicate); 40 μM N (nitrate:ammonium in a 50:50 ratio); 2.7 μM P (phosphate)). This nutrient concentration approximately reflects the nutrient concentration in the Kiel Fjord in early spring before the onset of the spring bloom. The stock cultures were maintained in a controlled climate chamber $16 \pm 1°C$ under-long day conditions (16:8 h light dark) and with a photon flux density of 45 ± 5 μmol photons m^{-2} s^{-1} (provided by fluorescent L36W/19 tubes.

Experimental design

Each experimental metacommunity consisted of three local communities with diatoms grown in individual cell culture flasks (40 ml; 9 cm^2 bottom area; 6.5 cm height) at three different light intensities (10, 20 and 40 μmol photons m^{-2} s^{-1}) to generate patch heterogeneity (Matthiessen et al. 2010a). The different light intensities were maintained by different black ink printed transparency sheets that created three levels of shading (Eggers et al. 2012). In order to prevent nutrient depletion at local scale, 20 ml of supernatant were exchanged with new medium every third day during the whole experiment. The concentrations of nitrate, ammonium, phosphate and silicate in the exchanged water of each local community were sampled four times over the course of the experiment and measured photometrically with an auto analyser following Grasshoff et al. (1999). In total the experiment ran for 43 days.

At the onset of the experiment, cell culture flasks with 40 ml medium were inoculated with all nine species comprising a total local biovolume of approximately 1.1×10^6 $μm^3$ cm^{-2}. Initially, each species contributed equally to total biovolume of the local communities and thus had equal chances to colonize the bottom area. We refer to surface bottom area because the three dimensional structure of the periphyton film is expected not to exceed approximately 0.5 mm in height. To test species-specific temperature tolerance, we ran additionally monocultures of the seven most common species during the experiment (all species except the rare species: *Licmophora* sp. and *Nitzschia sigma*; Supplementary material Appendix 2 Fig. A2). The monoculture experiment was performed after the main experiment was analysed.

Dispersal was manipulated in half of the metacommunities by simulating wave action and subsequently pipetting 5 ml out of each local community every second day. Wave action was simulated by turning the three flasks of each metacommunity carefully twice. This led to the effect that more loosely attached cells had a higher chance to disperse than strongly attached cells which resembles dispersal of these organisms in nature (Supplementary material Appendix 1 Table A2). The removed 5 ml were pooled for each metacommunity. This mixture (15 ml) was gently turned and 5 ml of the mix were distributed back into each local community. The applied dispersal rate was set at an intermediate level compared to earlier studies (Matthiessen et al. 2010b, Eggers et al. 2012), to ensure significant metacommunity dynamics but to avoid direct homogenization of the local communities by too high connectivity. To make sure that species specific effects of dispersal were not confounded by disturbance in connection with the turning of the flasks, we performed an additional control-experiment were we turned the flask but did not perform the actual

dispersal. The results showed that only turning the flasks at different frequencies over a period of 21 days did not have any significant effects on biomass of the different species. Thus, effects of the dispersal treatment were in our experiment due to dispersal and not disturbance dynamics.

Temperature stress was applied to half of the metacommunities by exposing them to a temperature profile that simulated a condensed version of shallow water temperatures in the western Baltic Sea during the 2003 European summer heat wave ('heat wave treatment', Supplementary material Appendix 1 Fig. A1) (Reusch et al. 2005). We condensed the heat wave by increasing the rate of change by two times, shortening the duration from 2 to 1 month. The other half of the metacommunities were kept at a constant level of the common water temperature level in western Baltic Sea during early summer (average of 16°C, 'continuous temperature treatment'). Variation between day and night temperatures (16:8 h light dark regime) was included in both temperature regimes (Supplementary material Appendix 1 Fig. A1). The two temperature levels were maintained in two independent climate rooms that first were tested for potential confounding room effects using two well-studied periphyton diatom species: *Stauroneis constricta* and *Amphora coffaeiformes* (Eggers et al. 2012). We found no differences between climate rooms in maximum population growth rates (one-way ANOVA's: *S. constricta*; F = 1.06, p = 0.36: *A. coffaeiformes*; F = 1.31, p = 0.32) or in carrying capacity (*S. constricta*; F = 2.45, p = 0.19: *A. coffaeiformes*; F = 2.74, p = 0.17).

In summary, the full experimental design included manipulation of three different factors: 1) dispersal (two levels – dispersal or not), 2) temperature (two levels – heat wave or not) and 3) light (three levels – low, medium and high). Dispersal and temperature were manipulated in a fully crossed factorial design among metacommunities while the light treatment was nested within each metacommunity. Each four metacommunity combination of dispersal and temperature treatments, were replicated twelve times. Sampling took place twice and was destructive: each time we removed six of the twelve replicates from the experiment and sampling time was therefore an independent factor in the analyses. The first sampling (T1; day 33) took place directly after the simulated heat wave. The second sampling (T2; day 43) followed 10 days after the heat wave to test for recovery after heat wave (Supplementary material Appendix 1 Fig. A1). We know from earlier studies of the same system that 10 days is enough to reflect the community composition at stationary phase (Matthiessen et al. 2010a, b, Eggers et al. 2012). Thus, the recovery after 10 days should reflect equilibrium species composition, rather than a transitional successional stage. Recovery was defined as no significant difference between a specific heat wave treatment and the corresponding control temperature treatment. In total, the experiment consisted of 48 metacommunities where each metacommunity contained three local patches with differing light intensities, resulting in a total of 144 local community flasks.

Sampling and analyses

At both sampling times (day 33 and 43) all the diatom species normally have reached stationary phase when grown in monocultures at 16°C (i.e. carrying capacity; Matthiessen et al. 2010a, Eggers et al. 2012). Forty-three days, with a mean vegetative growth rate of each local community of at least 0.5 day^{-1}, corresponds on average to 21 generations. Algae were sampled by carefully scraping of the entire bottom of the culture flasks (9 cm^2) with a cell scraper. The resulting cell suspension was sampled, fixed in 1–2% acid Lugol's iodine solution and analysed by inverted microscopy at 400 × magnification. These samples were used to calculate total and species-specific relative biomass (after Hillebrand et al. 1999). In order to avoid confounding results due to potentially altered cell sizes in comparison to the start of the experiment, the average cell biovolume per species (Hillebrand et al. 1999, Eggers et al. 2012) was measured after the experiment (Supplementary material Appendix 1 Table A1). Hereafter we refer to biovolume as biomass. Thus, with metacommunity biomass we refer to the average biovolume of the three respective local communities, calculated per unit bottom area (μm^3 cm^{-2}).

All data on mean local scale were tested for normality and homogeneity of variances prior the statistical analysis. The effect of the factors time, temperature, dispersal, light and their interactions were tested on local biomass by a mixed-effects model (using the lme4 package in R). To account for dependency between the three local communities within each metacommunity we included metacommunity as a random factor nested within the fixed factor dispersal. In addition, we tested experimental effects on the three most dominating species during the experiment (*Achnantes brevipes*, *Entomoneis paludosa* and *Melosira varians*) using the same mixed-effects model.

Results

Total biomass of all metacommunities increased over time between the samplings on day 33 (T1) and 43 (T2), but the rate of increase depended on contrasting effects of dispersal in the different temperature treatments (significant three-way interaction between sampling time,

Table 1. Mixed-effects model results for diatom biomass in local patches within a metacommunity, depending on sampling time (S); temperature regime (T); dispersal frequency (D); light availability (L) and their interactions. Bold numbers show significant results.

Factor	F	p
S	**48.92**	**<0.001**
T	**17.77**	**<0.001**
D	0.01	0.93
L	0.05	0.83
S×T	0.88	0.36
S×D	0.33	0.57
T×D	**6.05**	**<0.05**
S×L	1.28	0.26
T×L	**4.28**	**<0.05**
D×L	3.19	0.08
S×T×D	**7.57**	**<0.01**
S×T×L	1.88	0.17
S×D×L	0.06	0.80
T×D×L	0.37	0.55
S×T×D×L	0.19	0.67

temperature regime and dispersal: $F_{1,24} = 7.57$, $p < 0.01$; Table 1). In the continuous temperature treatment (metacommunities grown at 16°C, no heat wave), metacommunity biomass increased on average by 45.5% in the 10 days between sampling times T1 and T2. However, the increase was significantly lower in the metacommunities with dispersal compared to the metacommunities without dispersal (the increase between sampling time 1 and 2 was 29.4% with dispersal and 61.5% without dispersal; Fig. 1A). All local communities in the continuous temperature treatment were dominated by a large elliptic pennate diatom, *Achnanthes brevipes* (hereafter *Achnanthes*), contributing on average to $75 \pm 17\%$ of total biomass (mean ± SD) (Fig. 1A, 2A–D). *Achnanthes* built up biomass twice as fast as the other algae in the monocultures at 16°C, demonstrating its ability to quickly utilise space (Supplementary material Appendix 2 Fig. A2). In the absence of dispersal, the subdominant species *Entomoneis paludosa* (hereafter

Entomoneis) and *Melosira varians* had the highest biomass in the local patches with the highest light levels (299.2 and 160.2% higher than the local patches with the lowest light levels, respectively) while *Achnanthes* had the lowest biomass in the high light patches (25.1% lower than in the low and medium light level patches) (Fig. 2A–D, Table 2, Supplementary material Appendix 2 Fig. A3). Dispersal mitigated the shift in community composition at high light, promoting dominance by *Achnanthes* in all local communities. In the continuous temperature treatment, dispersal resulted in a significantly lower dissimilarity in species composition between local patches (Bray–Curtis dissimilarity index: mean ± SE, 0.24 ± 0.06 for metacommunities without dispersal and 0.06 ± 0.02 for metacommunities with dispersal; planned comparison using Fishers LSD test, $p < 0.002$; Supplementary material Appendix 2 Fig. A4). Thus, in continuous conditions, dispersal homogenised the local communities and prevented fine tuning of the species composition to the different light levels.

Right after the heat wave, biomass in the heated metacommunities was on average 38.7% lower than in the metacommunities kept at 16°C (Fig. 1). The initial negative effect of the heat wave on total biomass depended mainly on a strong decrease in *Achnanthes* (at sampling time T1 the average biomass of *Achnanthes* was 1099 ± 86 10^6 μm^3 cm^{-2} in the continuous temperature treatment compared to 246 ± 35 10^6 μm^3 cm^{-2} in the heat wave treatment; significant main effect of temperature: Table 2). *Achnanthes* did not increase significantly in the 10 days between sampling 1 and 2 after the heat wave (Fishers LSD test, $p = 0.36$). Instead, after 10 days of recovery the heat wave had induced a dominance shift from *Achnanthes* to the heat tolerant species *Entomoneis* in all metacommunities (Fig. 1B, 2E–H; Supplementary material Appendix 2 Fig. A5). High population growth of *Entomoneis* between T1 and T2 caused a general recovery of biomass after the initial loss due to the heat wave (Fig. 1). However, dispersal promoted recovery of biomass: after 10 days higher biomass was attained with dispersal than without in the heated communities, and there was no longer a significant difference comparing the heated communities with dispersal to any of the non-heated communities (Fig. 1, Table 1). Thus, dispersal promoted recovery of biomass after the heat wave enabling a full recovery in the heated metacommunities after 10 days.

There was a surplus of both nitrogen and phosphate available in the system in all treatments, but there were distinct differences in nutrient usage between the heated and continuous temperature treatments. In the continuous temperature treatment we detected limitation for silicate over time (below 0.1 $\mu mol\, l^{-1}$) and in the heated communities, phosphorus concentrations were more than three times higher than in the continuous temperature treatment (Supplementary material Appendix 2 Fig. A6).
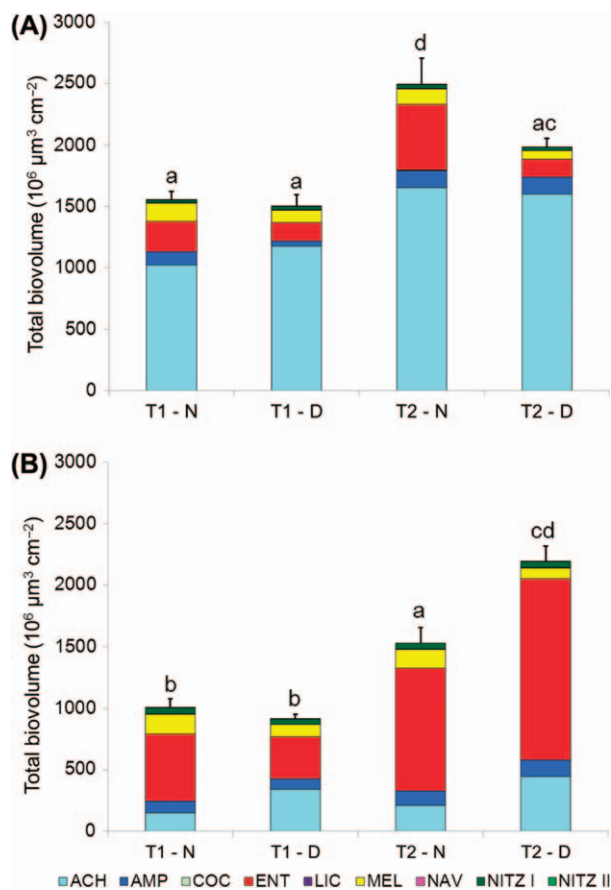

Figure 1. Average biomass in diatom metacommunities connected by dispersal (D) or not (N) and exposed to different temperature treatments: (A) continuous temperature treatment of 16°C and (B) heat wave treatment. Diatoms were sampled on day 33 (T1 – right after the heat wave) and 43 (T2 – 10 days after the heat wave) of the experiment. The different colors show the biomass contribution of each of the 9 diatom species. The abbreviations of the nine diatom species in the legend are explained in Supplementary material Appendix 1 Table A1. Error bars show the standard error of total biomass of all species. Letters above the bars show significant differences between treatment combinations according to Tukey's post hoc test ($p < 0.05$).
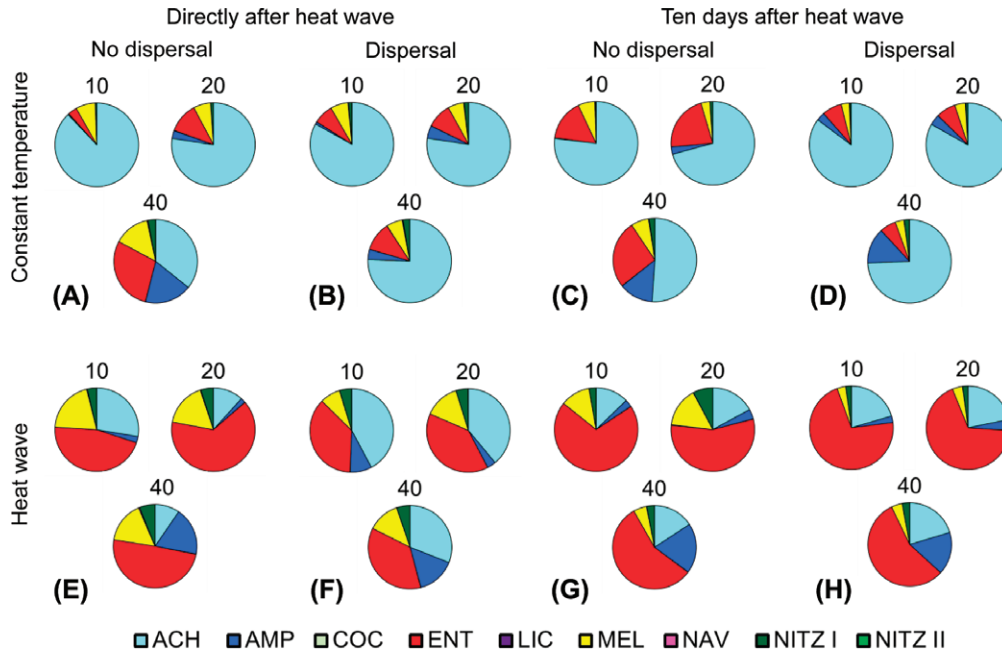
Discussion

The capacity of natural communities to reorganise or adapt in response to climate change will determine the extent to which we can expect changes in the structure and function of

Figure 2. Relative biomass of species in local communities at three different light intensities; 10, 20 and 40 μmol photons m^{-2} s^{-1}. These metacommunities are connected by dispersal or not and exposed to different temperature treatments: (A–D) continuous temperature treatment of 16°C (upper row) and (E–H) heat wave treatment (lower row). Diatoms were sampled directly after the heat wave and 10 days after the heat wave of the experiment. The different colors show the biomass contribution of each of the nine diatom species. The abbreviations of the 9 diatom species in the legend are explained in Supplementary material Appendix 1 Table A1.

ecosystems in coming decades (Walther et al. 2002, Millennium Ecosystem Assessment Report 2005, Urban et al. 2008, Gilman et al. 2010). So far, the limited body of climate change experiments that also manipulate dispersal seriously limits our ability to understand and predict local effects of warming (but see Eggers et al. 2012). With this study we demonstrate that dispersal can amplify the capacity of communities to maintain production by reorganizing species composition after a heat wave. However, we also show that dispersal decreases local biomass accumulation at stable conditions by homogenizing community

compositions. This demonstrates that regionally and locally driven processes interact, which suggests that dispersal generates a community level tradeoff between the capacity for recovery after disturbances and the ability to fine tune species compositions to heterogeneous environmental conditions (Urban et al. 2008). Thus, maximising the adaptive capacity of natural communities by managing connectivity on a landscape level poses inherent difficulties, because creating spatial insurance by promoting high dispersal may disrupt local niche dynamics and lower the equilibrium biomass of the target communities.

Table 2. Mixed-effects model results for the biomass of *Achnantes brevipes, Entomoneis paludosa* and *Melosira varians* in local patches within a metacommunity, depending on sampling time (S); temperature regime (T); dispersal frequency (D); light availability (L) and their interactions. The species represent the three most dominating diatom species in the experiment. Bold numbers show significant results.

Factor	*Achnantes brevipes*		*Entomoneis paludosa*		*Melosira varians*	
	F	p	F	p	F	p
S	**14.66**	**<0.001**	**57.25**	**<0.001**	1.21	0.28
T	**181.31**	**<0.001**	**85.40**	**<0.001**	0.81	0.37
D	2.77	0.10	0.75	0.39	**14.92**	**<0.001**
L	**11.58**	**0.001**	0.23	0.63	1.53	0.22
S×T	**7.76**	**<0.01**	**27.38**	**<0.001**	0.27	0.61
S×D	0.24	0.62	2.41	0.13	0.02	0.88
T×D	1.03	0.31	**9.33**	**<0.01**	0.11	0.74
S×L	0.51	0.5	**6.26**	**0.01**	2.40	0.13
T×L	**4.19**	**<0.05**	**18.21**	**<0.001**	**5.81**	**0.02**
D×L	2.98	0.09	**13.02**	**<0.001**	0.71	0.40
S×T×D	0.59	0.45	**15.77**	**<0.001**	0.003	0.96
S×T×L	<0.001	0.99	3.22	0.08	0.33	0.57
S×D×L	0.20	0.65	0.84	0.36	2.07	0.15
T×D×L	**6.07**	**<0.05**	0.55	0.46	**8.15**	**<0.01**
S×T×D×L	0.002	0.96	0.75	0.39	0.15	0.69

Biodiversity promotes ecosystem resilience because it increases the chance that species which are not able to cope with changing conditions can be replaced by well adapted and functionally similar species, leading to functional compensation through reorganisation of community structure (Peterson et al. 1998, Yachi and Loreau 1999, Gonzalez and Loreau 2009). Response diversity of a community refers to the range of responses to change that are dependent on species traits (Ives et al. 1999, Elmqvist et al. 2003). In our diatom communities, response diversity was provided by a tradeoff between monopolisation of nutrients by fast population growth and tolerance to heat stress. In the continuous temperature treatment, the rapid growing *Achnanthes* dominated all communities. *Achnanthes* uses high amounts of silicate and can dominate the Baltic periphyton community when silicate input is high (Sommer 1996). Accordingly, silicate decreased below limiting conditions in the continuous temperature treatment in our experiment, indicating that *Achnanthes* out-competed the other diatoms by quickly utilising the silicate added to the system. In the heat wave treatments, *Achnanthes* decreased strongly from the temperature stress, silicate was low but not limiting, phosphorus increased and the heat tolerant species *Entomoneis* became the dominating species instead. *Entomoneis* grew slower than *Achnanthes* and increased in the local patches with increasing light in the continuous temperature treatment. However, after the heat wave, *Entomoneis* increased in all local patches and thereby generated a general recovery of community biomass in all heated metacommunities. Dispersal quantitatively fuelled the population growth of *Entomoneis*, which significantly promoted the recovery of biomass after the heat wave. Earlier studies show that *Entomoneis* can dominate these periphyton communities when both silicate and phosphorus are abundant (Sommer 1996). This suggests that the decrease in *Achnanthes* performance after the heat wave decreased both silicate and phosphorus removal from the system, which shifted the competitive hierarchy and allowed *Entomoneis* to dominate the system. *Achnanthes* did not increase in biomass after 10 days of recovery, indicating that the shift to *Entomoneis* dominance reflects an equilibrium community state, rather than a transitional successional stage.

The interaction between dispersal and recovery after disturbance in our experiment has implications for understanding the resilience of ecological systems to climate change. The Spatial insurance hypothesis (Loreau et al. 2003) predicts that dispersal among local sites provides spatial insurance against locally changing conditions. However, in our study, the heat wave disturbance was regional and recovery was therefore not initiated by colonisers from undisturbed patches. Instead, recovery was caused by a general reorganisation of community structure that was driven by a shift in dominance to populations of species that also were exposed to the heat wave. The dominance shift was independent of dispersal because sufficient diversity of species was maintained in all local communities, enabling the dominance shift after temperature stress in all treatments. However, dispersal reinforced compensatory dynamics by subsidizing population growth of the dominant heat tolerant species in all patches, and thereby fuelled recovery.

Thus, the availability of a variety of response traits in the regional species pool allowed for major community reorganization after the heat stress, but full recovery after the heat wave was only possible in combination with dispersal.

Our results point towards a strong potential of communities connected by dispersal to maintain their function when subjected to a heat wave by utilising existing regional trait diversity. However, we tested the capacity of the metacommunity to respond towards one stressor only (heat stress) and we looked at only one functional response variable (total biomass). In a recent metacommunity study (Thompson and Shurin 2012), freshwater zooplankton communities were subjected to warming and salinity stress and the effects of regional diversity were tested on a number of relevant ecosystem rate and state variables. Whereas warming tolerant taxa immigrating from the region could compensate for some functions of declining species, there was no compensation for abundance decline due to salinity stress. This points out that in real world stress scenarios in which often multiple stressors act together the available regional trait diversity might be not sufficient for completely compensating species decline.

In a global change perspective, the capacity to cope with novel environmental and biological conditions through species sorting will be a critical property of natural communities to maintain their structure and function. Furthermore, next to local community dynamics driven by species sorting (Leibold et al. 2004) communities can also respond by phenotypic plasticity (Charmantier et al. 2008) or adaptive trait change within populations (evolution; Franks et al. 2007). Dispersal promotes adaptive trait change and species sorting by providing new genes through gene flow or new species through immigration, respectively. However, too high dispersal limits local adaptation and even causes maladaptation by flooding locally adapted genes. Similarly, too high dispersal limits species sorting by distributing species to all available habitats, including habitats to which they are poorly adapted (Urban et al. 2008). In our experiment at continuous temperature conditions, dispersal homogenised the metacommunities by favouring the dominant species *Achnanthes* in all local patches ('mass effect', Leibold et al. 2004). This disrupted species sorting by prohibiting the subdominant species *Entomoneis* and *Melosira varians* to accumulate biomass in patches with high light intensity, where they otherwise proliferated, with significant negative effects on metacommunity biomass. Thus, we demonstrate that dispersal limits the fine tuning of species compositions to a heterogeneous environment and thereby decreases equilibrium biomass of the experimental metacommunities. Genetic adaptation should be even more sensitive to dispersal than species sorting (Urban et al. 2008), indicating that the capacity for rapid adaptive evolution to novel conditions caused by climate change may be critically influenced by too high connectivity.

In conclusion, the interaction between dispersal and regional trait diversity has implications for understanding cumulative effects of anthropogenic drivers and the management of natural ecosystems. Species loss and habitat fragmentation are global phenomena that affect all biomes. Thus, if the interaction between dispersal and

community structure is widespread, a proactive management of ecosystem services should promote the capacity to maintain community function by focusing on ensuring sufficient connectivity and movement of populations to enable community reorganisation after regional disturbances. However, the observed detrimental mass effects of high dispersal on regional carrying capacity, suggest that we need to promote regional diversity at the same time as we avoid mass effects by regionally dominating species. This emphasises that the recent expansion of a few now globally distributed and functionally dominating invasive species together with globally decreasing endemic biodiversity (Pimm et al. 1995), may be a serious threat to the capacity of natural ecosystems to maintain their functions when the climate changes.

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Supplementary material (available online as Appendix oik-00927 at < www.oikosjournal.org/readers/appendix >). Appendix 1–2.