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A heatwave increases turnover and regional dominance in microbenthic metacommunities

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Abstract

While the effect of the global biodiversity crisis on local species loss is still debated, there is empirical evidence for major changes in local biodiversity attributed to increased species turnover. In communities exposed to a climate stressor, species turnover can lead to increased dominance of well-adapted species and consequently to an overall decline in species diversity. Despite the known importance of species turnover for community dynamics and functioning, experimental results on the connection between biodiversity loss and species turnover are scarce. We still do not fully understand which specific factors increase the rate of change in species composition, especially when considering natural compared to artificially lab assembled communities. In the present study, we experimentally tested whether a heatwave and dispersal increased species turnover and decreased species diversity in natural benthic diatom communities with different initial species compositions. We found that on the local scale, dispersal had overall positive effects on species richness while the relationship between exposure to the heatwave, species turnover, and diversity depended on initial community composition. However, on the regional (i.e. metacommunity) scale, exposure to the heatwave and dispersal both increased turnover and decreased Shannon diversity by almost 50%. Turnover in these metacommunities was not caused by a loss of species, but rather by a change in dominance patterns leading to homogenization, and consequently decreased diversity. Our study shows that climate change can destabilize community composition and degrade species diversity, but still after ca. 15 generations does not decrease the number of species in the community, demonstrating that the response of species diversity and richness to changing conditions can be fundamentally decoupled on ecological time scales.

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Keywords: Turnover; Biodiversity; Metacommunity; Heatwave; Benthic microalgae

Introduction

Amplified by human impacts, especially the emission of greenhouse gasses, the global climate is changing at an

alarming rate. Global sea surface temperature is increasing, and severe heatwaves, storms and droughts are becoming more frequent (IPCC 2014). Contrary to expectations of local species loss based on >180 small-scale warming experiments (Gruner et al., 2017), the observed changes in temperatures might not have led to a general decline in local-scale species numbers on land or in the ocean. (Dornelas et al., 2014; Elahi

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et al., 2015; Vellend et al., 2013) In fact, Elahi et al. (2015) showed a net increase in local species richness over the past decades by averaging 471 species richness time series from marine coastal ecosystems spanning from 1962 to 2015. Studies that claim no net loss of species on the local scale are challenged by other researchers, mainly due to criticism of the use of spatially biased datasets and the conclusions drawn from the analyses themselves (Cardinale, Gonzalez, Allington, & Loreau, 2018; Gonzalez et al., 2016; Wright et al., 2014). Either way, the global biodiversity crisis is concerning, and it is becoming increasingly clear that species richness poorly captures temporal dynamics of biodiversity in a changing environment (Hillebrand, Soininen, & Snoeijs, 2010; Hillebrand et al., 2018). Immigration and extinction events often take place on different time scales, which can lead to the decoupling of rates of changes in species richness and species composition (Hillebrand, Soininen, & Snoeijs, 2010; Hillebrand et al., 2018; Jones & Gilbert, 2018; Teittinen et al., 2016). Thus, to understand the impact of a changing climate on local scale biodiversity, we need to study effects of local impacts on turnover as determined by changes both in species relative abundances and identities (Hillebrand et al., 2018).

Even though the scientific literature on impacts on biodiversity changes is constantly growing (e.g. Kilpatrick, Salckeld, Titcomb, & Hahn, 2017; O'Connor et al., 2017; Pecl et al., 2017), experimental studies examining the connections between climate change, biodiversity loss, and species turnover are still rare. At the same time, if species turnover is measured, it is often done in local patches of habitats. This is limiting, however, because most natural communities are not isolated but connected by dispersal and form metacommunities (Leibold et al., 2004; Wilson, 1992). Thus, local patterns of biodiversity change can differ drastically from regional patterns. Metacommunities provide a larger regional species pool that allows for immigration and emigration between the local patches, which both influences species turnover and enables coexistence of otherwise inferior species (Tilman, 1994). Previous experiments have shown that a heatwave can cause dominance shifts in benthic microalgae metacommunities (de Boer et al., 2014; Eggers, Eriksson, & Matthiessen, 2012). However, these experiments were done with artificial species assemblages that poorly represent natural community patterns. To increase experimental realism, we used natural species assemblages and multiple spatial and temporal scales to study community processes in the present study.

In undisturbed communities under dispersal limitation, local diversity patterns and turnover should depend on local environmental conditions, initial community composition, and the resulting species interactions. In this scenario, changes in regional diversity and turnover will depend on the degree of synchrony between local patches (i.e. how similar or dissimilar the changes in community dynamics are in the separate local communities of a metacommunity), with no predictable expectation (Fig. 1(A)). In a metacommunity framework, diversity and turnover should depend on

the strength of dispersal and the scale of the disturbance. Regional disturbance events such as heatwaves create novel habitat conditions that favor the species best adapted to the new environment across all local communities in the region. This should increase both local and regional dominance of the best competitor (i.e. decrease diversity), homogenize the metacommunity, and increase regional species turnover (Fig. 1(B)) compared to the undisturbed state (Fig. 1(A)). Such dynamics are described for microalgae in thermal flumes, where increased temperature destabilized community composition and increased species turnover, although species richness did not change (Hillebrand, Soininen, & Snoeijs, 2010). Dispersal promotes the immigration of species or populations with adapted traits (Loeuille & Leibold, 2008; Urban et al., 2008) and should therefore speed up the homogenizing effect of regional disturbances by spreading the regionally best adapted species to all local patches of the metacommunity (de Boer et al., 2014; Eggers, Eriksson, & Matthiessen, 2012; Mouquet & Loreau, 2003), which leads to higher regional species turnover until all local patches are dominated by the best competitor (Fig. 1(C)).

In this study, we tested the effects of a regional heatwave disturbance on species turnover and diversity in a culture experiment with natural benthic diatom metacommunities. The metacommunities consisted of three local communities with different initial community compositions. In our full factorial design, half of the metacommunities were subject to dispersal and exposed to an experimental heatwave. We hypothesized that dispersal and warming increase metacommunity turnover and homogenize communities by promoting the dominance of a heat-tolerant species (Fig. 1).

Materials and methods

Set-up and sampling

We conducted a laboratory experiment with natural benthic diatom communities that we extracted from three separate locations ("A", "B", and "C") on the intertidal flat of the Wadden Sea close to Schiermonnikoog island, the Netherlands. We chose these locations, because varying hydrodynamic exposure history led to differences in species composition and biodiversity in the three locations. Thus, we had differences in initial species composition for the three local communities A, B, and C in our experiment (see Appendix A: Fig. 1). Using natural communities instead of artificial assemblages decreases the predictability of outcomes and is more difficult to replicate, but it gives the advantage of studying actual species interactions as they are observed in nature. Thus, using natural communities increases the realism of ecological experiments and allows for better extrapolation of laboratory results to the natural world. We extracted the benthic diatoms from the sediment immediately before the start of the experiment and kept them suspended in medium in separate culture flasks until

Fig. 1. Schematic representation of how a heatwave (i.e. regional disturbance) and dispersal can influence turnover in metacommunities by promoting the dominance of heat-adapted species in local patches. In all communities, local dominance patterns and thus local turnover will depend on initial community composition. (A) In communities without warming or dispersal, regional turnover will be relatively low, if turnover in the different local communities vary in such a way that they offset one another. (B) In communities exposed to a heatwave, the locally best adapted species will become locally dominant, which potentially leads to high regional turnover. However, the degree of species turnover depends on initial species composition, in particular the presence, abundance, and properties of heat-adapted species in the different local communities. (C) If the regional disturbance event is accompanied by dispersal, the best regional competitor will be spread among all the local patches and become both locally and regionally dominant, which leads to high regional turnover, independent of initial species composition in the local patches.

inoculation (one flask for community A, one for community B, one for community C). Benthic diatoms are the most important primary producers on many intertidal mudflats (Underwood & Kromkamp, 1999) and have short generation times, which can lead to rapid cell divisions under favorable growing conditions (Underwood & Paterson, 1993).

We used culture flasks (TPP, 60 mL, filter screw cap) filled with 40 mL sterile filtered North Sea water medium (N:Si:P added for final concentrations of 40:40:2.7 μM) as experimental units. We kept the culture flasks in temperature- and light-controlled climate cabinets (CTS Environmental Test System Type TP 0/600 L with OSRAM Biolux L 36 W/965 lights, 16:8 light:dark cycle; light level: 10.8 $\mu\text{mol m}^{-2} \text{s}^{-1}$) for the duration of the experiment. The benthic diatoms settle and eventually form biofilms on the bottom of the plastic flasks, comparable to biofilm formation on natural substrate. We replenished 20 mL of the overlying medium every third day to prevent nutrient limitation. We constructed 60 metacommunities by connecting three local communities with differing initial diatom species composition but similar initial biomass: Three culture flasks, one of each local community A, B, and C, formed one metacommunity. We simulated dispersal in half of the metacommunities (DISP) but not in the other half (NO.DISP), which led to two different dispersal treatments. To simulate dispersal in the DISP treatment, we created a metacommunity-specific dispersal mixture for each metacommunity separate. To do

so, we pipetted 3 mL solution out of each local flask of the metacommunity (e.g. 2A, 2B, 2C) into a sterile beaker. In the beaker we homogenized the solutions of the three local communities before returning 3 mL of the mixture (e.g. metacommunity 2 mixture) back into the separate local flasks (e.g. back into flask 2A, 2B, and 2C). Thus, we effectively added 1 mL, or 2.5% volume of each local flask into the respective other metacommunity flasks at each dispersal event. We simulated dispersal every other day. In the NO.DISP communities we did not simulate dispersal, and thus the separate flasks were not connected with one another. To be able to compare metacommunity dynamics in communities with and without dispersal, we nevertheless assigned three local flasks (one for each A, B, and C) to one metacommunity at the start of the experiment (e.g. flask 1A, 1B, and 1C formed metacommunity 1, even though the separate solutions were not mixed at any time during the experiment). Regardless of the dispersal treatment, on the day of dispersal, we turned all culture flasks (all DISP and all NO.DISP flasks) carefully three times before the DISP communities were mixed to diffuse the boundary layers around cells in all flasks in the same way. This prevents the creation of differential nutrient uptake dynamics in different flasks due to the dispersal treatment. At the same time, turning the flasks allowed us to indirectly include species-specific dispersal abilities, because more loosely attached species were more prone to be resuspended in the solution prior to

dispersal and thus more likely to be spread throughout the metacommunity.

We performed a 21-day-long experiment, during which time we exposed half of the metacommunities (30) to an experimental heatwave treatment (“HW”). The heatwave lasted 6 days and the treatment included a pre-adaptation time and a post-recovery time: the temperature for the 30 metacommunities exposed to warming was gradually increased from 19 °C to 33 °C on day 8, after which temperatures were gradually decreased again until they were back to 19 °C on day 15 (see Appendix B). The effective heatwave with temperatures over 25 °C was achieved from day 5 until day 11 (see Appendix B). See Appendix B for a figure showing the exact temperature on each experimental day. The remaining 30 metacommunities were kept at a constant temperature of 19 °C (“CONTROL”), which was the average air temperature in the sampling location during time of collection. The temperatures of the experimental heatwave were based on actual measurements of the summer heatwave in 2014 in the sampling location and represent values that should lead to decreased photosynthetic capacity in intertidal diatoms (Blanchard et al., 1996).

We ended the experiment after 21 days and sampled destructively (i.e. removed entire culture flasks) three times: before the heatwave (day 5), immediately after the heatwave (day 12), and longer after the heatwave (day 21). Each treatment was replicated five times. Overall, this led to a total replication of $n = 180$ local communities, forming 60 separate metacommunities (three sampling days (5, 12, 21), three local communities (A, B, C), two dispersal treatments (DISP, NO.DISP), two heat treatments (HW, CONTROL), and a replication of five flasks per treatment).

On each sampling day, we homogenized the diatom biofilm of each flask in the medium before taking any samples. This was achieved by scraping the entire biofilm off the bottom of the flask with a cell scraper and subsequent rigorous shaking of the bottle until all individuals of the biofilm were suspended in the culture medium and thus the sample homogenized. We collected 10 mL of the solution in brown glass bottles and fixed the microalgae with Lugol’s iodine solution. The samples then were stored in the dark at 4 °C until further processing. We used an inverted microscope (400× magnification) to obtain microalgae species richness, species composition, and biovolume using the Utermöhl counting technique (Utermöhl, 1958) and subsequent approximation of cell shapes to simple geometric forms (Hillebrand et al., 1999). We identified microalgae groups to the highest resolution possible (hereafter referred to as species; see Appendix A: Table 1) using several books (Hasle, Syvertsen, Steidinger, & Tangen, 1996; Hoppenrath, Elbrächter, & Drebes, 2009; Round, Crawford, & Mann, 1990). Even if we only name the genus, it only represents one species of this genus, which could not be determined more precisely with the methods that we used. We calculated species-specific cell biovolumes by directly measuring different dimensions (defined in Hillebrand et al., 1999) of

at least 25 cells per species (see Appendix A: Table 2). This allowed us to compute biovolume contribution of each species and total community biovolume. We use biovolume as a proxy for biomass and refer to it as biomass hereafter. We obtained regional biomass by adding the three values of each local community A, B, and C within a metacommunity. We calculated Shannon diversity and species turnover on the local and regional scale based on biomass data. For species turnover, we calculated Bray–Curtis dissimilarity for samples of the same treatment at different time points. We used Bray–Curtis dissimilarity as a measure for species turnover rather than a richness-based metric, because we were most interested in relative changes of species composition (relative abundances and changes in dominance) rather than the complete loss or replacement of species. In addition, the community dynamics in our experiment were mainly driven by one dominant species (*Entomoneis paludosa*), which further justifies the use of Bray–Curtis dissimilarity. However, we do provide results for turnover calculated with a richness-based method for comparison in Appendix C. Since we sampled destructively and removed entire culture flasks, we could not measure the exact same communities over time. Instead, we randomly assigned “time-replicates” to compare samples from the same treatment at different sampling times with one another. We calculated turnover values after 12 (dissimilarity between samples of the same treatment from day 5 and 12) and 21 days (dissimilarity between samples of the same treatment from day 5 and 21) to be able to compare the communities after the heatwave to the state before the heatwave and to see whether communities could recover with more time.

Statistical analysis

We performed all statistical tests with the vegan package (Oksanen et al., 2018) in R v. 3.3.2 (R Core Team, 2017) and created the graphs with ggplot (Wickham, 2016). We constructed full factorial ANOVA models for species turnover, species richness, and Shannon diversity on the local and on the metacommunity scale. On the local scale, we performed separate models for each local community (community A, B and C). On the metacommunity scale, we performed the analyses on summed data from communities A, B and C within each metacommunity. For species richness and Shannon diversity, we included the fixed factors sampling day, dispersal treatment, and warming treatment as independent factors. For species turnover, sampling day was included as a repeated measure in the ANOVA model, since turnover values on days 12 and 21 were related to the same starting community (day 5) and therefore depended on each other. Data that did not meet the assumptions of ANOVA were square-root or log10 transformed. For significant results, we subsequently conducted post-hoc comparisons of all contrasts within each sampling day. Thus, in comparison with a standard post-hoc analysis (such as Tukey’s HSD

test), we only compared a third of all possible pairs. To avoid excessive Type II error, we therefore calculated the least significant difference (student *t*-test) for all relevant comparisons and then performed a Bonferroni correction to account for multiple comparisons. In the text, we present the Bonferroni corrected *p*-values for all post-hoc tests.

Results

Local-scale results

At the local scale, initial community composition determined the effect of warming on species turnover and diversity, while dispersal increased species richness in general

(Fig. 2; see Appendix D for tables with complete statistical results). In community A, warming decreased species turnover over time, but only in the no-dispersal treatment (interaction day, warming, and dispersal: $F_{1,16}=6.4$, $p = 0.023$, Bonferroni day 21: $p = 0.036$; Fig. 2(A)). In contrast, in community B both warming and dispersal increased species turnover (main effect warming: $F_{1,16}=19.8$, $p<0.001$; interaction day and dispersal: $F_{1,16}=5.5$, $p = 0.032$, Bonferroni day 21: $p = 0.035$; Fig. 2(A)). In community C, turnover stayed relatively constant throughout time and was not significantly affected by warming (see Appendix D: Table 1; Fig. 2A). Warming initially increased species richness in community A, but only in the dispersal treatment, and this effect disappeared after the heatwave (interaction day, warming and dispersal: $F_{2,48}=3.4$, $p = 0.042$, Bonferroni day

Fig. 2. (A) Mean local turnover (based on changes in Bray–Curtis dissimilarity), (B) species richness, (C) and Shannon diversity at the different sampling days in the different local communities. In the heatwave treatment, day 5 is right before the heatwave, day 12 is immediately after the heatwave, and day 21 is longer after the heatwave (see Appendix B for graph of temperatures in the different treatments over the course of the experiment). For turnover, the sampling days denote the time frame in which turnover was measured, because it is based on changes over time rather than measurements taken on a specific day (i.e. sampling day 12 means the change in Bray–Curtis dissimilarity from day 5 to day 12; sampling day 21 is the change in Bray–Curtis dissimilarity from day 5 to day 21). The error bars represent standard errors.

5: $p = 0.021$; Fig. 2(B)). Dispersal increased species richness strongly, by two to five species, in all local communities (main effect of dispersal: A: $F_{1,48}=178.7$, $p<0.001$; B: $F_{1,48}=97.4$, $p<0.001$; C: $F_{1,48}=23.9$, $p<0.001$; Fig. 2(B)). In contrast, warming decreased Shannon diversity strongly in communities A and C (main effect of warming: A: $F_{1,48}=57.4$, $p<0.01$; C: $F_{1,48}=44.0$, $p<0.001$; Fig. 2(C)), while dispersal had minor effects. In community A, the negative effect of warming on Shannon diversity developed with time and was stronger without dispersal (interaction sampling day and warming: $F_{2,48}=10.1$, $p<0.001$; interaction warming and dispersal: $F_{1,48}=4.2$, $p = 0.045$; Fig. 2(C)).

The degree of local dominance of the most abundant species *Entomoneis paludosa* inversely reflected the described changes in Shannon diversity. Generally, relative abundance patterns of *Entomoneis paludosa* and abundance of rare species depended on the local communities (see Appendices E and F). In community A, *Entomoneis* dominated the communities from day 5 in all treatments and increased in dominance over time in all but the control treatment, in which it declined over time (interaction sampling day and warming: $F_{2,48}=3.2$, $p = 0.049$; see Appendix F: Fig. 1). Warming had the strongest effect on dominance in community A ($F_{1,48}=13.8$, $p<0.001$). Rare species composition in community A mostly changed in the communities subject to dispersal, in which the abundance of *Amphora* sp. increased over time, whereas several *Navicula* species abundance declined (see Appendix E: Fig. 2). In community B, *Entomoneis* relative abundance was low at day 5, but it increased over time, with a much stronger increase in the dispersal treatments compared to the no-dispersal treatment at day 21 (Sampling day: $F_{2,48}=50.5$, $p<0.001$, dispersal: $F_{2,48}=19.33$, $p<0.001$, interaction sampling day and dispersal: $F_{2,48}=6.9$, $p = 0.002$; see Appendix F: Fig. 1). The most abundant rare species in community B was *Gyrodinium acuminatum*, whose abundance decreased over time. In contrast, abundances of both *Amphora* species as well as a large *Stauroneis* sp. increased due to dispersal or a combination of the heatwave and dispersal (see Appendix E: Fig. 2). In community C, *Entomoneis* dominance was intermediate and remained so throughout the experiment, with slight increases over time in all but the control treatment (see Appendix F: Fig. 1). All factors and combinations significantly affected dominance in community C (see Appendix F: Table 1), where the most abundant rare species were *Amphora* sp. and a large *Stauroneis* sp., with the former's abundance increasing over time in all treatments. Both species' abundances were decreased by warming immediately after the heatwave compared to the control (day 12). Other rare species in community C remained relatively constant over time (see Appendix E: Fig. 2). For further information on dominance, including all statistical results, see Appendix F, and for graphs of total and rare species composition see Appendix E.

Metacommunity-scale results

On the metacommunity scale, warming and dispersal both increased species turnover and decreased Shannon diversity

(Fig. 3). However, while the effects of warming established immediately after the heatwave, the effect of dispersal developed over time (Fig. 3). Warming significantly increased metacommunity turnover on day 12 (directly after the heatwave), but this effect was not sustained after 21 days

Fig. 3. (A) Mean regional turnover (based on changes in Bray–Curtis dissimilarity), (B) species richness, (C) and Shannon diversity at the different sampling days in the different treatments. Regional turnover, Shannon diversity, and species richness were calculated based on regional biomass, which was obtained by summing the values of all three local communities A, B, and C within a metacommunity. Thus, mean regional values are averages from all five replicate metacommunities per treatment. In the heatwave treatment, day 5 is right before the heatwave, day 12 is immediately after the heatwave, and day 21 is longer after the heatwave (see Appendix B for graph of temperatures in the different treatments over the course of the experiment). For turnover, the sampling days denote the time frame in which turnover was measured, because it is based on changes over time rather than measurements taken on a specific day (i.e. sampling day 12 means the change in Bray–Curtis dissimilarity from day 5 to day 12; sampling day 21 is the change in Bray–Curtis dissimilarity from day 5 to day 21). The error bars represent standard errors.

(interaction effect sampling day and warming: $F_{1,16}=6.3$, $p = 0.023$; Bonferroni Day 12, $p = 0.042$; Day 21, $p = 1.00$; Fig. 3(A)). In contrast, dispersal increased metacommunity turnover only after 21 days (interaction effect sampling day and dispersal: $F_{1,16}=6.1$, $p = 0.025$; Bonferroni Day 12, $p = 0.144$; Day 21, $p < 0.001$; Fig. 3(A)). Species richness of the metacommunities remained relatively constant throughout the experiment, but restricting dispersal caused a 10% decrease in the number of species in the unheated communities after 21 days (interaction sampling day, warming and dispersal: $F_{2,48}=6.2$, $p = 0.004$; Bonferroni Day 21, $p < 0.001$; Fig. 3(B)). The increase in metacommunity turnover by warming and dispersal was best described by an increasing dominance of a single species, *Entomoneis paludosa* (see Appendix F), which caused Shannon diversity to drop in the warming treatment directly after the heatwave (interaction sampling day and warming: $F_{2,48}=8.1$, $p < 0.001$; Bonferroni Day 12 $p < 0.001$, Day 21 $p < 0.001$; Fig. 3(C)), and in the dispersal treatment after 21 days (interaction sampling day and dispersal: $F_{2,48}=13.8$, $p < 0.001$; Bonferroni Day 21 $p < 0.001$; Fig. 3(C)). Consequently, after 21 days, the unheated metacommunities with dispersal limitation had lost on average two species, but unlike the other metacommunities, they showed no loss of Shannon diversity compared to initial conditions (Fig. 3). For detailed information on species composition in the metacommunities see Appendix E.

Discussion

Species turnover despite invariant richness

In our metacommunity experiment, a simulated heatwave and dispersal both increased regional species turnover and strongly decreased regional species diversity (Shannon diversity). This was caused by the increased dominance of one superior species (*Entomoneis paludosa*) that homogenized communities across space and time. This is comparable to results obtained by de Boer et al. (2014) in an experiment using artificial species assemblages of benthic microalgae, where a heatwave and dispersal increased the biomass of *Entomoneis paludosa* after recovery. Despite increased turnover and decreased Shannon diversity, both the heatwave and dispersal counteracted species loss observed in the regional species pool in control communities after ca. 15 generations in our experiment. These results contrast with those obtained by Eggers, Eriksson, and Matthiesen (2012) where the heatwave decreased mean local species richness in the long run in an experiment with artificial microbenthic species assemblages.

Our results support studies of long-term data and modeling that indicate much faster responses of species composition to change in conditions, such as global warming, compared to species richness. This leads to the decoupling of rates of change in species richness and species

composition (Hillebrand, Soininen, & Snoeijs, 2010; Hillebrand et al., 2018; Teittinen et al., 2016). In fact, the results demonstrate that warming and connectivity can be detrimental to biodiversity when considering species composition, but still generate a positive impact on the number of species on ecologically relevant time scales. This suggests that to detect relevant biodiversity changes in the face of climate change and to predict extinction risks over time, we need to apply community-based metrics that not only focus on species richness, but also incorporate species identities and changes in relative species abundances over time. At the same time, it is important to make ecological experiments as realistic as possible to be able to extrapolate experimental results to natural systems. One step to achieve more realism is to use natural communities instead of artificial species assemblages as we have done in our experiment.

Importance of initial species composition

On the local scale, the effect of warming on species turnover and diversity depended on initial community composition. In all local communities, the same heat-tolerant species was promoted by warming (*Entomoneis paludosa*). In community A, *Entomoneis paludosa* already dominated the species composition at the start of the experiment (see Appendix A: Fig. 1), resulting in an even stronger decrease in both species turnover and diversity with warming. *Entomoneis paludosa* was present, but low in abundance in community C and below detection limit in community B at the start of the experiment (see Appendix A: Fig. 1). However, since it appeared in later samples of no-dispersal communities B and C, it must have been present initially. Thus, we assume that *Entomoneis* was favored under experimental conditions, including the heatwave and the dispersal treatments which led to a higher *Entomoneis* biomass after the heatwave (especially on day 21) compared to control and no-dispersal communities. Reasons for this dominance can only be speculated about, since we did not measure species-specific traits in this experiment. Generally, it seems like *Entomoneis* is a strong competitor under these experimental conditions and a good disperser. This is something that should be studied in more detail in future experiments. In the communities with higher diversity at the start of the experiment, warming either increased species turnover (community B) or decreased diversity (community C). The importance of initial community composition on local effects highlights the strength of using natural communities in experiments. Since the local results can differ drastically depending on the identities of initially present species, it is important to have realistic species assemblages to be able to see how communities might react in nature. Generally, any community that contains at least one species that is well-adapted to a climate stressor and at the same time shows good competitive and dispersal abilities should react in similar ways as *Entomoneis paludosa* did in our experiment.

Biodiversity effects depend on scale

The different community responses in local and regional communities show that the effect of warming was scale-dependent and thus we need to incorporate scale to understand climate change effects on biodiversity. Scale-dependent interactions are prevalent in ecology, and the influence of one driver can change in strength or direction with scale (Bergström, Englund, & Bonsdorff, 2002; Donadi et al., 2017; Kraan, Dormann, Greenfield, & Thrush, 2015). Notably, since regional warming in our study led to regional biodiversity declines that were not necessarily reflected in local trends, we cannot rely on local and spatially limited data series to monitor current changes.

The relationship between the heatwave and dispersal was also scale-dependent; indicating that different ecological drivers dominate at different scales. In contrast to the additive effects of warming and dispersal on the regional scale, dispersal did not add to the negative effects of warming on species diversity on the local scale. Instead, the main effect of dispersal was to prevent local species loss. Thus, dispersal strengthens warming effects at the regional scale, but weakens warming effects on the local scale. Such “cross-scale interactions”, where processes at one scale interact with processes at another scale, are poorly understood, but are increasingly described as generating non-linear interactions in different types of ecological systems (Donadi et al., 2017; Peters, Bestelmeyer, & Turner, 2007; Slocum et al., 2010; Soranno et al., 2014; Willig et al., 2007). The differing effects depending on scale exemplify the importance of looking at multiple spatial scales in biodiversity experiments to capture a more complete picture of what is happening in real world ecosystems. For example, in our study, dispersal rescued species and increased richness on the local scale by immigration, but at the same time decreased regional diversity by promoting the dominance of the best competitor.

Many factors influence metacommunity dynamics

It is important to note that (meta)community structure and dynamics always depend on multiple factors, including patch and metacommunity size and the configuration of the environment (Holyoak et al., 2005; Leibold et al., 2004). In our study, we constructed metacommunities with three local patches in a homogenous environment. Thus, we had a relatively small number of local patches compared to most natural metacommunities. If we had chosen to increase the metacommunity size, observed community dynamics would have taken longer to manifest. However, the general community response (i.e. increased species turnover with the heatwave and dispersal) would have stayed consistent with our results.

We also expect that local species dynamics would have been different if we had chosen to create heterogeneous environments in our metacommunities. Heterogeneous patches would have led to species sorting across the metacommunity,

possibly resulting in the dominance of different species in different local patches (Leibold et al., 2004; Mouquet & Loreau, 2003; Mouquet, Hoopes, & Amarasekare, 2005). To dominate in the heatwave treatment, the locally best competitors would also have to be stress resistant. Whereas species richness and Shannon diversity in heterogeneous environments are expected to change locally and regionally according to source-sink dynamics (Mouquet & Loreau, 2003), we do not expect turnover to differ in heterogeneous compared to homogenous metacommunities in response to dispersal and environmental stress. This is because turnover does not depend on species identities, but rather on changes in dominance patterns of the species present. In our experiment, when conditions were homogenous, *Entomoneis paludosa* was the best local and regional competitor and in addition, this species was stress-resistant. Despite the possibility of multiple different species being locally dominant, regional dominance of one superior species has previously also been demonstrated in heterogeneous systems (Matthiessen, Mielke, & Sommer, 2010; Mouquet & Loreau, 2002).

Negative effects on ecosystems can be delayed

The decoupling of compositional stability and species richness in our heatwave experiment highlights the challenge of documenting long-term effects of global change on biodiversity. While strong negative effects of a heatwave and connectivity on species turnover and compositional diversity were rapid and consistent throughout the experiment, the effect on the number of species was positive. Species extinctions can occur with considerable delay following disturbances and such extinction debt is a general challenge for biodiversity conservation (Kuussaari et al., 2009). Previous research has shown that biodiversity loss and strong dominance by certain species can lead to decreased ecosystem functioning (Cardinale et al., 2012; Hillebrand, Bennett, & Cadotte, 2008; Hooper et al., 2005; Lefcheck et al., 2015), which in turn can negatively affect ecosystem service provisioning (Worm et al., 2006) and render communities more vulnerable to perturbations (Isbell et al., 2015; Wagg et al., 2017). Consequently, if a global disturbance event homogenizes communities and decreases diversity, future perturbations may have disproportionately high impacts. The largest inherent problem of community homogenization is probably the decline of specialist species and thus trait diversity (Clavel, Julliard, & Devictor, 2011; Olden et al., 2004), which leads to loss of critical functions (Spaak et al., 2017). This shows that even without direct loss of species, increased species turnover can be an indicator for devastating effects in ecosystems, as it reflects changes in species composition (i.e. dominance patterns) and as such potential instability in communities.

In our experiment, the only measure of ecosystem functioning was biomass, which contrary to expectations increased with decreasing biodiversity (in the heatwave and

dispersal treatments; see Appendix E: Figs. 1 and 2). The increase in total biomass was clearly driven by strong biomass increases of the superior competitor in the system, *Entomoneis paludosa*, whose growth was additionally favored by the heatwave and dispersal. As such, *Entomoneis paludosa* could play an important role in the intertidal food web under extreme heat conditions as predicted with future climate change, because benthic microalgae fuel this system by acting as main food source for many organisms (Kromkamp et al., 2006; Markert et al., 2013; Rigolet, Thiébaud, & Dubois, 2014). Nevertheless, we do not know if other ecosystem functions decreased due to the strong dominance of one species, nor can we predict whether a future perturbation could negatively affect these metacommunities due to decreased response diversity. Thus, it is crucial to further investigate the effects of not only species loss, but also temporal changes in species composition on both local and regional scales to better understand the consequences of species turnover on community processes and functioning.

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2020.03.003.

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