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# Connectivity of communities interacts with regional heterogeneity in driving species diversity: a mesocosm experiment

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**Abstract.** According to metacommunity theory and previous experiments, inter-patch dispersal rates may alter species diversity at local to regional scales. In this study, we tested the predictions of metacommunity theory regarding the effect of dispersal rates on diversity, with a focus on the impact of environmental heterogeneity. Experiments were conducted in which the dispersal frequencies of freshwater nematode communities and the heterogeneity of local environmental conditions were factorial manipulated by maintaining mesocosms under homogeneous or heterogeneous temperature regime. The effect on biodiversity of the dispersal rate, environmental heterogeneity, and the interaction thereof were evaluated using linear (mixed) models, which showed a significant interaction of the dispersal rate and environmental heterogeneity for alpha- and gamma-diversity measures. Specifically, in homogeneous environments an increase in the dispersal rates led to a decline in diversity at local and regional scales. This was due to the increasing dominance of *Daptonema dubium*, which was favored by a higher patch connectivity that allowed it to invade local communities. In heterogeneous environments, diversity was unaffected, suggesting that rescue and source-sink effects did not play a role for many species, probably due to the wide temperature range. Diversity was also not impacted by high and low dispersal treatments, and the maximum change was already reached at a dispersal rate of <7% in 4 weeks. The communities were then sampled a second time to investigate the development of diversity when dispersal and thus community connectivity are suspended. After only 12 weeks of isolation, the homogenizing effect of dispersal on community disappeared. The results point to the degree of environmental heterogeneity as key factor in the metacommunity framework. They also demonstrate the need to increase experimental complexity in order to facilitate comparisons between experiments.

**Key words:** dispersal; mass effects; metacommunity; nematodes; temperature effects.

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## INTRODUCTION

Ecologists have long sought to identify the drivers of species diversity. In many of the early studies, the focus was on local scales, where species interactions, niche dimensions, and resource heterogeneity are key determinants of species diversity (MacArthur and Levins 1967). By contrast, the more recent metacommunity concept (Hanski 1999, Leibold et al. 2004) integrates regional factors, specifically dispersal, into the conceptual framework of species diversity. Nonetheless, much remains to be learned about how dispersal changes species diversity at different scales. Dispersal that is relatively homogeneous between species is generally considered to reduce beta-diversity, by homogenizing between local communities (Mouquet and Loreau 2003, Cottenie and De Meester 2004), whereas the effects on alpha-diversity vary. Theory predicts a

positive relationship between dispersal rates and local diversity due to (1) generally lower dispersal limitations, (2) rescue effects (Brown and Kodric-Brown 1977, Hanski 1999), which allow colonists to re-establish previously extinct populations, and (3) the source-sink effects (Pulliam 1988) [also referred to as mass effects (Shmida and Wilson 1985)] that occur when species persist in communities in which they are poor competitors because they constantly immigrate from communities where they are good competitors. Conversely, dispersal above a specific threshold may cause a decrease in diversity by allowing a regionally dominant competitor to invade local communities, thus reducing spatial refuges for inferior competitors and reducing local diversity (Amarasekare and Nisbet 2001, Forbes and Chase 2002, Mouquet and Loreau 2002). Regional (gamma) diversity and alpha-diversity are linked by beta-diversity (Gering and Crist 2002). Therefore, if dispersal decreases beta-diversity, then gamma-diversity may remain unaffected or will decrease as well (Mouquet and Loreau 2002).

A number of experimental studies aimed at testing these theorized predictions regarding diversity and its drivers have been conducted and have mostly provided support for several aspects of metacommunity theory. A meta-analysis of 23 studies showed that alpha-diversity generally increased with increasing dispersal and was highest at an intermediate dispersal rate (Cadotte 2006). A weak decrease in gamma-diversity across the included studies was also determined. However, because relatively few studies have considered regional diversity in their experimental setup, the latter result should be interpreted with caution (Cadotte 2006). In addition, conclusions regarding beta-diversity were not possible in that analysis due to the paucity of studies. Studies that included beta-diversity (most of them conducted after the meta-analysis in 2006) in some cases demonstrated the expected increase in community homogenization with increasing dispersal rate (Cadotte and Fukami 2005, Matthiessen et al. 2010, Vogt and Beisner 2011, Simonis and Ellis 2014) but others found no significant effect of dispersal on beta-diversity (Howeth and Leibold 2010, Schamp et al. 2015).

Although experimental results have provided modest support for the hump-shaped effect of dispersal on alpha-diversity, they have also identified the need for further experimental research to better understand the influence of dispersal on larger scales. Dispersal may with regard to the degree of heterogeneity among local habitat conditions have very different effects on local and regional diversities (Forbes and Chase 2002). However, most investigations into the relationship between dispersal and diversity have not considered the effects of heterogeneous environmental conditions across local communities (but see Matthiessen et al. 2010, Pedruski and Arnott 2011). Amarasekare and Nisbet (2001) predicted that in a homogeneous environment immigration cannot prevent the extinction of an inferior competitor whereas according to Leibold and Chase (2018) a heterogeneous environment is a prerequisite for mass effects. Accordingly, the ability of rescue and mass effects to increase alpha-diversity becomes less important with the increasing homogeneity of the biotic and abiotic factors that describe local habitats (Fig. 1). This would theoretically shift the threshold of the dispersal frequency above which alpha-diversity decreases (gray bar; Fig. 1). Matthiessen et al. (2010) found that dispersal indeed has a different effect on diversity depending on the presence or absence of an environmental gradient. In their study, local diversity and beta-diversity were shown to decrease with increasing dispersal in the presence of environmental heterogeneity, but there was no effect in its absence and diversity remained consistently low (Matthiessen et al. 2010). Moreover, field data from Heino (2013) indicated an interaction between environmental heterogeneity and the dispersal mode (and therefore the dispersal rates) that in turn affected diversity patterns.

In contrast to other environmental parameters such as pH or nutrient concentrations, dispersal is a relatively unstable event. Species populations from discrete sites that are dependent on passive dispersal may be connected only during a limited time period or through infrequent dispersal events (e.g., zoochory or transportation by wind). In field metacommunity studies, the degree of connection between communities is often inferred through their similarity despite their spatial separation. Whether the changes in

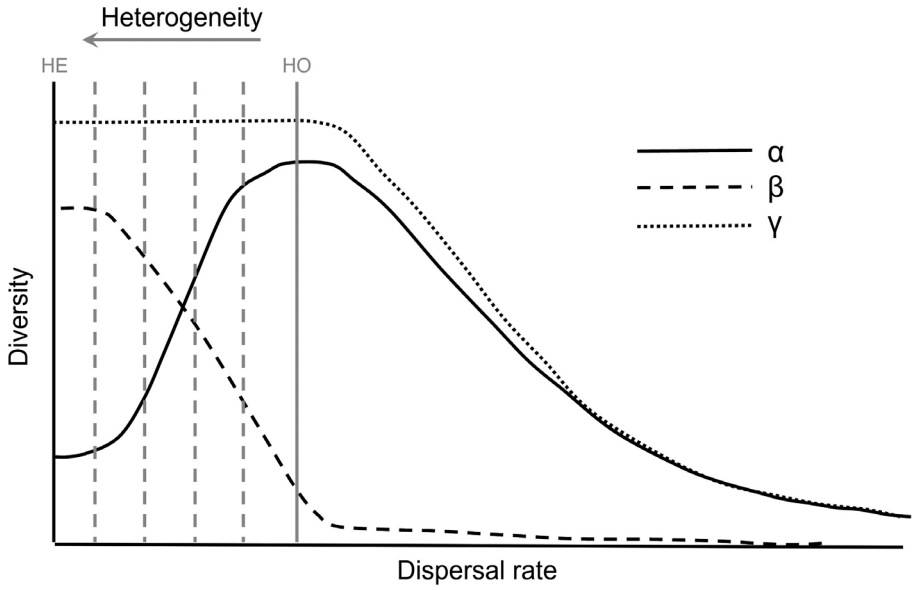


Fig. 1. Hypothesized relationship between the dispersal rate and alpha-diversity, beta-diversity, and gamma-diversity in the experimental setup. Under different degrees of environmental heterogeneity among local patches, the ordinate shifts either to the right (homogeneous environment, HO) or to the left (heterogeneous environment, HE). Note that within the closed experimental setup gamma-diversity depends on alpha-diversity and beta-diversity. (Modified from Mouquet and Loreau 2003 by adding the effect of heterogeneity.)

community assemblies induced by only temporarily connected sites are long-lasting is unclear. However, beta-diversity is likely to increase through stochastic dynamics in communities that are isolated from each other (Fukami 2010).

Most studies which have tested the predictions of metacommunity theory regarding the effect of dispersal on diversity have investigated artificial zooplankton and protozoan communities (see the studies cited in Cadotte 2006, as well as later studies, e.g., Howeth and Leibold 2010, Vogt and Beisner 2011, Verreydt et al. 2012, Schamp et al. 2015). By contrast, freshwater meiofauna, while a major contributor to the diversity of freshwater systems, have rarely been investigated within a metacommunity framework and experimental studies are lacking completely (Gansfort et al. 2020). However, pelagic organisms may differ from organisms within the interstitial of sediment in terms of their metacommunity processes, as the latter habitat is prone to patchiness and spatial limitations (Gansfort et al. 2018*a*). Among meiobenthic freshwater taxa, nematodes are the most abundant and diverse (Traunspurger 2002, Traunspurger et al. 2012). Other features, including their relatively short generation times and high species richness (in lakes, e.g., >100 species have been reported; Traunspurger et al. 2006), make them well suited as model organisms in laboratory studies.

On small (mm–cm) scales, freshwater nematodes actively move but their long-distance distribution depends on passive forces, either drifting within a water body (Palmer 1992) or dispersed overland by vectors such as wind, rain, or other animals (Vanschoenwinkel et al. 2008, Ptatscheck et al. 2018). For nematode metacommunities, temperature strongly contributes to environmental heterogeneity, as their growth rates are sensitive to temperature gradients, with considerable interspecific differences in their optimal temperatures and in their temperature tolerance ranges, even for species that co-occur in field sediments (Majdi et al. 2019). However, most nematode species can survive over a wide range of temperatures (from 10 to >30°C; Majdi et al. 2019), which accounts for their colonization of habitats such as phytotelmata, which undergo extreme temperature fluctuations, especially as

extreme climate events become more common (Thompson et al. 2013).

The aim of the present study was to test the predictions of metacommunity theory on the effect of dispersal on alpha-diversity, beta-diversity, and gamma-diversity, with a focus on the influence of environmental heterogeneity. Thus, metacommunities of benthic freshwater nematodes were collected from the field, transferred to mesocosms, and partly exposed to a temperature gradient. We manipulated both nematode dispersal frequencies between local communities and the heterogeneity of local environmental conditions; the latter was achieved by subjecting the mesocosms to homogeneous or heterogeneous temperature regimes. In accordance with the theoretical assumptions described above (Fig. 1), we hypothesized ($H_1$) that the higher connectivity of local communities resulting from increased dispersal leads to a homogenization of local communities and therefore to a decrease in beta-diversity, ($H_2$) that increasing dispersal frequencies result in an increased alpha-diversity under heterogeneous temperature conditions through the input of species and in a decrease under homogeneous temperatures through the displacement of species by the input of better competitors, and ($H_3$) that gamma-diversity remains unaffected under heterogeneous temperatures across local communities but declines when temperature conditions are homogeneous in local patches.

We further tested whether the effect of dispersal on nematode diversity lasted even when the dispersal-related connection between local communities was interrupted. In this context, ($H_4$) we hypothesize that the beta-diversity of communities increases again after their disconnection, due to the missing homogenizing effect of dispersal. However, both alpha-diversity and gamma-diversity were expected either to remain unaffected or to decrease after community disconnection, given the lack of further species inputs through dispersal.

## Materials and Methods

### *Experimental setup*

To obtain a rich pool of species, the sediment used in the experiment was taken from five locations in three different water bodies: two small lakes (Sandforther Lake [site 1: 52,026915, 8,347722; site 2: 52,026115, 8,345274], a fishing pond [52,020921, 8,345685]), and a stream (Johannisbach [site 1: 52,045997, 8,471103; site 2: 52,045274, 8,469890]). All samples were taken from the littoral zone. The sampling sites were located in similar geographic regions (max. distance between sites: 8.5 km). Water temperatures were in the range of 10–13°C. After the sediment had been carefully mixed, 1000 g was placed in each of 120 glasses (1700 mL volume, diameter 12 cm), resulting in a 5-cm layer of sediment. The glasses were then filled with 700 mL of tab water, and the final water level was marked to allow the subsequent replacement of the amount lost to evaporation. All glasses were equally aerated and incubated at 20°C in the dark. The benthic communities were left to grow and interact for 4 weeks prior to experimental dispersal, to eliminate species unable to survive under the conditions within the mesocosms.

Ten additional glasses were initially established to assess the homogeneity, diversities, and densities of the local nematode communities at the start of the experiment. Sediment (100 mL ≈200 g) samples were collected by inserting a corer (diameter 1.8 cm, piercing the sediment at eight locations) to a depth of 5 cm at different locations in the sediment. The nematodes in the samples were then extracted and identified as described below. Bray-Curtis and Sørensen indices were calculated to evaluate dissimilarities in abundance and in presence/absence determinations.

All other glasses were used in the different treatments (Fig. 2) resulting in 40 metacommunities (MCs), each consisting of three mesocosms (local communities, LCs). Of these, 20 MCs were placed in a homogeneous environment (HO) and 20 in a heterogeneous environment (HE). In the HO treatments, all glasses were left in the dark at 20° ± 1°C. In the HE treatments, glasses representing each of the MCs were placed at 12° ± 1°C, 20° ± 1°C and 28° ± 1°C. In addition, mesocosms in both the HO and the HE treatments were subject to four dispersal regimens: no dispersal, dispersal every 4 weeks, dispersal every 2 weeks, and dispersal every week. For each treatment, there were five replicates (Fig. 2).

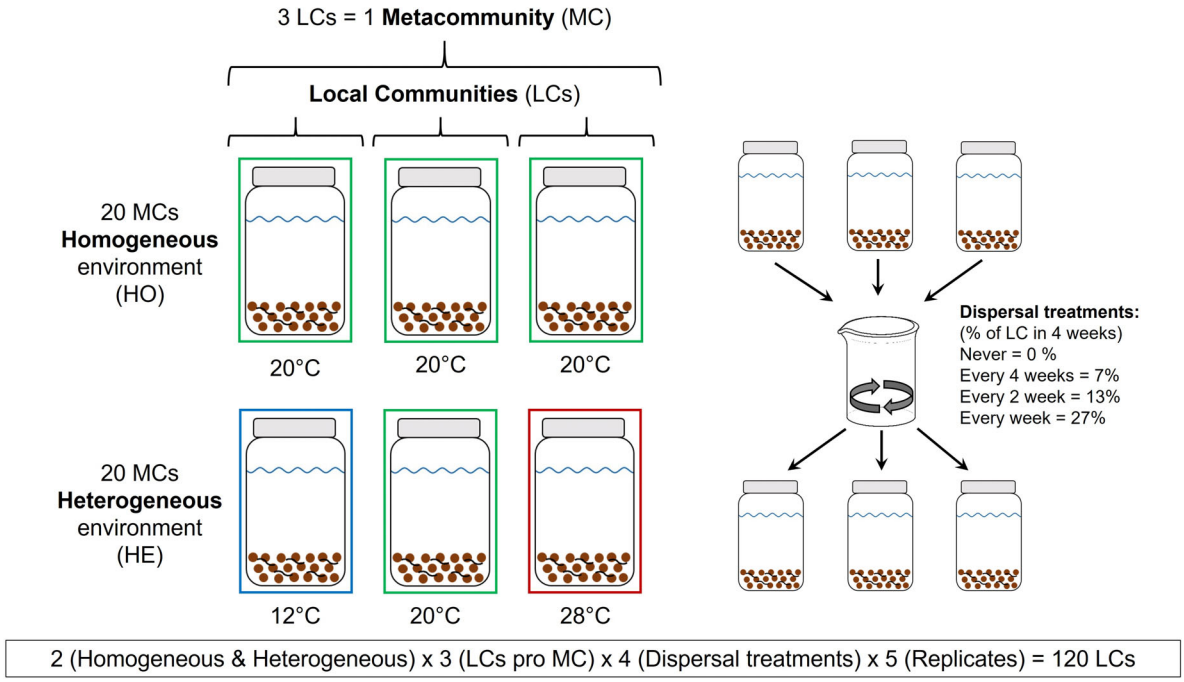


Fig. 2. Experimental setup. Glasses with sediment containing nematode communities were incubated under different temperature conditions (homogeneous temperatures: HO, heterogeneous temperatures: HE) and subjected to four different artificial dispersal treatments.

The positions of the glasses were rotated weekly, thus assuring comparable locations among LCs. During the experiment, the water parameters (conductivity, dissolved oxygen, pH, and temperature) were checked four times (every two months and at the end of the experiment) using a calibrated multiparameter meter (Hanna HI 9828; Hanna Instruments, Woonsocket, Rhode Island, USA). The LCs were randomly chosen but were balanced for each temperature and dispersal treatment ($n$ = 16 in the HE treatments for each temperature, $n$ = 32 in the HO treatments). The experiment lasted for 25 weeks, with sampling first conducted one week after the last dispersal event (Sampling 1) followed by a second sampling (Sampling 2) 12 weeks after the first one (and thus 13 weeks after the last dispersal event). During the interval between Samplings 1 and 2, there was no artificial dispersal between LCs. At both sampling dates, each LC was sampled by piercing corer (diameter 1.8 cm) four times to a depth of 5 cm at different locations in the sediment. This resulted in sediment samples of 50 mL, corresponding to 10% of the sediment in each LC. Although the whole LC was not sampled, diversity could be adequately measured. Nematodes mostly occupy the upper 1–3 cm (Traunspurger 2002, Gansfort et al. 2018*a*) of the sediment, and sampling from four locations should have included most species patches (Gansfort et al. 2018*a*). In addition, diversity was extrapolated to account for rare species (see *Statistical analysis*).

### *Artificial dispersal*

Depending on the dispersal treatment, 24 (every week), 12 (every 2 weeks), 6 (every 4 weeks), or no dispersal events were conducted in total. The artificial dispersal of the sediment between the three LCs of each MC was achieved as follows: For one dispersal event, 50 mL (= 100 g = 10% of the sediment of each glass) of sediment was removed from each glass using a corer (diameter 1.8 cm, pierced four times into the sediment) inserted to a depth of 5 cm at different locations in the sediment. The sediment samples (50 mL each) from the three LCs of one MC were then carefully mixed, and 50 mL of this

mixture was placed in each LC. Thus, 10% of the sediment was removed at each dispersal event and one third of this amount was transferred along with the other sediment samples (from the two other LCs) to the original LC. Thus, after 4 weeks, 27%, 13%, 7%, and 0% of the sediment of each glass had been dispersed according to the different dispersal treatments. To ensure treatment comparability, once a week each glass was disturbed as described above (sediment removed and put it back into the glasses), but the sediment was mixed only for genuine dispersal events.

### *Sample processing*

Benthic micro-invertebrates were extracted from the sediment using a density-centrifugation procedure and Ludox HS-40, following the method of Pfannkuche and Thiel (1988). The organic supernatant, containing invertebrates, was poured through 10-µm meshes. The organisms were preserved in 4% formaldehyde, stained with a few drops of Rose Bengal, and counted under a stereomicroscope (40× magnification). When available, the first 50 nematodes encountered during the counting procedure were removed from each sample, transferred to anhydrous glycerol and mounted on slides following the method of Seinhorst (1959). Nematodes were identified to the species level whenever possible (total of 5283 individuals identified).

### *Diversity measurements*

Diversity was measured on all three scales (alpha-diversity, beta-diversity, and gamma-diversity) using one index based on presence/absence data and another on abundance data. The indices for alpha-diversity and gamma-diversity were the species richness and evenness at the local (LC) and regional (MC) scales, respectively. As the number of nematodes identified varied between LCs and MCs, the species richness was extrapolated using Hill numbers (or the effective number of species, Hsieh et al. 2016) to allow fair comparisons across the assemblages. The $E_{\mathrm{var}}$ index was chosen to calculate the evenness. This method was recommended by Smith and Wilson (1996) based on its independence to species richness. The indices used to measure beta-diversity were the Bray-Curtis (Bray and Curtis 1957) and Sørensen (1948) dissimilarities of all LCs within one MC. Bray-Curtis dissimilarities reflect changes in the relative proportions of the different species while Sørensen dissimilarities indicate differences in species assemblages based solely on the incidences of those species.

The Bray-Curtis and Sørensen indices were calculated using the *vegan* package (Oksanen et al. 2018). Extrapolations of species richness were conducted using the *iNEXT* package (Hsieh et al. 2016) in the R environment (version 3.6.1, R Core Team 2019).

### *Statistical analysis*

Linear models (LMs) were calculated to test whether diversity is influenced by dispersal rates (as a continuous variable, 0–0.27), environmental heterogeneity (two factors: HO and HE), or the interactions thereof. The significances of the slopes were tested using transformed data when the assumption of a normal distribution of the residuals was not fulfilled by the original model. For alpha-diversity, the diversity measures from the three LCs within a MC that were connected by dispersal were not independent from each other (e.g., LCs were more likely to be inhabited by a greater number of species if one LC had a rich species pool). Therefore, linear mixed models (LMMs) with a random intercept were used to integrate the variance that might be caused by the different regional species pools. A forward selection procedure using likelihood ratio tests for nested models was performed to determine the significances of the individual predictors in the models identified using chi-square tests (McCulloch et al. 2008).

An ANOVA was used to test whether the physico-chemical variables differed between dispersal treatments. The normality and homogeneity of variances of these variables (conductivity, dissolved oxygen, pH, and temperature) were tested using the Shapiro-Wilk test and the Levene test, respectively. In case neither assumption could be confirmed even after data transformation, a Kruskal-Wallis test was conducted.

All analyses were done in the R environment (version 3.6.1). Linear mixed models were calculated using the *lme4* package (Bates et al. 2020). As in LMMs, the degrees of freedom cannot be determined, *P* values cannot be calculated in the conventional manner. Instead, the *lmerTest* package (Kuznetsova et al. 2017), which implements

Satterthwaite's method of approximating degrees of freedom, was used for the $t$ and $F$ tests. Two measures were used to assign $r^2$ values for the LMs and LMMs: the variance explained by fixed effects and the variance explained by the whole model, including fixed and random effects. This was done using the *r.squaredGLMM* function of the *MuMIn* package. Details of the calculations are provided in Bartoń (2019).

## Results

### *Nematode communities*

The samples taken from the 10 communities at the start of the experiment contained 11.4 ± 1.5 nematode species at a mean density of 83 ± 32 individuals per 50 mL sediment. Of these, six species occurred in every community (for the species list, see Appendix S1: Table S1), four in >50% of the samples, and five in only one community. The mean value of the Bray-Curtis and Sørensen dissimilarities was 0.44 ± 0.09 and 0.35 ± 0.16, respectively. In the experimental setup, the treatment comparable to the initial conditions was the HO treatment without dispersal. At the end of the experiment, the mean local richness determined in this treatment was 11.2 ± 4.5, with a mean density of 90.1 ± 58.3 individuals per 50 mL sediment. The mean values of the Bray-Curtis and Sørensen dissimilarities were 0.59 ± 0.20 and 0.43 ± 0.13, respectively. Therefore, local species richness remained constant during the experiment while the beta-diversity increased, thus excluding effects of heterogeneity and dispersal.

In general, there was no large difference between the determined and the extrapolated species number (a mean of two more extrapolated than found species). Altogether, we found 35 nematode species within the samples. Of these, 20 species were found in the HO treatments (Appendix S1: Table S2, whole species list), where the mean nematode density was 73.6 ± 45.1 individuals per sample (= 50 mL sediment). Only one nematode individual was detected in two LCs of one MC (HO, dispersal rate = 0.13), which was therefore excluded from further analysis. The most dominant species within the HO treatments without dispersal was *Tripyla glomerans*, which was present in every MC except one (Appendix S1: Fig. S1, Table S2). In treatments with dispersal between local assemblages, *Daptonema dubium* largely dominated the nematode MCs. *Eumonhystera longicaudatula* and *Prodesmodora circulata* reached higher abundances in some of the MCs subjected to dispersal than in the MCs without dispersal. All other species had reduced abundances or were absent in the dispersal treatments. Samples of the HE treatments contained 33 species, with a density of 87.3 ± 55.9 individuals per sample. In the MCs with a temperature gradient, *T. glomerans* was the most abundant species in the treatments without dispersal (Appendix S1: Fig. S1, Table S2). In those with dispersal, *Dorylaimus stagnalis* dominated the nematode MCs but high abundances were also reached by *D. dubium, P. circulata,* and *T. glomerans*. A separation of the results in the HE treatments according to temperature revealed differences in the responses of the different species to increasing temperatures (Appendix S1: Fig. S2); thus, while some species increased in abundances (e.g., *D. stagnalis* and *P. circulata*), others decreased (e.g., *T. glomerans* and *Mesotheristus crassimus*). The abundant species *D. dubium* occurred in the non-dispersed treatments only at a temperature of 20°C.

### *Physico-chemical variables*

The measured physico-chemical variables were uniform across the different experimental treatments incubated at the same temperature (see Appendix S1: Table S3 for details). Within the HO treatments, the mean conductivity (892 ± 208 µS/cm), dissolved oxygen (DO) (8.37 ± 0.48 mg/L), pH (8.42 ± 0.15), and temperature (20.98° ± 0.6°C) did not differ significantly between dispersal treatments (ANOVA, $P_{Cond} = 0.750$, $P_{pH} = 0.651$, $P_{Temp} = 0.403$; Kruskal-Wallis, $P_{DO} = 0.890$). In the HE treatments, the dispersal frequencies did not influence the measured parameters (ANOVA, $P > 0.05$; Appendix S1: Table S3). Increasing temperatures caused an increase in conductivity and a decrease in DO (12°C treatments: temperature 11.8 ± 0.3, conductivity 637.5 ± 51.0 µS/cm, pH 8.41 ± 0.23, $DO_2$ 9.55 ± 0.46 mg/L; 20°C treatments: temperature 21.1 ± 1.3, conductivity 667.8 ± 73.2 µS/cm; pH 8.49 ± 0.08, DO 8.45 ± 0.27 mg/L; 28°C treatments: temperature 28.3 ± 0.4, conductivity 708.9 ± 100.4 µS/cm; pH 8.48 ± 0.16, DO 8.07 ± 0.59 mg/L).

*Diversity measurements*

Because alpha-diversity, beta-diversity, and gamma-diversity generally differed between the HE and HO treatments, environmental heterogeneity was included in five of the six models during model selection (Appendix S1: Table S4). However, diversity was significantly higher in the HE treatments based on Bray-Curtis dissimilarities and regional evenness (Table 1, Fig. 3d, f). The dispersal rate was chosen as an explanatory variable in both beta-diversity models, as the Bray-Curtis and Sørensen dissimilarities of the communities significantly decreased with increasing dispersal (Table 1, Fig. 3e, f). The interaction of environmental heterogeneity and dispersal rate was selected as an explanatory variable in three models (Appendix S1: Table S4) given that in the HO and HE treatments the dispersal rate differentially affected diversity with respect to local and regional species richness and local evenness. Thus, in the HO treatments these measures significantly decreased (in case of local evenness marginal significant $P = 0.053$) with increasing

Table 1. Fixed effects for the linear mixed models (alpha-diversity) and linear models (beta-diversity and gamma-diversity) of the different diversity measures as response variables and the two predictors, environmental heterogeneity (Env) (two factors: homogeneous [HO], heterogeneous [HE]) and dispersal rate (Disp) (continuous, 0–0.27).

| Response variable | Explanatory variable | Estimate | SE | Trans | *t* | *P* |
|---|---|---|---|---|---|---|
| Alpha-diversity (Fixed effects) | | | | | | |
| Richness | Intercept (HE) | 10.09 | 1.12 | log | 17.3 | **<0.001** |
| | Env (HO) | −0.67 | 1.59 | | −0.3 | 0.786 |
| | Env (HE) : Disp | 5.45 | 7.76 | | 0.8 | 0.442 |
| | Env (HO) : Disp | −20.55 | 7.77 | | −3.3 | **0.002** |
| Evenness | Intercept (HE) | 0.62 | 0.03 | log | −8.27 | **<0.001** |
| | Env (HO) | −0.04 | 0.05 | | −1.13 | 0.265 |
| | Env (HE) : Disp | 0.08 | 0.25 | | 0.28 | 0.780 |
| | Env (HO) : Disp | −0.44 | 0.25 | | −1.98 | 0.053 |
| Beta-diversity | | | | | | |
| Sørensen | Intercept | 0.46 | 0.03 | log+1 | 18.5 | **<0.001** |
| | Disp | −0.62 | 0.18 | | −3.4 | **0.001** |
| Bray-Curtis | Intercept (HE) | 0.69 | 0.04 | log+1 | 20.5 | **<0.001** |
| | Env (HO) | −0.23 | 0.04 | | −6.1 | **<0.001** |
| | Disp | −0.97 | 0.20 | | −4.7 | **<0.001** |
| Gamma-diversity | | | | | | |
| Richness | Intercept (HE) | 19.69 | 2.61 | log | 15.8 | **<0.001** |
| | Env (HO) | −6.26 | 3.71 | | −1.6 | 0.116 |
| | Env (HE) : Disp | −0.73 | 11.40 | | −0.1 | 0.905 |
| | Env (HO) : Disp | −19.74 | 11.41 | | −2.6 | **0.014** |
| Evenness | Intercept (HE) | 0.49 | 0.03 | log | −13.0 | **<0.001** |
| | Env (HO) | −0.09 | 0.04 | | −3.1 | **0.004** |
| Alpha-diversity for HE only (fixed effects) | | | | | | |
| Richness | Intercept (12) | 16.81 | 1.64 | log | 18.4 | **<0.001** |
| | Temp (20) | −10.15 | 2.25 | | −4.3 | **<0.001** |
| | Temp (28) | −10.16 | 2.25 | | −4.3 | **<0.001** |
| | Temp (12) : Disp | −15.75 | 10.68 | | −0.9 | 0.367 |
| | Temp (20) : Disp | 26.77 | 10.68 | | 2.7 | **0.010** |
| | Temp (28) : Disp | 6.23 | 10.68 | | 0.4 | 0.670 |
| Evenness | Intercept | 0.62 | 0.01 | | 46.4 | **<0.001** |

*Notes:* The presented models are those that best fit the data in the context of model selection. The estimated intercepts considered a heterogeneous environment and a dispersal rate of 0. When the residuals of the models were not normally distributed, the response variables were transformed (Trans) for the significance tests. For the local species richness and evenness of the HE treatments, the fixed effects of an additional linear mixed models are shown with the two predictors temperature (three factors for temperature: 12°C, 20°C, and 28°C) and dispersal rate (Disp) (continuous, 0–0.27). The estimated intercepts considered a temperature of 12°C and a dispersal rate of 0. SE, standard error. Significant values ($P < 0.05$) are shown in bold.

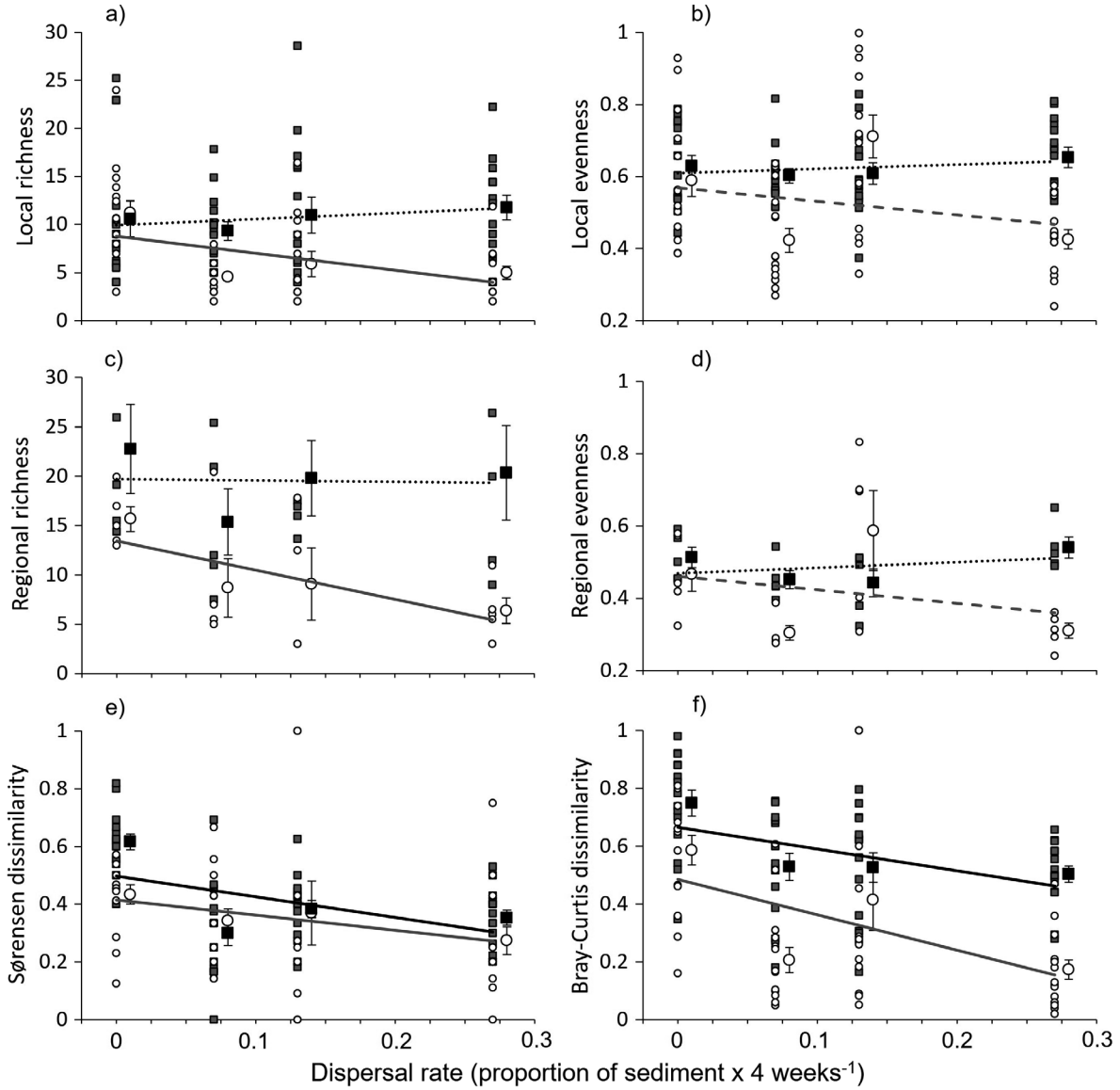


Fig. 3. Alpha-(a, b) diversity, gamma-(c, d) diversity, and beta-(e, f) diversity ($n$ = 15 for local communities; $n$ = 5 for metacommunities; one replicate [homogeneous, dispersal rate = 0.13] was excluded from the analysis) of nematode communities placed in homogeneous (white circles, large white circle: mean ± standard error [SE]) and heterogeneous (gray squares, large black square: mean ± SE) environments and subjected to four degrees of dispersal. The linear regressions are shown and indicate a significant (solid lines) or not significant (dotted lines) regression slope ($P < 0.05$) according to the linear (mixed) models (Table 1).

dispersal rate while in the HE treatments, no significant effects on measures of diversity were observed (Fig. 3a–c, Table 1). In the LMMs, random effects accounted for a variance of 7.27 ± 2.70 and 0.01 ± 0.10 in terms of local species richness and local evenness, respectively. In both models, the proportion of variance explained by the models was much larger when random effects were included (Appendix S1: Table S4).

Regarding alpha-diversity of the HE treatments only for local richness the inclusion of

temperature and dispersal improved the model. In contrast, no model including these variables performed significantly better in explaining the local evenness than the null model (including only the intercept). The LMM calculated for local richness (Appendix S1: Table S4; Table 1) in the HE treatments revealed a significantly more species in the 12°C treatments than in either of the warmer treatments (Table 1). The interaction between dispersal rate and temperature was chosen for the model of local richness (Appendix S1: Table S4) due to the significantly increasing slope of this variable within the 20°C treatments and the increasing dispersal rate (Appendix S1: Fig. S3; Table 1). In the other two temperature regimes was no significant influence of dispersal. In the respective LMMs, random effects showed a variance of 3.35 ± 1.83 for species richness. As the null model best explained the evenness data, the distinction between random and fixed effects was not relevant. For the model of species richness, the $r^2$ values were better when random factors were included (Appendix S1: Table S4).

As there was no recognizable increasing or decreasing trend in the diversity measures between dispersal treatments such that the main difference was due to "no dispersal" vs. any of the other dispersal treatments, we re-calculated the model by excluding the no-dispersal treatments. The results showed that, in the context of model selection, neither the dispersal rate nor the interaction of dispersal rate and environmental heterogeneity was the relevant explanatory variable. Thus, there was no significant linear relation between diversity measures and dispersal intensity.

### *Do dispersal effects on diversity persist when connectivity disappears?*

The second sampling was conducted 12 weeks after the first (and 13 weeks after the last dispersal or disturbance event) in order to determine whether the significant effects in the first sampling remained even when the artificial connectivity between LCs was no longer maintained. As the comparisons were solely based on the detection of a significant effect between the no-dispersal treatments and the dispersal treatments in general, the following analysis was conducted only for the no- and low- (dispersal rate of 7% in 4 weeks) dispersal treatments. We assessed whether (1) local and (2) regional richness as well as (3) beta-diversity (Bray-Curtis and Sørensen dissimilarity) were lower in the HO treatments than in the treatments without dispersal. For the (4) HE treatments, this was only tested for the 20°C treatments, as a significant effect of dispersal was determined only for these treatments. Samplings 1 and 2 were pairwise compared using a *t* test (normality was tested in advance, and the data were log-transformed if necessary).

The analysis of the HO treatment showed that after 3 months without dispersal all diversity measures, except the Sørensen dissimilarities, that had decreased under the dispersal treatments increased again. During this same time period, there was no change in the measures in the treatments without dispersal (Fig. 4a, c, d, e). Specifically, (1) local species richness significantly increased (Fig. 4a, $P < 0.001$) such that the mean species number (9.0 ± 2.5) was almost as high as in the treatments without dispersal during the whole experiment (mean species number 10.5 ± 5.9). (2) Beta-diversity rose again after the period without artificial dispersal, as determined from the Bray-Curtis dissimilarities (from 0.2 ± 0.17 to 0.4 ± 0.17; $P < 0.001$; Fig. 4c), but the Sørensen dissimilarities declined slightly although not significantly (from 0.34 ± 0.17 to 0.25 ± 0.14; $P = 0.102$; Fig. 4d). (3) Regional richness increased, but due to the high standard deviations, the effect was not significant (from 8.7 ± 6.6 to 13.8 ± 6.2; $P = 0.123$; Fig. 4e).

In the HE treatments, local species richness increased from the first to the second sampling in treatments without and with dispersal (Fig. 4b). Thus, the species richness in those five LCs with a low dispersal rate for 6 months before the first sampling increased from 8.4 ± 3.3 to 15.9 ± 8.8 ($P = 0.056$; Fig. 4b).

## Discussion

Biodiversity is largely affected by the degree of environmental heterogeneity (Chesson 2000) while habitat connectivity via species dispersal determines the range of environmental conditions which species may experience (Leibold et al. 2004). Our finding of an interaction of these two factors in their effect on biodiversity when both of these theoretical assumptions were linked was therefore not surprising. However,

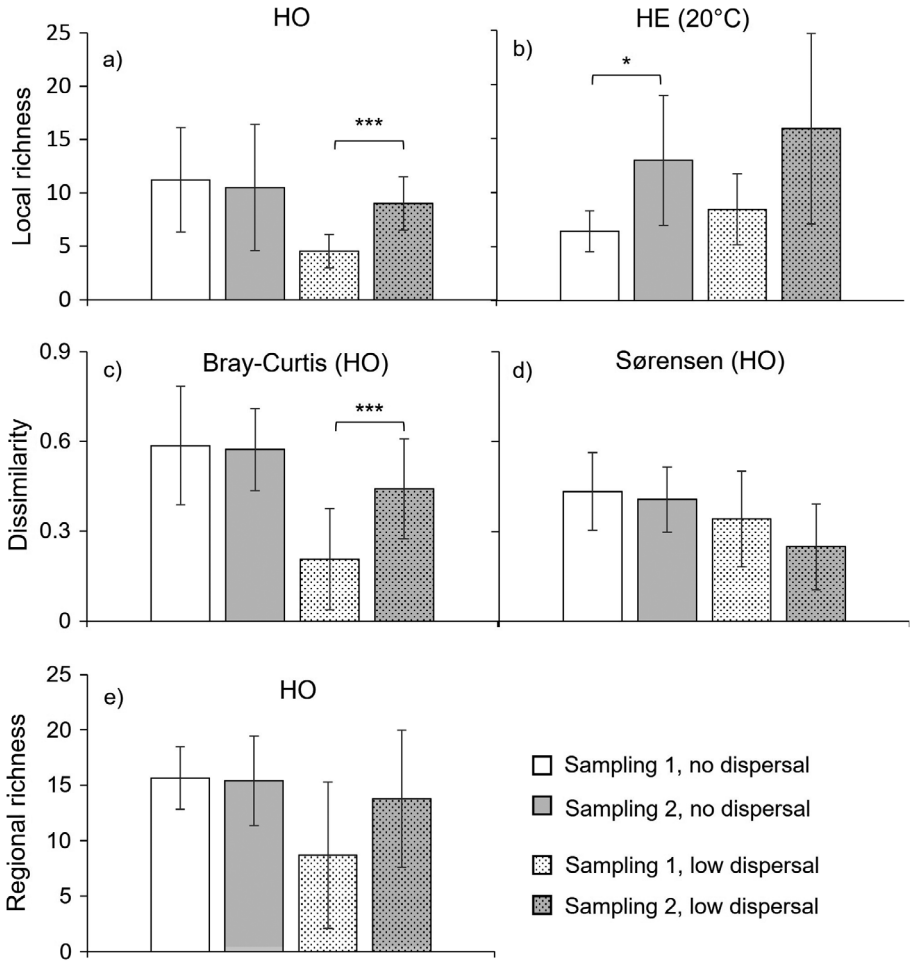


Fig. 4. Alpha-(a, b) diversity, beta-(c, d) diversity, and gamma-(e) diversity (mean ± standard deviation) of local (a–d) and regional (e) nematode communities in homogeneous (HO, a, c–e, $n = 15$ for a, c and d; $n = 5$ for e) and heterogeneous (HE, b, $n = 5$) environments. Data from the two sampling dates are depicted as follows: directly after 6 months with (dotted bars) or without (clear bars) dispersal (Sampling 1, white bars) and then 12 weeks later, with no dispersal during the intervening time span (Sampling 2, gray bars). Samplings 1 and 2 with the same dispersal treatments were tested against each other using a *t* test; significant results are shown: $^{*}P < 0.05$; $^{***}P < 0.001$.

the interesting aspect of our experiment was its demonstration of an interaction involving direction and ecology (mode of action). Specifically, in the homogeneous environments an increase in the dispersal rate led to a decline in diversity at the local and regional scales while in the heterogeneous environments diversity was unaffected. By contrast, environmental heterogeneity was irrelevant for the homogenization of communities and had no effect on beta-diversity, which decreased with an increasing dispersal rate. The decrease in local diversity and regional diversity can be attributed to the predominance of *D. dubium*. The abundance of this very successful species (at a temperature <20°C) was favored by the presence of patch connectivity, which allowed invasion of the LCs, and in turn, a potential reduction in the number of spatial refuges available for less abundant species such as *Eumonhystera vulgaris* and *Eumonhystera barbata* (Appendix S1: Fig. S1). Our experimental findings therefore differ from metacommunity

theory and contradict our hypotheses, solely in one point: Alpha-diversity did not increase in response to the higher connectivity of the LCs ($H_2$). A positive effect of dispersal on local diversity has been demonstrated in several studies (Pedruski and Arnott 2011, Schamp et al. 2015), including the meta-analysis of Cadotte (2006). Going back to theory, this local diversity increase was explained by rescue (Brown and Kodric-Brown 1977, Hanski 1999) and source-sink (Pulliam 1988) effects. The lack of increase in diversity with increasing patch connectivity therefore suggests that the respective dynamic does not act (or only acts weakly) in the respective system. Forbes and Chase (2002) also found no effect of habitat connectivity on the local species diversity of the zooplankton communities in their experiment, in which the nutrient supply varied across communities. The authors accordingly argued that zooplankton species may not be able to persist in sink habitats long enough to be rescued by immigrants. Also, in the studies of Holmes et al. (2016) and Simonis and Ellis (2014), the absence of an increase in alpha-diversity was explained by the presence of environmental conditions that overlapped the effect of rescue and source-sink effects as well as by the stochastic extinction of rare species. Application of these arguments to our experimental results can explain why a significant increase in local diversity related to dispersal intensity occurred only in the 20°C treatments. At this temperature, all species in the mesocosms should have positive growth rates whereas at lower temperatures growth rates will typically be slower and at higher temperatures only those species with a broad enough temperature range (e.g., *P. circulata* and *D. stagnalis*) will be able to reproduce (Majdi et al. 2019). Thus, over the wide range of temperatures tested in our study, source-sink effects would not have been relevant for species such as *Semitobrilus pellucidus*, which were not detected at higher temperatures (Appendix S1: Fig. S1), while rescue effects would not have played a role for rare species such as *Chromadorita leuckarti* and *Filenchus vulgaris*, both of which were completely absent from the dispersal treatments (Appendix S1: Table S2). By contrast, *D. dubium*, *P. circulata*, and *T. glomerans* were subject to source-sink dynamics, which were necessary for the presence of these species in all of the tested temperature treatments (Appendix S1: Fig. S2). Thus, although the mean alpha-diversity did not increase with dispersal, the communities were homogenized and the beta-diversity of both the heterogeneous and the homogeneous environments decreased, as predicted by hypothesis ($H_1$).

Our study of the effects of dispersal on biodiversity is one of the few to include environmental heterogeneity in its design. The results clearly show that dispersal heterogeneity and environmental heterogeneity interact in shaping biodiversity, and specifically alpha-diversity and gamma-diversity. A significant interaction of environmental heterogeneity and patch connectivity was previously reported by Matthiessen et al. (2010), who included a light gradient as an environmental condition to differ between patches of microalgal metacommunities, and by Östman et al. (2006), who used disturbance to create heterogeneous conditions for protist and rotifer communities. However, the changes in diversity determined by our study differed from those described in the latter two studies: For example, our results showed that, in response to dispersal, regional diversity in the heterogeneous MCs was unaffected whereas it declined in the homogeneous MCs, in accordance with hypothesis ($H_3$). By contrast, regional diversity increased in the heterogeneous treatments applied in the study of Östman et al. (2006) and decreased slightly in response to those in the study of Matthiessen et al. (2010). The different community responses to dispersal and heterogeneity can be explained by several reasons, but a combination thereof was most likely responsible for the different study outcomes: (1) Theory predicts different responses of diversity according to different degrees of site heterogeneity (Fig. 1). However, it is hard to arrange MC responses along a continuum as objective measurements of "environmental heterogeneity" are lacking. (2) The degree of connectivity (amount of dispersal) determines whether diversity will increase or decrease (Fig. 1 and see the following discussion of dispersal rates). (3) Processes other than dispersal and environmental filtering may weaken or change the relationship between dispersal and diversity. For example, the resident community may monopolize resources within patches, such that patch variation persists even when dispersal is high (Weiher et al. 2011, Symons and Arnott 2014). MC responses to dispersal can also be

altered by the stochastic extinctions of species (Holmes et al. 2016) and due to differences in the regional species pools at the start of an experiment. The latter effect was included in the LMMs of our study, such that a relevant part of the variance was explained solely by the MC affiliations (and therefore the connection to a specific regional species pool) of the LCs. In addition, inter- or intraspecific biological interaction (e.g., predation or facilitation, Gansfort et al. 2018*b*) can influence population densities by interacting either synergistically (Kneitel and Miller 2003, Verreydt et al. 2012) or additively (Cadotte et al. 2006) with dispersal to shape biodiversity. Finally, (4) habitat types may play a role in the community responses to dispersal and heterogeneity. For example, for poorly competing species (e.g., *E. barbata*, which solely occurred in samples without dispersal), the patchy environment of the sediment may offer spatial refuges (Gansfort et al. 2018*a*) that are not similarly available to pelagic communities of zooplankton. Therefore, the interstitial might favor less competitive species.

The main effect of dispersal on diversity was the change from no connection to a general connection between LCs, such that there was no significant linear trend from the lowest to the highest dispersal treatment. This finding was unexpected, as the dispersal rates in the various treatments differed by fourfold. This suggests that the lowest connection level within our experiment was already high enough to induce maximum effects on nematode biodiversity. Indeed, compared to previously reported experiments (Matthiessen et al. 2010, Schamp et al. 2015), the dispersal rates in our study were high, ranging within 4 weeks from a minimum of 7% to a maximum of 27%. Vogt and Beisner (2011) found that a threshold dispersal rate of 1% every 3.5 weeks caused a significant change in the beta-diversity of zooplankton communities. Pedruski and Arnott (2011) showed that a weekly dispersal rate of 2.5% had the same effect on diversity as a rate that was five times higher. However, such comparisons of pure dispersal rates are difficult as a standardized and comparable dispersal rate has to take into account both species generation times and the number of dispersal events (Cadotte 2006). The generation time of free-living freshwater nematodes varies largely from some days (e.g., Rhabditis) to some months (e.g., Tobrilids, Dorylaimids) but is unknown for most species. Here, we calculate with a generation time of ˜20 d (Muschiol and Traunspurger 2007, Kreuzinger-Janik et al. 2017), which is already longer than that of other studied organisms, such as microbes (Cadotte and Fukami 2005) and rotifers (Schamp et al. 2015). Calculation of a standardized dispersal rate according to Cadotte (2006) and based on a generation time of 20 d would yield a rate of 0.05 (dispersal every 4 weeks) to 0.19 (dispersal every week). Thus, compared to the 23 studies included in the meta-analysis (Cadotte 2006), the dispersal rates applied in our study were not very high but spanned a wide range of connectivity levels. Nonetheless, a lower dispersal rate would likely show a more continuous response of diversity whereas the rates in our study may already represent "dispersal-saturation." Verreydt et al. (2012) reported that a dispersal rate of 0.02% is high enough to have enormous consequences for community responses to environmental heterogeneity. More gradual dispersal treatments are needed if the aim is to examine the shape of dispersal response curves rather than response direction, the main objective of this study.

A further aim of this study was to evaluate whether dispersal-induced changes remain even when the connectivity between local communities is interrupted. We expected an increase in the beta-diversity of the isolated LCs ($H_4$), which was indeed determined with respect to the Bray-Curtis dissimilarity of the communities but not in terms of the Sørensen coefficient. This might have been due to the fact that the Bray-Curtis dissimilarity is based on the abundance composition of species, and the Sørensen dissimilarity on the pure species assemblies (presence/absence). This is plausible because the species composition among the communities remained similar since species were exchanged during the connectivity period. However, species abundances may have developed differently among LCs, such as due to priority effects or random drift in the relatively small and isolated communities (Fukami 2010).

Contrary to our expectation, both local species richness and regional species richness increased after the period without dispersal. Consequently, those species that had been replaced by competitively dominant invaders (mostly *D. dubium*) were able to benefit from their isolation from

other communities. Most likely, these species (e.g., many from Eumonhystera; Appendix S1: Fig. S4) either survived at very low abundances or entered a dormant stage (such as eggs) until the competitive pressure of the invaders stopped. This ability may be common for nematodes, as many species are able to at least partly resist unfavorable conditions for as long as decades (Ptatscheck and Traunspurger 2020). Generally, this result suggests that dispersal-induced diversity changes can be reversed rather quickly. Therefore, it might be assumed that the spatially structured beta-diversity determined in field samples is a result of the continuous connections of communities rather than irregular dispersal events between nematode communities.

A persisting problem regarding all experiments that address the question of dispersal-diversity relationships is the degree to which artificially imposed dispersal reflects the dispersal actually occurring in nature (Zobel and Kalamees 2005). The natural dispersal rates of nematodes have been investigated in only a few studies. Palmer (1992) found a maximum of 0.03% of nematodes from the sediment drifting in the water column of a stream. Clifford (1972) reported 26,473 nematode individuals drifting in 20 min in one cubic meter of stream water. The overland dispersal rates of nematodes have rarely been examined, but Ptatscheck et al. (2018) found a monthly maximum of 3000 nematodes/$m^2$ wind-dispersed over short distances and 500 individuals/$m^2$ distributed over long distances. However, determinations of exact dispersal rates in the field are nearly impossible (Zobel and Kalamees 2005). Although experimental connectivity levels might be similar to those found in stream drifts (Clifford 1972), continuity and strength are in most cases probably higher under experimental conditions than in the field but are still useful to create and validate theoretical models. A further important difference between our artificial dispersal procedure and processes occurring in nature is the fact that in our study species were randomly selected for dispersal (by happening to be in the dispersed sediment and depending on the LC to which they were transferred). Naturally, dispersal probability is affected by species traits, such that small species (De Bie et al. 2012) and those that are better swimmers (examples for nematode species are only published for marine habitats, e.g., Thomas and Lana 2011) may have a higher dispersal potential. Consequently, this study provides insights into the processes of environmental and interaction filters but not of dispersal filters on (meta-)community structure (Cadotte and Tucker 2017).

A further point that requires clarification is that the community used for this experiment may not be truly considered natural. Firstly, the sediments were pooled from several different habitats, and secondly, the experimental conditions in the mesocosms led to a pre-selection of some species able to tolerate the experimental conditions, as also described in other mesocosm studies of nematodes (Ristau et al. 2012, Haegerbaeumer et al. 2018). However, the time between sediment transfer and the start of the experiment should have been long enough to eliminate those species, such that all later effects could be attributed to the effects of dispersal and heterogeneity. This was evidenced by the fact that species richness remained constant in the homogeneous non-dispersal treatments (which were disturbed in the same way as the dispersal treatments) over the course of the experiment. The increase in beta-diversity can be explained by the isolation of the communities in a small system and the increasing role of stochastic dynamics (Fukami 2010). Nematode densities were slightly higher at the end than at the beginning of the experiment but were always in the lower, naturally occurring range of nematode densities in the field (Traunspurger et al. 2020). Also, while nematode species richness is usually higher in the field, the presence of 10 species in our experiment is in line with the number of species found in a comparable area of field sediment (Gansfort et al. 2018*a*).

Along with the community, the environmental conditions, and specifically the temperature regime, were artificial such that the related results can be questioned. The sediments used in this study are typically subjected to a seasonal temperature range of 0 to >20°C. Such that a temperature of 28°C may have been too high for some sediment inhabiting nematode species. Indeed, our data showed that many species were unable to adapt to this high temperature. However, intentionally created conditions that favored some, not all species. Moreover, as passive dispersers transported overland by wind or zoochory, nematodes

species that are good dispersers have to survive very harsh (temperature) conditions during their passage (see, e.g., the review of Ptatscheck and Traunspurger 2020). It is also likely that "stop-over" habitats (e.g., small-water bodies such as puddles), which are important for nematode dispersers, undergo extremely large fluctuations in temperature. Therefore, species that are good "adapters," including to a wide range of temperatures, will be better able to disperse and thus to colonize new habitats.

The diversity measurements (alpha, beta, and gamma) were based on presence/absence data and on abundance data. We considered this to be an important distinction, as in the case of dispersal-related community changes presence/absence data should more readily correspond to dispersal as they are more strongly influenced by rare species (Heino et al. 2010) whereas abundance data better reflect environmental heterogeneity (Soininen 2014). Indeed, in our study the Bray-Curtis dissimilarity was significantly higher in the HE than in the HO environments while the Sørensen dissimilarity, which is based on presence/absence measurements, did not significantly differ between treatments. Further, neither the local nor the regional evenness was significantly affected by dispersal, in contrast to the local species richness and regional species richness.

So far, studies that investigated the interactions between the effects of dispersal and environmental heterogeneity on diversity yielded somewhat contradictory results; similarly, our study was not completely consistent with theoretical assumptions. This suggests that in the metacommunity framework the interaction of many different dynamics hampers their description in simple models. The manifold possibilities to combine niche-based, dispersal and stochastic factors in experimental set-ups would require increasing the experimental complexity to enable comparisons of experimental outcomes. This would allow a better assessments of the relative importance of multiple processes (Weiher et al. 2011) in different habitat types and thus yield insights into metacommunity dynamics that can be integrated within a holistic theoretical framework applicable to the conservation management of biodiversity. As such, our study is a further step in the integrated assessment of environmental heterogeneity and benthic meiofaunal assemblages.

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## Literature Cited

Amarasekare, P., and R. M. Nisbet. 2001. Spatial heterogeneity, source-sink dynamics, and the local coexistence of competing species. American Naturalist 158:572–584.

Bartoń, K. 2019. MuMIn: multi-model inference. R package version 1.43.17. https://cran.r-project.org/web/packages/MuMIn/index.html

Bates, D., et al. 2020. lme4: linear mixed-effects models using 'Eigen' and S4. R package version 1.1-26. https://cran.r-project.org/web/packages/lme4/index.html

Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27:325–349.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography. Effect of immigration on extinction. Ecology 58:445–449.

Cadotte, M. W. 2006. Dispersal and species diversity: a meta-analysis. American Naturalist 167:913–924.

Cadotte, M. W., A. M. Fortner, and T. Fukami. 2006. The effects of resource enrichment, dispersal, and predation on local and metacommunity structure. Oecologia 149:150–157.

Cadotte, M. W., and T. Fukami. 2005. Dispersal, spatial scale, and species diversity in a hierarchically structured experimental landscape. Ecology Letters 8:548–557.

Cadotte, M. W., and C. M. Tucker. 2017. Should environmental filtering be abandoned? Trends in Ecology & Evolution 32:429–437.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31:343–366.

Clifford, H. F. 1972. Drift of invertebrates in an intermittent stream draining marshy terrain of west-central Alberta. Canadian Journal of Zoology 50:985–991.

Cottenie, K., and L. De Meester. 2004. Metacommunity structure: synergy of biotic interactions as selective agents and dispersal as fuel. Ecology 85:114–119.

De Bie, T., et al. 2012. Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. Ecology Letters 15:740–747.

Forbes, A. E., and J. M. Chase. 2002. The role of habitat connectivity and landscape geometry in experimental zooplankton metacommunities. Oikos 96:433–440.

Fukami, T. 2010. Community assembly dynamics in space. Pages 45–54 *in* H. A. Verhoef and P. J. Morin, editors. Community ecology. Processes, models, and applications. Oxford University Press, Oxford, UK.

Gansfort, B., D. Fontaneto, and M. Zhai. 2020. Meiofauna as a model to test paradigms of ecological metacommunity theory. Hydrobiologia 847:2645–2663.

Gansfort, B., W. Traunspurger, I. Threis, and N. Majdi. 2018*a*. Wide variation in a tiny space. The microdistribution of meiobenthos in an artificial pond. Freshwater Biology 63:420–431.

Gansfort, B., J. Uthoff, and W. Traunspurger. 2018*b*. Interactions among competing nematode species affect population growth rates. Oecologia 187:75–84.

Gering, J. C., and T. O. Crist. 2002. The alpha-beta-regional relationship. Providing new insights into local-regional patterns of species richness and scale dependence of diversity components. Ecology Letters 5:433–444.

Haegerbaeumer, A., S. Höss, P. Heininger, and W. Traunspurger. 2018. Response of nematode communities to metals and PAHs in freshwater microcosms. Ecotoxicology and Environmental Safety 148:244–253.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press, Oxford, UK.

Heino, J. 2013. Environmental heterogeneity, dispersal mode, and co-occurrence in stream macroinvertebrates. Ecology and Evolution 3:344–355.

Heino, J., L. M. Bini, S. M. Karjalainen, H. Mykrä, J. Soininen, L. C. G. Vieira, and J. A. F. Diniz-Filho. 2010. Geographical patterns of micro-organismal community structure. Are diatoms ubiquitously distributed across boreal streams? Oikos 119:129–137.

Holmes, C. J., S. Figary, K. L. Schulz, and C. E. Cáceres. 2016. Effects of diversity on community assembly in newly formed pond communities. Ecosphere 7: e01377.

Howeth, J. G., and M. A. Leibold. 2010. Species dispersal rates alter diversity and ecosystem stability in pond metacommunities. Ecology 91:2727–2741.

Hsieh, T. C., K. H. Ma, A. Chao, and G. McInerny. 2016. iNEXT. An R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods in Ecology and Evolution 7:1451–1456.

Kneitel, J. M., and T. E. Miller. 2003. Dispersal rates affect species composition in metacommunities of *Sarracenia purpurea* inquilines. American Naturalist 162:165–171.

Kreuzinger-Janik, B., M. Brinke, W. Traunspurger, and N. Majdi. 2017. Life history traits of the free-living nematode, *Plectus acuminatus* Bastian, 1865, and responses to cadmium exposure. Nematology 19:645–654.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. lmerTest package: tests in linear mixed effects models. Journal of Statistical Software 82. http://doi.org/10.18637/jss.v082.i13

Leibold, M. A., et al. 2004. The metacommunity concept. A framework for multi-scale community ecology. Ecology Letters 7:601–613.

Leibold, M. A., and J. M. Chase. 2018. Metacommunity ecology. Princeton University Press, Princeton, New Jersey, USA.

MacArthur, R., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. American Naturalist 101:377–385.

Majdi, N., W. Traunspurger, H. Fueser, B. Gansfort, P. Laffaille, and A. Maire. 2019. Effects of a broad range of experimental temperatures on the population growth and body-size of five species of free-living nematodes. Journal of Thermal Biology 80:21–36.

Matthiessen, B., E. Mielke, and U. Sommer. 2010. Dispersal decreases diversity in heterogeneous metacommunities by enhancing regional competition. Ecology 91:2022–2033.

McCulloch, C. E., S. R. Searle, and J. M. Neuhaus. 2008. Generalized, linear, and mixed models. John Wiley & Sons, Hoboken, New Jersey, USA.

Mouquet, N., and M. Loreau. 2002. Coexistence in metacommunities. The regional similarity hypothesis. American Naturalist 159:420–426.

Mouquet, N., and M. Loreau. 2003. Community patterns in source-sink metacommunities. American Naturalist 162:544–557.

Muschiol, D., and W. Traunspurger. 2007. Life cycle and calculation of the intrinsic rate of natural increase of two bacterivorous nematodes, *Panagrolaimus* sp. and *Poikilolaimus* sp. from chemoautotrophic Movile Cave, Romania. Nematology 9:271–284.

Oksanen, J., et al. 2018. vegan: community ecology package. R package version 2.5.-6. https://cran.uni-muenster.de/web/packages/vegan/index.html

Östman, Ö., J. M. Kneitel, and J. M. Chase. 2006. Disturbance alters habitat isolation's effect on biodiversity in aquatic microcosms. Oikos 114:360–366.

Palmer, M. A. 1992. Incorporating lotic meiofauna into our understanding of faunal transport processes. Limnology and Oceanography 37:329–341.

Pedruski, M. T., and S. E. Arnott. 2011. The effects of habitat connectivity and regional heterogeneity on artificial pond metacommunities. Oecologia 166:221–228.

Pfannkuche, O., and H. Thiel. 1988. Sample processing. Pages 134–145 *in* R. P. Higgins and H. Thiel, editors. Introduction to the study of meiofauna. Smithsonian Institution Press, Washington, D.C., USA; London, UK.

Ptatscheck, C., B. Gansfort, and W. Traunspurger. 2018. The extent of wind-mediated dispersal of small metazoans, focusing nematodes. Scientific Reports 8:6814.

Ptatscheck, C., and W. Traunspurger. 2020. The ability to get everywhere: dispersal modes of free-living, aquatic nematodes. Hydrobiologia 22:71.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652–661.

R Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ristau, K., M. Faupel, and W. Traunspurger. 2012. The effects of nutrient enrichment on a freshwater meiofaunal assemblage. Freshwater Biology 57:824–834.

Schamp, B. S., S. E. Arnott, and K. L. Joslin. 2015. Dispersal strength influences zooplankton co-occurrence patterns in experimental mesocosms. Ecology 96:1074–1083.

Seinhorst, J. W. 1959. A rapid method for the transfer of nematodes from fixative to anhydrous glycerin. Nematologica 4:67–69.

Shmida, A., and M. V. Wilson. 1985. Biological determinants of species diversity. Journal of Biogeography 12:1–20.

Simonis, J. L., and J. C. Ellis. 2014. Bathing birds bias β-diversity: Frequent dispersal by gulls homogenizes fauna in a rock-pool metacommunity. Ecology 95:1545–1555.

Smith, B., and J. B. Wilson. 1996. A consumer's guide to evenness indices. Oikos 76:70–82.

Soininen, J. 2014. A quantitative analysis of species sorting across organisms and ecosystems. Ecology 95:3284–3292.

Sørensen, T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and 1st application to analyses of the vegetation on Danish commons. Biologiske Skrifter 5:1–34.

Symons, C. C., and S. E. Arnott. 2014. Timing is everything. Priority effects alter community invasibility after disturbance. Ecology and Evolution 4:397–407.

Thomas, M. C., and P. C. Lana. 2011. A new look into the small-scale dispersal of free-living marine nematodes. Zoologia (Curitiba) 28:449–456.

Thompson, R. M., J. Beardall, J. Beringer, M. Grace, and P. Sardina. 2013. Means and extremes. Building variability into community-level climate change experiments. Ecology Letters 16:799–806.

Traunspurger, W. 2002. Nematoda. Pages 63–104 *in* S. D. Rundle, A. L. Robertson, and J. M. Schmid-Araya, editors. Freshwater meiofauna. Biology and ecology. Backhuys, Leiden, The Netherlands.

Traunspurger, W., S. Höss, A. Witthöft-Mühlmann, M. Wessels, and H. Güde. 2012. Meiobenthic community patterns of oligotrophic and deep Lake Constance in relation to water depth and nutrients. Fundamental and Applied Limnology/Archiv für Hydrobiologie 180:233–248.

Traunspurger, W., I. C. Michiels, and Eyualem-Abebe. 2006. Composition and distribution of free-living freshwater nematodes: global and local perspectives. Pages 46–76 *in* Eyualem-Abebe, I. Andrássy, and W. Traunspurger, editors. Freshwater nematodes. Ecology and taxonomy. CABI Pub, Wallingford, UK; Cambridge, Massachusetts, USA.

Traunspurger, W., B. Wilden, and N. Majdi. 2020. An overview of meiofaunal and nematode distribution patterns in lake ecosystems differing in their trophic state. Hydrobiologia 847:2665–2679.

Vanschoenwinkel, B., S. Gielen, M. Seaman, and L. Brendonck. 2008. Any way the wind blows – frequent wind dispersal drives species sorting in ephemeral aquatic communities. Oikos 117:125–134.

Verreydt, D., L. De Meester, E. Decaestecker, M.-J. Villena, K. van der Gucht, P. Vannormelingen, W. Vyverman, and S. A. J. Declerck. 2012. Dispersal-mediated trophic interactions can generate apparent patterns of dispersal limitation in aquatic metacommunities. Ecology Letters 15:218–226.

Vogt, R. J., and B. E. Beisner. 2011. Assessing the impact of dispersal on zooplankton community structure. Journal of Plankton Research 33:1757–1761.

Weiher, E., D. Freund, T. Bunton, A. Stefanski, T. Lee, and S. Bentivenga. 2011. Advances, challenges and a developing synthesis of ecological community assembly theory. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 366:2403–2413.

Zobel, M., and R. Kalamees. 2005. Diversity and dispersal – Can the link be approached experimentally? Folia Geobotanica 40:3–11.

## Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3749/full