esa ECOSPHERE

Midge-stabilized sediment drives the composition of benthic cladoceran communities in Lake Mývatn, Iceland

KYLE C. WEBERT,[1,]† CRISTINA M. HERREN,[1] ÁRNI EINARSSON,[2,3] MIREIA BARTRONS,[1,4]
ULF HAUPTFLEISCH,[5] AND ANTHONY R. IVES[1]

[1]*Department of Zoology, University of Wisconsin-Madison, Madison, Wisconsin 53706 USA*
[2]*Mývatn Research Station, Skútustaðir IS-660 Iceland*
[3]*Faculty of Life and Environmental Sciences, University of Iceland, Reykjavik 101 Iceland*
[4]*Aquatic Ecology Group, University of Vic–Central University of Catalonia, Vic, Catalonia 08500 Spain*
[5]*Faculty of Earth Sciences, University of Iceland, Reykjavik 101 Iceland*

Citation: Webert, K. C., C. M. Herren, Á. Einarsson, M. Bartrons, U. Hauptfleisch, and A. R. Ives. 2017. Midge-stabilized sediment drives the composition of benthic cladoceran communities in Lake Mývatn, Iceland. Ecosphere 8(2):e01659. 10.1002/ecs2.1659

Abstract. The importance of environmental disturbances as drivers of ecological communities depends not only on the magnitude of the disturbance, but also on the disturbance-specific sensitivity of the community. Organisms that alter the physical structure of their surroundings can affect the sensitivity of their habitat to environmental disturbance, and may alter the potential for disturbance to shape ecological communities. Such organisms therefore act as ecosystem engineers by indirectly modifying the resources available to other species. The benthos of shallow, eutrophic Lake Mývatn, Iceland, is frequently disturbed by wind events that lead to sediment resuspension. The impact of wind, however, depends on the abundance of midges (Chironomidae) whose larval tubes bind sediment and reduce wind-driven resuspension. Here, we investigate the long-term effect of fluctuations in midge abundance on the benthic cladoceran community using two lake sediment cores representing 30 and 140 years of deposition. In both cores, midge remains show a significant positive correlation with abundance of a large benthic surface-dwelling cladoceran, *Eurycercus lamellatus*, relative to the abundance of a small within-sediment-dwelling cladoceran, *Alona rectangula*. To experimentally investigate whether this shift could have been caused by midges acting as ecosystem engineers, we subjected cladoceran communities to sediment resuspension events within mesocosms. We found a significant decrease in abundance of the large epibenthic *E. lamellatus* relative to the abundance of small infaunal *Alona* spp. when subjected to disturbance. These findings show that physical alteration of benthic sediment and hence the sensitivity of the sediment to disturbance may explain the community shift in cladocerans observed with fluctuating midge abundance in Lake Mývatn.

Key words: benthic cladoceran; chironomid; disturbance; ecosystem engineer; *Eurycercus lamellatus;* mesocosm; Mývatn; sediment core.

Received 29 November 2016; accepted 30 November 2016. Corresponding Editor: Debra P. C. Peters.

† **E-mail:** webert@wisc.edu

INTRODUCTION

Disturbances are important determinants of community composition. Disturbances alter community composition by interrupting normal successional patterns (Connell and Slatyer 1977, Sousa 1979, Turner et al. 1998, Roxburgh et al. 2004). If disturbances are spatially heterogeneous, creating a mosaic of communities in different stages of succession, then disturbances will increase regional community diversity (Connell 1978, Chambers et al. 2013). Disturbances can also generate local resource heterogeneity, thereby allowing an increase in spatial niche partitioning and preventing dominance by any one competitor (Hubbell 1979, Huston 1979, Hastings 1980, Nee and May 1992, Amarasekare 2003). Finally, disturbances can alter the physical structure of the environment, thereby modifying habitats to favor or disfavor different suites of species (Dayton 1971, Levin and Paine 1974, Paine and Levin 1981, Sousa 1984, Marvier et al. 2004). Ecosystem engineers create, modify, or maintain the physical structure of their environment and thereby modify the resources available to other species (Jones et al. 1994). Therefore, if species act as ecosystem engineers in ways that alter the effects of disturbances on physical structure, then they will also likely alter the composition of ecological communities.

For aquatic communities, the role of disturbance in shaping species composition is well documented in stream and river systems where the effects of altered flow regimes and sediment mobilization impact many communities (Gray and Fisher 1981, Resh et al. 1988, Townsend 1989, Lake 2000, Stanley et al. 2010). Empirical work has demonstrated these effects of disturbance on community composition, with evidence for direct mortality caused by sediment mobilization (McAuliffe 1984), displacement of superior competitors (Sousa 1979, Hemphill and Cooper 1983), and spatial reshuffling of top-down effects (Power et al. 1985). In contrast to lentic systems, lakes are generally thought to have lower rates of disturbance and host more-stable communities. Nonetheless, shallow lakes are exposed to disturbances caused by winds, which can impact the entire water column including the water–sediment interface. Sediment resuspension events are common in shallow, soft-bottom habitats (Bloesch 1995) and can have large effects on the structure of pelagic and benthic communities (Probert 1984, Bloesch 1995). Biotic drivers can also cause resuspension. Sediment resuspension by benthivorous fish may enhance phytoplankton biomass and alter community structure in shallow lakes (Roozen et al. 2007).

While benthic deposit feeders are most often considered to be sediment resuspenders, and hence agents of disturbance, they can also reduce disturbances. Sediment stabilization by meio- and macrofauna in soft-bottom habitats has been hypothesized to affect the resulting community, maintaining a trophically mixed macrofauna that does not become dominated by deposit feeders (Probert 1984). Tube-building deposit feeders can reduce resuspension of sediment through a variety of mechanisms including sediment binding, roughening surfaces, and shifting particle size distributions (McCall and Tevesz 1982, Rhoads and Boyer 1982, Black et al. 2002). Tube-dwelling invertebrates, such as midges, are increasingly thought to have large effects on ecosystem properties of shallow lakes (Hölker et al. 2015).

Lake Mývatn, Iceland, is 37 km^2 yet has a maximum natural depth of only 4 m, making it particularly sensitive to the strong wind events that are common in the region. Midges, primarily *Tanytarsus gracilentus* (Holmgren), form dense mats of larval tubes in the muddy diatomaceous ooze of the benthos, which have been shown to reduce sediment resuspension through sediment binding (Ólafsson and Paterson 2004, see Fig. 1). This effect is often marked, as midge larval densities can reach >500,000/m^2 in the benthos (Thorbergsdóttir et al. 2004). However, the midge population shows dramatic fluctuations through time, which are likely caused by resource limitation (Einarsson et al. 2002, Ives et al. 2008). Therefore, the role of midges in binding sediment and reducing resuspension changes on a roughly 4- to 8-year time scale as midge populations fluctuate between high and low abundance.

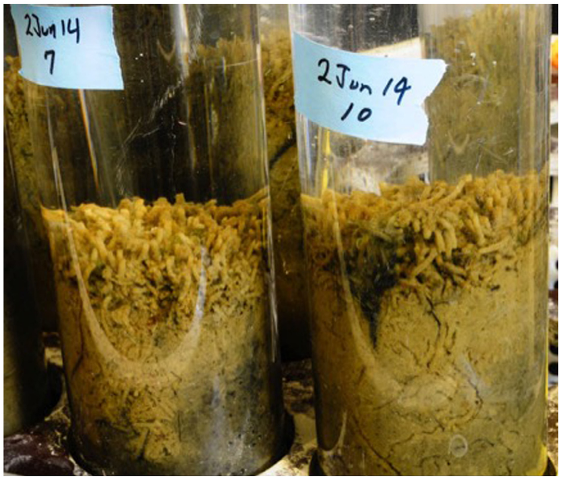

Fig. 1. Photograph of sediment cores taken in a year of high midge abundance in Lake Mývatn. The structures on top are chironomid tubes. Photo credit: Claudio Gratton.

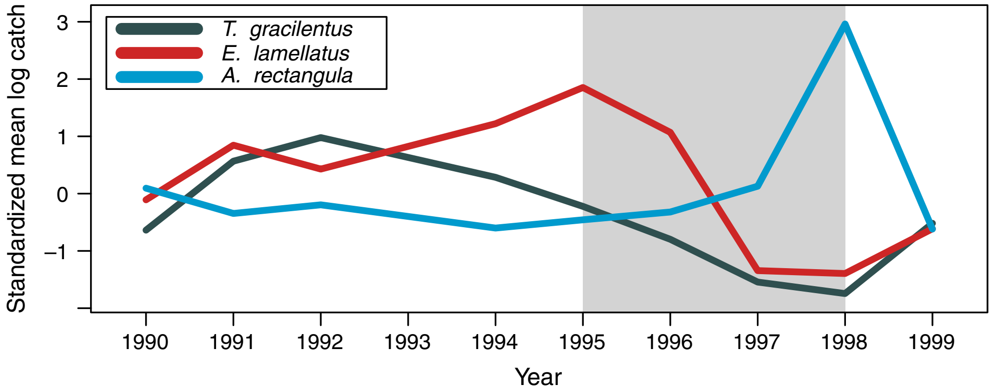

Fig. 2. Standardized mean log catch per unit effort of adult *Tanytarsus gracilentus* (black) at two traps on the shore of the South Basin of Lake Mývatn, and mean log counts of two benthic microcrustaceans, *Eurycercus lamellatus* (red) and *Alona rectangula* (blue), over a 9-year period (redrawn from Einarsson and Örnólfsdóttir 2004). Note the shift from peak abundance of *E. lamellatus* in 1995 to peak abundance of *A. rectangula* in 1998 (shaded region), which coincides with a sustained decrease in *T. gracilentus* abundance to the observed minimum in 1998.

Eurycercus lamellatus (Müller) is a dominant epibenthic cladoceran species in Lake Mývatn. It is the largest cladoceran found in the lake and is a significant food source for fish and diving ducks (Gardarsson 1979, Gardarsson and Einarsson 1994). Monitoring of benthic cladocerans from 1990 to 1999 (Fig. 2) revealed a significant shift in cladoceran community (Einarsson and Örnólfsdóttir 2004). For the first 7 years, there was a relatively stable community with high abundance of *E. lamellatus*. However, in 1997 *E. lamellatus* became scarce and a previously rare small-bodied infaunal cladoceran, *Alona rectangula* (Sars), became abundant. This shift in community coincided with a prolonged decline of the midge population, when abundance of adult *T. gracilentus* dropped approximately four orders of magnitude in traps around the lake (Einarsson et al. 2002, Hauptfleisch et al. 2012). Einarsson and Örnólfsdóttir (2004) hypothesized that lower midge larvae density led to less sediment binding and consequently greater disturbance of the sediments, which favored the infaunal *A. rectangula*.

Here, we investigate whether the observed relationships between *E. lamellatus*, *Alona* spp., and chironomids extend beyond the decade-long monitoring presented in Einarsson and Örnólfsdóttir (2004). We performed a time-series correlation analysis on the density of cladoceran exuviae and chironomid egg capsules in two sediment cores obtained from Lake Mývatn. A 34 cm long core taken in 2006, which corresponds to approximately 1975–2005, provided direct comparisons to both 30-year monitoring data on adult chironomid abundance near the lake and concurrent decade-long monitoring data on cladoceran abundance within the lake (Hauptfleisch et al. 2012). A 259 cm long core taken in 2006 was used to investigate cladoceran and chironomid abundance over approximately 1849–1994.

We also investigate experimentally whether disturbance-driven physical alteration of the benthic substrate from solid to soft could affect the change in benthic cladoceran communities in Lake Mývatn, with small *Alona* spp. replacing large *E. lamellatus* when resuspension rates are high. We hypothesized that the large-bodied epibenthic *E. lamellatus* would have higher population growth rates in the absence of disturbance, because it is more effective in grazing relatively nutrient-dense patches of diatoms occurring as biofilms in undisturbed benthos (Smirnov 1962, Fryer 1963). In contrast, higher disturbance rates would favor the small infaunal *Alona* spp. because they are more effective foragers for smaller food parcels occurring in mixed, low-quality sediment (Adalsteinsson 1979). To test whether *E. lamellatus* had lower, and *Alona* spp. had higher, population growth rates in disturbed vs. undisturbed conditions, we constructed mesocosms containing a mixed community of both large-bodied epibenthic cladoceran and small infaunal cladoceran collected from Lake Mývatn in 2012, a year of a midge population crash when both *E. lamellatus* and *Alona* spp. were available (but midges were not). We performed a 2 × 2 factorial experiment, with one factor the presence/absence of regular resuspension disturbances and the other factor the presence/absence of cladocerans. At the end of the experiment, we measured the abundance of cladoceran species (in treatments in which they were present) and the composition of the diatom community. This design allowed us to investigate not only the effect of the disturbance on the cladoceran community, but also possible effects of disturbances on diatom communities that might be responsible for treatment effects on the population growth rates of *E. lamellatus* and *Alona* spp.

METHODS

Study species

The main study species are the chydorid cladocerans *E. lamellatus*, *A. rectangula*, *A. quadrangularis* (Müll.), and *A. affinis* (Leydig). *Eurycercus lamellatus* is by far the largest of these, with a maximum length of 3.3 mm (Einarsson and Örnólfsdóttir 2004). It is a deposit and diatom feeder with a diet consisting mainly of microalgae, detritus, and bacteria (Smirnov 1962 citing Smirnov 1959 [in Russian], Fryer 1963, Desvilettes and Bourdier 1997, Einarsson et al. 2004). *Eurycercus lamellatus* uses specialized cephalic and trunk appendages to crawl along the benthic surface while scraping surfaces for food particles and occasionally attaching to the benthic surface or plants (Smirnov 1962, Fryer 1963, Adalsteinsson 1979). In contrast to *E. lamellatus*, *A. rectangula* is an infaunal suspension feeder (Adalsteinsson 1979). *Alona rectangula* is the smallest (max. length 0.43 mm) of the three *Alona* species in Lake Mývatn and is the only one of the three to exhibit the shift in abundance after chironomid populations crash (Einarsson and Örnólfsdóttir 2004). *Alona quadrangularis* and *A. affinis* are larger than *A. rectangula*, but likely play similar ecological roles. Because we were unable to consistently separate the three species of *Alona*, they were combined for the experimental component of this study. Nonetheless, grouping species together as *Alona* spp. provides a conservative estimate of the effect of the experimental manipulation, because only *A. rectangula* was expected to respond strongly to the disturbance treatment.

Sediment cores

The sediment cores KB-1 and R-1 used for time-series correlation analyses are described in detail in Hauptfleisch et al. (2012) and Hauptfleisch (2012). Briefly, the short core (34 cm long), KB-1, was collected with a Kajak-Brinkhurst corer and extruded vertically in the field. The uppermost 2 cm was separated into 1-cm slices, and the remainder of the core was sliced at 0.5-cm intervals. The long core (259 cm long), R-1, was collected with a "Russian peat borer" (Jowsey 1966) in 0.5-m sections and placed horizontally in trays made of longitudinally cut plastic tubes. In the laboratory, the core was cut into 1-cm slices, avoiding zones of smearing. All core slices were stored in individual sealed plastic bags at 4°C.

For counting midge and cladoceran abundance, 2-ml aliquots of wet sediment from each slice were deflocculated by heating in 10% KOH (weight/volume) at 80°C for 2 h and sieved through a 63-μm mesh. Sieve residue was then separated by water floatation into organic (mostly chitinous) and mineral components (sand). Organic components were then identified under 100× magnification in water under the compound microscope. Chironomid eggs were identified by their appearance (see Hauptfleisch et al. 2012, Fig. 2), and cladoceran exuviae by the method recommended in Frey (1986) with the exception that head shields were not counted except those of *E. lamellatus* (Hauptfleisch et al. 2012).

Dating of the cores was achieved by using a combination of markers in the sediment including tephra, Cs-137 (a radioactive isotope of cesium linked to atomic bomb tests), and historical peaks in fossil-producing biota (Hauptfleisch 2012).

Mesocosm experiments

A mesocosm incubation system was constructed at the Mývatn Research Station. Three polystyrene-insulated containers, each approximately 100 L, were filled with non-chlorinated well water. A continual source of fresh water was delivered into each container throughout the course of the experiment. Two tubes connected all adjacent containers approximately 10 cm from the bottom and just below the water surface to provide water exchange and equal water levels among containers.

Light was provided by two high-pressure sodium grow lamps on a 12-h light/dark schedule.

White polyester mesh was placed over the containers to equalize light levels to those observed at the bottom of the lake during high light (around 500 μmol$\cdot$m$^{-2}\cdot$s^{-1}) and avoid possible photoinhibition of diatoms. Light levels were measured with a light meter (LI-COR LI-250A Light Meter, Lincoln, Nebraska, USA).

Mesocosms were constructed from 400-ml plastic containers with snap lids (UniPak 5110; RPC Superfos Denmark, Taastrup, Denmark). The center of the snap lid was cut out and covered with 63-μm mesh to facilitate water exchange with the larger holding tank while retaining cladocerans. Twelve cups were arranged 3 × 4 in each polystyrene container for a total of 48 mesocosms. We used a clean toothbrush to remove any biofilm growing on the mesh daily to avoid variability in shading among cups.

Sediment for mesocosms was collected from the center of Lake Mývatn on 17 July 2012, using three Ekman grab samples. The three grab samples were combined and allowed to settle for approximately 8 h in the laboratory, and the excess water was poured off. The settled sediment was then sifted through a 63-μm sieve to remove all benthic invertebrates and large primary producers (mostly filamentous green algae). The sifted sediment was allowed to settle for an additional 24 h, and then the liquid was poured off and the sample homogenized. Aliquots of 80 ml homogenized lake sediment were added to all 36 mesocosms.

Cladocerans were collected over 24 h with a benthic cladoceran sampler at two locations in Lake Mývatn where both *E. lamellatus* and *Alona* spp. occur (Örnólfsdóttir and Einarsson 2004). Samples were homogenized, and 300 ml was added to each mesocosm. Thus, the density of cladocerans in mesocosms was equal to that collected using passive activity traps of the same radius over 24 h.

Cladoceran addition and resuspension treatments were applied in a 2 × 2 factorial design with nine mesocosm replicates for each of the four treatments. The four treatments were Undisturbed-No-Cladocerans, Undisturbed-With-Cladocerans, Disturbed-No-Cladocerans, and Disturbed-With-Cladocerans. Each incubation container held three mesocosms of each treatment. Placement of the four treatments was randomized within columns and rows in the 3 × 4 array of mesocosms within each incubation container, so that each treatment was present once in each column and no more than once in each row. The Disturbance treatment was administered by swirling all "disturbed" mesocosms by hand haphazardly one to three times daily for 20 s with just enough vigor to suspend the sediment; this disturbance level was designed to ensure that biofilms could not develop on the sediment surface. The experiment ran for 27 d, when a complete destructive sample was taken of all mesocosms.

Mesocosms containing cladocerans were completely sieved with a 63-μm mesh. Cladocerans and remaining sediment were transferred from the sieve to 50-ml tubes and preserved with 1% Lugol's solution for later analysis. Immediately before counting, the 50-ml preserved samples were sieved again and transferred to a counting tray. Counting of major cladoceran taxa was performed using a Bogorov counting tray and dissecting microscope. The three commonly observed *Alona* species, *A. rectangula*, *A. quadrangularis*, and *A. affinis*, were grouped due to the difficulty in consistently separating them. The other taxa counted include *E. lamellatus*, *Macrothrix hirsuticornis* (Norman and Brady), *Chydorus sphaericus* (Müll.), and *Acroperus harpae* (Baird).

To sample diatom composition, a micropipette with enlarged tip was used to sample sediment. Six haphazard samples of 500 μl were taken just below the sediment surface of each cup. These samples were homogenized, and 1 ml was taken from each and preserved in Lugol's solution. Diatom composition was obtained from 200 random point-intercept counts on prepared slides, with the following taxa counted: *Fragilaria* spp., *Cymatopleura* spp., *Amphora* spp., *Navicula* spp., *Cymbella* spp., *Epithemia* spp., and *Cocconeis* spp.

Statistical analyses

Correlations between time-series data are complicated by autocorrelation within the individual series, which will likely lead to type I errors (false positives) in standard statistical tests (Blaauw et al. 2010). Furthermore, the patterns that we are interested in occur on an annual time scale, and variation in sedimentation rates makes it difficult to standardize counts of midge and cladoceran remains with sufficiently fine temporal resolution. Therefore, we used a statistical approach modified from Einarsson et al. (2016). We used two methods to assess patterns in the time series. First, we used the correlation between log-transformed ratio of *E. lamellatus* to *A. rectangula* counts (i.e., $\log[(N_{\mathrm{El}} + 1)/(N_{\mathrm{Ar}} + 1)]$) and the log-transformed proportion of midge remains (i.e., $\log[(N_{\mathrm{midge}} + 1)/(N_{\mathrm{midge}} + N_{\mathrm{El}} + N_{\mathrm{Ar}} + 3)]$). Second, we computed the three correlations between the proportions of midge, *E. lamellatus,* and *A. rectangula* counts (i.e., $\log[(N_{\mathrm{midge}} + 1)/(N_{\mathrm{midge}} + N_{\mathrm{El}} + N_{\mathrm{Ar}} + 3)]$, $\log[(N_{\mathrm{El}} + 1)/(N_{\mathrm{midge}} + N_{\mathrm{El}} + N_{\mathrm{Ar}} + 3)]$, and $\log[(N_{\mathrm{Ar}} + 1)/(N_{\mathrm{midge}} + N_{\mathrm{El}} + N_{\mathrm{Ar}} + 3)]$). The second measure could be biased toward negative correlations, because the values share the same denominator. Nonetheless, the statistical tests account for this bias. The first measure is unlikely to show this bias.

Statistical tests involved first fitting the three individual times series of the log-transformed count data to autoregressive-moving average models, ARMA (p, q), using the method of Ives et al. (2010). The value of p gives the number of autoregressive lags and q gives the number of moving average lags; the values of p ($p = 1, 2, 3$) and q ($q = 1, 2, 3$) were selected using Akaike's information criterion corrected for small sample sizes (AIC$_c$). We then simulated data from the best-fitting ARMA models and computed the same two correlation measures we used for the real data. Repeating this for 100,000 simulated data sets gives the approximate distribution of the estimator of the correlation coefficients under the null hypothesis that the time series are independent but temporally autocorrelated (Efron and Tibshirani 1993), and we used this to compute P-values. Note that this parametric bootstrap approach accounts for possible bias in correlations between proportions (our second method), since this bias will be included in the bootstrap simulations. Because we were interested in fluctuations in the response variables, we detrended the transformed variables (both real and simulated data) with a linear function, $\log(x(t) + 1) = c_0 + c_1 t$, and standardized the residuals to have SD 1. Finally, because we did not distinguish among *Alona* species in the mesocosm experiment, we repeated these analyses using the combined total counts of all three *Alona* species.

Cladoceran counts were analyzed using quasi-Poisson generalized linear regression. Cladoceran count data for individual taxa were analyzed by disturbance treatment with the addition of a term for incubation container. Periphyton counts were analyzed using generalized linear mixed models with a Poisson-lognormal distribution and crossed factors of disturbance and presence/absence of cladocerans with random terms for incubation container and individual observation. The random term for individual observation accounts for greater than Poisson variation in the counts. Separate analyses were performed for each diatom taxon independently. For *Fragilaria* spp. and *Cymatopleura* spp., post hoc Tukey's tests were performed for each of the four treatment combinations using honestly significant difference (HSD) to correct for multiple comparisons. All statistics were performed in R version 3.2.4, using the *base* and *stats* packages (R Core Team 2016) for generalized linear regressions and Tukey's HSD tests, *lme4* (Bates et al. 2015) and *lmerTest* (Kuznetsova et al. 2014) for generalized linear mixed models.

RESULTS

Sediment cores

Both R-1 and KB-1 cores (Fig. 3) showed positive correlations between chironomid eggs and the ratio of *E. lamellatus* to *A. rectangula* (R-1: $r = 0.35$, $P = 0.002$; KB-1: $r = 0.54$, $P = 0.005$); the results using combined counts for all three *Alona* spp. were similar (R-1: $r = 0.33$, $P = 0.002$; KB-1: $r = 0.51$, $P = 0.004$). In the analyses using proportions of the different taxa, there were positive correlations between the proportions of chironomid eggs and *E. lamellatus* in both cores (R-1: $r = 0.34$, $P = 0.005$; KB-1: $r = 0.40$, $P = 0.009$) and negative correlations between chironomid eggs and *A. rectangula* in both cores (R-1: $r = -0.21$, $P = 0.075$; KB-1: $r = -0.44$, $P = 0.024$), although the correlation in the R-1 core was not significant. The results using combined counts for all three *Alona* spp. were similar, with positive correlations between chironomid eggs and *E. lamellatus* (R-1: $r = 0.40$, $P = 0.001$; KB-1: $r = 0.34$, $P = 0.0004$) and negative correlations between chironomid eggs and *A. rectangula* (R-1: $r = -0.15$, $P = 0.19$; KB-1: $r = -0.38$, $P = 0.05$), although the correlation in the R-1 core was not significant. Although using proportions in principle could lead to spurious negative correlations due to our use of proportions that have the same denominator, the simulated distributions of the estimators of the correlations were in fact not biased; the mean values of the correlations in the simulations were all less than 0.01.

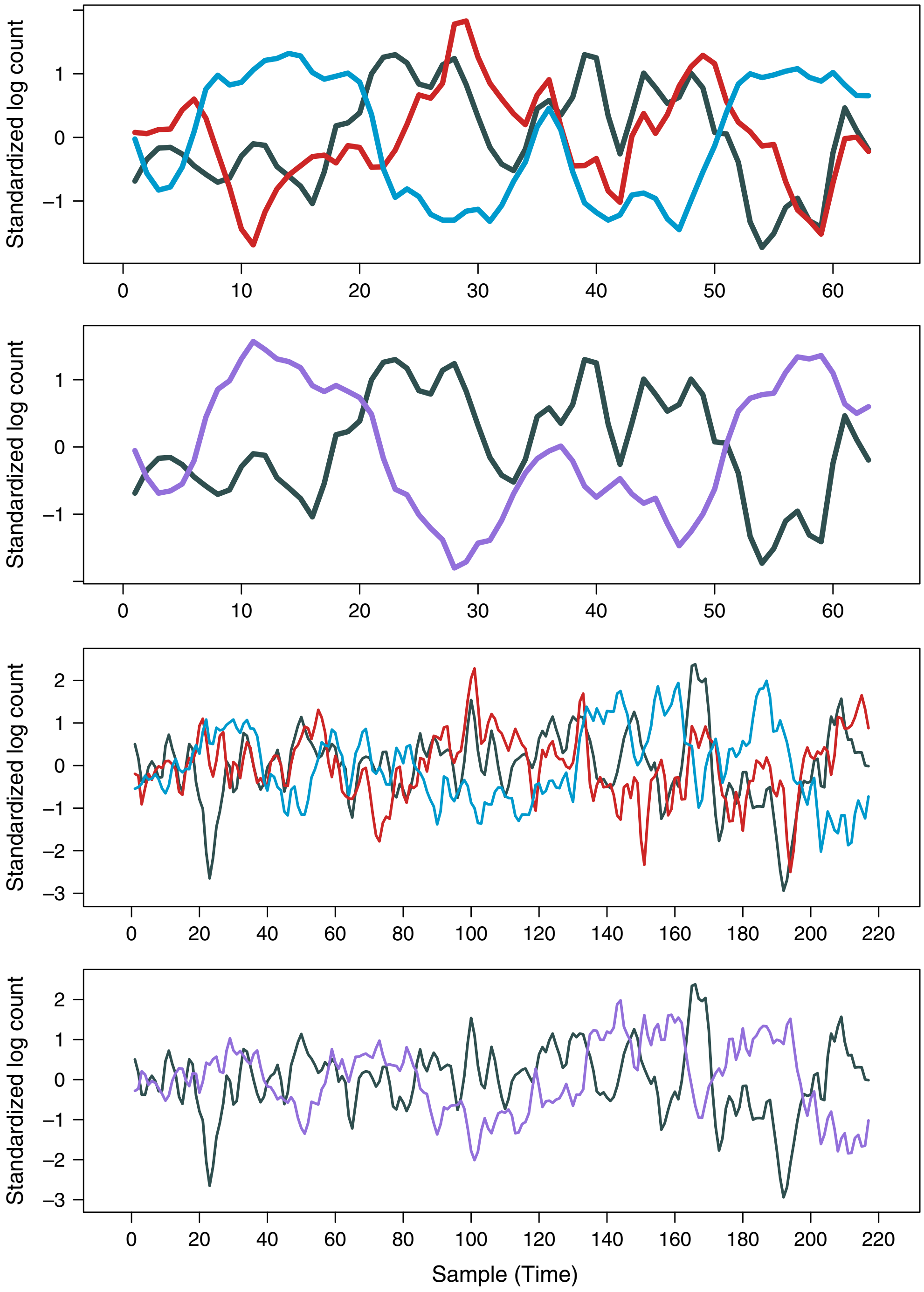

Fig. 3. Standardized log counts of *Tanytarsus gracilentus* egg capsules (black), *Eurycercus lamellatus* (red), *Alona rectangula* (blue), and the ratio of *A. rectangula* to *E. lamellatus* (purple) from the KB-1 (top 2 panels, approximately 1975–2005) and R-1 (bottom two panels, approximately 1849–1994) sediment cores (see Hauptfleisch et al. 2012). Counts were log(x + 1)-transformed, linearly detrended, standardized to have a SD of one, and smoothed using a moving average filter with a window size of 3 with weightings 0.25, 0.5, and 0.25.

Table 1. Responses of *Eurycercus lamellatus* and *Alona* spp. abundance to sediment disturbance in 18 mesocosms with cladocerans present (nine undisturbed and nine disturbed).

Parameter	β	SE	*t*-value (df = 13)	Probability > |*t*|
E. lamellatus				
Intercept	2.2412	0.2811	7.974	≪0.0001***
Disturbed	−3.58	0.8816	−4.061	0.00135**
Block 2	0.4919	0.3562	1.381	0.19053
Block 3	0.5447	0.352	1.548	0.14573
Alona spp.				
Intercept	6.5188	0.1228	53.078	≪0.0001***
Disturbed	0.3276	0.1176	2.785	0.0155*
Block 2	0.1939	0.1456	1.332	0.2057
Block 3	0.0843	0.1414	0.596	0.5612

Notes: The mesocosms were blocked into three incubation containers containing 12 mesocosms each, six with cladocerans. Results are from a quasi-Poisson generalized linear model. $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Mesocosm experiments

Opposing responses to disturbance in mesocosms were observed for *E. lamellatus* and *Alona* spp. abundance. *Eurycercus lamellatus* abundance was lower in the disturbance treatment compared to undisturbed (β = −3.58, *P* = 0.001), while *Alona* spp. abundance was higher in the disturbance treatment compared to undisturbed (β = 0.33, *P* = 0.015; Table 1, Fig. 4). The remaining cladoceran taxa did not show significant responses to the disturbance treatment, which was expected since these taxa did not show historic population shifts with midge abundance. *Eurycercus lamellatus*, *C. sphaericus*, and *Acroperus harpae* all showed reduced abundance from the estimated number added to the mesocosms at the beginning of the experiment. However, the *Alona* spp. and *M. hirsuticornis* increased in abundance in the mesocosms over the course of the experiment.

Diatom composition

Fragilaria spp. was the most common diatom in all mesocosms, making up 50–70% of diatom point-counts. There was a positive effect of disturbance on percent composition of *Fragilaria* spp. with a significant interaction between disturbance and presence of cladocerans (disturbance main effect: *P* < 0.001; interaction: *P* = 0.035, Table 2) in the generalized linear mixed model; the presence of cladocerans had a positive effect in the undisturbed treatment and a negative effect in the disturbed treatment (Fig. 5, top panel). There was a negative effect of disturbance on percent composition of *Cymatopleura solea* and a significant interaction with cladoceran presence (disturbance main effect: *P* < 0.001; interaction: *P* = 0.045, Table 2, Fig. 5, bottom panel). The remaining diatom taxa were scarce and did not show clear differences between treatments.

DISCUSSION

Tanytarsus gracilentus populations measured from adults caught in traps on the shore of Lake

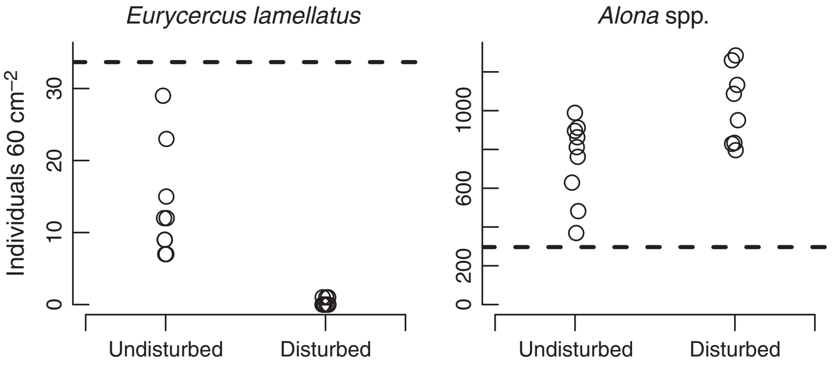

Fig. 4. *Eurycercus lamellatus* abundance was lower in mesocosms experiencing regular disturbance compared to undisturbed mesocosms after 27 d (left panel, β = −3.58, *P* = 0.001). However, the *Alona* spp. shows the opposite pattern (right panel, β = 0.3276, *P* = 0.015). Each point represents a single replicate, and points are horizontally jittered for clarity. The dashed line represents the estimated number of individuals added to mesocosms on day 0.

Table 2. Responses of *Fragilaria* spp. and *Cymatopleura* spp. abundance to sediment disturbance, presence of cladocerans, and random terms for block (incubation container) and individual observation (accounting for overdispersion).

Parameter	Coefficient	SE	*z*-value	$Pr < \|z\|$
Fragilaria spp.				
Fixed effects	β			
Intercept	4.69401	0.03336	140.69	$<2 \times 10^{-16}$
Disturbed	0.18418	0.04500	4.09	4.25×10^{-5}
Cladocerans	0.06492	0.04617	1.41	0.1597
Disturbed × Cladocerans	−0.13403	0.06361	−2.11	0.0351
Random effects	Variance			
Block	4.266×10^{-05}			
Observation	7.338×10^{-04}			
Cymatopleura spp.				
Fixed effects	β			
Intercept	3.48591	0.10195	34.19	$<2 \times 10^{-16}$
Disturbed	−0.39277	0.11616	−3.38	0.000721
Cladocerans	−0.01693	0.1093	−0.15	0.876881
Disturbed × Cladocerans	0.32045	0.16044	2.00	0.045795
Random effects	Variance			
Block	0.01324			
Observation	0.02321			

Notes: Included in this analysis are 36 mesocosms (nine mesocosms of each combination of cladoceran presence/absence and undisturbed/disturbed). Results are from a quasi-Poisson generalized linear mixed model.

Mývatn fluctuate by over four orders of magnitude on a decadal time scale (Gardarsson et al. 2004, Ives et al. 2008). Because these tube-forming midges are ecosystem engineers that stabilize the sediment in this shallow lake (Ólafsson and Paterson 2004), the fluctuations in midge abundance generate fluctuations in the sensitivity of the benthos to wind disturbance events. Direct monitoring of the benthic cladoceran community from 1990 to 1999 showed a shift from the large-bodied epibenthic *E. lamellatus* to the small infaunal *A. rectangula* coincident with declines in *T. gracilentus* abundance (Einarsson and Örnólfsdóttir 2004, Fig. 2). Our analyses of microfossils from two sediment cores (Fig. 3) show a significant positive correlation between midge egg abundance and ratio of *E. lamellatus* to *A. rectangula*, extending the pattern observed in the 1990–1999 monitoring data for 140 yr.

Einarsson and Örnólfsdóttir (2004) argue that the shift from high *E. lamellatus* abundance to high *A. rectangula* abundance is likely caused by frequent disturbance and resulting resuspension of sediment in the absence of midge larvae. Midges can have multiple effects on the benthic environment in addition to sediment stabilization (Ólafsson and Paterson 2004, Hölker et al. 2015), including changing nutrient fluxes (Tátrai 1988, Nogaro et al. 2008), altering rates of benthic productivity (Herren et al., *in press*), and changing the composition of diatoms by their feeding. Therefore, we designed our experiment to isolate the resuspension effect of disturbance to separate these confounding effects of the presence of midge larvae. Manual disturbance of our experimental mesocosms reproduced the same patterns expected from direct monitoring and from our sediment cores, with *Alona* spp. increasing relative to *E. lamellatus* in the presence of disturbance. This suggests that the ecosystem engineering effect of midges stabilizing the sediment is a causal mechanism underlying the shift in the cladoceran community observed with midge density in the sediment cores. Our experiment does not exclude other possible effects of midges on cladoceran composition, although it does show that the effect of sediment stability on cladoceran population dynamics is sufficiently large to be observed in a relatively short experiment.

Our mesocosms showed clear differences between *E. lamellatus* and *Alona* spp. in their population growth rates under different disturbance regimes. We cannot directly separate the

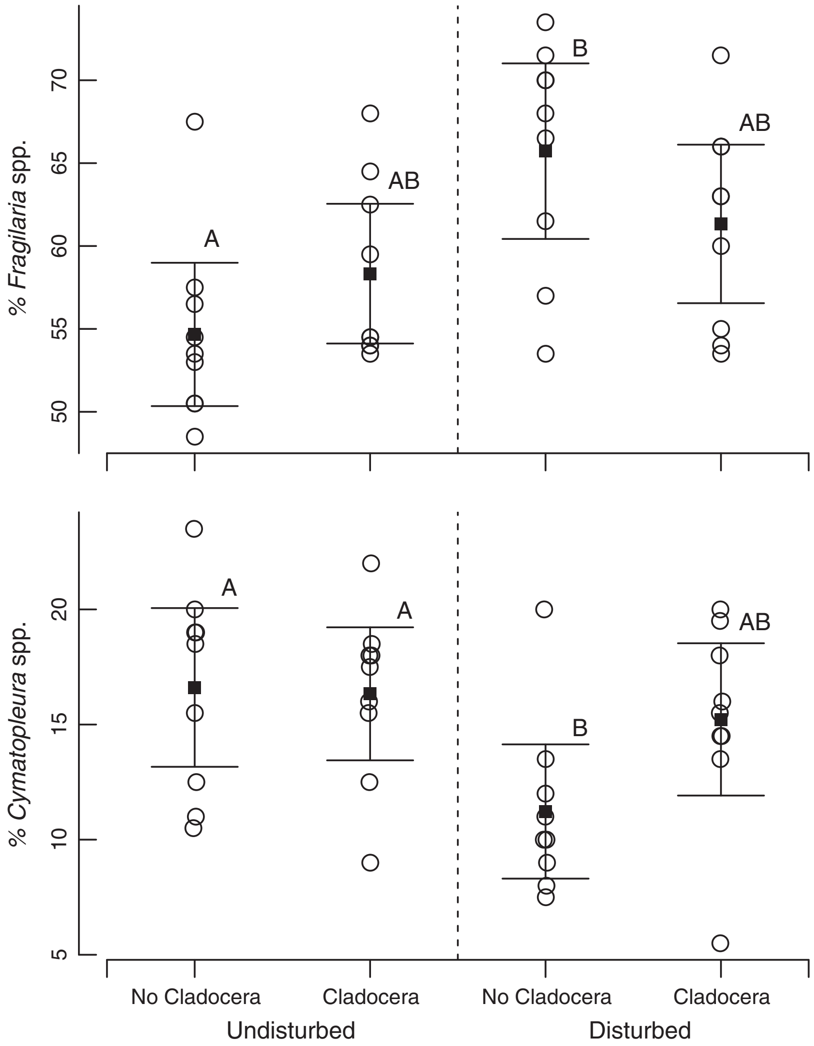

Fig. 5. Percent composition (±1 SE) of *Fragilaria* spp. (top panel) and *Cymatopleura* spp. (bottom panel) in sediment from experimental mesocosms after 27 d. Significance groups were determined with Tukey's HSD procedure from a model with a term to account for incubation container.

effects of disturbance on mortality vs. recruitment. Nonetheless, the treatment means for the number of *E. lamellatus* at the end of the experiment were below the initial treatment means at the start of the experiment, whereas the opposite was true for *Alona* spp. This suggests that disturbance increased mortality of *E. lamellatus* and increased recruitment of *Alona* spp. Although the likely cause for this difference is differences in feeding rates of the two taxa under the disturbance regimes, an additional possible explanation is differences in annual phenology between taxa. However, simultaneous monitoring in Lake Mývatn showed that the density of *E. lamellatus* increased, while the density of *Alona* spp. stayed relatively unchanged over the period of the mesocosm experiment (publicly available data, https://lter.limnology.wisc.edu/datafile/ltreb-benthic-microcrustacean-counts-lake-myvatn). Therefore, our experimental results are unlikely to have been caused by phenological differences in the age or stage distribution of taxa. No cladocerans other than *E. lamellatus* and *Alona* spp. showed significant response to disturbance treatments.

The contrasting responses of *E. lamellatus* and *Alona* spp. to disturbance make sense in light of their differing biology. *Eurycercus lamellatus* is more selective of food particles than suspension feeders like *A. rectangula* (Fryer 1963). Therefore, high rates of sediment resuspension, and the consequent mixing of high-quality diatom food resources with detritus, will likely have a large impact on *E. lamellatus* feeding rates. In contrast, the non-selective *A. rectangula* can effectively use this mix of food. Romanovsky and Feniova (1985) found that under a low-quality resource regime, small-bodied pelagic cladocerans are able to outcompete juveniles of larger cladocerans. However, other studies found the opposite, and there remains controversy over size efficiency and food thresholds for zooplankton (Hart and Bychek 2011). To our knowledge, the issue of size and foraging efficiency has not been previously addressed explicitly for benthic cladocerans.

In the experimental treatments without cladocerans, there were a higher proportion of small-celled *Fragilaria* spp. in disturbed conditions and a higher proportion of large-celled *Cymatopleura* in undisturbed conditions. This shows that disturbance changes the diatom composition in the mesocosms, potentially favoring *Alona* spp. by increasing the abundance of small-celled *Fragilaria* spp. Although there is no information in the literature about the ability of *Alona* spp. to handle colonial filaments of small-celled *Fragilaria* spp., small-bodied *Daphnia* are known to be more effective grazers of filamentous cyanobacteria than large-bodied *Daphnia*, with filaments less likely to clog their filtering apparatus than for large-bodied zooplankton (Sikora and Dawidowicz 2014). Although *Fragilaria* spp. was the most common diatom both in the mesocosm experiment and in Lake Mývatn, a previous sediment core from the lake showed a higher percent of *Fragilaria* spp. than found in our mesocosms and little variation in diatom composition over the last 1400 years of the 2300-year core (Jónasson 1979, Einarsson 1982).

In conclusion, our results show that low midge densities in Lake Mývatn are associated with a shift from large-bodied epibenthic *E. lamellatus* to the small-bodied infaunal *A. rectangula*, a pattern that emerges over the 140 years represented by sediment cores. Our mesocosm experiment gives support for the hypothesis that this association is driven by the ecosystem engineering of the midges, as larvae create mats of tubes that stabilize the sediment against resuspension events in this shallow lake. These findings illustrate not only the potential for disturbances to drive changes in community composition, but also the role that ecosystem engineers can play in modifying the sensitivity of ecosystems to disturbance.

ACKNOWLEDGMENTS

The authors would like to thank P. Klas, S. Jennings, A. Linz, R. Nobre, and E. de Vries for their assistance in the laboratory and field; the Mývatn Research Station for technical and logistical support in Iceland; the Ives Lab at UW-Madison, C. Gratton, and M. J. Vander Zanden for many helpful discussions. A National Science Foundation Graduate Research Fellowship (DGE-1256259) to K. Webert, and a LTREB (DEB-1052160) awarded to A. R. Ives supported this work.

LITERATURE CITED

Adalsteinsson, H. 1979. Seasonal variation and habitat distribution of benthic Crustacea in Lake Mývatn in 1973. Oikos 32:195–201.

Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: a synthesis. Ecology Letters 6:1109–1122.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Blaauw, M., K. D. Bennett, and J. A. Christen. 2010. Random walk simulations of fossil proxy data. Holocene 20:645–649.

Black, K. S., T. J. Tolhurst, D. M. Paterson, and S. E. Hagerthey. 2002. Working with natural cohesive sediments. Journal of Hydraulic Engineering 128:2–8.

Bloesch, J. 1995. Mechanisms, measurement and importance of sediment resuspension in lakes. Marine and Freshwater Research 46:295–304.

Chambers, J. Q. J. Q., R. I. R. I. Negron-Juarez, D. M. D. M. Marra, A. Di Vittorio, J. Tews, D. Roberts, G. H. P. M. G. H. P. M. Ribeiro, S. E. S. E. Trumbore, and N. Higuchi. 2013. The steady-state mosaic of disturbance and succession across an old-growth Central Amazon forest landscape. Proceedings of the National Academy of Sciences USA 110:3949–3954.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302–1310.

Connell, H. J., and O. R. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111:1119–1144.

Dayton, P. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 41:351–389.

Desvilettes, C., and G. Bourdier. 1997. Use of fatty acids for the assessment of zooplankton grazing on bacteria, protozoans and microalgae. Freshwater Biology 38:629–637.

Efron, B., and R. J. Tibshirani. 1993. Introduction to the bootstrap. Chapman & Hall/CRC, New York, New York, USA.

Einarsson, Á. 1982. The palaeolimnology of Lake Myvatn, northern Iceland: plant and animal microfossils in the sediment. Freshwater Biology 12: 63–82.

Einarsson, Á., A. Gardarsson, G. M. Gislason, and A. R. Ives. 2002. Consumer–resource interactions and cyclic population dynamics of *Tanytarsus gracilentus* (Diptera: Chironomidae). Journal of Animal Ecology 71:832–845.

Einarsson, Á., U. Hauptfleisch, R. P. Leavitt, and A. R. Ives. 2016. Identifying consumer-resource population dynamics using paleoecological data. Ecology 97:361–371.

Einarsson, Á., and E. B. Örnólfsdóttir. 2004. Long-term changes in benthic Cladocera populations in Lake Mývatn, Iceland. Aquatic Ecology 38:253–262.

Einarsson, Á., G. Stefánsdóttir, H. Jóhannesson, J. S. Ólafsson, G. M. Gíslason, I. Wakana, G. Gudbergsson, and A. Gardarsson. 2004. The ecology of Lake Mývatn and the River Laxá: variation in space and time. Aquatic Ecology 38:317–348.

Frey, D. G. 1986. Cladocera analysis. Pages 677–692 *in* B. E. Berglund, editor. Handbook of Holocene palaeoecology and palaeohydrology. John Wiley and Sons, Chichester, New York, USA.

Fryer, G. 1963. XIV. – The functional morphology and feeding mechanism of the chydorid cladoceran *Eurycercus lamellatus* (O. F. Müller). Transactions of the Royal Society of Edinburgh 65:335–381.

Gardarsson, A. 1979. Waterfowl populations of Lake Mývatn and recent changes in numbers and food habits. Oikos 32:250–270.

Gardarsson, A., and Á. Einarsson. 1994. Responses of breeding duck populations to changes in food supply. Hydrobiologia 279:15–27.

Gardarsson, A., Á. Einarsson, G. M. Gíslason, T. Hrafnsdóttir, H. R. Ingvason, E. Jónsson, and J. S. Ólafsson. 2004. Population fluctuations of chironomid and simuliid Diptera at Mývatn in 1977–1996. Aquatic Ecology 38:209–217.

Gray, L., and S. Fisher. 1981. Postflood recolonization pathways of macroinvertebrates in a lowland Sonoran Desert stream. American Midland Naturalist 106:249–257.

Hart, R. C., and E. A. Bychek. 2011. Body size in freshwater planktonic crustaceans: an overview of extrinsic determinants and modifying influences of biotic interactions. Hydrobiologia 668:61–108.

Hastings, A. 1980. Disturbance, coexistence, history, and competition for space. Theoretical Population Biology 18:363–373.

Hauptfleisch, U. 2012. High-resolution palaeolimnology of Lake Mývatn, Iceland. Dissertation. University of Iceland, Reykjavik, Iceland.

Hauptfleisch, U., Á. Einarsson, T. J. Andersen, A. Newton, and A. Gardarsson. 2012. Matching thirty years of ecosystem monitoring with a high-resolution microfossil record. Freshwater Biology 57:1986–1997.

Hemphill, N., and S. Cooper. 1983. The effect of physical disturbance on the relative abundances of two filter-feeding insects in a small stream. Oecologia 58:378–382.

Herren, C. M., K. C. Webert, M. D. Drake, M. J. Vander Zanden, Á. Einarsson, A. R. Ives, and C. Gratton. *In press*. Positive feedback between chironomids and algae creates net mutualism between benthic primary consumers and producers. Ecology. https://doi.org/10.1002/ecy.1654

Hölker, F., et al. 2015. Tube-dwelling invertebrates: Tiny ecosystem engineers have large effects in lake ecosystems. Ecological Monographs 85:333–351.

Hubbell, S. P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. Science 203: 1299–1309.

Huston, M. 1979. A general hypothesis of species diversity. American Naturalist 113:81–101.

Ives, A. R., K. C. Abbott, and N. L. Ziebarth. 2010. Analysis of ecological time series with ARMA (p, q) models. Ecology 91:858–871.

Ives, A. R., A. Einarsson, V. A. A. Jansen, and A. Gardarsson. 2008. High-amplitude fluctuations and alternative dynamical states of midges in Lake Mývatn. Nature 452:84–87.

Jónasson, P. M. 1979. The Lake Mývatn ecosystem, Iceland. Oikos 32:289–305.

Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos 69: 373–386.

Jowsey, P. C. 1966. An improved peat sampler. New Phytologist 65:245–248.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2014. LmerTest: tests for random and fixed effects for linear mixed effect models. R package, version 2.0-3.

Lake, P. S. 2000. Disturbance, patchiness, and diversity in streams. Journal of the North American Benthological Society 19:573–592.

Levin, S. A., and R. T. Paine. 1974. Disturbance, patch formation, and community structure. Proceedings of the National Academy of Sciences USA 71: 2744–2747.

Marvier, M., P. Kareiva, and M. G. Neubert. 2004. Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multispecies metapopulation. Risk Analysis 24: 869–878.

McAuliffe, J. 1984. Competition for space, disturbance, and the structure of a benthic stream community. Ecology 65:894–908.

McCall, P. L., and M. J. S. Tevesz. 1982. The effects of benthos on physical properties of freshwater sediments. Pages 105–176 *in* P. L. McCall and M. J. S. Tevesz, editors. Animal-sediment relations. Springer US, Boston, Massachusetts, USA.

Nee, S., and R. M. May. 1992. Dynamics of metapopulations: habitat destruction and competitive coexistence. Journal of Animal Ecology 61: 37–40.

Nogaro, G., F. Mermillod-Blondin, B. Montuelle, J. C. Boisson, and J. Gibert. 2008. Chironomid larvae stimulate biogeochemical and microbial processes in a riverbed covered with fine sediment. Aquatic Sciences 70:156–168.

Ólafsson, J., and D. Paterson. 2004. Alteration of biogenic structure and physical properties by tube-building chironomid larvae in cohesive sediments. Aquatic Ecology 38:219–229.

Örnólfsdóttir, E. B., and Á. Einarsson. 2004. Spatial and temporal variation of benthic Cladocera (Crustacea) studied with activity traps in Lake Mývatn, Iceland. Aquatic Ecology 38:239–251.

Paine, R. T., and S. A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecological Monographs 51:145–178.

Power, M., W. Matthews, and A. Stewart. 1985. Grazing minnows, piscivorous bass, and stream algae: dynamics of a strong interaction. Ecology 66:1448–1456.

Probert, P. K. 1984. Disturbance, sediment stability, and trophic structure of soft-bottom communities. Journal of Marine Research 42:893–921.

R Core Team. 2016. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Resh, V., A. Brown, A. Covich, and M. Gurtz. 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society 7:433–455.

Rhoads, D. C., and L. F. Boyer. 1982. The effects of marine benthos on physical properties of sediments. Pages 3–52 *in* P. L. McCall and M. J. S. Tevesz, editors. Animal-sediment relations. Springer US, Boston, Massachusetts, USA.

Romanovsky, Y., and I. Feniova. 1985. Competition among Cladocera: effect of different levels of food supply. Oikos 44:243–252.

Roozen, F. C. J. M., M. Lürling, H. Vlek, E. A. J. Van Der Pouw Kraan, B. W. Ibelings, and M. Scheffer. 2007. Resuspension of algal cells by benthivorous fish boosts phytoplankton biomass and alters community structure in shallow lakes. Freshwater Biology 52:977–987.

Roxburgh, S. H., K. Shea, and J. B. Wilson. 2004. The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. Ecology 85:359–371.

Sikora, A., and P. Dawidowicz. 2014. Do the presence of filamentous cyanobacteria and an elevated temperature favor small-bodied *Daphnia* in interspecific competitive interactions? Fundamental and Applied Limnology/Archiv für Hydrobiologie 185:307–314.

Smirnov, N. 1962. *Eurycercus lamellatus* (O. F. Müller) (Chydoridae, Cladocera): field observations and nutrition. Hydrobiologia 20:280–295.

Sousa, W. P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecology 60:1225–1239.

Sousa, W. P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15:353–391.

Stanley, E. H., S. M. Powers, and N. R. Lottig. 2010. The evolving legacy of disturbance in stream ecology: concepts, contributions, and coming challenges. Journal of the North American Benthological Society 29:67–83.

Tátrai, I. 1988. Experiments on nitrogen and phosphorus release by *Chironomus* ex gr. plumosus from the sediments of Lake Balaton, Hungary. Internationale Revue der gesamten Hydrobiologie und Hydrographie 73:627–640.

Thorbergsdóttir, I. M., S. R. Gíslason, H. R. Ingvason, and Á. Einarsson. 2004. Benthic oxygen flux in the highly productive subarctic Lake Myvatn, Iceland: in situ benthic flux chamber study. Aquatic Ecology 38:177–189.

Townsend, C. 1989. The patch dynamics concept of stream community ecology. Journal of the North American Benthological Society 8:36–50.

Turner, M. G., W. L. Baker, C. J. Peterson, and R. K. Peet. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. Ecosystems 1:511–523.