

## LETTER

# Rapid local adaptation mediates zooplankton community assembly in experimental mesocosms

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### Abstract

Adaptive evolution can occur over similar timescales as ecological processes such as community assembly, but its particular effects on community assembly and structure and their magnitude are poorly understood. In experimental evolution trials, *Daphnia magna* were exposed to varying environments (presence and absence of fish and artificial macrophytes) for 2 months. Then, in a common gardening experiment, we compared zooplankton community composition when either experimentally adapted or *D. magna* from the original population were present. Local adaptation of *D. magna* significantly altered zooplankton community composition, leading to a suppression of abundances for some zooplankton taxa and facilitation for others. The effect size of *D. magna* adaptation was similar to that of adding fish or macrophytes to mesocosms, two important drivers of zooplankton community structure. Our results suggest that substantial amounts of variation in community composition in natural systems may be unexplained if evolutionary dynamics are ignored.

### Keywords

Community assembly, *Daphnia*, evolving metacommunity, local adaptation.

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## INTRODUCTION

A primary goal of community ecology is to understand how and which deterministic and stochastic processes influence the assembly, structure, and function of communities in natural landscapes. Environmental and spatial features, as well as historical and stochastic processes, typically explain only part of the variation in community composition observed in nature (Cottenie 2005; Meynard *et al.* 2011), leaving the drivers of a substantial part of the variation in community structure unexplained. The traditional niche-based explanatory paradigms that predict a match between species and their environment, such as community assembly (Drake 1990) and species sorting (Chase & Leibold 2003), treat the species-specific traits that determine the outcome of assembly and species sorting as fixed and do not consider that community structure can be contingent on the genetic properties of the species involved. Yet several studies have provided evidence that genetic identity and diversity can impact community assembly. For example, the susceptibility of freshwater zooplankton communities to invasion can depend on the genetic identity of resident and colonising species (De Meester *et al.* 2007; Pantel *et al.* 2011b), the establishment success of immigrants in stands of goldenrod (*Solidago altissima*) is impacted by genotype identity and diversity (Crutsinger *et al.* 2008), the assembly of herbivore communities can depend on the genetic identity of the host plant (Johnson & Agrawal 2005; Wimp *et al.* 2005), and the outcome of competition between a grass and a sedge species depends on the genetic identity of both species (Fridley

*et al.* 2007). Genetic contingency can thus influence the assembly and structure of communities and warrants consideration alongside other properties such as competitive differences among species and priority effects (Antonovics 1992; Whitham *et al.* 2003).

Evolution can proceed at a rapid enough pace, over just a few to a few tens of generations in many cases (Hendry & Kinnison 1999), that both ecological and evolutionary processes can occur on overlapping timescales and thus may interact with one another (Schoener 2011). Fukami *et al.* (2007) showed in a simple microcosm experiment that adaptive phenotypic diversification in *Pseudomonas fluorescens* to available niche space was greatly constrained when other pre-adapted *P. fluorescens* strains were inoculated before the focal strain. Similarly, adaptive radiation in *P. fluorescens* was limited in the presence of a naturally diverse soil bacterial community (Gómez & Buckling 2013). In these studies, the relative speeds of ecological (community assembly through immigration) and evolutionary (local adaptation of residents) processes determine how available niche space is filled with inter- or intraspecific phenotypic variation.

A growing number of experiments quantified the impact of evolutionary divergence on community- and ecosystem-level responses. Many of these studies employed a common gardening approach (Matthews *et al.* 2011), where distinct genotypes (clones, families, or populations) associated with distinct phenotypes of interest were put in the same environmental conditions and their differential effects on communities and ecosystems were measured. This approach was successfully

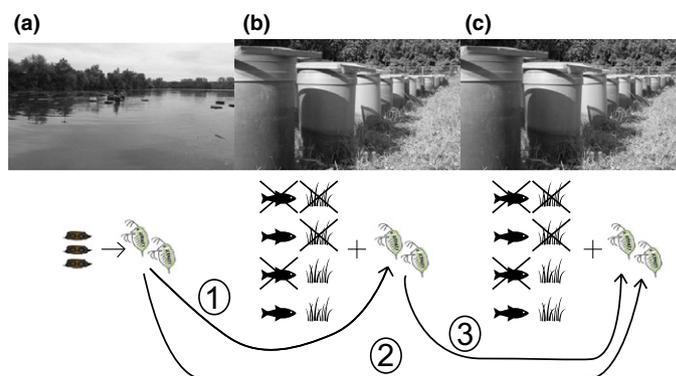
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applied in fish (Post *et al.* 2008; Harmon *et al.* 2009; Bassar *et al.* 2010), zooplankton (De Meester *et al.* 2007; Pantel *et al.* 2011b; Walsh *et al.* 2012), and plant systems (Crutsinger *et al.* 2008; Terhorst *et al.* 2014). In some instances the assumption underlying these studies, that phenotypic differences among stocked populations reflect adaptive responses to natural environmental gradients, is substantiated with supporting historical evidence (e.g. Reznick *et al.* 1990; Crutsinger *et al.* 2006; Pantel *et al.* 2011a). Very few common gardening studies have considered both the evolutionary impacts of environmental selection pressures as well as the ecological impacts of the resulting adaptive divergence in the same experimental setting. Of these studies, one focused on the structure of communities that assembled on adaptively diverged hosts (Terhorst *et al.* 2014) while the other considered the effects of evolution on pairwise species interactions and on ecosystem functioning in a group of bacteria (Lawrence *et al.* 2012). The goal of our study was to explicitly link environmental variation with evolved phenotypic variation in a strong competitor and then link this phenotypic variation with variation in the assembly of communities of competitors occupying the same trophic level in one sequence of experiments. We therefore conducted both a selection experiment, in which we induced genetic changes in response to environmental selection pressures in a focal species, the water flea *Daphnia magna*, and subsequently a community assembly experiment, in which we monitored the impact of these evolved changes on the composition of crustacean zooplankton communities, which are *D. magna*'s primary competitors.

Our experimental study involved three phases (Fig. 1). First, we collected and hatched dormant eggs from a wild population of the keystone zooplanktonic grazer, *D. magna*, to obtain a representative sample of naturally occurring levels of genetic diversity in a single population. Second, in a selection experiment, we exposed replicate samples of hatchlings to different environmental conditions. These conditions, factorial combinations of the presence and absence of artificial macrophytes and planktivorous fish, are known selection pressures that exert a strong influence on zooplankton community structure (Brooks & Dodson 1965; Scheffer 1998). Third, we inoculated either adapted *D. magna* harvested at the end of the selection experiment or *D. magna* hatched from the original source pond into mesocosms with the same environmental conditions experienced in the selection experiment (i.e. a factorial combination of fish and artificial macrophyte presence and absence) and quantified community assembly after inoculation with a diverse zooplankton community. This approach allowed us to assess the impact of adaptive evolution in a key interactor on community assembly and to compare this impact to the effect size of environmental drivers known to be important determinants of zooplankton community structure. We hypothesised (1) that evolution of a strong competitor, the large-bodied cladoceran *D. magna*, in response to environmental selection pressures would influence subsequent community assembly, (2) that the effect size of *D. magna* evolution would be appreciable but smaller than that of the environmental drivers (presence of fish and artificial macrophytes), and (3) that adapted *D. magna* would suppress the establishment and population growth of competitors during



**Figure 1** Overview of our experimental design to determine how adaptive genetic differentiation influences composition and structure in a community of competitors, spanning three stages: (a) We generated an initial *D. magna* population by hatching dormant eggs from surficial sediment collected from a single source pond. (b) We used hatched clones (1) to stock a selection experiment to induce adaptive evolution in response to factorial combinations of fish and artificial macrophytes, two important drivers of zooplankton community structure. A diverse community of zooplankton competitors was present in all treatments of the selection experiment. (c) We then placed either (2) non-adapted *D. magna* clones hatched from the source pond or (3) adapted *D. magna* from the selection experiment in a community assembly experiment in the presence and absence of fish and artificial macrophytes and in the presence of a diverse community of zooplankton competitors. The selection and assembly experiments were conducted in two different years. Maternal effects were purged from *D. magna* clonal lineages by culturing in common garden conditions for at least two generations.

community assembly. Our experimental results confirmed that *D. magna* evolution significantly influenced zooplankton community structure. However, the magnitude of this effect was stronger than expected, comparable to the effect of fish or artificial macrophytes. Abundances of individual zooplankton taxa were also both suppressed and enhanced by *D. magna* evolution.

## MATERIALS AND METHODS

### Initial *D. magna* population

For our selection experiment, we sought to inoculate mesocosms with a standardised, genetically diverse *D. magna* population meant to represent the sample of genotypes that would hatch at the beginning of a growing season in a natural pond. In February 2006, we collected surficial sediment from the upper three cm of pond OM2 (Vijvers Abdij van 't Park, 50°49'40" N 04°39'39" E). The sediments were kept in the dark for several months (until just prior to the beginning of the selection experiment) at 4 °C then sediments were sieved to extract dormant eggs. Eggs were exposed to conditions that stimulate hatching (20 °C, 14 h light/10 h dark regime, fresh ADAM medium; De Meester & De Jager 1993; Klüttgen *et al.* 1994) and hatchlings were transferred to favourable growing conditions (up to 30 hatchlings in a 1 L jar filled with aged tap water, 20 °C, 14 h light/10 h dark photoperiod, fed the unicellular alga *Scenedesmus obliquus* at a concentration of  $0.5 \times 10^5$  cells/mL).

### Selection experiment

In summer 2006, we conducted a selection experiment to allow *D. magna* from pond OM2 to adapt to four different environmental conditions, which were factorial combinations of the presence or absence of predatory fish (three-spined stickleback, *Gasterosteus aculeatus*) and artificial macrophytes intended to mimic structural complexity in ponds. Each condition was replicated three times, resulting in a total of 12 mesocosms. The mesocosms were 200 L containers filled with 170 L of tap water 1 week prior to inoculating *D. magna*. The artificial macrophyte treatment was implemented immediately and consisted of *c.* 30 plastic strips of 1 m length placed outside the fish cage (used for the fish treatment, described in a subsequent section) that reached from the bottom to the water surface (Figure S1). These plastic strips mimic plants in terms of structure, but do not produce chemical exudates that sometimes have a repellent effect on zooplankton. The fish treatment was implemented later in the experiment when densities of the zooplankton were high enough to reduce the risk of chance extinctions upon predator addition. Because our selection experiments purposefully included natural food webs with bacterio-, phyto-, and zooplankton, it is likely that the selective environments included both direct effects of fish and macrophytes as well as indirect effects through alterations of food webs and species interactions.

Individual *D. magna* hatched from the dormant egg bank of OM2 were cultured in the laboratory until they were 4 days old, at which time they were used to inoculate the experimental mesocosms. On May 22, 2006, each mesocosm received 115 individual 4-day-old *D. magna*. *Daphnia magna* dormant eggs result from sexual reproduction, so all hatchlings were genetically distinct and each mesocosm's 115 genotypes represent a random sample of source pond genetic diversity. Mesocosms received inocula of the unicellular alga *S. obliquus* on May 22, June 20, and June 27.

Four weeks after *D. magna* inoculation, all mesocosms received inocula of a diverse zooplankton community to create a more natural environment with competitors. We collected zooplankton samples (by hauls of a 100 µm plankton net) from multiple ponds near the city of Leuven (Belgium) that lack natural *D. magna* populations, pooled the samples, mixed the contents of the pooled samples to create a relatively uniform distribution of zooplankton taxa, and subdivided this mixture into 1 L aliquots to reduce among-aliquot variation. Aliquots were further filtered over a 64 µm mesh and added to each mesocosm as a 50 mL sample. The inocula contained *c.* 1250 individuals per mesocosm of ten cladoceran species (*Alona rectangula*, *Bosmina longirostris*, *Ceriodaphnia pulchella*, *Ceriodaphnia quadrangula*, *Chydorus sphaericus*, *Daphnia longispina*, *Daphnia pulex*, *Pleuroxus denticulatus*, *Scapholeberis mucronata*, and *Simocephalus vetulus*) as well as cyclopoid copepods and ostracods. On July 24 we added one *G. aculeatus* (*c.* 5 cm standard length) to each of six mesocosms randomly assigned to the fish treatment. Fish movement was constrained by a cylindrical cage made from plastic gauze with a 5 mm mesh size that did not limit the movement of zooplankton (Figure S1). The cages covered *c.* 25% of total water volume and were placed in the middle of the mesocosm,

leaving refugia at the outer edge and bottom of the mesocosm. Treatments without fish received empty cages.

On August 29, 36 days after exposure to fish and 99 days after exposure to artificial macrophytes, a random sample of 20 female *D. magna* individuals was collected from each mesocosm and used to start clonal lineages in the laboratory. Each clonal lineage was cultured in a different jar, kept in a walk-in climate room at 20 °C with a 14 h light/10 h dark photoperiod, and fed *S. obliquus* cells until the community assembly experiment was initiated the following year (subsequent summer period). For at least two generations prior to the community assembly experiment, the clonal lineages were cultured under standardised conditions (20–25 individuals in a 1L jar, dechlorinated tap water refreshed for 25% every second day, 20 °C, 14 h light/10 h dark photoperiod, daily feeding of  $1.10^5$  *S. obliquus* cells/mL). The resulting clonal lineages are referred to as 'adapted *D. magna*' in the remainder of the text, as they were isolated from mesocosms after 36–99 days of selection in mesocosm environmental conditions.

### Non-adapted *D. magna*

Appropriate 'non-adapted' clones for the community assembly experiment should originate from the same source population as those in the selection experiment but should not have experienced the selection conditions. To obtain this non-adapted population, we hatched *D. magna* directly from the same dormant egg bank used to initiate the selection experiment. Hatching was induced by removing dormant eggs from the dark and cold storage conditions and exposing them to previously described hatching conditions. Hatchlings were transferred to 1 L jars and reared under identical standardised conditions as described previously for the adapted clones for at least two generations before their use in the assembly experiment. We cultured 20 clones to represent the non-adapted *D. magna* population.

### Community assembly experiment

In late summer 2007 we used adapted and non-adapted *D. magna* in a mesocosm experiment to determine how adaptation influences community assembly of zooplankton in the presence and absence of fish and artificial macrophytes. On August 30, twenty-four 200 L mesocosms were filled with 180L of tap water, given an inoculum of the alga *S. obliquus*, and covered with a 1 mm mesh to prevent colonisation by other zooplankton and macroinvertebrates. On September 8th, 100 individual *D. magna* (five juveniles < 24 h old from each of 20 different clonal lineages) were added to each mesocosm. Each replicate of all treatments initially contained a genetically identical *D. magna* population. Each 'non-adapted' *D. magna* treatment received the same 20 clones descended from individuals hatched directly from pond OM2 sediment. Each 'adapted' *D. magna* treatment received 20 clonal lineages isolated from mesocosms in the selection experiment with a similar environment (fish and artificial macrophytes present vs. absent; therefore 'adapted' *D. magna* were placed only in the environment they were previously exposed to during the selection experiment). These 20 clonal lineages were chosen at

random from those isolated at the end of the selection experiment and remaining after stochastic extinction of some lineages in laboratory cultures. Each treatment was replicated three times. We introduced a diverse community of potential competitors on September 14th. We collected zooplankton from various ponds in the neighbourhood of Leuven that were known to not harbour *D. magna*. The inoculum added to each mesocosm contained on average 1646 individuals representing 12 cladoceran species (*B. longirostris*, *C. quadrangula*, *C. sphaericus*, *D. longispina*, *D. pulex*, *Eurycercus lamellatus*, *Leydigia quadrangularis*, *P. aduncus*, *P. denticulatus*, *Polyphemus pediculus*, *S. mucronata* and *S. vetulus*), together with some cyclopoid copepods and ostracods.

Mesocosms were subject to one of eight treatments in a factorial combination of *D. magna* adaptation (yes or no), artificial macrophytes (present or absent), and fish (present or absent). Artificial macrophyte and fish treatments were implemented in the same manner as in the selection experiment. Fish were added on September 25th.

Zooplankton communities were sampled on October 24th, c. 1 month after fish were inoculated in the mesocosms, by gently mixing mesocosm contents, using a tube sampler (plexi-glass tube of 7.5 cm diameter with a magnet-operated closing lid at the bottom) to sample 10 L of water, and filtering contents over a 64 µm mesh. Zooplankton were fixed in 70% ethanol and identified to species level, except for Cyclopoida (identified to order), Chydoridae (identified to family), and *Ceriodaphnia* (identified to genus). *Daphnia* were identified as *D. magna*, *D. pulex*, or *D. longispina* species complex (called *D. longispina* subsequently). All data were analysed as the total number of individuals in a mesocosm (number of individuals per 180 L, estimated from counts of 10 L samples).

### Statistical analysis

To determine whether *D. magna* evolution in response to the applied environmental selection pressures influenced community assembly (hypothesis 1) and to quantify its effect size (hypothesis 2), we analysed *D. magna* abundance and composition of the non-*D. magna* community from the community assembly experimental mesocosms. We then evaluated abundances of individual zooplankton taxonomic groups to assess whether evolved *D. magna* led to lower (suppressed) or higher (facilitated) abundances of competitors (hypothesis 3).

We tested the influence of treatments on *D. magna* abundance in mesocosms from the assembly experiment by fitting generalised linear models with artificial macrophytes (present vs. absent), fish (present vs. absent), local adaptation (adapted vs. non-adapted), and their interactions as factors (see Supporting Information Methods).

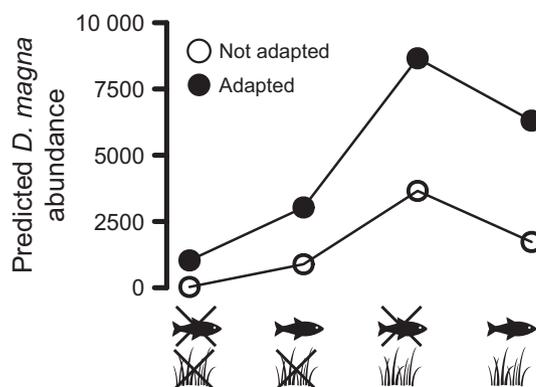
We tested the influence of fish, artificial macrophytes, and adaptation on non-*D. magna* community similarity using PERMANOVA (Anderson *et al.* 2006) of the Hellinger distance (Legendre & Gallagher 2001) between all pairs of mesocosm communities and estimated treatment effect size using partial  $R^2$  values. Compositional similarity within and among treatment groups was visualised with a non-metric multidimensional scaling (NMDS) plot. We also tested the dependence of non-*D. magna* community composition on fish, artificial

macrophytes, and adaptation using MANOVA of Hellinger-transformed abundance values for each taxonomic group. Data were Hellinger transformed to reduce the weight of rare taxa (Legendre & Gallagher 2001). *Post hoc* tests for individual taxa were conducted using factorial ANOVA. The response of individual zooplankton to adapted *D. magna* was evaluated via these *post hoc* ANOVA tests and by calculating the average partial contribution of each individual taxon to the Hellinger distance between non-*D. magna* zooplankton communities in treatments with adapted vs. non-adapted *D. magna* populations.

We estimated the effect of fish, artificial macrophytes, *D. magna* local adaptation, and their interactions on three community ecological response variables – the score from the first axis of an (NMDS) analysis on zooplankton community Hellinger distance, species richness, and Simpson's diversity index ( $1 - D$ , the probability that two individuals taken at random from a mesocosm belong to different taxa), calculated for all non-*D. magna* zooplankton taxa in each mesocosm – using methods adapted from Ellner *et al.* (2011). Instead of reporting effects as a change from one state (environmental or genetic) to another (as described in Ellner *et al.* 2011), we instead asked how moving from a state halfway between the fish environmental (fish absent and present), macrophyte environmental (artificial macrophytes absent and present), and genetic (non-adapted and adapted *D. magna*) states to each observed state influenced community ecological response variables (formulas given in Supporting Information Methods). We also calculated the bootstrap standard deviations obtained by repeating calculations for 10 000 bootstrap samples. Statistical analyses were conducted in R (version 3.1.1, 2014) using the base package and the 'vegan' package (Oksanen *et al.* 2013).

### RESULTS

The best-fit model of *D. magna* abundance (a zero-inflated negative binomial regression model; Supporting Information Results) indicated that fish, artificial macrophytes, *D. magna* adaptation and their interactions all significantly influenced

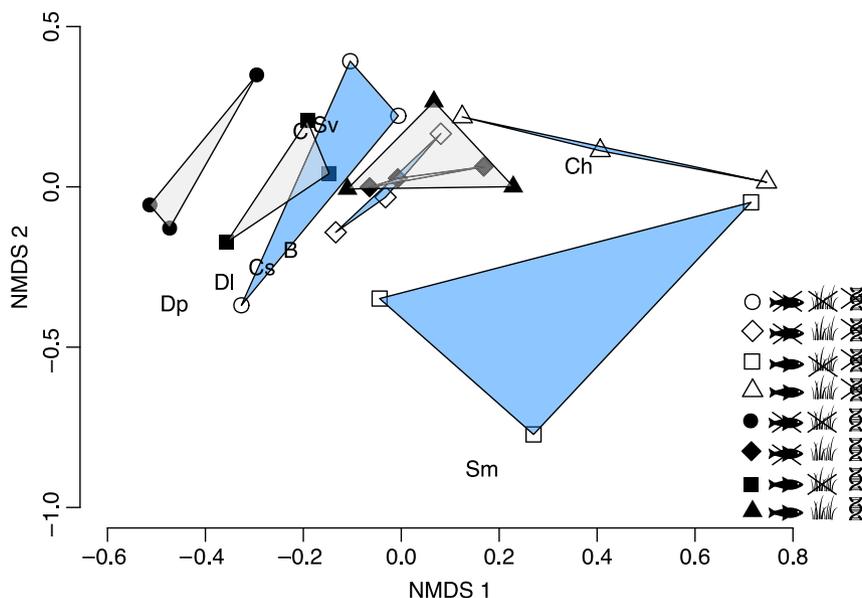


**Figure 2** Predicted values of *Daphnia magna* abundance in the community assembly experiment from our best-fit regression model (Table S2) for each artificial macrophyte × fish treatment combination. Treatments with non-adapted *D. magna* are depicted with open circles and treatments with adapted *D. magna* are depicted with filled circles.

the count of *D. magna* (Fig. 2; Supporting Information Results; Figure S2; Table S2).

Taxonomic composition of non-*D. magna* zooplankton communities in each treatment more closely resembled communities in the same treatment than communities in other treatments (fish:  $F$ -ratio = 3.11,  $P = 0.03$ ; adapted:  $F$ -ratio = 3.70,  $P = 0.01$ ; artificial macrophytes:  $F$ -ratio = 5.02,  $P < 0.01$ ; Fig. 3). These treatment effects did not interact (Table 1). The fish, adapted, and artificial macrophyte treatments explained 10, 11, and 15% of variation in community compositional similarity respectively.

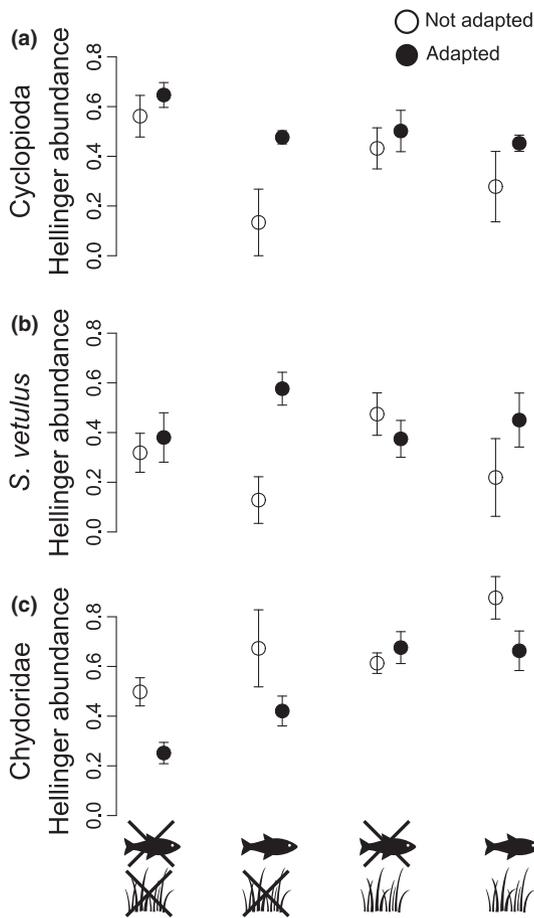
Species composition of zooplankton (excluding *D. magna*) communities significantly differed depending on fish (MANOVA: Pillai's trace = 0.76,  $F_{1,16} = 3.58$ ,  $P = 0.04$ ), artificial macrophytes (Pillai's trace = 0.89,  $F_{1,16} = 9.32$ ,  $P < 0.01$ ), adapted *D. magna* (Pillai's trace = 0.82,  $F_{1,16} = 5.20$ ,  $P = 0.01$ ), and the interaction of fish and artificial macrophytes (Pillai's trace = 0.77,  $F_{1,16} = 3.74$ ,  $P = 0.03$ ). All other effects were not significant (Table S3). *Post hoc* ANOVA tests indicated three taxa with significant 'adapted' treatment effects: Cyclopoida, *S. vetulus*, and Chydoridae. (Table S4, Fig. 4, Figure S3).



**Figure 3** NMDS plot of Hellinger distances for all non-*D. magna* zooplankton communities in the community assembly experiment. Treatments with adapted *D. magna* are connected with grey triangles and treatments with non-adapted *D. magna* are connected with blue triangles. Each taxon's position along NMDS axes is indicated by abbreviations: C = Cyclopoida, DI = *D. longispina*, Dp = *D. pulex*, Sv = *S. vetulus*, Sm = *S. mucronata*, Cs = *Ceriodaphnia spp.*, Ch = Chydoridae, and B = *B. longirostris*.

	d.f.	Sums of Sq	Mean Sq	$F$ model	$R^2$	Pr(> $F$ )
Fish	1	0.516	0.516	3.105	0.095	<b>0.022</b>
Adapted	1	0.615	0.614	3.699	0.113	<b>0.006</b>
Macrophytes	1	0.834	0.834	5.023	0.154	<b>0.001</b>
Fish × Adapted	1	0.318	0.318	1.914	0.059	0.121
Fish × Macrophytes	1	0.174	0.174	1.046	0.032	0.351
Macrophytes × Adapted	1	0.209	0.209	1.258	0.039	0.264
Fish × Macrophytes × Adapted	1	0.103	0.103	0.622	0.019	0.674
Residuals	16	2.658	0.166		0.490	
Total	23	5.427			1.000	

**Table 1** Results of PERMANOVA testing the effects of fish, artificial macrophytes, adapted *D. magna*, and their interactions on non-*D. magna* zooplankton community similarity (Hellinger distance). Treatments with  $P$  values less than 0.05 are highlighted in bold.

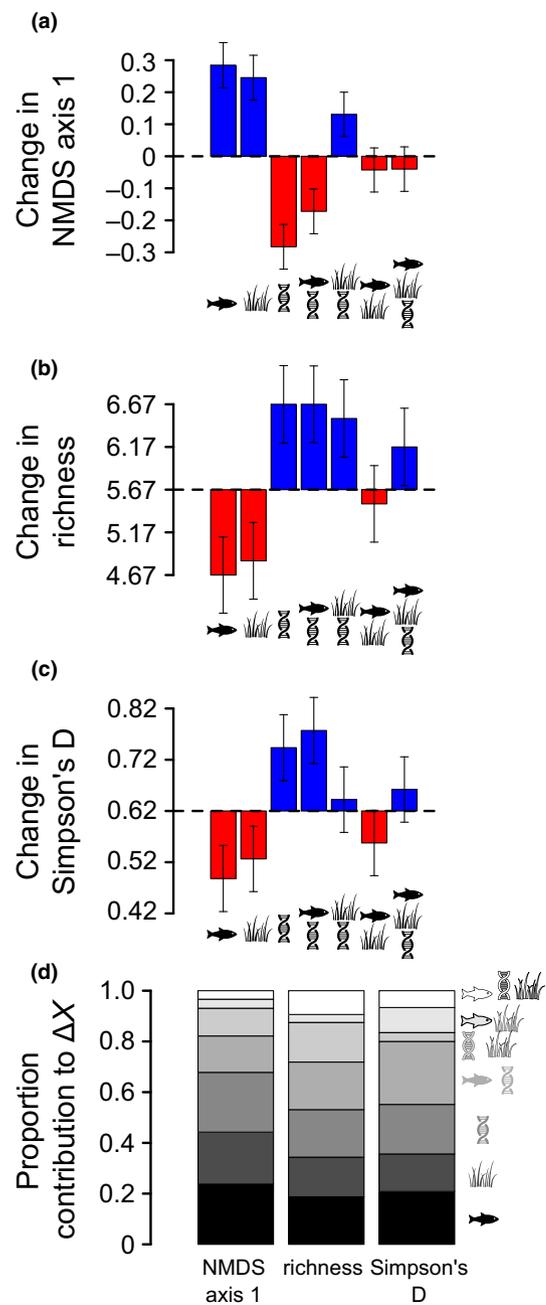


**Figure 4** Hellinger abundance in the community assembly experiment for (a) Cyclopoda, (b) *S. vetulus*, and (c) Chydoridae. Points are mean values of three replicate mesocosms for each artificial macrophyte×fish×adapted *D. magna* treatment and error bars are ± one standard error.

(± 0.06) (for richness and diversity respectively) and by −0.83 (± 0.44) and −0.09 (± 0.06) for artificial macrophytes (Fig. 5b and c). Interaction effects of *D. magna* adaptation with other factors (except the adapted × artificial macrophyte interaction effect for NMDS axis 1) were in the same direction as the *D. magna* adaptation main effect (Fig. 5).

**DISCUSSION**

The genetic differences that accumulated in our experimental *D. magna* populations, which were initiated from the standing genetic variation present in a single natural population and exposed to environmental selective pressures for a relatively short period (36 and 99 days for fish and artificial macrophytes, respectively), significantly influenced zooplankton composition in the subsequent community assembly experiment. Communities with non-adapted *D. magna* populations diverged in taxonomic composition in ways that reflected species sorting to match environmental conditions, such as an increase in the abundance of Chydoridae when artificial macrophytes were present (Smirnov 1996) and a decrease in the abundance of large-bodied taxa such as *S. vetulus* when fish were present and artificial macrophytes were absent (Perrow *et al.* 1999; Fig. 4). The presence of adapted *D.*



**Figure 5** Direction and magnitude of the effects of fish, artificial macrophytes, and *D. magna* local adaptation on community ecological properties. In (a–c), bars are the means of the absolute values of each effect size as a deviation from the intercept value, dashed lines are the means of the intercept values, and error bars are ± 1 standard deviation from 10 000 bootstrapped estimates of effect sizes. In (d), the stacked bars depict the mean of the absolute value of effect sizes as a proportion of the total differences observed in property *X* (position along NMDS axis 1, richness, or Simpson's *D*).

*magna* significantly influenced community composition, leading to communities that were more similar to one another than to communities experiencing identical environmental conditions but with non-adapted *D. magna* (Fig. 3). This effect was most evident in Cyclopoda and *S. vetulus*, where the negative effect of fish predation on abundances was min-

imised or reversed in the presence of locally adapted *D. magna* (Fig. 4). Local adaptation in *D. magna* thus interfered significantly and in repeatable ways with zooplankton community assembly in our experiment.

The impact of *D. magna* local adaptation varied among zooplankton taxa. Some taxa were suppressed by *D. magna* adaptation, such as the Chydoridae, while other taxa were actually facilitated, such as Cyclopoida and *S. vetulus* (Fig. 4). We cannot derive the precise mechanism leading to these changes from our study. However, the suppression of Chydoridae aligns with our expectation that local adaptation would increase *D. magna* competitive strength, leading to increased *D. magna* abundance and decreased abundance of competitors. Although we did not anticipate the observed facilitation of Cyclopoida and *S. vetulus* (Fig. 4a and b), this finding can be explained by expected adaptations of *D. magna* to fish predation. In the presence of fish, *D. magna* generally evolve to become smaller and mature faster (Boersma *et al.* 1998; Mikulski *et al.* 2005), to engage in diel vertical migration (moving to deeper and darker water layers during the day to escape visual predators; Cousyn *et al.* 2001), and to engage in diel horizontal migration (Michels *et al.* 2007). These adaptations, which reduce *Daphnia's* likelihood of encountering and visibility to fish, may explain why *D. magna* abundance in the adapted treatment exceeded that in the non-adapted treatment. However, because body size in zooplankton is generally associated with competitive ability (size efficiency hypothesis; e.g. Brooks & Dodson 1965; Gliwicz 1990), the reduced size at maturity and overall body size would also decrease *D. magna's* competitive strength, benefiting other large cladocerans such as *S. vetulus* that are commonly associated with predators (Louette & De Meester 2007). Migration to the bottom and along the walls of mesocosms would also reduce *D. magna's* grazing capacity, leading to increased food resources to benefit other taxa.

Several other studies have provided evidence that genetic properties can alter the outcome of community assembly, but these differ from our study in important ways. Some studies evaluated genetic differentiation in a species that serves as a niche on which other species assemble (e.g. herbivore assemblages on host plants, Wimp *et al.* 2005; bacterial and fungal communities associated with host plants, Terhorst *et al.* 2014), whereas we considered genetic variation in a species that competes with other species in the assembling communities. Another group of studies evaluated intraspecific variation and its implications for competitors but focused more specifically on the effects of genetically diverse vs. uniform populations (e.g. Crutsinger *et al.* 2008) or of genetic identity (De Meester *et al.* 2007; Pantel *et al.* 2011b). These common gardening studies did provide evidence of the principle that evolved genetic differences can influence community composition, but they did not follow the system through the complete sequence from evolution in response to environmental selective pressures to its impacts on community assembly. Our study provides evidence that natural populations of *D. magna* harbour the evolutionary potential to rapidly adapt to changing environments and that one consequence of this adaptive response is altered community assembly trajectories. Evolu-

tion over as few as 36 days (*c.* 3–4 generations of clonal sorting) is sufficient to alter assembly trajectories.

Our results align with some predictions from theory on eco-evolutionary interactions between competitors and also offer new perspectives that may stimulate further theoretical work. For example, Urban *et al.* (2008) showed in a simple model that evolution in one species may interfere with colonisation and growth of another species, while Urban & De Meester (2009) showed in a landscape-scale evolving metacommunity model that local adaptation in the first species to arrive in a habitat can enhance priority effects. We observed this interference in some instances, such as when locally adapted *D. magna* led to reduced abundances of Chydoridae. However, the facilitation observed in other taxa serves as a reminder that the dynamic reciprocal interactions of ecological and evolutionary processes may lead to complex and surprising outcomes. Another surprising result was the relative homogenisation of zooplankton communities with adapted *D. magna* compared to communities with non-adapted *D. magna* (Fig. 3). This suggests that locally adapted *D. magna*, through their increased abundances in all experimental conditions, may have a large and similar impact on the entire zooplankton community that acts in opposition to the diverging impacts associated with the presence of fish and artificial macrophytes. Our results add to the evidence that fundamental ecological theory may require full integration of the genetic differences within species to maximise its explanatory power (Bolnick *et al.* 2003; Schoener 2011).

Our experiment did not consider evolution in response to environmental conditions for other zooplankton species in the community or a shared coevolutionary history between *D. magna* and its competitors. Adaptive responses in other taxa could reduce the impact of *D. magna* adaptation on community structure observed in our experiment. However, considering evolution in only one focal species does not necessarily overestimate the impact of evolution. Even if evolution in other taxa led to less divergence between 'adapted' and 'non-adapted' treatments, the main driver of composition in the 'adapted' treatments would still be evolution. In such an instance the evolution in various species would on balance produce no observed turnover in species composition, but evolution would still be responsible for this pattern. It is also important to note that *D. magna* in our selection experiment likely evolved in response to the suite of environmental conditions in mesocosms, including the containers themselves as well as the array of indirect trophic and environmental shifts induced by the selection conditions. Therefore, some of the observed effects of evolution are likely contingent on the specific conditions chosen for this experiment. However, the evidence that *D. magna* adaptively responded to the main selection pressures – the presence and absence of fish and artificial macrophytes – is clearly observed in the divergent consequences of evolution for community composition in the differing environments. For instance, the increased facilitation of *S. vetulus* in mesocosms with fish aligns with the expectation that *D. magna* would evolve behaviours and decreased body size in the presence of fish that would favour large competitors such as *S. vetulus*.

One of the most intriguing findings of this study was that the effect size of *D. magna* adaptation on zooplankton community composition was similar in magnitude to that of fish or artificial macrophyte presence (Table 1; Fig. 5). Fish and macrophytes are two well-studied and important drivers of zooplankton community structure. The influence of fish on zooplankton community structure is one of the cornerstones not only of limnology but also of modern ecological concepts such as indirect effects and top-down control of ecosystems (Hairston *et al.* 1960; Brooks & Dodson 1965; Ives *et al.* 1999). The presence vs. absence of macrophytes lies at either end of alternative stable states in lake ecosystems and can substantially impact the structure of zooplankton communities (Scheffer 1998; Perrow *et al.* 1999). Our results support the importance of these environmental drivers in determining zooplankton community structure, but also indicate that local adaptation in a strong competitor, the large-bodied cladoceran *D. magna*, can impact community composition with a similar magnitude as fish or macrophytes. This result speaks to the importance of synthesising ecological and evolutionary perspectives to best understand dynamics of natural systems (Schoener 2011). Although attention to contemporary evolution and its implications for ecological processes is growing (Fussmann *et al.* 2007; Pelletier *et al.* 2009), it has been claimed that this field can establish its importance only if researchers demonstrate that the effects of evolution on ecological processes are as significant as traditionally considered ecological drivers such as environmental properties or interactions with other species. Our results add to recent work (e.g. Ellner *et al.* 2011; Becks *et al.* 2012) showing this is clearly the case, as the amount of variation in zooplankton communities and the percentage of total change in community ecological properties such as richness and diversity explained by *D. magna* adaptation ( $R_{\text{adj}}^2 = 0.113$ , 19%, and 20%, respectively) is comparable to that explained by artificial macrophyte addition ( $R_{\text{adj}}^2 = 0.154$ , 16%, and 15% respectively) and fish presence ( $R_{\text{adj}}^2 = 0.095$ , 19%, and 21% respectively) in our standardised and replicated mesocosm experiment. We therefore conclude that failing to consider genetic differentiation within species may partially account for the substantial unexplained fractions of community structure observed in nature.

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## Supplementary Information

### SUPPLEMENTARY METHODS

#### Generalized Linear Models

We tested the influence of treatments on *D. magna* abundance in mesocosms from the assembly experiment by fitting generalized linear models with artificial macrophytes (present vs. absent), fish (present vs. absent), local adaption (adapted vs. non-adapted), and their interactions as factors. We selected among a suite of models with various error structures (Gaussian, Poisson, negative binomial, Tweedie, zero-inflated Poisson, zero-inflated geometric, and zero-inflated negative binomial) by comparing their Akaike information criterion. We assessed significance of the model with the lowest AIC value by comparing the difference between its log likelihood value and the log likelihood value of a null model with no predictors using a  $\chi^2$  test. Significance of model coefficients was assessed with partial Wald tests. Analyses were conducted using R packages 'pscl' (Zeileis et al. 2008; Jackman 2015), 'tweedie' (Dunn 2014), and 'MASS' (Venables & Ripley 2002).

#### Treatment effect size and direction

To estimate the effects of *D. magna* adaptation, fish, artificial macrophytes, and their interactions on each ecological response variable  $X$ , we adapted the discrete-time approach presented by Ellner et al. (2011) to include three factors. We refer to each ecological response variable as  $X$  and the factors as  $k_f$ ,  $k_m$ , and  $g$  (for fish, artificial macrophytes, and *D. magna* adaptation, respectively). We solved the least-squares normal equation for the model coefficients of the following regression model:

$$X = \alpha_0 + \beta_g g + \beta_{k_f} k_f + \beta_{k_m} k_m + \gamma_{g \times k_f} g \times k_f + \gamma_{g \times k_m} g \times k_m + \gamma_{k_f \times k_m} k_f \times k_m + \gamma_{g \times k_f \times k_m} g \times k_f \times k_m + error ,$$

where  $\alpha_0$  is the intercept,  $\beta_g$ ,  $\beta_{k_f}$  and  $\beta_{k_m}$  are the main effects of *D. magna* adaptation, fish, and artificial macrophytes, respectively,  $\gamma_{g \times k_f}$  is the interaction effect between *D. magna* adaptation and fish,  $\gamma_{g \times k_m}$  is the interaction effect between *D. magna* adaptation and artificial macrophytes,  $\gamma_{k_f \times k_m}$  is the interaction effect of fish and artificial macrophytes, and  $\gamma_{g \times k_f \times k_m}$  is the three-way interaction effect. We solved the least-squares normal equation of the regression model by coding each factor as  $\pm 0.5$  (factor absent or present, instead of 0 or 1 as in Ellner et al. 2011; done because the Ellner et al. formulation is appropriate when there is a clear temporal directionality of genetic and environmental state change, while that is not the case in our analysis) and produced eight formulas to estimate effects. In the formulas,  $X_{ijk}$  represents the mean of variable  $X$  in the  $i$ th *D. magna* evolutionary history treatment (non-adapted or adapted,

$i = 1$  or  $2$ ), the  $j$ th fish environment (absent or present,  $j = 1$  or  $2$ ), and the  $k$ th artificial macrophyte environment (absent or present,  $k = 1$  or  $2$ ).

The overall effect of *D. magna* evolutionary history estimated the difference between  $X$  in mesocosms with adapted and non-adapted *D. magna*, averaged across each fish and artificial macrophyte environment state:

$$\beta_g = \frac{(X_{211} - X_{111}) + (X_{221} - X_{121}) + (X_{212} - X_{112}) + (X_{222} - X_{122})}{4}$$

The overall ecological effect of fish estimated the difference between  $X$  in mesocosms with fish present and absent, averaged across each *D. magna* evolutionary history and artificial macrophyte environment state:

$$\beta_{k_f} = \frac{(X_{121} - X_{111}) + (X_{221} - X_{211}) + (X_{122} - X_{112}) + (X_{222} - X_{212})}{4}$$

The overall ecological effect of artificial macrophytes estimated the difference between  $X$  in mesocosms with artificial macrophytes present and absent, averaged across each *D. magna* evolutionary history and fish environment state:

$$\beta_{k_m} = \frac{(X_{112} - X_{111}) + (X_{212} - X_{211}) + (X_{122} - X_{121}) + (X_{222} - X_{221})}{4}$$

The interaction between *D. magna* evolutionary history and fish environment estimated the extent to which an evolutionary effect in one fish environment differed from an evolutionary effect in the other fish environment, averaged across both artificial macrophyte environments:

$$\gamma_{g \times k_f} = \frac{\left[ \frac{(X_{221} - X_{121}) - (X_{211} - X_{111})}{2} \right] + \left[ \frac{(X_{222} - X_{122}) - (X_{212} - X_{112})}{2} \right]}{2}$$

The interaction between *D. magna* evolutionary history and artificial macrophyte environment estimated the extent to which an evolutionary effect in one artificial macrophyte environment differed from an evolutionary effect in the other artificial macrophyte environment, averaged across both fish environments:

$$\gamma_{g \times k_m} = \frac{\left[ \frac{(X_{212} - X_{112}) - (X_{211} - X_{111})}{2} \right] + \left[ \frac{(X_{222} - X_{122}) - (X_{221} - X_{121})}{2} \right]}{2}$$

The interaction between fish and artificial macrophyte environment estimated the extent to which a fish effect in one artificial macrophyte environment differed from a fish effect in the other artificial macrophyte environment, averaged across both *D. magna* evolutionary states:

$$\gamma_{k_f \times k_m} = \frac{\left[ \frac{(X_{222} - X_{212}) - (X_{221} - X_{211})}{2} \right] + \left[ \frac{(X_{122} - X_{112}) - (X_{121} - X_{111})}{2} \right]}{2}$$

We estimated the three-way interaction between *D. magna* evolutionary history, fish environment, and artificial macrophyte environment, which measures the extent to which the evolution×fish interactive effect varied across both artificial macrophyte environments:

$$\gamma_{g \times k_f \times k_m} = \frac{\left[ \frac{(X_{222} - X_{122}) - (X_{212} - X_{112})}{2} \right] - \left[ \frac{(X_{221} - X_{121}) - (X_{211} - X_{111})}{2} \right]}{2}$$

The intercept was estimated as the average of  $X$  in all states:

$$\alpha_0 = \frac{X_{121} + X_{111} + X_{221} + X_{211} + X_{122} + X_{112} + X_{222} + X_{212}}{8}$$

## SUPPLEMENTARY RESULTS

The best-fit model of *D. magna* abundance was a zero-inflated negative binomial regression model (Table S1). A zero-inflated model combines two processes, a point mass at zero and a proper count distribution (Zeileis 2008). The 'zero' component of the model was a binary model with a logit link function giving the probability of the zero mass and the 'count' component was a negative binomial model with a log link function giving the expected count of *D. magna*. The zero-inflated negative binomial model with seven regressors (the main effects of fish, artificial macrophytes, and *D. magna* adaptation, all two-way interactions, and their three-way interaction) for the count model and no regressors other than the intercept for the zero model (corresponding to a simple inflation model where all zero counts have the same probability of belonging to the zero component) had a lower AIC value (281.61) than a null model with no predictors (AIC = 290.11,  $p < 0.01$ ), a zero-inflated negative binomial model with all seven regressors for the zero model (AIC = 285.42), and a standard negative binomial model (AIC = 73870.23). Fish, artificial macrophytes, *D. magna* adaptation, and their interactions all significantly influenced the count of *D. magna* in this best-fit model (Table S2).

## SUPPLEMENTARY REFERENCES

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**Table S1** AIC values of all fit GLM models regressing *D. magna* abundance against fish, artificial macrophytes, *D. magna* adaptation, and their interactions.

family	link	AIC
Gaussian	log	474.30
Poisson	log	73890.00
negative binomial	log	73870.23
Tweedie	log (variance link = 1.2)	296.72
Tweedie	log (variance link = 1.4)	290.68
Tweedie	log (variance link = 1.6)	295.12
Tweedie	log (variance link = 1.8)	307.85
zero-inflated Poisson	log	14366.52
zero-inflated geometric	log	297.33
zero-inflated negative binomial	log	285.42

**Table S2** Results of zero-inflated binomial regression regressing *D. magna* abundance against fish, artificial macrophytes, *D. magna* adaptation, and their interactions.

model	term	estimate	standard error	z value	Pr(> z )
count	intercept	4.500	0.421	10.691	< 0.001
	fish	3.388	0.586	5.779	< 0.001
	adapted	3.538	0.586	6.036	< 0.001
	macrophytes	3.704	0.482	7.679	< 0.001
	fishxadapted	-2.311	0.822	-2.810	0.005
	fishxmacrophytes	-3.038	0.752	-4.041	< 0.001
	macrophytesxadapted	-2.675	0.674	-3.969	< 0.001
	fishxmacrophytesxadapted	2.049	1.018	2.013	0.044
	log(theta*)	1.795	0.382	4.696	< 0.001
zero	intercept	-0.167	0.410	-0.408	0.683

\*Theta is the dispersion parameter of the negative binomial distribution.

**Table S3** Results of MANOVA testing the effects of fish, macrophytes, adapted *D. magna*, and their interactions on the Hellinger abundance of zooplankton taxa.

Df	Pillai	approx F	num Df	den Df	Pr(>F)
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fish	1	0.761	3.582	8	9	<b>0.037</b>
macrophytes	1	0.892	9.319	8	9	<b>0.001</b>
adapted	1	0.822	5.201	8	9	<b>0.012</b>
fish×macrophytes	1	0.769	3.744	8	9	<b>0.033</b>
fish×adapted	1	0.595	1.656	8	9	0.234
macrophytes×adapted	1	0.644	2.031	8	9	0.156
fish×macrophytes×adapted	1	0.591	1.626	8	9	0.242
Residuals	16					

**Table S4** Results of ANOVA testing the effects of fish, macrophytes, adapted *D. magna*, and their interactions on Hellinger-transformed abundance for individual zooplankton taxa.

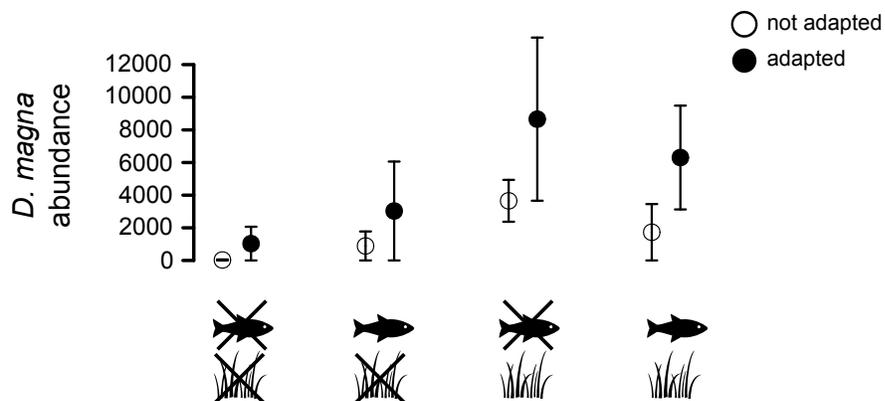
taxa	effect	df	SS	MS	F	p
Cyclopoida	fish	1	0.241	0.241	10.176	<b>0.006</b>
	macrophytes	1	0.009	0.009	0.376	0.548
	adapted	1	0.170	0.169	7.169	<b>0.017</b>
	fish×macrophytes	1	0.058	0.058	2.471	0.136
	fish×adapted	1	0.049	0.049	2.079	0.169
	macrophytes×adapted	1	0.013	0.013	0.534	0.475
	fish×macrophytes×adapted	1	0.009	0.009	0.370	0.552
	residuals	16	0.378	0.024		
D. longispina	fish	1	0.069	0.069	1.426	0.250
	macrophytes	1	0.031	0.031	0.636	0.437
	adapted	1	0.056	0.056	1.159	0.298
	fish×macrophytes	1	0.058	0.058	1.204	0.289
	fish×adapted	1	0.019	0.019	0.398	0.537
	macrophytes×adapted	1	0.012	0.012	0.247	0.626
	fish×macrophytes×adapted	1	0.012	0.012	0.239	0.631
	residuals	16	0.773	0.048		
D. pulex	fish	1	0.003	0.003	1.562	0.229
	macrophytes	1	0.000	0.000	0.091	0.767
	adapted	1	0.000	0.000	0.083	0.777
	fish×macrophytes	1	0.002	0.002	1.015	0.329
	fish×adapted	1	0.002	0.002	0.987	0.335
	macrophytes×adapted	1	0.000	0.000	0.002	0.964
	fish×macrophytes×adapted	1	0.001	0.001	0.437	0.518
	residuals	16	0.030	0.002		
S. vetulus	fish	1	0.011	0.011	0.384	0.544
	macrophytes	1	0.005	0.005	0.168	0.687
	adapted	1	0.154	0.154	5.252	<b>0.036</b>

	fish×macrophytes	1	0.013	0.013	0.439	0.517
	fish×adapted	1	0.193	0.193	6.579	<b>0.021</b>
	macrophytes×adapted	1	0.054	0.054	1.831	0.195
	fish×macrophytes×adapted	1	0.001	0.001	0.040	0.845
	residuals	16	0.470	0.029		
S. mucronata	fish	1	0.046	0.046	2.758	0.116
	macrophytes	1	0.108	0.108	6.496	<b>0.022</b>
	adapted	1	0.038	0.038	2.303	0.149
	fish×macrophytes	1	0.037	0.037	2.216	0.156
	fish×adapted	1	0.018	0.018	1.101	0.310
	macrophytes×adapted	1	0.067	0.067	4.006	0.063
	fish×macrophytes×adapted	1	0.025	0.025	1.492	0.240
	residuals	16	0.266	0.017		
Ceriodaphnia spp.	fish	1	0.002	0.002	0.139	0.714
	macrophytes	1	0.298	0.298	17.880	<b>0.001</b>
	adapted	1	0.007	0.007	0.402	0.535
	fish×macrophytes	1	0.002	0.002	0.127	0.726
	fish×adapted	1	0.002	0.002	0.148	0.706
	macrophytes×adapted	1	0.016	0.016	0.982	0.336
	fish×macrophytes×adapted	1	0.005	0.005	0.330	0.574
	residuals	16	0.267	0.017		
Chydoridae	fish	1	0.133	0.133	6.774	<b>0.019</b>
	macrophytes	1	0.364	0.364	18.623	<b>0.001</b>
	adapted	1	0.158	0.158	8.074	<b>0.012</b>
	fish×macrophytes	1	0.003	0.003	0.169	0.687
	fish×adapted	1	0.030	0.030	1.521	0.235
	macrophytes×adapted	1	0.045	0.045	2.322	0.147
	fish×macrophytes×adapted	1	0.027	0.027	1.395	0.255
	residuals	16	0.313	0.020		
B. longirostris	fish	1	0.012	0.012	1.142	0.301
	macrophytes	1	0.019	0.019	1.920	0.185
	adapted	1	0.032	0.032	3.150	0.095
	fish×macrophytes	1	0.000	0.000	0.005	0.943
	fish×adapted	1	0.004	0.004	0.413	0.529
	macrophytes×adapted	1	0.002	0.002	0.211	0.652
	fish×macrophytes×adapted	1	0.023	0.023	2.331	0.146
	residuals	16	0.161	0.010		

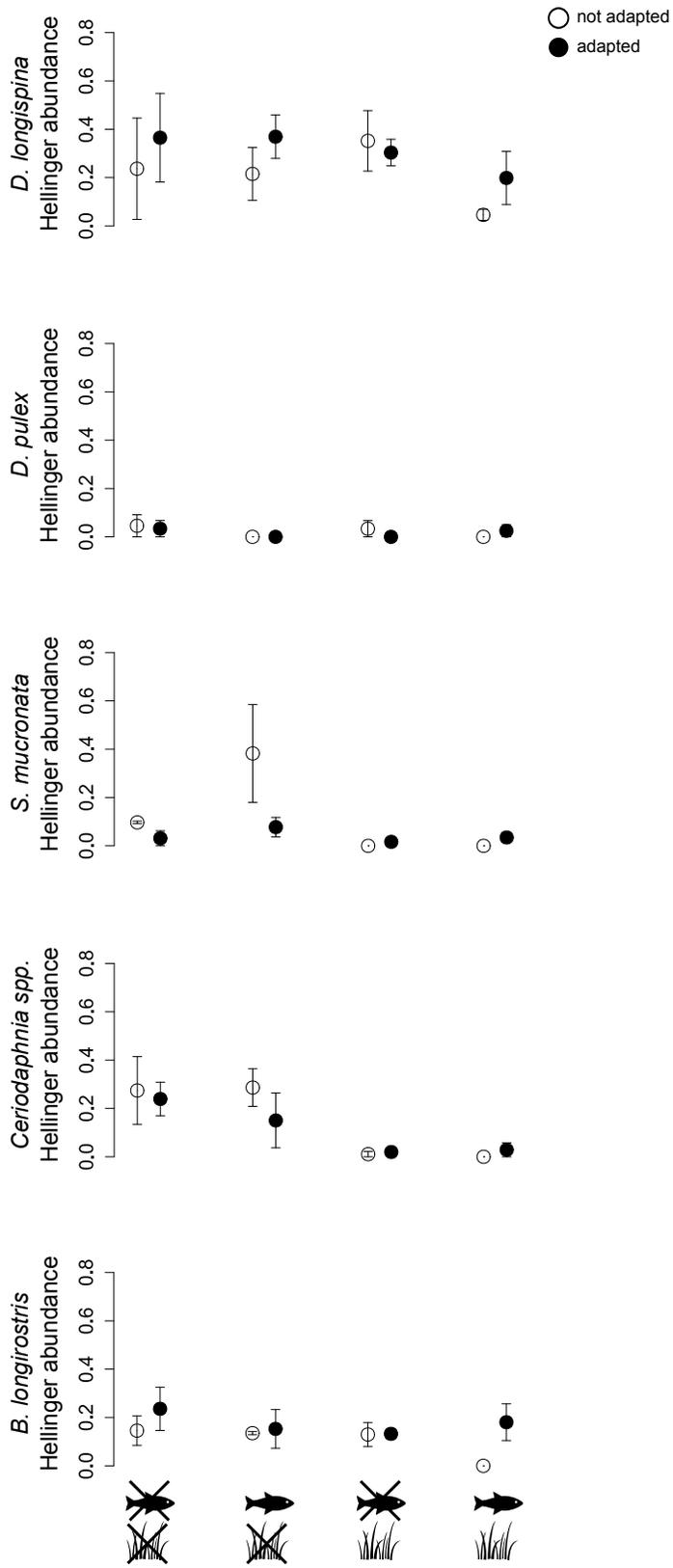
**Figure S1** Picture of mesocosm with a fish cage and artificial macrophytes used in the selection and community assembly experiment. In the fish treatment, the fish cage contained a single three-spined stickleback (*G. aculeatus*).



**Figure S2** Average ( $\pm 1$  s.e.) *D. magna* abundance (number of individuals in mesocosm) for all treatments in the community assembly experiment. Black points are for treatments with adapted *D. magna* and white points are for treatments with non-adapted *D. magna*.



**Figure S3** Average ( $\pm 1$  s.e.) Hellinger abundance for all treatments of (a) *D. longispina*, (b) *D. pulex*, (c) *Scapholeberis mucronata*, (d) *Ceriodaphnia* spp., and (e) *B. longirostris*. Black points are for treatments with adapted *D. magna* and white points are for treatments with non-adapted *D. magna*.



**Figure S4** Average partial contribution of each taxon to the Hellinger distance between zooplankton communities in the presence of adapted vs. non-adapted *D. magna* populations for all treatments in the assembly experiment.

partial contribution to Hellinger distance

