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Experimental thermal microevolution in community-embedded *Daphnia* populations

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ABSTRACT: There are an increasing number of studies documenting effects of global warming on the distribution and ecology of a wide variety of organisms. However, much less is known about evolutionary responses in species to increasing temperature. As a result, thermal microevolution is often ignored when making predictions about the impact of global warming on the distribution of organisms and the composition of communities. We investigated the ability of 2 large-bodied *Daphnia* species, *D. magna* and *D. pulex*, to genetically respond to increased temperature under semi-natural conditions. *Daphnia* populations were exposed for 6 mo to different temperature treatments in large outdoor mesocosms that simulated small pond systems. The selection experiment was followed by a common garden experiment in which we quantified thermal microevolution in important life history traits. Intrinsic growth rate did not respond to thermal selection. Instead, we observed an effect of selection temperature on size at maturity, indicating that *Daphnia* may genetically adapt to increased temperature within one growing season. In a previous laboratory study on thermal microevolution using single-species cultures of *D. magna*, we documented the opposite pattern with thermal microevolution in intrinsic growth rate but not in size at maturity. These observations suggest that the ecological context (semi-natural conditions compared to single species cultures) is very important in determining with which traits species adapt to global warming.

KEY WORDS: Rapid microevolution · Temperature adaptation · Global warming · *Daphnia* · Mesocosm experiment

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1. INTRODUCTION

Rapid climate change is one of the main drivers affecting biodiversity and ecosystems (IPCC 2007, Thuiller 2007). Insight into evolutionary responses to current rates of temperature increase is important to make predictions on the persistence of local populations under global warming. There is increasing evidence of rapid evolutionary responses to global warming (e.g. Bradshaw & Holzapfel 2006, Franks et al. 2007, Van Doorslaer et al. 2007, Jump et al. 2008). Yet evolutionary responses are often still ignored in simulation models aiming at predicting the impact of global warming on species, populations and ecosystems (but see Kearney et al. 2009), amongst other reasons because of a lack of information on the capacity of species to genetically adapt to rising temperatures (e.g. Pearson & Dawson 2003, Thuiller et al. 2008). Not incorporating evolutionary responses is likely to lead to erroneous predictions, as genetic change may profoundly alter ecological interactions (e.g. Skelly et al. 2007, Lennon & Martiny 2008, Loeuille & Leibold 2008, Urban & De Meester 2009). More specifically, in an evolutionary metacommunity context (Urban et al. 2008), evolu-

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tionary change may increase the importance of local dynamics and reduce the impact of regional dynamics. Results of a recent experiment with the water flea *Daphnia* indeed suggest that evolutionary adaptation may result in a reduced regional impact in the context of climate change (Van Doorslaer et al. 2009a).

The projected changes in temperature and precipitation are predicted to profoundly impact the characteristics and even the occurrence of freshwater ecosystems (e.g. Pyke 2005). In addition, an increase in temperature is expected to seriously impact the organisms inhabiting freshwater ecosystems. Most aquatic organisms are ectothermic, so their metabolic rates are directly controlled by ambient temperature. Under climate change, temperatures may also locally exceed the thermal tolerance limits of species (e.g. Stillman 2002). The impact of global warming on the presence and ecology of keystone species may therefore lead to cascading effects up or down the trophic web and thus impact freshwater ecosystem functioning (e.g. Poff et al. 2002, Jeppesen et al. 2010). Both direct and indirect temperature effects need to be considered, as temperature change may also impact the ecology of species through increased hypoxia or altered competitive, predatory and parasitic interactions, which are important in shaping the life history and fitness of many organisms (e.g. Moore et al. 1996). Despite the major changes freshwater ecosystems are facing under global warming, little research has been conducted to quantify the ability of freshwater species to genetically adapt to higher temperatures (but see Van Doorslaer et al. 2007, 2009a).

The main aim of the present study was to investigate the capacity of local populations of the water flea *Daphnia* to genetically adapt to increasing temperature related to global warming by using an experimental evolution approach under semi-natural conditions. A large-scale outdoor thermal selection experiment using mesocosms was carried out at the University of Liverpool, UK, simulating global warming under semi-natural field conditions. We quantified microevolutionary responses in life history traits in response to the temperature selection regimes through a life table experiment in a common garden environment at different temperatures. Experiments under semi-natural conditions have the added value of incorporating the complexity of trade-offs in relation to a diversity of selection pressures, including biotic stresses such as competition, predation and parasitism and abiotic stresses such as oxygen availability and light. We compared the results obtained in the present mesocosm experiment with those of a previous study in which we quantified the genetic response to a change in temperature of *D. magna* populations that were kept in isolation under standardized laboratory conditions (Van Doorslaer et al. 2009a). This comparison is informative on the impact of the ecological context (multi-species setting under semi-natural conditions compared to single-species cultures) on the characteristics of the microevolutionary response to rising temperature (Reznick & Ghalambor 2005).

2. MATERIALS AND METHODS

2.1. Study species and experimental set-up

The water fleas *Daphnia magna* (Straus 1820) and *D. pulex* (Leydig 1860) are keystone grazers in shallow freshwater ecosystems (Peters & de Bernardi 1987). They are strong competitors and fulfill an important ecological role by profoundly influencing phytoplankton communities in terms of biomass as well as species composition. As *Daphnia* are a preferred prey for both invertebrate and vertebrate predators, they act as an important link between the lower and higher trophic levels of the aquatic food web (Lampert 1987). Like most *Daphnia* species, *D. magna* and *D. pulex* are cyclic parthenogens that reproduce parthenogenetically when conditions are favourable and engage in sexual reproduction when environmental conditions deteriorate (De Meester et al. 2004). Sexual reproduction leads to the production of dormant eggs. As these hatch at the start of a new growing season, they yield a genetically diverse population due to the release of hidden genetic variation by sexual recombination (Lynch & Spitze 1994).

In October 2005, a 2-yr large-scale mesocosm experiment was initiated at the outdoor experimental area of the University of Liverpool at Ness Botanic Gardens (53° 16′ N, 3° 03′ W). This experiment involved exposure of active zooplankton communities (originating from ponds and shallow lakes in the vicinity of the experimental site) and a mixture of zooplankton dormant eggs from a natural population (Brown Moss, north Shropshire, UK), harbouring *Daphnia magna* and *D. pulex*, to all factorial combinations of 2 temperatures (ambient temperature [non-heated] and ambient temperature + 4°C [heated]; following IPCC climate predictions (IPCC 2001a,b); see also Houghton et al. 2001), 3 levels of nutrient loading (a standard nutrient load added every 2 wk; high level: 2500 µg l^{-1} N and 50 µg l^{-1} P; intermediate level: 250 µg l^{-1} N and 50 µg l^{-1} P; low level: no nutrient additions) and 2 levels of predation (presence or absence of sticklebacks *Gasterosteus aculeatus*). Each treatment combination was replicated 4 times, resulting in a total of 48 mesocosms of 3000 l each. Detailed information on the mesocosm experiment is given in Feuchtmayr et al. (2009); for a schematic overview, see Fig. 1. To ensure

the presence of *D. magna* in all mesocosms, we inoculated all mesocosms in March 2006 with the same set of 150 *D. magna* clones (one individual per clone) hatched from sediment collected from the same pond (Brown Moss) from which the dormant eggs that were inoculated in the mesocosms at the start of the experiment originated.

2.2. Quantifying microevolutionary responses

To study thermal microevolution in *Daphnia*, we focused on a subset of 6 mesocosm populations with intermediate nutrient level loading in the absence of fish, as these mesocosms harboured relatively dense populations of both study species (Fig. 1). We studied 3 replicate populations of the non-heated and heated mesocosms for *D. magna* and 2 replicate populations of both temperature treatments for *D. pulex* to compare thermal adaptation between the 2 temperature selection environments. In August 2006, after 6 mo of thermal selection, we collected a random set of 10 adult females of *D. magna* and 5 adult females of *D. pulex* from each mesocosm to establish clonal lineages, which were later used in a life table experiment at different temperatures.

In a common garden experiment, we quantified key life history variables at 2 test temperatures, 20 and 24°C, under standardized laboratory conditions. Test temperatures corresponded to the mean (± SE) summer temperatures in the mesocosm experiment (non-heated mesocosms: 20.40 ± 0.28°C, heated mesocosms: 24.14 ± 0.31°C). We evaluated in a life table experiment a total of 80 clones (*Daphnia magna*: 6 mesocosms × 10 clones; *D. pulex*: 4 mesocosms × 5 clones) for the presence of thermal microevolution in the mesocosms. Each clone was tested at the 2 test temperatures, and clones were used as replicates at the population level. This resulted in a total of 160 individuals.

To minimize interference from maternal effects, all animals were cultured for more than 5 generations under standardized conditions (14 h light:10 h dark, 20×10^6 algae cells per individual) before the actual start of the life table experiment. After several generations in the laboratory as clonal cultures in 500 ml jars, all clonal lineages were cultured for 2 generations as individuals in isolation, in 100 ml glass jars. Newborns of the second clutch were used to found the mother generation. When the mother individuals produced their second clutch, one juvenile was randomly assigned to each of the 2 test temperatures (20 and 24°C). After culturing the animals for another 2 generations at

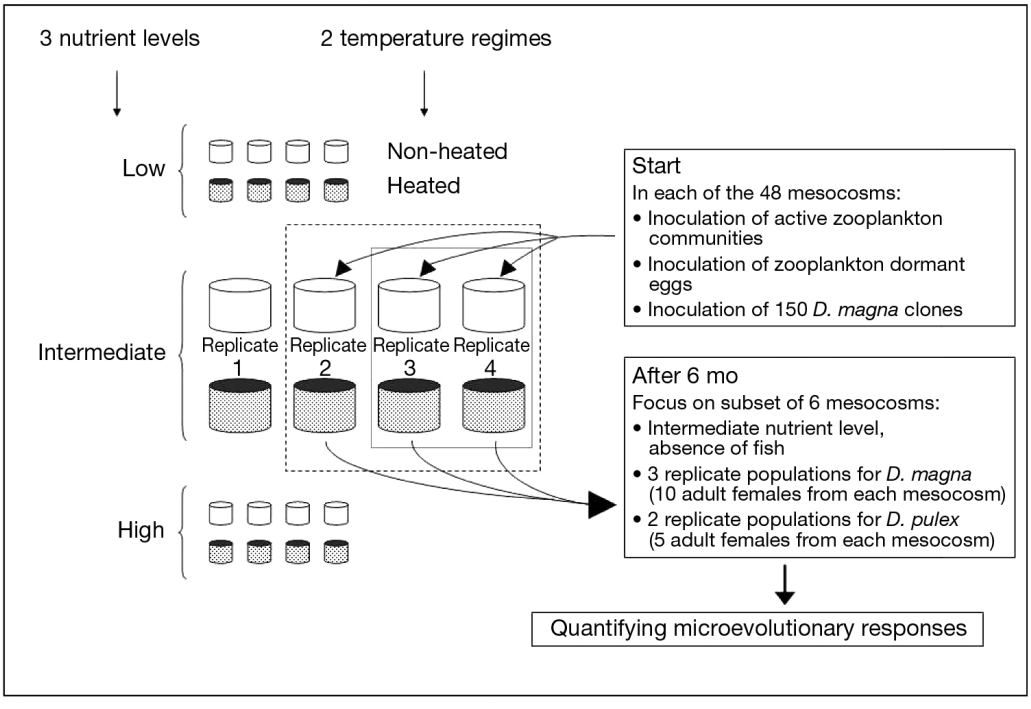

Fig. 1. Schematic overview of the experiment. A total of 48 mesocosm communities were exposed to all factorial combinations of 2 temperature regimes, 3 nutrient levels and 2 predation regimes (the last treatment is not shown). Each treatment was replicated 4 times. At the start, all mesocosms were inoculated with a mixture of active zooplankton communities, zooplankton dormant eggs and 150 clones of *Daphnia magna*. After 6 mo of thermal selection, *D. magna* and *D. pulex* were collected from a subset of heated and non-heated mesocosms of the intermediate nutrient level treatment without fish to evaluate the presence of thermal microevolution in a subsequent common garden experiment, in which life history traits were scored

their test temperature, the experimental generation started off with second-clutch juveniles all born within a 24 h time interval. These animals were checked daily and medium was refreshed every day until they produced their second clutch. To assess performance of clones, we calculated the intrinsic rate of natural increase, *r*, using the Lotka-Euler equation (see Van Doorslaer et al. 2007). In order to calculate *r*, we measured the following 4 life history traits: age at release of the first and the second clutch, and the number of offspring produced in the first and the second clutch. In addition, we measured size at maturity, as body size is an important life history trait that may be strongly influenced by temperature selection (cf. the temperature–size rule, Atkinson 1994) and is important in interactions with predators and competitors (e.g. Lampert 1987, Gliwicz 1990).

2.3. Monitoring the mesocosm populations

At the time we isolated the clones for the life table experiment (August 2006) we sampled the subset of 4 mesocosm populations harbouring both *Daphnia magna* and *D. pulex* using a tube sampler. We quantified population densities of both *Daphnia* species as an indication of their relative performance. An equal number of samples were taken from the outer edge and central zone of each mesocosm and pooled to a total of 40 l. All samples were poured through a zooplankton net (mesh size 50 µm) and fixed using sugar formalin (4%).

In addition, we monitored whether or not active populations of the 2 *Daphnia* species were present in all replicate mesocosms (n = 8, both temperature treatments, intermediate nutrient level, absence of fish) during the course of the entire 2 yr mesocosm experiment, with a total of 6 sampling events in spring (March 2006, 2007), early summer (July 2006, June 2007) and late summer (September 2006, August 2007).

2.4. Statistical analyses

We tested for the effect of selection temperature (i.e. mesocosm temperature), test temperature and species on 2 life history traits that are considered to be closely linked to fitness, namely *r* and size at maturity, using separate repeated-measures ANOVAs in the PROC MIXED module of SAS 9.1 (SAS Institute). We treated the responses of a clone measured at the 2 test temperatures as repeats and included mesocosm nested in selection temperature as a random factor in the model. We used the Satterthwaite approximation to estimate the denominator degrees of freedom.

We tested for the effect of selection temperature (i.e. mesocosm temperature) and species on *Daphnia* densities in the mesocosms using a repeated-measures ANOVA. We treated the densities of both species isolated from the same mesocosm as repeats of that mesocosm. To meet ANOVA assumptions, we performed a log + 1 transformation on *Daphnia* density. In a 1-way ANOVA, we tested for the effect of selection temperature on the relative abundance of *D. magna* to *D. pulex* in the mesocosms. Mesocosm nested in selection temperature was included as a random factor in the model.

3. RESULTS

3.1. Intrinsic rate of increase

r was higher at test temperature 24°C than at test temperature 20°C, and this effect was stronger for *Daphnia pulex* clones, as indicated by the significant test temperature × species interaction (Table 1, Fig. 2A). No effect of mesocosm temperature or interactions with mesocosm temperature was found, indicating no microevolutionary response for this trait.

3.2. Size at maturity

Daphnia pulex clones were smaller at maturity than *D. magna* clones (Table 1, Fig. 2B). For both species, size at maturity decreased with increasing test temperature. Overall, clones isolated from the heated mesocosms were larger than those isolated from the non-heated mesocosms, indicating a microevolutionary response for size at maturity after 6 mo of temperature adaptation

Table 1. Repeated-measures ANOVAs testing for the effect of mesocosm temperature, test temperature, species and their interactions on the intrinsic rate of natural increase *r* and size at maturity in *Daphnia magna* and *D. pulex*. Statistically significant differences ($p < 0.05$) are highlighted in **bold**; marginally significant differences ($p < 0.1$) are indicated by *

Effect	*r*			Size at maturity		
	df	*F*	p	df	*F*	p
Mesocosm temp (MT)	1, 4.48	1.43	0.29	1, 68.7	4.15	**0.046**
Test temp (TT)	1, 137	267.38	**<0.0001**	1, 68.3	23.09	**<0.0001**
Species (S)	1, 141	4.26	**0.041**	1, 68.7	572.90	**<0.0001**
MT × TT	1, 137	1.38	0.24	1, 68.3	2.17	0.15
MT × S	1, 141	2.08	0.15	1, 68.7	3.08	0.084*
TT × S	1, 137	6.42	**0.012**	1, 68.3	1.22	0.27
MT × TT × S	1, 137	0.20	0.66	1, 68.3	0.02	0.90

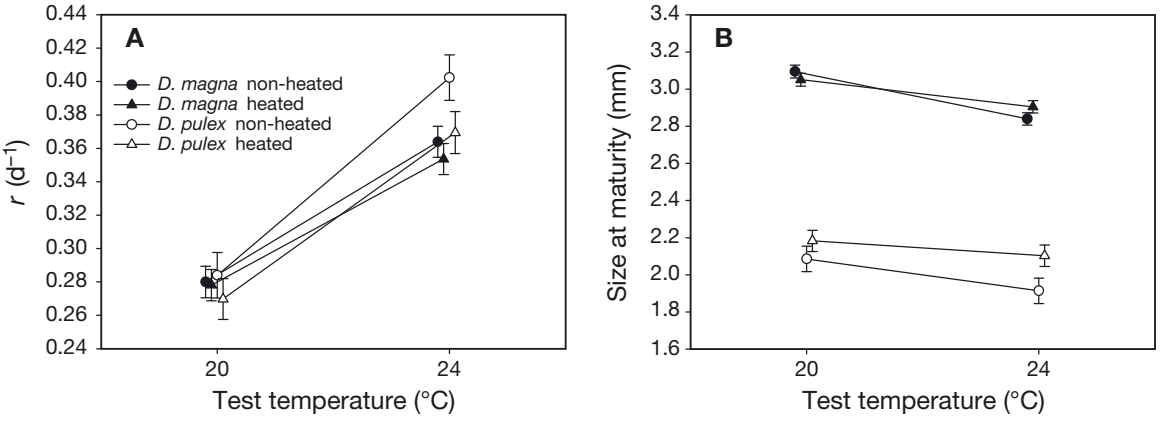

Fig. 2. *Daphnia magna* and *D. pulex*. (A) Intrinsic rate of natural increase, *r*, and (B) size at maturity as a function of mesocosm temperature, test temperature and species. Means are given ±1 SE

(Table 1, Fig. 2B). This effect tended to be more pronounced in *D. pulex* than in *D. magna*, as indicated by the marginally non-significant mesocosm temperature × species interaction (p = 0.084; Table 1, Fig. 2B).

3.3. *Daphnia* abundance in the mesocosms

A repeated-measures ANOVA showed that in August, *Daphnia* densities were lower in the heated mesocosms than in the non-heated mesocosms (mesocosm temperature: $F_{1,12}$ = 14.86, p = 0.023). There was no significant effect of species, indicating no differences in densities between the 2 species in the mesocosms ($F_{1,12}$ = 2.45, p = 0.14; Fig. 3A). A 1-way ANOVA on relative abundance of *D. magna* to *D. pulex* indicated, however, a tendency for the relative abundance of *D. magna* to be higher in the heated than in the non-heated mesocosms (mesocosm temperature: $F_{1,5}$ = 6.54, p = 0.051; Fig. 3B).

Fig. 4 shows that, overall, *Daphnia* population densities were higher throughout the season in the non-heated than in the heated mesocosms. In 2007, both *Daphnia* species had disappeared from most mesocosms in summer.

4. DISCUSSION

Both key life history traits, *r* and size at maturity, were highly dependent on test temperature. The observed thermal plasticity in both traits is in agreement with several other studies showing an increase in *r* and a decrease in size at maturity at higher temperature (e.g. in *Daphnia*: Mitchell & Lampert 2000, Weetman & Atkinson 2004). The latter result follows the temperature–size rule (Atkinson 1994; for an example in the copper butterfly, see Fischer & Karl 2010, this Special). After 6 mo of temperature selection in the mesocosms, however, we also found a microevolutionary response,

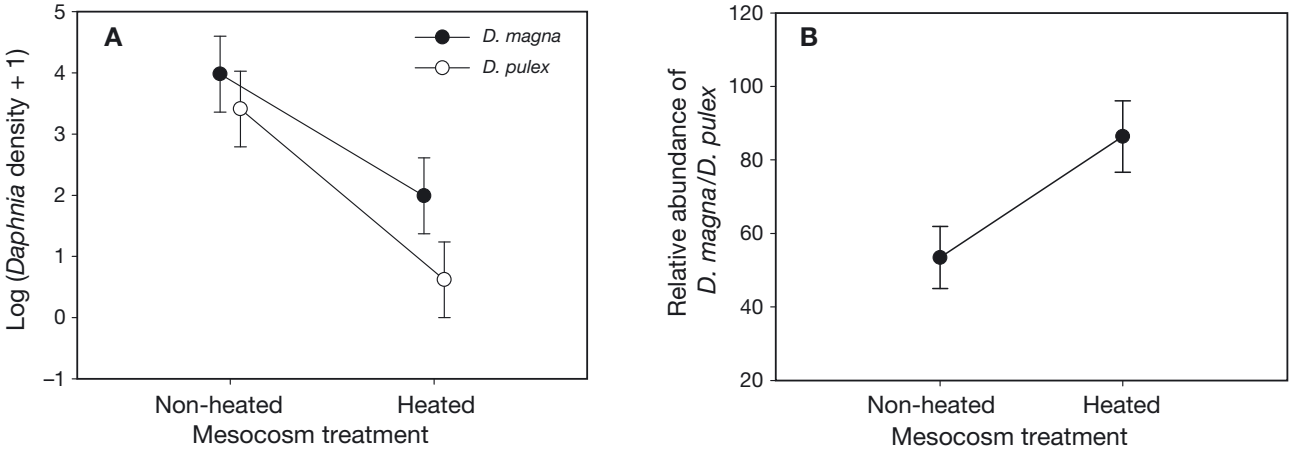

Fig. 3. *Daphnia magna* and *D. pulex*. (A) Population density of both *Daphnia* species and (B) relative abundance of *D. magna* to *D. pulex* as a function of mesocosm temperature 6 mo after the start of the mesocosm experiment (August 2006). Means are given ±1 SE

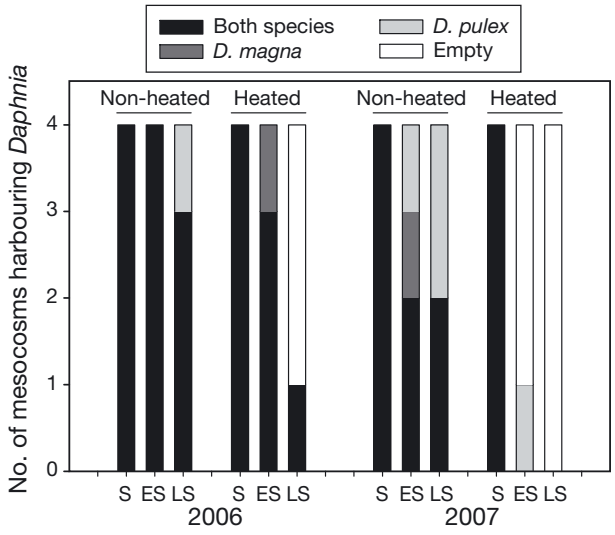

Fig. 4. *Daphnia magna* and *D. pulex*. Species presence in the 4 non-heated and 4 heated mesocosms that were monitored for *Daphnia* presence during the entire 2 yr experiment. Experimental mesocosm populations were monitored during 2 growing seasons (2006, 2007) in spring (S), early summer (ES) and late summer (LS)

with a larger size at maturity for both *D. magna* and *D. pulex* in the heated temperature treatment compared to the non-heated mesocosms. This indicates a fast evolutionary response. Intriguingly, the evolutionary response in both species is in the opposite direction to the plasticity response to test temperature. To a certain degree, the microevolutionary response thus compensates for temperature-induced plasticity. Although the observed microevolutionary response for size at maturity may seem not straightforward to explain in an adaptive context, this response may reflect the complexity of the selection environment we created in the mesocosms, as these mesocosms contained competitors, predators and parasites. As typical, the mesocosm approach, in which semi-natural conditions are established, trades off a higher level of realism against a full mechanistic understanding of the observed patterns. Yet there is evidence from a follow-up experiment that the microevolutionary changes we report here are adaptive. Van Doorslaer et al. (2009b) compared strength in competition of heat-adapted and non-heat-adapted genotypes from the present experiment in competition trials with a set of genotypes from southern France that are expected to be pre-adapted to the high temperature regime. In that experiment, we observed that the French genotypes performed better at high temperatures than the UK genotypes, but that the difference in fitness was smaller in the heat-adapted than in the non-heat-adapted UK genotypes. It thus seems that the compensatory microevolutionary response in terms of size at maturity is adaptive.

Both studied life history traits differed between the 2 *Daphnia* species studied. *D. magna* is at both temperatures by far the larger species of the two. *D. pulex* showed a higher *r* at test temperature 24°C compared to *D. magna*. This did not result, however, in higher population densities of *D. pulex* or a higher relative abundance of this species in the heated compared to the non-heated mesocosms. These observations are more in agreement with the size-efficiency hypothesis, stating that larger bodied species are better competitors for food than small-bodied species (see Gliwicz 1990), rather than the r-max hypothesis (i.e. species with the highest intrinsic rate of increase are the better competitors; Goulden et al. 1978). Although no differences in abundance of macroinvertebrate predators of *Daphnia* were observed between the heated and non-heated mesocosm communities (abundances of *Chaoborus* and *Notonecta*; R. Moran unpubl. data), the higher temperature in the heated mesocosms may have resulted in an increased activity of invertebrate predators (Weetman & Atkinson 2004). As these predators show a preference for small individuals (Zaret 1980), this might explain the decrease in relative abundance of *D. pulex* in the heated mesocosms. It may also be a driving force of the (partial) compensation for the temperature-induced plastic shift to smaller body size by microevolution in both species.

Evolutionary adaptation may strongly impact the response of populations and species to global warming (Schaefer et al. 2008, Van Doorslaer et al. 2009b). Yet the capacity to evolve should not be seen as a safeguard by itself (Gomulkiewicz & Holt 1995), for several reasons. First, there is the observation that global warming has already had a clear impact during the past decades, including species replacements, mismatches in interactions between species, local extinctions and invasion of warm-adapted species (e.g. Thomas et al. 2004, Hickling et al. 2006, Durant et al. 2007, van der Wal et al. 2008). Second, one should not expect perfect genetic tracking of changes in a way that the interactions of species with their abiotic environment or other species would not change. Species differ in their capacity to evolve because of differences in generation time, genetic variation and ecological, genetic and phylogenetic constraints. This will change interactions among species, including interactions with food, competitors, predators and parasites. In addition, genetic responses are complex and often involve trade-offs, so that evolutionary adaptation to global warming may make populations more vulnerable (e.g. through reduced energy or reduced evolutionary potential) to other stressors, including biotic interactions such as competition, predation and parasitism, as well as anthropogenic ones such as pollution or habitat fragmentation (e.g. Eränen et al. 2009, Joubert &

Bijlsma 2010, this Special). In short, temperature is not the only environmental selective force organisms encounter in their habitat. Indeed, in our experiment we observed that thermal evolution is no guarantee for survival of local populations, as several of the resident *Daphnia* populations in the high temperature mesocosms did not survive for the whole experimental period of 2 yr. Each year, populations of both species disappeared from the active community towards the end of the summer; this was more prominent in 2007 than in 2006 (Fig. 4). This is probably related to the massive occurrence of aquatic macrophytes during the summer of 2007, with the macrophytes, through competition, lowering the densities of phytoplankton, thus resulting in food shortage in *Daphnia* (Feuchtmayr et al. 2009). Although the *Daphnia* can re-emerge from dormant eggs during the next growing season, our results suggest that the microevolutionary response observed in our mesocosms is not sufficient for keeping their position as a dominant species in summer.

Starting with a random sample of clones originating from the same *Daphnia magna* population as used in the present experiment, we monitored genetic adaptation to increased temperature in a parallel laboratory experiment in which the *D. magna* populations were kept in isolation, i.e. in the absence of competitors, predators and parasites (Van Doorslaer et al. 2009a). Several aspects of the design were different between both experiments (size of the culturing units: 10 l aquaria vs. 3000 l mesocosms; ecological complexity: isolation vs. community; length of the selective protocol: 3 vs. 6 mo), making a direct quantitative comparison impossible. Yet crucial aspects of the 2 experiments are similar, such as the starting population (random collection of clones from the same natural population; 240 clones were used in the aquarium experiment whereas 150 clones were used in the present mesocosm experiment, but this difference in numbers is unlikely to strongly impact trait values) and selection and test temperatures. This allows a cautious qualitative assessment of the extent to which the ecological setting (semi-natural conditions in the mesocosms compared to no interspecific biotic interactions in the laboratory aquaria) influences the genetic response to increased temperature. We found thermal microevolution with respect to r in the laboratory (Van Doorslaer et al. 2009a), whereas in the present mesocosm experiment a genetic change in size at maturity in response to higher temperature was observed. This suggests that the ecological context is very important in determining with which traits the study species adapt to increased temperature. In their review on experimental studies, Reznick & Ghalambor (2005) similarly stress that studies under controlled laboratory conditions may yield quite different outcomes in stress responses of organisms compared to field studies where species are subjected to a wide variety of selective forces, including trade-offs between different stressors. Our observation that the broader ecological context (including both biotic and abiotic factors as well as direct and indirect effects) strongly influences the resulting microevolutionary responses is important, as it stresses the complexity of predicting evolutionary responses, and cautions against a too bold extrapolation of laboratory experiments that are carried out in an oversimplified environment. The observed response in size at maturity is not completely unexpected, given the importance of size at maturity in determining vulnerability to invertebrate and vertebrate predators as well as competitive strength (Lampert 1987).

Our results suggest that genetic adaptation to higher temperature can occur rapidly (for an example in fly species, see Rezende et al. 2010, this Special). Such rapid evolutionary responses may alter the ecological responses of populations and communities to environmental change (e.g. Yoshida et al. 2003, De Meester et al. 2007, Crutsinger et al. 2008, Lennon & Martiny 2008, Schaefer et al. 2008). It is therefore important to incorporate evolutionary responses in models that aim to predict the response of populations and communities to global warming (Skelly et al. 2007); this will allow more accurate predictions of climatic impacts on species' distribution ranges. For example, Kearney et al. (2009) demonstrated that incorporation of evolutionary responses in range-limiting traits (i.e. resistance to cold and egg desiccation resistance) in the mosquito *Aedes aeqypti* considerably increased the predicted probability of establishment in new regions under climate change. In order to quantify the impact of evolutionary responses on ecological interactions, we have, in a follow-up study, quantified the degree to which the observed genetic change in mesocosms influences the establishment success of southern immigrant genotypes, thus impacting effective migration from warmer regions (Van Doorslaer et al. 2009b). Using the selected *Daphnia magna* populations from the present mesocosm experiment in competition trials, we showed that the evolutionary changes in response to higher temperature reported here indeed have important ecological consequences as we observed a significant increase in the capacity of warm-adapted resident UK populations to compete with southern French immigrant genotypes (Van Doorslaer et al. 2009b).

In conclusion, we found a fast adaptive microevolutionary response in size at maturity in *Daphnia* populations exposed to increased temperature under semi-natural conditions. In a parallel experiment reported elsewhere, we also observed a fast genetic response in *Daphnia* to temperature change in isolated laboratory cultures (Van Doorslaer et al. 2009a). However, the

traits that showed a genetic change upon thermal selection differed among experiments, stressing the importance of ecological context in driving microevolution. Furthermore, in a follow-up study, we showed that the observed microevolutionary response reported here is indeed adaptive and has non-marginal ecological implications (Van Doorslaer et al. 2009b).

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