

# Climate change and evolution: disentangling environmental and genetic responses

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## Abstract

Rapid climate change is likely to impose strong selection pressures on traits important for fitness, and therefore, microevolution in response to climate-mediated selection is potentially an important mechanism mitigating negative consequences of climate change. We reviewed the empirical evidence for recent microevolutionary responses to climate change in longitudinal studies emphasizing the following three perspectives emerging from the published data. First, although signatures of climate change are clearly visible in many ecological processes, similar examples of microevolutionary responses in literature are in fact very rare. Second, the quality of evidence for microevolutionary responses to climate change is far from satisfactory as the documented responses are often — if not typically — based on nongenetic data. We reinforce the view that it is as important to make the distinction between genetic (evolutionary) and phenotypic (includes a nongenetic, plastic component) responses clear, as it is to understand the relative roles of plasticity and genetics in adaptation to climate change. Third, in order to illustrate the difficulties and their potential ubiquity in detection of microevolution in response to natural selection, we reviewed the quantitative genetic studies on microevolutionary responses to natural selection in the context of long-term studies of vertebrates. The available evidence points to the overall conclusion that many responses perceived as adaptations to changing environmental conditions could be environmentally induced plastic responses rather than microevolutionary adaptations. Hence, clear-cut evidence indicating a significant role for evolutionary adaptation to ongoing climate warming is conspicuously scarce.

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## Introduction

Almost every alteration in a species' environment — whether natural or human-induced, biotic or abiotic — is a potential source of new or intensified directional selection on traits important for fitness. When faced with new selection pressures — such as those imposed by ongoing climate change (Houghton *et al.* 2001; Jones *et al.* 2001) — populations can respond basically in three ways (e.g. Holt 1990, Davis *et al.* 2005). First, they can evade by dispersing to suitable habitats elsewhere. Second, they can stay put and adjust to the changed conditions by means of phenotypic

plasticity without altering their genetic constitution. Third, they can adapt to the changed conditions by means of genetic changes through the process of evolution. While evading will lead to local extinction but persistence elsewhere, phenotypic plasticity and adaptation can prevent local extinction.

The relative importance of these three different mechanisms as ways of coping with environmental changes is likely to vary depending on the timescale considered, organisms' life history, rate and extent of environmental change, and availability of alternative habitats and species' dispersal ability (Holt 1990; Meyers & Bull 2002; Sultan & Spencer 2002; Davis *et al.* 2005; Kokko & López-Sepulcre 2006). Naturally, a combination of these responses is also possible; perhaps even likely (Davis & Shaw 2001).

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There is no doubt that range-shifts are often important means of coping with climate change: evidence for such shifts in response to ongoing climatic changes is overwhelming (e.g. Parmesan & Yohe 2003; Root *et al.* 2003; Perry *et al.* 2005). Likewise, phenotypic plasticity provides an important mechanism to cope with changing environmental conditions (e.g. Bradshaw 1965; Przybylo *et al.* 2000; see below), but there are limits to plastic responses (de Jong 2005; Pigliucci 1996; DeWitt *et al.* 1998) and they are unlikely to provide long-term solutions for challenges faced by populations experiencing continued directional environmental change.

Although microevolutionary adaptations are generally envisioned to be ubiquitous (Hendry & Kinnison 2001 and references therein) and are a requisite for coping with environmental changes in the long run (e.g. Stockwell *et al.* 2003, e.g. Davis *et al.* 2005), no clear picture has yet emerged as to how effective microevolution will be in mitigating consequences of ongoing environmental changes. In fact, the views in this respect range from one extreme to another: while some treatments stress the importance of range shifts (e.g. Bradshaw & McNeilly 1991; Bradshaw 1991; Huntley 1991; Jackson *et al.* 2000) and others suggest an important role for plasticity (e.g. Przybylo *et al.* 2000; Price *et al.* 2003; Réale *et al.* 2003a; Réale *et al.* 2003b), many tend to stress the importance of adaptation (e.g. Davis & Shaw 2001, Berteaux *et al.* 2004; Pulido & Berthold 2004; Davis *et al.* 2005; Thomas 2005). This despite the fact that results of theoretical treatments suggest that predicted rate of climate warming may be too rapid for many populations to sustain continued response (Lynch & Lande 1993; Bürger & Lynch 1995; Lynch 1996; see also Gomulkiewicz & Holt 1995).

Disentangling microevolutionary responses from plastic responses is important for two reasons. First, phenotypic plasticity has some limits in terms of development (DeWitt *et al.* 1998): a plastic genotype is typically (at least in the long run) unable to develop as extreme phenotypes as it is possible to produce via microevolutionary responses. This limitation becomes important when environmental change progresses to a point where plastic responses cannot anymore mitigate loss of fitness. Second, coping with climate change via plastic responses is possible only as long as the relationship between existing reaction norm and fitness remains unchanged over time. However, this seems unlikely in the case of climate change. For instance, as the rate of temperature increase is predicted to vary between regions and seasons (Easterling *et al.* 1997; Luterbacher *et al.* 2004), and the life cycle of most species integrates more than one region and season (e.g. migratory birds), existing reaction norms are unlikely to remain adaptive in the future. This was illustrated by Visser *et al.* (1998) who demonstrated that climate change has disrupted the link between the cue controlling laying date and the peak in food abundance in great tits (*Parus major*). As a consequence, the

current reaction norm is no longer adaptive (Visser *et al.* 2006). Since the breeding-time reaction norm in this population is heritable (Nussey *et al.* 2005), phenotypic plasticity itself can evolve, but such changes would not classify as plastic responses but as examples of microevolution.

Here, our aim was to review and discuss the empirical evidence for microevolutionary responses to climate change in longitudinal studies. Although there have been several reviews of this topic both in the past (e.g. Holt 1990, Hoffmann & Blows 1993; Travis & Futuyma 1993) and more recently (Berteaux *et al.* 2004; Pulido & Berthold 2004; Davis *et al.* 2005; Jump & Penuelas 2005; Thomas 2005; see also Stockwell *et al.* 2003; Parmesan 2006), our treatment differs from these in several respects. In particular, we hope to emphasize the following three perspectives. First, although signatures of climate change are clearly visible in many ecological processes (e.g. Walther *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003, Parmesan 2006), similar examples of microevolutionary responses are in fact very rare. Second, the quality of evidence is far from satisfactory as the documented responses are often — if not typically — based on nongenetic data. We will reinforce the view that it is as important to make the distinction between genetic (evolutionary) and phenotypic (includes a nongenetic, plastic component) responses clear, as it is to understand the relative roles of plasticity and genetics in adaptation to climate change. Third, in order to highlight the difficulties involved in detection of microevolution in response to natural selection, we will review the studies on microevolutionary responses to natural selection from the perspective of quantitative genetics in the context of long-term studies of vertebrates.

### Evidence for adaptive responses — where is it?

During the past couple of decades, an increasing number of studies have documented 'rapid' evolutionary transitions that have occurred within a time span of a few generations or so (see Hendry & Kinnison 1999; Kinnison & Hendry 2001; Reznick & Ghalambor 2001; for reviews). This suggests that microevolutionary responses to recent climate change — if they are occurring — should also be detectable, at least in principle, even in relatively short time-series. Yet, many of the studies in animal and plant responses to temporal environmental heterogeneity in general, and to those in response to climate change in particular, often provide little evidence that microevolutionary responses would be frequently occurring.

One reason for this is that most of the available data does not allow us to evaluate whether any genetic response, and hence evolution, has actually occurred or not. In other words, most studies are purely phenotypic, and therefore, unable to separate plastic responses from genetic responses. This is illustrated, for instance, by counting the proportion

of studies providing genetic evidence for climate-mediated responses in the two recent meta-analyses (Parmesan & Yohe 2003; Root *et al.* 2003). Excluding all studies on range shifts, density and community changes in which the possible role of microevolution is hard to assess, we found that only three out of 105 studies in Parmesan & Yohe (2003) and Root *et al.* (2003) provide genetic evidence for observed population responses.

While neither of the meta-analyses mentioned above, nor most of the case studies included in them were designed to detect microevolutionary responses in the first place, one might expect to see better representation of genetic approaches in studies explicitly focused on detecting microevolutionary responses to environmental heterogeneity. A look at the recent general reviews on microevolution reveals that purely phenotypic data is still frequently used as a basis for evolutionary inference. For instance, 11 out of 47 examples of rapid evolution in Reznick & Ghalambor (2001) are based on purely phenotypic data. Similarly, the inference about microevolution in 11 out of 21 (52%) studies in Hendry & Kinnison (1999) and 25 out of 46 (54%) in Kinnison & Hendry (2001) were based on entirely phenotypic data.

The situation is even more unsatisfactory in the case of studies focusing on ecotypic variation in the context of global climate change (Millien *et al.* 2006). Several studies have recently discovered temporal decline in mean body size of birds (e.g. Yom-Tov 2001; Schmidt & Jensen 2005; Yom-Tov *et al.* 2006) and mammals (e.g. Smith *et al.* 1995; Schmidt & Jensen 2003; Millien 2004; Yom-Tov & Yom-Tov 2004), and these trends have been interpreted as microevolutionary responses to warming climate. Yet, none of the studies have provided evidence that the observed trends have a genetic basis. However convincing these kinds of temporal phenotypic trends are, longitudinal quantitative genetic studies reviewed below illustrate that these kinds of trends can also be expected in the absence of any genetic component to the observed changes.

Studies in avian breeding time advances in response to climate warming provide yet another context where information about genetic details is scarce. Since the early reports (Järvinen 1989; Crick *et al.* 1997) the number of studies reporting advancement of breeding dates with warming climate has increased tremendously (Bergmann 1999; Koike & Higuchi 2002; Both *et al.* 2005; Pearce-Higgins *et al.* 2005; Torti & Dunn 2005; Møller *et al.* 2006; and references in Parmesan & Yohe 2003; Root *et al.* 2003). Although there is some heterogeneity in observed responses among different studies, species (e.g. Crick *et al.* 1997) and populations (e.g. Sanz 2002; Visser *et al.* 2003; Both *et al.* 2004), the overall pattern is clearly in support of ubiquitous climate associated advancement of breeding schedules. Still, as clear as these patterns are, virtually none of the above-mentioned studies have measured climate medi-

ated selection on breeding time or addressed the critical question as to whether the observed advancement was a product of phenotypic plasticity or microevolution. In fact, there are only two avian studies which have been able to test for genetic basis of breeding time advancements, and neither of these found evidence for genetically based response (Sheldon *et al.* 2003; Gienapp *et al.* 2006). Admittedly, some genetic response might be taking place but its rate may be too low to be detected by available methods (Postma 2006). Yet, several studies have shown now that plastic responses can easily accommodate the observed climate responses in avian breeding time (e.g. Przybylo *et al.* 2000; Schiegg *et al.* 2002; Brommer *et al.* 2005; Nussey *et al.* 2005; Reed *et al.* 2006).

Under the assumption that much of the observed changes in avian breeding time in response to climate change are due to phenotypic plasticity as suggested by the evidence reviewed above, we can gain some insights on the potential importance of phenotypic plasticity by expressing the observed advances in breeding time in terms of haldanes ( $h$ ), i.e. per-generation advances in breeding times expressed in standard deviation units (Hendry & Kinnison 1999). Table 1 shows these rates for 20 case studies of birds, the average  $h$  equalling 0.19. As compared to typical rates of evolution, this value is very high; in their review of 224 haldane estimates, Hendry & Kinnison (1999) found that 92% did not exceed  $h = 0.18$ . If we were to assume that the haldane rates in Table 1 were microevolutionary responses, and that the typical heritability for breeding time is *c.* 0.3 (Sheldon *et al.* 2003; p. 416), this rate of evolution would correspond to selection intensity of approximately  $0.20/0.3 = 0.67$  standard deviation units in each generation (cf. Hendry & Kinnison 1999). This would be very strong selection for any trait (median selection intensity in Kingsolver *et al.* (2001) = 0.16), risking the population persistence due to a large number of selective deaths in each generation. Also, theoretical work (e.g. Lynch & Lande 1993; Bürger & Lynch 1995) suggested the maximum sustainable rate of evolution for even large populations should not exceed more than a few per cent of the phenotypic standard deviation per generation. As the average rate of change in haldanes is 19.2%, the observed advances in avian breeding time would be unsustainable from a microevolutionary point of view, suggesting an important role for phenotypic plasticity in mitigating fitness loss in climate-change responses.

### Evidence for genetic changes in response to climate change — recent case studies

Having emphasized above the lack of evidence for genetically based responses to climate change, it is instructive to look at the case studies where a microevolutionary response to climate change has been actually reported. Bradshaw &

**Table 1** Examples of avian studies reporting advances in mean egg-laying dates over time. Shown are the rates of change expressed in haldanes (SD unit/generation), days/year (slope of the regression of average egg-laying date against year; note that all trends reported here are statistically significant,  $P < 0.05$ ) and advancement over the study period

Species	Country	Slope (days/year)	Length of study (years)	Advancement (days)	Haldanes	Reference
<i>Ficedula hypoleuca</i>	CH	-0.31	23	6.8	-0.09	1
<i>Ficedula hypoleuca</i>	NL	-0.36	17	5.7	-0.11	1
<i>Ficedula hypoleuca</i>	NL	-0.34	22	7.5	-0.14	1
<i>Ficedula hypoleuca</i>	NL	-0.47	23	10.3	-0.14	1
<i>Ficedula hypoleuca</i>	NL	-0.42	23	8.6	-0.15	1
<i>Ficedula hypoleuca</i>	NL	-0.29	23	5.7	-0.11	1
<i>Ficedula hypoleuca</i>	D	-0.49	21	10.8	-0.17	1
<i>Ficedula hypoleuca</i>	D	-0.40	23	8.7	-0.14	1
<i>Parus major</i>	D	-0.24	26	6.0	-0.15	2
<i>Parus major</i>	B	-0.51	20	9.7	-0.22	3
<i>Parus major</i>	B	-0.67	20	12.7	-0.30	3
<i>Parus major</i>	NL	-0.40	20	7.7	-0.18	3
<i>Parus major</i>	UK	-0.53	20	10.0	-0.18	3
<i>Parus caeruleus</i>	D	-0.20	26	5.0	-0.12	2
<i>Parus caeruleus</i>	B	-0.54	20	10.2	-0.24	3
<i>Parus caeruleus</i>	B	-0.59	20	11.3	-0.23	3
<i>Parus caeruleus</i>	UK	-0.58	20	11.0	-0.22	3
<i>Sturnia philippensis</i>	JP	-0.73	15	14.6	-0.68	4
<i>Sterna paradisaea</i>	DK	-0.88	70	18.0	-0.23	5
<i>Aphelocoma ultramarina</i>	USA		28	10.1	-0.10	6
Average		-0.47	24	9.5	-0.20	

<sup>1</sup>Both *et al.* (2004), <sup>2</sup>Winkel & Hudde (1997); <sup>3</sup>Visser *et al.* (2003), <sup>4</sup>Koike & Higuchi (2002), <sup>5</sup>Møller *et al.* (2006), <sup>6</sup>Brown *et al.* (1999).

Holzapfel (2001) compared the length of the critical photoperiod that terminates diapause in pitcher-plant mosquitoes (*Wyeomyia smithii*) between populations sampled at different locations and in different years. Using laboratory experiments, they demonstrated that the critical photoperiod of the northern populations has shifted toward that of the southern populations over a 24-year period, apparently as a response to climate warming in the north, allowing mosquitoes to exploit a prolonged growth season.

Parallel latitudinal clines in body size, chromosomal arrangements and Adh polymorphism in *Drosophila* species have traditionally been interpreted in the context of climatic adaptation (e.g. James *et al.* 1997; Rodríguez-Trelles & Rodríguez 1998; Umina *et al.* 2005). Recent studies demonstrating temporal shifts in mean body size (Huey *et al.* 2000) and frequencies of different chromosomal arrangements (Levitan 2003; Levitan & Etges 2005; Balanya *et al.* 2006) and Adh alleles (Umina *et al.* 2005) provide some of the strongest evidence for microevolution in response to climate changes. Yet, the mechanisms or selective factors linking particular genotypes/phenotypes to climate are not well understood in these examples and require further studies to be established.

Warm spring temperatures and increased cone abundance have been associated with advanced parturition

dates in Canadian red squirrels (*Tamiasciurus hudsonicus*; Réale *et al.* 2003b). Using an 'animal model', Réale *et al.* (2003b) predicted breeding values for parturition date and demonstrated that the observed phenotypic changes were partly caused by phenotypic plasticity (87% of the change) and partly by an evolutionary response (13% of the change) to selection on parturition date (Réale *et al.* 2003a, b). The predicted microevolutionary change in parturition date coincided with the observed change in breeding values, providing additional support for the genetic basis of observed response. Apart from providing one of the first clear-cut examples of microevolutionary response to climate change, this study remains — at least to our knowledge — the only one where the relative importance of genetic and plastic components has been quantified.

Another possible example of climate-driven evolutionary response is provided by the evolution of new migration pattern in German blackcaps (*Sylvia atricapilla*; Berthold *et al.* 1992; Bearhop *et al.* 2005). The inference in this case study is patched together with an impressive variety of approaches and various lines of evidence but without explicit demonstration of involvement of climatic selection. In the same vein, the microevolutionary responses of Darwin's finches (*Geospiza fortis*) on two episodes of climate-mediated selection (Grant & Grant 1995, 2002)

provide one of the best documented examples of evolution in action. This work also nicely illustrates the context dependency and difficulty of predicting the course of evolutionary transitions (cf. Holt 1990): the selection imposed by drought favoured larger beaks in 1977 in absence of competition, and smaller beaks in 2004 when competition was involved (Grant & Grant 2006).

Another two recent studies worth mentioning in this context due to their important heuristic value, are those of Spottiswoode *et al.* (2006) and Jonzén *et al.* (2006) showing climate-mediated responses in spring arrival schedules of migrant birds. Although the inference put forth in these studies is consistent with microevolutionary explanations, lack of evidence for genetic responses precludes disentangling plastic and evolutionary responses even in these cases.

To sum up, a conclusive demonstration that a population has responded adaptively to climate change requires three conditions to be fulfilled. First, selection of the trait under consideration needs to be demonstrated or at least inferred. Second, reasonable evidence should be provided that this selection is caused by – or intimately linked to – climatic change. Alternatively, there should be good evidence to show that certain trait values are favoured over others under changed climatic conditions, e.g. by linking the trait to environmental conditions affected by climate change from knowledge of physiological mechanisms. Third, a genetic change in the trait in question has to be demonstrated: purely phenotypic measures will not suffice (e.g. Conover & Schultz 1995 see below). Fulfilling all these conditions in a single study can be a daunting but important task if we are to understand microevolution and avoid the potential fallacy of ‘adaptive story telling’ (cf. Gould & Lewontin 1979).

### Lessons from quantitative genetic studies of wild populations

From above, it should be clear that genetic evidence for microevolutionary responses to climate-mediated natural selection from longitudinal studies is rather uncommon, circumstantial, and often quite weak at best. While it is true that the current climate warming is so recent that the detection of possible evolutionary responses, especially in long-lived organisms, might be still lagging behind, the high prevalence of ecological signatures (e.g. Parmesan 2006) and high rates of microevolution even over short time intervals (Hendry & Kinnison 1999; Kinnison & Hendry 2001) suggests that this is not the whole story. One possible contributing factor to the paucity of evidence is a detectability problem: the responses might be taking place, but the methods used are not able to filter the response out of the observations. This could occur, for instance, if the genetic and environmental influences on a trait are

opposing each other over time as envisioned under the ‘counter-gradient’ hypothesis (Conover & Schultz 1995), or if the statistical power of the methods used is too low. Furthermore, constraints stemming from genetic correlations among traits (e.g. Etterson & Shaw 2001), lack of sufficient genetic variability (e.g. Hoffmann *et al.* 2003) and inbreeding in shrinking populations (e.g. Potvin & Tousignant 1996; Schiegg *et al.* 2002) have all been suggested to be constraining adaptation to climate change. Yet, one of the foremost possible reasons for the paucity of solid evidence for microevolutionary responses is simply that the needed genetic evidence is hard to obtain. While molecular genetic basis of most traits of ecological importance are yet to be uncovered (but see French-Constant *et al.* 1993; McKenzie & Batterham 1998; Raymond *et al.* 2001; Rank & Dahlhoff 2002; Colosimo *et al.* 2004, 2005; Abzhanov *et al.* 2006; Hanski & Saccheri 2006), quantitative genetic approaches provide—at least in principle—a readily available framework to investigate (e.g. Réale *et al.* 2003b; Gienapp *et al.* 2006) and evaluate (e.g. Billington & Pelham 1991; Savolainen *et al.* 2004) the interplay between selection and genetics in the context of climate change. In what follows, we will briefly summarize a few lessons for climate-change studies born out of the research in long-term studies of vertebrates. Although most of these studies do not explicitly deal with climate-change-driven selection (but see Réale *et al.* 2003b; Gienapp *et al.* 2006), they do serve to illustrate some of the problems that might be faced by studies seeking to detect climate-change-driven microevolutionary responses, or by studies inferring microevolutionary responses from phenotypic data.

### Expected vs. observed selection responses

A straightforward prediction from quantitative genetic theory is that heritable traits under consistent directional selection should respond to selection according to the simple relationship given by the equation (Falconer & Mackay 1996):

$$R = h^2 * S \quad (\text{eqn 1})$$

where  $R$  is the selection response (phenotypic) over one generation,  $h^2$  is the heritability of the trait and  $S$  is the selection differential, indicating intensity and direction (sign) of the selection acting on a given trait. The utility and accuracy of this predictive model depends on a number of assumptions (e.g. Falconer & Mackay 1996; Merilä *et al.* 2001c; Kruuk *et al.* 2003), namely: (i)  $h^2$  and  $S$  have been reasonably well estimated, (ii) there are no constraining genetic correlations between focal and other traits, and (iii) the environment influencing trait expression has remained constant over generations. If these assumptions are met, the equation should provide a reasonable approximation of  $R$ , or at least its sign.

Yet, as pointed out by Merilä *et al.* (2001c), the observed and expected selection responses from studies in the wild are frequently in conflict with each other. To illustrate this, we summarized the available evidence for expected and observed selection responses from long-term studies of vertebrates (see Table S1 for more details). Of the 30 cases in which the traits were found to be under directional natural selection and heritable, a phenotypic response to expected direction was seen in 40% ( $n = 12$ ) of the cases. In six (20%) cases, the response was in the opposite direction than expected, and in 12 (40%) cases, there was no observable response. Hence, in 60% of the cases, there was a discrepancy between the observed and expected selection responses.

There are a number of possible methodological and biological explanations for these discrepancies (see Merilä *et al.* 2001c for detailed discussion), but there is also substantial evidence to indicate that one of the main reasons might be the frequent violation of the assumption that the environment has remained constant over generations (Cooke *et al.* 1990; Cooch *et al.* 1991; Merilä *et al.* 2001a; Garant *et al.* 2004a). If so, the results reviewed in Table S1 underline the difficulty of basing evolutionary inference on purely phenotypic data: a heritable trait under directional selection may not always display a response to selection. Conversely, a heritable trait under directional selection exhibiting a significant change in its mean value over generations — as in the case of studies listed in Table 1 — is not itself proof that it has responded to selection. Also, the timescale of the study is important: in long-lived organisms, viability selection operating during the timescale of a study can shift phenotypic distributions within a generation without any evolutionary response. A demonstration that a trait has responded to microevolution requires either a common garden experiment (e.g. Bradshaw & McNeilly 1991) or statistical control over environmental influences on the expression of the trait of interest (e.g. Réale *et al.* 2003b).

#### *Phenotypic vs. genetic trends in population means*

Information about actual genetic — rather than phenotypic (includes an environmental component) — changes in mean trait values between generations can be achieved using predicted breeding values estimable from pedigree-based data with an ‘animal model’ approach (Kruuk 2004). Population means of these breeding values — which in essence are measures of the total additive genetic effects on the trait (Lynch & Walsh 1998) — can then be compared across time (or space) to test for changes in the genetic composition of the population over time (or space).

To illustrate the utility of the predicted breeding values in inferring causes of temporal changes in mean phenotypes over time, we compiled data on breeding values from long-term studies of wild populations and asked how

often the observed trends in phenotypic means were concordant with trends in mean predicted breeding values (i.e. underlying genetic trends).

We found altogether 15 studies of nine species which had estimated both mean phenotypic and mean predicted breeding values for at least one trait (Table 2). Altogether, these studies report 23 pairwise estimates, many of which may not be independent because of correlations between traits and because the same data has been analysed for different fractions of the given population. Focusing on those traits which display a significant change in phenotypes or genotypes over time ( $n = 14$ ), we found that in only five cases (36%) phenotypes and breeding values show a qualitatively consistent trend (Table 2). If we restrict the focus to only those seven cases where both the phenotypic and genetic trends are statistically significant, five (71%) of them classify as concordant and two (29%) as clearly discordant (Table 2). Hence, the phenotypic trends are not concordant with genotypic trends in a fair proportion of the cases. How should we interpret these findings and reconcile them with the notion of ‘rapid evolution’ and climate-change responses?

#### **Explaining the discrepancies**

For the first, in cases where observations meet the expectations, there should not be too much to worry: populations are responding to selection as expected giving us some confidence to believe that responses to selection are not hopelessly constrained by ecological or genetic complexity. Furthermore, many of the data sets reviewed above are actually rather short relative to the study organisms’ generation times. Given that the observed rates of evolution scale negatively with generation time (Hendry & Kinnison 2001), it is possible that the data above is biased towards making detection of (small) selection responses difficult. This detection problem might be especially relevant in cases where expected selection responses are small compared to annual fluctuations in highly plastic traits such as avian breeding time. As suggested by Gienapp *et al.* (2006; see also Sheldon *et al.* 2003), detection of a selection response at the phenotypic level in such cases can become a simple matter of statistical power.

Having said this, it is also important to point out a possible bias toward the converse; as pointed out by Postma (2006), parallelism in phenotypic and breeding values over time provides evidence for the genetic basis of the observed phenotypic trend only under the assumption that the breeding values have been properly estimated. If the information content of pedigrees used to predict breeding values is poor, and/or there is a failure to correct for obvious environmental effects (e.g. site and year effects), the predicted breeding values may become biased towards the phenotypic values (Postma 2006). If so, this could give

**Table 2** Trends in mean phenotypic and mean predicted breeding values for quantitative traits from studies of wild populations. Plus or minus indicates a significant increase/decrease; zero indicates no significant trend. Only significant trends of phenotypes and genotypes in the same direction were interpreted as consistent, all other combinations as inconsistent. Cases where both phenotypic and genetic trend was significant are highlighted with bold font

Species	Trait	No. of years	Phenotypic	Genotypic	Change	Reference
<i>Cervus elaphus</i>	Antler mass	24	–	0	Inconsistent	1
<i>Ovis canadensis</i>	Body size	29	–	–	<b>Consistent</b>	2
<i>Ovis canadensis</i>	Horn size	26	–	–	<b>Consistent</b>	2
<i>Tamiasciurus hudsonicus</i>	Parturition date	10	–	–	<b>Consistent</b>	3
<i>Cygnus olor</i>	Clutch size	26	+	+	<b>Consistent</b>	4
<i>Larus novahollandiae</i>	Body weight	42	–	0	Inconsistent	5
<i>Ficedula albicollis</i>	Body condition	18	–	+	<b>Inconsistent</b>	6
<i>Ficedula albicollis</i>	Forehead patch (old)	22	–	0	Inconsistent	7
<i>Ficedula albicollis</i>	Wing patch (old)	22	–	0	Inconsistent	7
<i>Ficedula albicollis</i>	Laying date	20	0	0	Consistent*	8
<i>Ficedula albicollis</i>	Tarsus length	18	0	0	Consistent	9
<i>Parus caeruleus</i>	Body mass (M population)	9	0	0	Consistent*	10
<i>Parus caeruleus</i>	Body mass (P population)	14	0	0	Consistent*	10
<i>Parus caeruleus</i>	Body mass (R population)	12	0	0	Consistent*	10
<i>Parus caeruleus</i>	Tarsus length (M population)	9	0	0	Consistent*	10
<i>Parus caeruleus</i>	Tarsus length (P population)	13	0	0	Consistent*	10
<i>Parus caeruleus</i>	Tarsus length (R population)	12	0	0	Consistent†	10
<i>Parus major</i>	Fledging mass (East Wytham)	36	–	–	<b>Consistent</b>	11
<i>Parus major</i>	Fledging mass (North Wytham)	36	0	+	Inconsistent	11
<i>Parus major</i>	Fledging mass	36	–	+	<b>Inconsistent</b>	12
<i>Parus major</i>	Laying date	31	0	0	Consistent	13
<i>Perisoreus infaustus</i>	Body weight	20	–	0	Inconsistent	14
<i>Perisoreus infaustus</i>	Body weight	10	+	0	Inconsistent	14

<sup>1</sup>Kruuk *et al.* 2002, <sup>2</sup>Coltman *et al.* 2005, <sup>3</sup>Réale *et al.* (2003b), <sup>4</sup>Charmantier *et al.* 2006, <sup>5</sup>Teplitsky, Milis, Alho & Merilä, unpublished data, <sup>6</sup>Merilä *et al.* (2001a), <sup>7</sup>Garant *et al.* 2004b, <sup>8</sup>Sheldon *et al.* (2003), <sup>9</sup>Kruuk *et al.* (2001), <sup>10</sup>Charmantier *et al.* 2004, <sup>11</sup>Garant *et al.* (2004a), <sup>12</sup>Garant *et al.* (2004a), <sup>13</sup>Gienapp *et al.* (2006), <sup>14</sup>Gienapp, Alho, Lillandt & Merilä, unpublished data.

\*Derived from figures in the reference; †genotypic data derived from data from figures in the reference.

the false impression of microevolutionary response over time. Accounting for this possible source of bias becomes especially important in studies of climate-change responses when both environmental and genetic influences on trait means are expected to change over time in parallel fashion.

Turning to cases where estimates of genetic and phenotypic patterns were nonconcordant, the cases where phenotypic means were changing without corresponding genetic trends provide an important lesson for studies of climate-change responses. Namely, they show that directional changes in population mean phenotypes comparable to those observed in many purely phenotypic studies (e.g. Millien *et al.* 2006; Table 1) can occur due to simple environmental induction. The results from the red-billed gulls (*Larus novahollandiae*; Table 2) are a case in point: the mean body size in this population has declined steadily over the 44-year long (1958–2002) study period, but the breeding values — estimated from large (> 16 000 individuals) pedigrees — show absolutely no trend over the same time

period (Celine Teplitsky, James A. Mills, Jussi Alho and Juha Merilä, unpublished data). Since the mean average ambient temperatures in this New Zealand study population have increased over the study period (D. Wratt and J. Salinger, personal communication), inference based on phenotypic means would lead support to the 'adaptive' climate response explanation (*sensu* Millien *et al.* 2006). Yet, the absence of any signal of selection in estimated breeding values, as well as the absence of any consistent selection on body size over this period suggests that the phenotypic trend is a simple reflection of directional change in environmental conditions experienced during the development.

In two of case studies listed in Table 2, the temporal patterns of phenotypic and genetic divergence were opposing each other. Although examples of this kind of opposing patterns in temporal data sets are still relatively rare (Table 2, Merilä *et al.* 2001a; Garant *et al.* 2004a), the phenomenon — recognized a good while ago (Levins 1969) and termed as counter-gradient variation by Conover & Schultz (1995) —

is apparently quite frequent in the context of spatial differentiation (e.g. Conover & Schultz 1995; Arendt & Wilson 1999; Laugen *et al.* 2003). Occurrence of counter-gradient variation in temporal data sets underline the contention that inferences about rates and directions of microevolution based on temporal changes in the mean values of phenotypic traits in the wild can easily end up being grossly misleading.

Counter-gradient phenomenon may be important in the context of climate-change response also because it may lead to rapid phenotypic changes — even in absence of genetic changes — if the environmental constraints suppressing the genetic (and hence also phenotypic) expression of traits are suddenly removed. For instance, given all else equal, increased ambient temperatures at high altitudes and latitudes can be expected to release many ectothermic organisms from constraints imposed by low ambient temperatures which could be easily — and erroneously — perceived as genetic responses to climate change. Such a response would be expected, e.g. in developmental and growth rates of amphibians displaying counter-gradient variation along altitudinal (e.g. Berven *et al.* 1979; Berven & Gill 1983) and latitudinal (e.g. Laugen *et al.* 2003) clines.

Finally, and for the sake of completeness, we note that some of discrepancies listed above and in Table 2 might be due to other methodological and biological issues not covered above. For instance, unrealistic selection response expectations could result from overestimated heritabilities due to spatial or temporal auto-correlation of environmental effects among relatives (e.g. van der Jeugd & McCleery 2002). Yet, at least the animal-model-based estimates should be fairly robust against this caveat (Kruuk 2004). However, since the amount of additive genetic variance expressed at phenotypic level may depend on environmental conditions (Hoffmann & Merilä 1999; Charmantier & Garant 2005), negative temporal covariance between heritability and selection intensity — as demonstrated recently in study of Soay sheep (*Ovis ares*) (Wilson *et al.* 2006) — might also bias the expectations upwards. Although it seems unlikely that a lack of genetic variation would turn out to be the major obstacle for climate-change responses except when population sizes are small (Potvin & Tousignant 1996), this may well be the case in some particular instances already at the outset (e.g. Hoffmann *et al.* 2003).

Another potential explanation for the lack of correspondence between expected and observed selection responses is biased estimates of intensity of selection either due to problems with fitness estimates (Sheldon *et al.* 2003) or due to environmental covariance between fitness and the trait in focus (Scheiner *et al.* 2002; Stinchcombe *et al.* 2002; Kruuk *et al.* 2003). The details are beyond the scope of this review, but several recent studies have tested for environmental bias in selection (Kruuk *et al.* 2001, 2002; Merilä *et al.* 2001b; Gienapp *et al.* 2006). Of these, only Kruuk *et al.* (2002) found strong evidence for environmental

covariance between fitness and the focal trait, suggesting that the lack of expected selection response in the antler size of red deer (*Cervus ephalus*; Table 2) was probably due to a spurious correlation between fitness and antler size.

Last but not least, gene flow can be a source of discrepancy between observed and expected responses. Most wild populations are not closed and immigrants can make up a substantial fraction of breeders. It is typically assumed that immigrants have undergone a similar selection and that they have a similar genetic background as the local individuals, which may not be true (e.g. Garant *et al.* 2005; Postma & van Noordwijk 2005). Again, although immigration has a potential to explain the discrepancies between observed and expected evolutionary transitions, it cannot explain the discrepancies in closed island populations, such as in those of collared flycatchers and red deer in Table 2. Nevertheless, as exemplified in the two case studies above, immigration can be a potent factor influencing microevolution — or the lack of it thereof — in response to climate change in most continental populations subject to range shifts (e.g. Møller & Merilä 2004).

To sum up, in the light of the discussion and examples above, it is quite clear that changes in environmental conditions might trigger phenotypic responses observable as changes in population mean trait values without any (at least immediate) corresponding changes at the genetic level of the population. Therefore, caution should be exercised in interpretations of changes in population mean values as a response to directional environmental changes.

## Future

Given the logistical difficulties in inferring evolutionary responses with quantitative genetic methods, genomic approaches based on the detection of changes in actual genes or genomic regions involved with adaptation to changing environments may provide alternatives to identify adaptations (e.g. Jump *et al.* 2006; Hoffmann & Daborn 2007). These types of approaches are likely to be most useful for traits with a relatively simple genetic basis, and more challenging in the case of complex polygenic traits such as body size. Furthermore, as illustrated by studies which have picked up clear signatures of climate-change-driven microevolution with genetic markers (Umina *et al.* 2005; Balanya *et al.* 2006), pinning down the actual target or mechanism of selection may be difficult. For instance, even after several decades of research, it remains unclear why *Adh* and chromosomal polymorphisms in *Drosophila* are selected differently in different climatic conditions. Nevertheless, as exemplified by several recent studies in other contexts (e.g. Abzhanov *et al.* 2004; Colosimo *et al.* 2004; Shapiro *et al.* 2004; Abzhanov *et al.* 2006; Hanski & Saccheri 2006), functional polymorphisms with known ecological relevance are becoming uncovered with increasing pace.

Another way to gain a better understanding of the relative roles of genetic adaptation and phenotypic plasticity in climate-change responses — as well as allow identifying the causal agents of selection — is to do experimental work. Organisms with short generation times (e.g. *Drosophila* or bacteria) could be used in experiments in which populations are pushed past the limits of normally experienced (and ecologically relevant) environmental ranges to see what the plastic and microevolutionary responses are. While such studies can be always criticized from scarification of ecological and evolutionary realism, they could be at least used as rigorous complements to studies in the wild.

## Conclusions

Taken together, while the evidence for climate- and habitat-change-driven phenotypic responses in wild populations is indisputable, it is often far less clear what the underlying mechanisms are causing these changes. The evidence reviewed here points to the conclusion that many responses perceived as adaptations to changing environmental conditions could be environmentally induced plastic responses. At the same time, cryptic genetic changes masked by environmental heterogeneity are possible, and apparently even quite common. This highlights the fundamental importance of using detailed genetic data when inferring the nature of phenotypic responses to changing environments. All in all, our understanding of microevolutionary adaptation to climate change is still very much at the same point as it was over 15 years ago when Holt (1990) noted that: 'There is almost no species for which we know enough relevant ecology, physiology and genetics to predict its evolutionary response to climate change'. Sadly, in one of the best-understood cases where such a prediction is possible, it is that extinction rather than adaptation is a likely outcome of climate warming (Hoffmann *et al.* 2003).

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Philip Gienapp, Celine Teplitsky, Jussi Alho and Juha Merilä work with avian long-term data sets in context of evolution and adaptation to environmental heterogeneity mainly using quantitative genetic approaches. James A. Mills has been studying and collecting data on Red-billed Gull population breeding in Kaikoura, New Zealand, and is interested on various aspects of population biology of this species.

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## Supplementary material

The following supplementary material is available for this article:

**Table S1** Long-term studies on wild population of vertebrates, which have estimated heritabilities ( $h^2$ ), selection intensities ( $s'$ ) and selection gradients ( $\beta$ ) and made predictions about expected and observed responses to selection.

This material is available as part of the online article from:

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