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INVITED REVIEW

Monitoring adaptive genetic responses to environmental change

MICHAEL M. HANSEN,* ISABELLE OLIVIERI,† DONALD M. WALLER,‡ EINAR E. NIELSEN§ and THE GEM WORKING GROUP¶

Department of Bioscience, Aarhus University, Ny Munkegade 114, DK-8000 Aarhus C, Denmark, †Institut des Sciences de l'Evolution de Montpellier (ISEM), Université Montpellier II, CNRS, UMR 5554, 34095 Montpellier Cedex 05, France, ‡Department of Botany, University of Wisconsin-Madison, Madison, WI 53706, USA, §National Institute of Aquatic Resources, Technical University of Denmark, Vejlsøvej 39, DK-8600 Silkeborg, Denmark, ¶The NCEAS/NESCent Working Group on Genetic Monitoring (GeM) is chaired by F.W. Allendorf, University of Montana, USA, and M.K. Schwartz, USDA Forest Service, USA. The other members are: C.S. Baker (Oregon State University, USA), D.P. Gregovich (University of Alaska, USA), M.M. Hansen (Aarhus University, Denmark), J.A. Jackson (Oregon State University, USA), K.C. Kendall (US Geological Survey, USA), L. Laikre (Stockholm University, Sweden), K. McKelvey (USDA Forest Service, USA), M.C. Neel (University of Maryland, USA), I. Olivieri (Université de Montpellier II, France), N. Ryman (Stockholm University, Sweden), R. Short Bull (University of Montana, USA), J.B. Stetz (University of Montana, USA), D.A. Tallmon (University of Alaska Southeast, USA), C.D. Vojta (USDA Forest Service, USA), D.M. Waller (University of Wisconsin, USA) and R.S. Waples (National Marine Fisheries Service, USA)

Abstract

Widespread environmental changes including climate change, selective harvesting and landscape alterations now greatly affect selection regimes for most organisms. How animals and plants can adapt to these altered environments via contemporary evolution is thus of strong interest. We discuss how to use genetic monitoring to study adaptive responses via repeated analysis of the same populations over time, distinguishing between phenotypic and molecular genetics approaches. After describing monitoring designs, we develop explicit criteria for demonstrating adaptive responses, which include testing for selection and establishing clear links between genetic and environmental change. We then review a few exemplary studies that explore adaptive responses to climate change in *Drosophila*, selective responses to hunting and fishing, and contemporary evolution in *Daphnia* using resurrected resting eggs. We further review a broader set of 44 studies to assess how well they meet the proposed criteria, and conclude that only 23% fulfill all criteria. Approximately half (43%) of these studies failed to rule out the alternative hypothesis of replacement by a different, better-adapted population. Likewise, 34% of the studies based on phenotypic variation did not test for selection as opposed to drift. These shortcomings can be addressed via improved experimental designs and statistical testing. We foresee monitoring of adaptive responses as a future valuable tool in conservation biology, for identifying populations unable to evolve at sufficiently high rates and for identifying possible donor populations for genetic rescue. Technological advances will further augment the realization of this potential, especially next-generation sequencing technologies that allow for monitoring at the level of whole genomes.

Keywords: contemporary evolution, genetic monitoring, global change, historical DNA samples, population genomics, quantitative trait

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Introduction

Species across the globe are experiencing drastic changes in environmental conditions as a result of

Correspondence: Michael M. Hansen, Tel.: +45 40247191; Fax: +45 89422722; E-mail: michael.m.hansen@biology.au.dk

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human activities. Climate change induced by increased greenhouse gas emissions has emerged as a top concern, both scientifically and politically (Kerr 2007; Moss *et al.* 2010), with increasing evidence that it has already affected populations of many plant and animal species (Parmesan 2006). Organisms also confront other environmental challenges like pollution (Anderson *et al.* 1994), emerging pathogens (Parker & Gilbert 2004), and newly introduced species that alter patterns of predation or competition (Mack *et al.* 2000). Finally, the intensified harvesting of wild populations via fishing and hunting radically alters population demographics and selection regimes (Allendorf *et al.* 2008; Coltman 2008).

These pervasive environmental changes have precipitated public policy debates and conservation efforts, although they are primarily focused on ecosystem and species components of biodiversity. Diversity at the genetic level and how environmental changes affect selection regimes and evolutionary trajectories of species and populations have attracted relatively less interest (Laikre *et al.* 2010). Recently, however, the content of several reviews (Palumbi 2001; Stockwell *et al.* 2003; Reusch & Wood 2007; Coltman 2008; Gienapp *et al.* 2008; Hendry *et al.* 2008; Hoffmann & Willi 2008; Hoffmann & Sgro 2011), empirical studies (Bradshaw & Holzapfel 2001; Coltman *et al.* 2003; Olsen *et al.* 2004; Phillips & Shine 2004; Umina *et al.* 2005; Balanya *et al.* 2006; Teplitsky *et al.* 2008; Pulido & Berthold 2010; Williams & Oleksiak 2011) and conferences (Smith & Bernatchez 2008) marks an increased focus on contemporary evolution in response to human-altered selection regimes.

In the short term, animals and plants acclimate to shifting environmental conditions via phenotypic plasticity, developing and expressing particular traits in response to local environmental conditions. Over the longer term, in a second kind of response, organisms may disperse to more favorable sites, potentially over long distances. A third type of response is via genic selection leading to adaptation. It is important to be able to differentiate among these types of responses and to consider their relationships. Of note, some organisms cannot disperse to more favorable conditions because of low vagility or habitat fragmentation in human-altered environments. For this reason, their ability to acclimate or adapt locally becomes vital and is all the more important because fragmentation itself selects against dispersal propensity (Ronce 2007). A firm distinction must also be made between acclimation resulting from phenotypic plasticity, which allows for response to environmental change in the short term, and adaptive evolutionary change, which allows for adaptation to a continually changing environment beyond the limits of possible responses attributable to phenotypic plasticity (Gienapp *et al.* 2008); Box 1 addresses this issue in more detail.

As the preceding makes evident, reasons are numerous for studying adaptive responses to environmental change in wild populations. In a general scientific context, human-disturbed environments represent a series of unplanned, large-scale, 'natural' experiments for observing evolution in action. From an applied perspective, we are interested in (i) evaluating and forecasting if and how populations and species can adapt to and

Box 1 Types of response – acclimation or adaptation to environmental change?

Phenotypic traits appear to be changing faster in populations subject to obvious anthropogenic forces than in those persisting in more natural habitats (Hendry *et al.* 2008). Inferring adaptation from shifts in phenotype, however, runs the risk of confusing short-term, plastic responses with longer-term genetic changes (Gienapp *et al.* 2008; Hendry *et al.* 2008). Most individuals have the capacity to respond to local environmental conditions via phenotypic plasticity. If phenotypic changes mostly reflect plasticity, responses to continuing environmental change will be limited (Gienapp *et al.* 2008). However, plasticity can also serve to provide an initial rapid response to environmental change that can then facilitate subsequent genetic adaptation via 'genetic assimilation' (Lande 2009). In addition, when environmental stresses reverse, as could be the case when policies to harvest wild populations change, phenotypic changes reflecting plasticity would also reverse rapidly, in contrast to genetic changes, which would be harder to reverse.

To infer actual adaptive change and to forecast longer-term responses to environmental change, we need to rigorously distinguish genetic adaptation from plasticity. This distinction can be a complex task because most phenotypic traits are polygenic and genes can interact epistatically. Dissecting the genetic basis for quantitative traits usually requires experiments such as common garden or reciprocal transplant setups (Endler 1986; Lynch & Walsh 1998). These classic approaches decompose total variation into its components, namely additive genetic, non-additive genetic, environmental, and genetic-by-environment ($G \times E$) interactions (Lynch & Walsh 1998).

Plasticity reflects shifts in phenotype due to non-genetic responses to variation in environmental conditions. However, because these reaction norms themselves have a genetic basis, they can also evolve (Pigliucci & Schlichting 1998; Czesak *et al.* 2006). It would therefore be interesting to monitor changes in these reaction norms using, e.g. resurrection techniques involving diapausing seeds or eggs from different time periods (Cousyn *et al.* 2001; Franks *et al.* 2007).

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persist in human-altered environments; (ii) assessing if individual populations can invoke an adaptive response and, if not, take measures such as genetic rescue (Richards 2000; Ingvarsson 2001) to assist adaptive processes; (iii) assessing and mitigating unintended consequences of anthropogenic change, such as selection imposed by harvesting of wild populations and (iv) using evidence for adaptive responses as an indicator of environmental stress that warns of incipient population declines. Concerning the latter point, it is important to note that even if adaptive responses occur, extinction of populations may still result. An increasing 'lag load' may develop as environmental changes accumulate and accelerate, whereas at the same time, the mean phenotype of the population increasingly lags behind the optimal phenotype, leading to an increasing burden of selective deaths (Box 2).

Tracking adaptive responses in populations requires monitoring, i.e. sampling and analysing populations over time. In ecology, a common practice is to trade time for space, and studying phenotypic traits or molecular markers within the same species across environmental gradients can be used for *forecasting* adaptive responses to environmental change in local populations (e.g. Byars *et al.* 2007; Jensen *et al.* 2008; Riba *et al.* 2009). Nevertheless, in many cases, populations have experienced different evolutionary histories and differ in important demographic characteristics such as effective population size and gene flow and in adaptation to local environments. Populations may therefore from the onset differ in standing genetic variation of potential adaptive value under environmental change. Furthermore, empirical evidence has shown that parallel phenotypic change in different populations can reflect both similar and different genetic architecture of traits. For instance, threespine sticklebacks (*Gasterosteus aculeatus*) from marine populations have repeatedly colonized freshwater habitats, and extensive parallel evolution of armor loss has occurred. In all cases examined, this adaptive response has involved variation at the Ectodysplasin (Eda) locus (Colosimo *et al.* 2005). In sharp contrast, different genetic architecture of the same phenotypic trait underlies parallel evolution of adaptive colour variation in rock pocket mice (*Chaetodipus intermedius*) (Nachman *et al.* 2003) and beach mice (*Peromyscus polionotus*) populations (Hoekstra *et al.* 2006). We therefore argue that adaptive responses to environmental change are best studied by observing the process using a temporal approach, i.e. genetic monitoring, rather than predicting responses based on the distribution of adaptive variation across populations in different environments. Of interest, one of the classic textbook examples of contemporary evolution, industrial melanism in the peppered moth (*Biston betularia*), can be considered an example of genetic monitoring of adaptive change (Bateson 1900; Kettlewell 1961).

In this review, we explore how to monitor the genetic composition of populations to infer whether adaptive changes are occurring. Schwartz *et al.* (2007) broadly defined genetic monitoring as the tracking of neutral genetic markers through time to estimate demographic and/or population genetic parameters. Here, we focus on studies using temporal genetic data to identify adaptive genetic changes and how such changes can be

Box 2 Lag load and rates of evolution

Following Haldane (1949), evolutionary biologists characterize evolutionary change as a change in mean trait value relative to the variation we observe around that mean wherein one *Haldane* represents the change in mean per generation relative to its phenotypic standard deviation (for details, see Hendry & Kinnison 1999). Phenotypic means can also change because of phenotypic plasticity, so this measure refers only to changes resulting from genic selection. *Haldanes* are measured relative to generation time, which necessitates adjustment of this quantity to compare rates of adaptation among organisms and to rates of environmental change. In particular, to measure absolute rates of evolutionary change (RoE) in units of phenotypic standard deviations, we need to adjust by generation time as follows:

$$\text{RoE} = \text{Haldanes}/\text{generation time}.$$

This unit of measure allows comparison of the rates at which traits evolve among populations and species.
Such evolutionary responses are key for understanding how well populations can track changes in their environment. Felsenstein (1971) and Maynard Smith (1978) first developed the idea of *lag load* to refer to the situation in which continuous changes in the environment produce a gap between the optimum trait value and the mean genotypic value for that trait actually observed in a population. The size of this lag load depends on the rate of environmental change relative to the rate of adaptation. As environmental change accelerates and this lag load increases, the intensity of selection will also increase. The amount of selection that can occur, however, is limited by both the reproductive excess present in the population and the heritability (h^2) of fitness in these new environments. Each of these will tend to decline as selection forces intensify and diversify and as populations depart further from their optima. Theory suggests that most populations' maximum sustainable rate of evolution is considerably less than 0.1 *Haldanes* per generation (Lynch & Lande 1993; Burger & Lynch 1995).

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related to changing environments. We consider analyses of both molecular markers [e.g. candidate genes, quantitative trait loci (QTLs), or genome scans] and phenotypic traits. Our overarching aim is to provide a practical framework for identifying adaptive evolutionary responses to environmental change using genetic monitoring. We first describe and discuss the use of molecular markers and phenotypic traits in genetic monitoring. Next, we develop specific criteria for demonstrating adaptive evolutionary responses to specific shifts in environmental conditions. In this case, we are inspired by the approach by Endler (1986) for developing criteria for inferring natural selection in the wild. We then search the literature for and identify examples of genetic monitoring of adaptive change to illustrate the various possible approaches. This groundwork leads into a review of a larger body of studies, again with reference to how well they meet the criteria for demonstrating adaptive responses. Finally, we discuss the conservation applications and future perspectives of monitoring adaptive change in populations.

Molecular markers and phenotypic traits for genetic monitoring of adaptive change

Two targets exist for monitoring adaptive change: molecular markers or phenotypic traits, the latter encompassing qualitative traits preferably exhibiting simple Mendelian inheritance or quantitative traits. Each approach has its advantages and disadvantages. For example, a major challenge in monitoring quantitative traits is distinguishing between phenotypic plasticity and adaptive genetic responses (Box 1). Monitoring molecular markers avoids this problem but raises another, namely how to associate genetic variation at particular loci with variation in phenotypic traits and the selective agent acting on that variation (Vasemägi & Primmer 2005).

Molecular markers

The options for monitoring adaptive change using molecular markers have so far primarily been limited to analysing candidate loci known to encode ecologically important genes like the major histocompatibility complex (MHC) genes involved in immune responses (Bernatchez & Landry 2003), heat shock protein (Hsp) genes involved in responses to temperature stress (Sørensen *et al.* 2003), or circadian genes involved in phenological traits (Liedvogel *et al.* 2009; Jimenez *et al.* 2010). Previously identified QTLs represent another source of genes for monitoring, with the caveat that QTLs may be population and environment specific and that the effects of selection on individual QTLs may be small (Lynch & Walsh 1998; McKay & Latta 2002; Pritchard & Di Rienzo 2010). Several reviews describe the possibilities and challenges involved in identifying ecologically important functional variation (Vasemägi & Primmer 2005; Bouck & Vision 2007; Stinchcombe & Hoekstra 2008).

An alternative method involves using an outlier test approach to identify anonymous markers under possible diversifying hitch-hiking selection across geographically and ecologically divergent populations (Storz 2005). Such markers can then be monitored over time within populations (e.g. Jump *et al.* 2006). A disadvantage with this approach is that it may be difficult to identify the specific selective agent acting on an anonymous marker. However, methods from the emerging field of landscape genomics (Joost *et al.* 2007; Coop *et al.* 2010; Manel *et al.* 2010) and the related field of genetic association studies, as applied particularly in human genetics (Pritchard *et al.* 2000; Stranger *et al.* 2011), hold much promise for associating specific markers with environmental conditions (e.g. Bradbury *et al.* 2010; Poncet *et al.* 2010; Williams & Oleksiak 2011).

It will almost always be necessary to evaluate genetic change at candidate loci under possible selection against a background of several presumably neutral loci, such as microsatellites or single nucleotide polymorphisms (SNPs). The number of loci needed for background will depend on the power of the specific test applied, but as a general recommendation derived from one of the most commonly applied statistical tests, it should exceed 20 (Beaumont & Nichols 1996).

Because most adaptive traits have a polygenic genetic architecture, failure to demonstrate genetic change at a specific candidate locus does not rule out that change has occurred at other loci affecting the same trait. This complexity argues for analysing many loci (hundreds to thousands) to densely cover the genome and possibly identify other loci under selection from the same environmental stressors. Fortunately, this approach is now becoming feasible with the advent of next-generation sequencing methods (Margulies *et al.* 2005). Transcriptome sequencing provides rich sources of SNPs (Barbazuk *et al.* 2007), facilitating identification of the genes involved in adaptive change (e.g. Renaut *et al.* 2010; Williams & Oleksiak 2011). An exciting recent development is the use of reduced-representation genome-wide sequencing; thousands of short fragments are sequenced throughout the genome, allowing for genotyping by sequencing of thousands of SNPs and narrowing the gap between model and non-model species (Allendorf *et al.* 2010; Davey *et al.* 2011).

We are often limited in our ability to collect samples on a sufficiently long temporal scale, particularly for species with long generation times. However, we can use ''retrospective sampling'' to extend the time scale

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using either samples or data from previous studies. For instance, Umina *et al.* (2005) and Balanya *et al.* (2006) analysed adaptive responses to climate change in *Drosophila* species based on ca. 25-year-old historical data. The disadvantage of this approach is that molecular analyses of contemporary samples have to be based on the same approaches as those used in the historical studies; in the case of *Drosophila*, these methods involved analysis of allozyme and chromosome polymorphisms. If historical samples are available, such as herbarium specimens of plants or hard parts from animals (e.g. bones, feathers, or fish scales), they can be used as sources of DNA. Wandeler *et al.* (2007), Leonard (2008) and Nielsen & Hansen (2008) have reviewed these approaches along with the inherent challenges of DNA degradation and potential contamination. It should be noted that current protocols for reduced-representation genome-wide sequencing require high amounts of high-quality DNA (Davey *et al.* 2011), thus limiting their applicability for historical DNA samples.

Testing for selection at molecular markers

Genetic monitoring of adaptive change at the molecular level involves testing for selection on ecological time scales. This calls for the use of outlier test approaches in which loci under putative selection (either hitchhiking or direct selection) are identified as outliers in terms of genetic differentiation and/or reduced variation (selective sweep) against a background of supposedly neutral markers (Storz 2005). Although we have not found any empirical examples, it should in principle also be possible to test for association between allelic variation and environmental parameters that change over time, using some of the available landscape genomics and association tests, notably that described by Coop *et al.* (2010). In Table 1, we list tests of relevance for monitoring, along with their requirements and potential drawbacks, and we elaborate on some of the methods below.

Analysing large numbers of mapped markers, obtained either by linkage mapping, reduced-representation genome-wide sequencing and alignment to a reference genome (Davey *et al.* 2011), or analysing whole genomes, holds many advantages because it allows for fine-scale mapping by identifying signatures of selection along a chromosomal region (Nielsen 2005; Wiehe *et al.* 2007). Tests relying on signals from several linked markers reduce the number of false positives and also allow for more exact identification of the chromosomal region under selection (Nielsen 2005; Wiehe *et al.* 2007; Mäkinen *et al.* 2008). There is as yet very little reported experience with using genome-wide data for genetic monitoring of adaptive change in eukaryotes. However, Burke *et al.* (2010) used this type of approach to investigate the genomic footprints of selection in lines of *Drosophila melanogaster* selected for accelerated developmental time over 600 generations. Using next-generation sequencing of pooled samples, they identified several genomic regions with increased divergence between selected and control lines, presumably reflecting selection, but no regions where classical selective sweeps had led to fixation of alleles.

If clinal variation at molecular markers reflects selection, then monitoring clinal patterns can provide evidence for adaptive responses to environmental change, such as climate change (Umina *et al.* 2005; Balanya *et al.* 2006). It should be noted, however, that clines can also reflect neutral processes, particularly isolation-by-distance (Vasemägi 2006). Testing for associations between loci and environmental gradients is therefore important to substantiate assumptions of an adaptive basis of the clines, e.g. using landscape genomics and genetic association tests (Joost *et al.* 2007; Coop *et al.* 2010; Manel *et al.* 2010; Stranger *et al.* 2011). There are no generalized test frameworks available for analysing temporal shifts of clines, but a study of *Drosophila subobscura* by Balanya *et al.* (2006) serves as an illustrative example (this and related studies are reviewed in more detail later in the paper). They analysed changes of clinal patterns of chromosome polymorphisms coinciding with increasing temperatures resulting from climate change. First, they constructed a 'temperature index' based on PC1 of principal component analyses of monthly temperatures for each locality and time period. Next, they calculated a 'chromosome index' based on PC1 of principal component analyses of chromosome polymorphisms, again for each locality and time period. The 'chromosome index' was inversely correlated with both latitude and the 'temperature index', indicating an association between climate and polymorphisms. Both the 'temperature index' and the 'chromosome index' had increased significantly over the study period, documenting climate change and genetic change. Finally, shifts in the 'chromosome index' were parallel to shifts in 'temperature index' for almost all localities, suggesting genetic change in the direction of 'warm-adapted' polymorphisms.

Do we then have the required statistical toolbox for monitoring adaptive change at molecular markers? Much can be done with the statistical tests already at hand, but the field would clearly benefit from tests specifically aimed at genetic monitoring, i.e. temporal analysis. The F_{ST}-based tests listed in Table 1 use simulations to generate expected confidence intervals of differentiation for neutral loci. These simulations are based on demographic models in which geographically different populations exchange migrants, whereas genetic

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Table 1 Tests and approaches for genetic monitoring of adaptive changes using molecular data

Test/method	Principle	Requirements	Potential problems for genetic monitoring	References
F_{ST}-based outlier tests	Detection of loci that show significantly high (or low) differentiation. Significance determined by simulations assuming specific population structure models	Co-dominant (in some cases also dominant) markers. Many loci, >20. Temporal samples, increasing statistical power with number of samples	Geographical demographic models are assumed, whereas monitoring involves temporal sampling from the same populations	Beaumont & Nichols (1996), Beaumont & Balding (2004) and Foll & Gaggiotti (2008)
Detection of selective sweeps; ln(RH) and ln(RV)	Selective sweeps lead to reduced variation. Comparison of the ratio R of $\Theta = 4N_e\mu$ for each locus between a pair of populations (N_e = effective population size, μ = mutation rate). Θ is estimated based on V (variance in repeat number at microsatellite loci) or H (expected heterozygosity). Outliers detected empirically, assuming normal distribution of ln(RH) or ln(RV). A Bayesian test based on ln(RV) has been developed that allows for analysing multiple populations (Marshall & Weiss 2006)	Co-dominant markers, lnRV applicable only to microsatellite loci. Many loci (preferably >20), as significance is determined from empirical distributions. Temporal samples, pairwise tests (or tests involving multiple samples using the method by Marshall & Weiss (2006))	Different phases of selective sweeps may generate patterns other than decreased variation. For instance, positive selection for a rare allele at a bi-allelic locus will initially increase heterozygosity	Schlotterer (2002), Kauer *et al.* (2003) and Marshall & Weiss (2006)
Landscape genomics and genetic association tests	Testing for correlation between allelic variation and environmental parameters while controlling for neutral population structure	Temporal data on relevant environmental parameters. SNPs or other bi-allelic markers, though multi-allelic markers also useful for the method by Pritchard *et al.* (2000). Several (>>2) temporal samples required, depending on specific test	Assumes geographical structure, but should be applicable to temporal data	Pritchard *et al.* (2000) and Coop *et al.* (2010)
Temporal change of clinal patterns	No generalized framework. Test procedures should verify that (i) clinal patterns reflect adaptive responses to environmental gradients; (ii) clines have changed over time and (iii) this corresponds to a change in environmental gradients	Temporal data on relevant environmental parameters and markers showing clinal patterns	Research possibilities restricted to cases where clines occur	Example of study design and test procedures provided by Balanya *et al.* (2006)
Genome scans using mapped markers or markers aligned to reference genome	Testing for selection along chromosomes or linkage groups across time periods. Can involve both tests for diversifying selection and selective sweeps, e.g. using sliding windows approaches	Temporal samples involving hundreds to thousands of markers. Linkage map, alignment of sequences to reference genome, or analysis of whole genomes	Feasible, but as yet technically highly demanding	Tests and examples provided in Nielsen (2005), Nielsen *et al.* (2005), Wiehe *et al.* (2007) and Burke *et al.* (2010)

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monitoring involves temporal sampling of the same populations. It would therefore be preferable to develop outlier tests that specifically simulate temporal sampling, e.g. by incorporating estimates of effective population size, to identify loci that show more temporal divergence (and thereby lower effective population size) than would be expected by drift alone.

Monitoring phenotypic traits

Analysing change in phenotypic traits holds the clear advantage of focusing on characters of direct relevance to the specific environmental change, e.g. flowering time in plants experiencing climate change (Franks *et al.* 2007) or age at reproduction in overharvested fish populations (Olsen *et al.* 2004). Qualitative traits with simple Mendelian inheritance would be ideal for monitoring, but except for the classic case of industrial melanism in the peppered moth (Kettlewell 1961; van't Hof *et al.* 2011), it is probably difficult to find such traits that are at the same time relevant in the context of a specific environmental change. The vast majority of traits will therefore be quantitative, which requires separating genetic from environmental components of phenotypic variance and separating evolution from phenotypic plasticity (Box 1). Where these traits cannot be studied directly, some studies use narrow-sense heritability (h^2) estimates for the traits from other populations of the same species or even related species (Edeline *et al.* 2007; Nussle *et al.* 2009). Although this approach provides an indication of the genetic basis for the trait, we should recall that heritabilities often depend on the environments in which they are estimated (Hoffmann & Merila 1999). For instance, Larsson (1993) obtained h^2 estimates for tarsus length in the barnacle goose (*Branta leucopsis*) ranging from 0.16 (and not significantly different from zero) under poor growth conditions to 0.67 under good conditions. Although there are no universal patterns of h^2 increase or decrease in stressful environments, several cases have nevertheless involved a drastic decrease in h^2, presumably because of higher environmental variance as stress conditions increase (Hoffmann & Merila 1999). In such instances, studies that report phenotypic change and at the same time rely on h^2 estimates measured under favorable conditions could arrive at erroneous conclusions; phenotypic change may be ascribed to adaptive genetic change when it may in reality reflect phenotypic plasticity. The degree to which heritability estimates differ across environments is expected to vary among specific traits, but the recommendation is to estimate h^2 for the specific populations and environments to the greatest possible extent, or at least to obtain h^2 estimates for more than one population and environment.

Testing for selection at phenotypic traits

Genetic monitoring of adaptive change at the phenotypic level, just as for the molecular level, involves testing for selection on ecological time scales. We summarize some of the methods and tests in Table 2.

A major challenge of most of the approaches concerns documenting the heritable basis of the traits while at the same time keeping in mind that h^2 estimates may differ among populations and environments, as discussed above. Moreover, it should be kept in mind that h^2 is defined as V_A/V_P, where V_A denotes additive genetic variance and V_P total phenotypic variance. If a trait is under directional selection, then V_A is expected to decrease and h^2 may eventually approach zero. Hence, what should really be of interest is the genetic basis of temporal phenotypic variance and temporal change of V_A. One approach controls for this issue, namely studies based on pedigreeing of populations and estimation of quantitative genetics parameters using the Animal Model (Kruuk 2004; Garant & Kruuk 2005; Pemberton 2008; Wilson *et al.* 2010). Some of these studies reveal the importance of monitoring not only phenotypic change, but also change in V_A as the environment changes.

As an example illustrating these issues, the classical Bergmann's rule predicts that mean body size in ectotherms will increase with increasing geographical latitude because of energetic adaptations to colder climates. This rule raises the possibility that decreasing body size and shifts in 'Bergmann's clines' could reflect adaptive responses to global warming (Millien *et al.* 2006). Teplitsky *et al.* (2008) tested this hypothesis in a red-billed gull (*Larus novaehollandiae scopulinus*) population that had been monitored for 47 years. Even though temperature had increased, body size had decreased, and h^2 of body size had been estimated at 0.33 and 0.27 for males and females, respectively, V_A had not changed over the time period. Hence, the decreased body size was interpreted as reflecting phenotypic plasticity rather than an adaptive genetic response.

Criteria for demonstrating adaptive genetic change

How should we judge the evidence supporting adaptive genetic change? We define six criteria needed to convincingly demonstrate adaptive evolutionary change based on analyses of either quantitative traits or molecular markers (Table 3). In particular, we should ensure that (i) suitable genetic variation exists; (ii) the monitored traits or genes are relevant to the specific environmental stress; (iii) traits or genes are analysed over time; (iv) selection is tested; (v) shifts in traits or allele

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Table 2 Tests and approaches for genetic monitoring of adaptive change using phenotypic traits

Test/method	Principle	Requirements	Potential problems for genetic monitoring	References
Q_{ST}–F_{ST}	Differentiation at quantitative traits can be estimated as: $Q_{ST} = \sigma^2_{GB} / (\sigma^2_{GB} + 2\sigma^2_{GW})$, where σ^2_{GB} and σ^2_{GW} represent additive genetic variance between and within samples, respectively. Q_{ST} is compared to F_{ST} at molecular markers. If $Q_{ST} > F_{ST}$, this may indicate diversifying selection. Although designed for geographically different populations, it is applicable also to temporal analysis	Estimates of additive variance for trait(s) obtained in common garden set-up. Estimates of F_{ST} obtained from molecular markers. The ideal design should consider at least two test environments resembling the environmental conditions at the time periods considered	Logistically demanding. Continuous monitoring possible by rearing individuals every few generations under identical environmental conditions to estimate additive variance. Better suited for organisms where seeds or resting eggs from different time periods can be resurrected. Q_{ST}–F_{ST} is controversial, particularly due to some studies estimating phenotypic or broad-sense genetic variance instead of additive variance (Pujol *et al.* 2008)	Merilä & Crnokrak (2001) and Leinonen *et al.* (2008)
Observing direction of trait changes in the wild	If the environment changes in a specific direction, then a consistent change is expected for traits under selection. Hypotheses about the direction of change can be tested by runs or sign tests	The heritability of traits must be demonstrated. Time series of trait measurements must include several sampling points (≥5) for statistical tests to be meaningful	Even though heritability of traits has been demonstrated, h^2 may differ across populations and environments	Lande (1977)
Temporal change of clinal patterns	No generalized statistical framework. Similar to molecular markers (Table 1), it must be tested that changes of phenotypic clines coincide with changes of environmental gradients	Temporal data on relevant environmental parameters and traits showing clinal patterns. The heritability of traits must be demonstrated	Even though heritability of traits has been demonstrated, h^2 may differ across populations and environments	See Bradshaw & Holzapfel (2001) for an example
Testing the neutrality of rates of evolution	If t denotes the number of generations between two points in time, z the mean phenotypic change, h^2 the heritability, and σ the standard deviation of the trait value, then the maximum expected effective population size compatible with a pure drift scenario, N^*, can be estimated: $N^* = (1.96)^2 h^2 t/(z/\sigma)^2$. If the actual effective population size, $N_e > N^*$, then the hypothesis of neutrality is rejected (at a 5% significance level)	Requires estimates of N_e, heritability and phenotypic data from two points in time. If N_e cannot be estimated, then as a minimum it can be assessed if N^* represents an unrealistically low N_e value	Assumes that h^2 is constant over time	Lande (1976)
Pedigreeing and estimation of quantitative genetics parameters using Animal Model	By pedigreeing and measurement of quantitative traits, quantitative genetics parameters are estimated using the Animal Model, and temporal change of V_A can be assessed. Using estimates of life-time reproductive success, selection gradients and differentials can be estimated (Lande & Arnold 1983), and the predicted response to selection can be calculated from the Breeder's Equation (Falconer & McKay 1996): $R = h^2 S$, where R denotes evolutionary response measured in standard deviations and S denotes selection differential	Requires pedigree and measurements of relevant quantitative traits	Logistically highly demanding as populations must be pedigreed over several generations. Unsuitable for organisms with large population sizes, e.g. insects, or species that are continuously distributed over large geographical areas	Kruuk (2004), Garant & Kruuk (2005) and Wilson *et al.* (2010)

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Table 3 Criteria for demonstrating adaptive genetic responses to environmental change

	Approach for demonstrating criteria	
Criterion	For molecular markers:	For quantitative traits:
1. *Demonstrate that suitable genetic variation exists*	a) Analyse candidate loci previously demonstrated to be under selection b) Identify loci (with known or unknown functions) suggested to be under direct or hitch-hiking selection on a spatial scale, e.g. using genome scan approaches (Storz 2005)	Identify traits likely to be under selection. Is there genetic variation for the trait in the original population? a) Estimate additive genetic variance in the wild (Kruuk 2004). Ideally, estimate h^2 as the environment changes as part of the monitoring design b) Use 'common garden', reciprocal transplant, and/or field experiments to demonstrate genetic vs. environmental bases for trait variation (Lynch & Walsh 1998) c) As a last resort, use traits where heritability has previously been demonstrated in other populations of the same species
2. *Link this genetic variation to a specific environmental stress*	Do we expect the gene to be under selection due to the specific environmental stress? This could be based on prior knowledge, the expected function of the locus, or empirical data For example: a) Analyse candidate loci of specific relevance to the environmental stress, such as MHC genes involved in immune response (Bernatchez & Landry 2003) or Hsp genes involved in thermal stress response (Sørensen *et al.* 2003) b) Test for associations between genetic variants and environmental variables associated with a specific environmental stress (Manel *et al.* 2010)	Do we expect the trait to be under selection due to the specific environmental stress? This could be based on prior knowledge, the expected function of the trait, or empirical data For example: a) Do traits covary in the expected way across experimental or field populations that vary in this stress? b) Does this trait variation enhance fitness?
3. *Test genetic change over time*	Do the identified allele(s) vary over generations? a) Initiate a continuous sampling program starting at the present b) Sample retrospectively using archived samples, e.g. herbarium specimens, bones, skins, feathers, or fish scales (Wandeler *et al.* 2007; Leonard 2008; Nielsen & Hansen 2008)	Do the identified trait(s) vary over generations? a) Initiate a continuous sampling program starting at the present. Alternatively, pedigree analyses may serve to track variation among families over generations b) Track trait change by growing out historical and newer individuals from seeds or eggs into a common environment (resurrection studies) c) If resurrection is impossible, track historical changes in traits known to have a strong genetic basis
4. Test that selection has occurred	Do the changes in allele frequency reflect selection? a) Conduct specific test for selection, e.g. using one or more of the methods listed in Table 1 b) Test a specific hypothesis, e.g. expected change of clinal patterns at traits due to a certain environmental change	Do the changes in trait values reflect selection? a) Conduct specific analysis/test for selection, e.g. using one or more of the methods listed in Table 2 b) Test a specific hypothesis, e.g. expected change of clinal patterns at loci due to a certain environmental change
5. Link the observed genetic change(s) to selection attributable to a particular environmental factor	Do observed shifts in a trait or allele frequencies reflect selection due to the identified environmental factor? Assess or test that the observed adaptive change coincides with the specific environmental change. If possible, obtain information on many environmental parameters to rule out confounding variables	
6. *Conduct tests to rule out simple replacement – the possibility that a more adapted population replaced the original population*	a) Demonstrate genetic continuity over time using molecular markers, e.g. by estimating temporal differentiation. If possible, analyse several populations and conduct a hierarchical F_{ST}-analysis to document that differentiation among populations exceeds differentiation among temporal samples within populations b) If immigration from other populations is unlikely, e.g. due to isolation on an island or in a closed lake, then this should be stated explicitly	

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frequencies coincide with the changes expected in response to the environmental change in question and (vi) we do not infer adaptive genetic change when simple replacement by a genetically different population has instead occurred.

Collectively, these defined criteria represent a stringent set of conditions. In the following, we present some empirical cases that illustrate different approaches to genetic monitoring of adaptive change and provide examples of how they have met the criteria listed in Table 3. We also review a larger body of studies and assess the extent to which they have met the criteria (Tables S1 and S2, Supporting information).

Empirical cases

Response to climate change in Drosophila

Some of the most convincing results suggesting adaptive responses to ongoing climate change are derived from wild populations of *D. melanogaster* (Umina *et al.* 2005) and *D. subobscura* (Balanya *et al.* 2006). These studies represent exemplary cases of genetic monitoring of adaptive change and address almost all of our criteria (Table 3). Both species display latitudinal (i.e. North–South) clines in both phenotypic traits thought to reflect thermal adaptation and genetic markers involving well-characterized genes and chromosome inversions. These clines appear to reflect temperature-related selection as supported by laboratory experiments (Umina *et al.* 2005). They also provide evidence that the polymorphisms are relevant candidates for being under selection (criterion 1) and that links exist between these polymorphisms and a specific environmental factor (criterion 2). Umina *et al.* (2005) further demonstrated temporal genetic change (criterion 3) in *D. melanogaster* introduced to Australia approximately 100 ya by analysing clines at two enzyme-coding loci and two chromosome inversions observed in 1979–1982 and 2002–2004. For one enzyme locus and one inversion, no significant temporal change was evident, but at the alcohol dehydrogenase locus and the other inversion, there were significant shifts in the clines even as the slopes remained unchanged. The authors confirmed that temperature had increased over the monitoring period and moreover that the shifts occurred in the direction expected if populations were responding evolutionarily to those increased temperatures. Hence, by testing a previously stated hypothesis (criterion 4), the study provided evidence for genetic change resulting from selection. Of interest, these cline shifts corresponded to latitude shifts of 3.9° and 7.3°, respectively, considerably more than the shift expected from changes in individual climate change factors (increasing temperature, decreasing rainfall and decreasing humidity). The authors interpreted this outcome to mean that these populations are responding to a combination of climatic factors rather than to single factors acting independently. Thus, the authors linked the observed adaptive response to a specific environmental change (criterion 5). They presented no evidence, however, to confirm that these changes reflect adaptive responses *within* populations (as opposed to immigration of individuals from other populations; criterion 6). Nevertheless, the Australian *D. melanogaster* clines arose *de novo* since the introduction of the species ca. 100 ya, confirming that temperature-related adaptation can proceed rapidly.

In terms of both design and results, the work of Balanya *et al.* (2006) with *D. subobscura* resembles that of Umina *et al.* (2005). Balanya *et al.* took advantage of the fact that *D. subobscura* is native to Europe but has been introduced to North and South America, allowing them to replicate their results and demonstrate recent cline shifts in response to climate change on all three continents.

Rodriguez-Trelles & Rodriguez (2007) subsequently criticized this study, arguing that the study design could not rule out whether seasonal cycles of allele frequency change created the apparent cline shifts. Balanya *et al.* (2007) later presented empirical data refuting this criticism. Nevertheless, the criticism raises an important issue for monitoring adaptive responses to climate change in organisms with short generation times. Such studies should control for possible seasonal cycles of selection regimes and evaluate how climate change alters seasonal timing. Life histories could also possibly exist where individuals from panmictic populations disperse to environmentally different foraging areas where they are subject to diversifying selection. However, this within-generation response is obliterated following each event of panmictic breeding. Such a scenario may be particularly relevant in marine fishes with high dispersal potential (Nielsen *et al.* 2009a), and particularly in panmictic species like the European eel (*Anguilla anguilla*; Als *et al.* 2011).

Selection imposed by hunting and fishing

Human predators represent perhaps the most significant factor modifying traits in most exploited species (Allendorf & Hard 2009; Darimont *et al.* 2009). One approach for studying selection imposed by hunting involves pedigreeing wild populations and estimating quantitative genetic parameters using the Animal Model (Table 2). Using such a setup, Coltman *et al.* (2003) tracked individual phenotypes in a pedigreed bighorn sheep (*Ovis canadensis*) population in Alberta, Canada, under pressure from trophy hunting (focusing

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on the horns) for 30 years. They used microsatellite paternity analysis to confirm the high heritability of horn and body size. They also documented significant declines in horn size, an apparently adaptive evolutionary response to hunting. Body weight had also declined, representing a correlated response. Such results suggest that selective hunting can substantially alter prey characteristics over relatively short periods of time.

Rutter (1904) wrote more than a century ago that '*A large fish is worth more on the market than a small fish; but so are large cattle worth more on the market than small cattle, yet a stock raiser would never think of selling his fine cattle and keeping only the runts to breed*', expressing his concern about selective fishing for large Sacramento River salmon. Fisheries-induced evolution has thus long been recognized. Modern intense size-selective fishing favours faster-growing, early-maturing genotypes, as has been observed in many exploited fish populations (Jørgensen *et al.* 2007; Sharpe & Hendry 2009). Do these changes reflect environmentally induced changes in the demography of populations or true genetic changes? A number of studies have attempted to disentangle these factors using phenotypic data [see reviews by Jørgensen *et al.* (2007) and Heino & Dieckmann (2008) and empirical studies by Olsen *et al.* (2004), Edeline *et al.* (2007) and Nussle *et al.* (2009)]. In general, these studies documented phenotypic change over time, but the genetic basis of the observed change and identification of the specific selection regime (i.e. fisheries-induced selection as opposed to other environmental change) often remains uncertain (reviewed in Table S2, Supporting information). Mesocosm experiments involving simulated selective fisheries have confirmed that this pressure can lead to evolutionary genetic change in the predicted direction and in as few as four generations (Conover & Munch 2002), but obviously this type of study involves much less complex environmental conditions than those encountered in the wild. However, we now also see attempts to estimate fisheries-induced evolution using genetic markers, moving towards the molecular level and providing tools for monitoring wild populations (Nielsen *et al.* 2009a).

Analyses of DNA from historical collections of scales and otoliths allow us to infer both demographic processes, such as temporal changes in migration rates and genetically effective population sizes (Nielsen & Hansen 2008), and decadal shifts at genes of adaptive value (e.g. Nielsen *et al.* 2009b; Hansen *et al.* 2010). Such candidate gene approaches can also be used to infer fisheries-induced evolution. Although growth and maturation are likely highly polygenic in fish, a few master genes may govern these processes. The 'growth axis' appears to be determined by a system of hormones, including growth hormone and insulin-like growth factors, as well as various promoters, inhibitors and receptors (De-Santis & Jerry 2007). The 'maturation axis' appears to be similarly regulated by other hormones (e.g. follicle-stimulating hormone and luteinizing hormone) and their respective receptors, promoters and inhibitors (Weltzien *et al.* 2004). Genetic variation in and around these genes can be identified by sequencing as a prelude to screening for polymorphisms (e.g. SNPs) in historical and contemporary population samples (Hemmer-Hansen *et al.* 2011).

All the caveats and criteria described previously also apply to marine organisms. Criterion 6 – ruling out replacement by a different population – is particularly important, given the potentially high vagility of marine fishes. A recent SNP-based genome scan of Atlantic cod (*Gadus morhua*) was used to identify genomic signatures of adaptive variation across populations and also confirmed the temporal stability of apparent selection based on analysis of historical samples (Nielsen *et al.* 2009b). Neutral genetic change over time was limited, confirming the genetic continuity of populations. Hence, we now have the markers, samples and conditions needed to monitor fisheries-induced evolution at the molecular level.

Resurrection ecology and contemporary evolution in Daphnia

Time and resources limit our ability to monitor phenotypic traits across generations. Plants and animals that produce diapausing seeds or eggs, however, allow tracking of genetic changes over much longer periods by 'resurrection' of dormant seeds and eggs (Bennington *et al.* 1991; Kerfoot *et al.* 1999; Cousyn *et al.* 2001; Decaestecker *et al.* 2007; Franks *et al.* 2007). By rearing individuals from historical and contemporary populations in a common environment, we can detect adaptive responses over time and estimate rates of evolution.

Water fleas such as *Daphnia* play crucial roles in aquatic ecosystems by grazing on phytoplankton and providing food for fish. Their diapausing eggs can be recovered and 'resurrected' from stratified sediments, allowing establishment of experimental populations corresponding to different time points. Cousyn *et al.* (2001) used this approach to study contemporary evolution over ca. 30 years in *Daphnia magna* in a small pond that had experienced high variation in predator abundance. The study focused on a behavioural trait, phototactic behaviour, that results in diel vertical migration: at night, zooplankton move up in the water column to feed but retreat to deeper water during the day to avoid predators. Phototactic behaviour was known to differ among *D. magna* populations in lakes with different fish

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densities, but whether contemporary evolution could occur at this trait was unknown. The prediction was that if phototactic behaviour in the presence of fish adaptively evolved within the time frame of the study, then (i) differentiation, Q_{ST}, at the quantitative trait should exceed F_{ST} at neutral microsatellite loci among temporal populations resurrected from different time periods; and (ii) there should be higher plasticity in phototactic response with exposure to predators in populations adapted to higher fish densities. Plasticity was measured by comparing phototactic responses in the absence of fish predators to responses when *Daphnia* were exposed to a fish kairomone (a substance released by the predator that is perceived by the prey). While Q_{ST} ranged from 0.19 to 0.20, F_{ST} was much smaller (<0.022), suggesting that selection had dramatically changed the phototactic response in the predicted direction. The study thereby fulfills all criteria for demonstrating temporal evolutionary adaptive change by demonstrating selection at the trait, associating the observed selection with a specific selection regime, testing an extrinsic hypothesis concerning the predicted direction of adaptive change, and demonstrating genetic continuity of the population using microsatellite markers (Table 3). This study also demonstrates that reaction norms can evolve quickly.

Resurrection ecology studies of *D. magna* have provided other important insights. For instance, this system has been used to analyse Red Queen dynamics by studying host–parasite coevolution across temporal resurrected populations (Decaestecker *et al.* 2007). Resurrected *D. magna* populations have also been used to assess evolution at the gene expression level. Pauwels *et al.* (2007) demonstrated temporally increasing levels of Hsp60 expression and estimated evolutionary rates between 0.08 and 0.12 *Haldanes* among different resurrected populations, probably in response to the increasing abundance of an ectoparasite.

The resurrection studies in *Daphnia* and other species demonstrate the power of this approach for monitoring evolutionary adaptive change. The approach is obviously restricted to organisms with diapausing seeds or eggs, but it can yield important general insights into the evolutionary potential of species and populations for adapting to altered environments. It thus remains the most feasible means for retrospective genetic monitoring of phenotypic traits, including monitoring the evolution of reaction norms and differences in gene expression.

Review of studies

We searched the literature to identify studies employing genetic monitoring to study adaptive change. This was performed by searching Web of Science for papers containing the terms *genetic monitoring*, *adaptive change*, *adaptation*, *contemporary evolution*, *environmental stress*, *selection*, *time series* and *temporal* in different combinations. Papers deemed to represent genetic monitoring of adaptive change were supplemented with other papers already known to us. In total, we identified 44 papers/studies, 15 employing molecular markers and 29 based on quantitative traits. Tables S1 and S2 (Supporting information) summarize the experimental designs and main results of the studies. We also assessed the extent to which the papers fulfilled the criteria for having demonstrated adaptive change, as defined in Table 3.

Few studies (23%) fulfilled all six suggested criteria (Fig. 1). None of the studies based on molecular markers fulfilled all criteria, but all of them fulfilled four or five of the criteria. The lowest and highest fulfillment of criteria was found among the studies based on phenotypic traits; 24% of the studies fulfilled only 1–3 criteria, but on the other end of the spectrum, another 34%, corresponding to ten studies, fulfilled all six. Of note, seven of these latter studies were based on pedigreed populations and estimation of quantitative genetics parameters using the Animal Model, underlining the usefulness of this approach.

Is there a pattern in the criteria that were not fulfilled? Approximately half of all studies (43%) and 55% of studies based on phenotypic traits failed to address criterion 6 by not ruling out simple population replacements (Fig. 2). In some studies, such as of fishes in closed lakes (Edeline *et al.* 2007; Nussle *et al.* 2009), replacement could be ruled out because of the nature of the system, although this rationale was not specifically

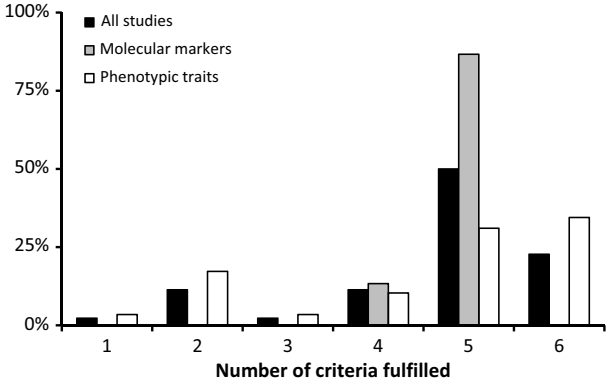

Fig. 1 Overview of the number of fulfilled criteria, as listed in Table 3, in studies attempting to demonstrate adaptive evolutionary responses using genetic monitoring. The results are based on a review of 44 studies, 15 employing molecular markers and 29 based on quantitative traits. The studies and their main results are summarized in Tables S1 and S2 (Supporting information).

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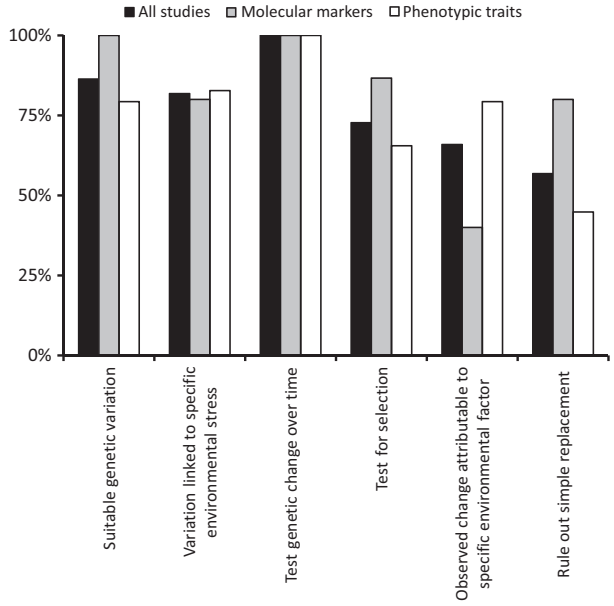

Fig. 2 Overview of fulfillment of the specific criteria for demonstrating adaptive evolutionary response using genetic monitoring (see Table 3), based on 44 studies summarized in Tables S1 and S2 (Supporting information).

highlighted in the papers. Other studies were based on pedigreed or very closely monitored populations, thus providing a control for immigration (e.g. Grant & Grant 2002; Coltman *et al.* 2003). Among the remaining studies based on phenotypic traits, only a few specifically addressed the possibility of population replacement (e.g. Cousyn *et al.* 2001; Decaestecker *et al.* 2007). In total, this pattern demonstrates that monitoring of phenotypic traits could be improved by using molecular markers to assess temporal stability within populations and/or to document that differentiation is higher among different populations than among temporal samples within populations. Nevertheless, even if the temporal stability of a population is documented, limited gene flow among populations cannot be ruled out. Even a few immigrants could introduce adaptive variation resulting in higher fitness in a changing environment. From a conservation perspective, it would be important to know if adaptive responses result from standing genetic variation within a population or from variation provided by gene flow. Unless populations are pedigreed, demonstrating genetic rescue will be difficult, but the potential for genetic rescue could be assessed by methods for estimating dispersal among populations based on molecular markers (e.g. Paetkau *et al.* 2004).

Thirty-four percent of the studies monitoring phenotypic traits did not test whether selection as opposed to genetic drift caused the observed changes (Fig. 2). Although such testing can be a challenge, several possible tests exist, as described in Table 2. It seems realistic that one or more of these analyses could have been applied in the cases in which selection was not tested. For instance, studies measuring rates of evolution could examine if the observed change is compatible with a scenario involving only drift (Lande 1976; see Table 2).

Only 16% of all studies reported no adaptive change (Fig. S1, Supporting information). This finding could reflect publication bias if research that identifies no adaptive response goes unpublished. We find it striking that 36% of all studies provided evidence for adaptive responses but at the same time could not link the observed responses to a specific environmental change (Fig. S1, Supporting information). These reports included studies that did not specifically test for associations between adaptive and environmental changes and those that conducted such tests but found no significant association. Because selection regimes can be complex, this pattern emphasizes the importance of detailed collection of environmental data to identify the specific selection forces involved.

In total, only a minority of the reviewed studies fulfilled all the criteria needed to convincingly demonstrate adaptive change via genetic monitoring. We therefore recommend that future studies be specifically designed to address all criteria for demonstrating adaptive change, such as those provided in Table 3. If, for some reason, not all criteria can be fulfilled, any that were not met should be explicitly highlighted in publications, and conclusions should obviously be tempered accordingly.

Genetic monitoring of adaptive change as a tool in conservation biology

The reviewed studies collectively demonstrate that monitoring adaptive genetic change in field populations is feasible and thus could be used as a practical conservation tool. In addition to general questions concerning adaptability and adaptive responses of populations, we would like to draw attention to the following potential applications of genetic monitoring.

1 Where populations are declining and show evidence of little adaptive response, genetic rescue can be considered as a conservation option. Genetic rescue has so far been used primarily to introduce new variation into populations suffering from inbreeding depression (e.g. Hedrick 1995; Westemeier *et al.* 1998). This application has generally proven successful, although caveats concerning outbreeding depression and swamping of indigenous adaptive variation have also been raised (Tallmon *et al.* 2004). In addition to providing evidence

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for low adaptability of specific populations, genetic monitoring could also assist in identifying potential donor populations. Thus, where several populations are monitored simultaneously, those showing adaptive responses could be considered as candidate donors for genetic rescue of other declining populations showing no adaptive responses. With the ongoing integration of genomics methodology into population and conservation genetics (Allendorf *et al.* 2010; Ouborg *et al.* 2010), our understanding of the genomic basis of adaptation to various kinds of environmental change could even advance to an ability to predict which particular source populations, or even alleles at specific loci, might most benefit a local, non-adapting population. This potential application raises the possibility of contributing not only more genotypes but also genotypes enriched in just the kinds of genetic variation most likely to benefit the population at risk.

2 Genetic monitoring could identify harvested populations suffering from increased lag load (Box 2) and thus potentially approaching collapse. This information could be used for managing exploited populations of fish and wildlife by regulating harvesting (Olsen *et al.* 2004).

A strict demonstration of lag load is complicated but might, for example, involve genetic monitoring along with monitoring of demographic trends. Alternatively, the theoretically maximum sustainable rate of evolution of <0.1 *Haldanes* per generation (Lynch & Lande 1993; Burger & Lynch 1995) could serve as a threshold, and evolutionary rates approaching this magnitude should be cause for concern.

3 Which species and populations will not adapt fast enough? This is a central question when forecasting the consequences of environmental change, such as global warming. Genetic monitoring of adaptive change could provide predictive tools for this purpose. Theoretically, we would predict that organisms with features such as small populations, long generation time, asexuality and complex interactions with their environment would adapt slowly to environmental change. However, for organisms that show intermediate values with respect to these traits, predictions will be more difficult. There may also be many more as-yet-unidentified life-history and demographic features that could influence adaptability to a certain environmental stress. A comparative approach based on genetic monitoring of several species experiencing similar environmental change but representing diversity in a variety of traits could highlight the most important factors involved in adaptability and thus improve our basis for forecasting.

Future perspectives

Our review of studies reveals that genetic monitoring of adaptive change is already a diverse field involving many different approaches. We particularly foresee important future developments in three directions, as follows.

First, most genetic monitoring studies based on quantitative traits have focused on a few traits individually. In reality, quantitative traits within an organism show various degrees of correlation that can be described with a matrix of additive genetic variances and covariances, the G-matrix (Lande 1979). Depending on the strength of correlation and selection acting on the different traits, there may be constraints on adaptation of individual traits. Hence, the outcome of selection on a single trait may not be readily predictable, an important consideration when interpreting results of genetic monitoring. Moreover, the G-matrix itself can evolve (reviewed by Steppan *et al.* 2002; Arnold *et al.* 2008), and reconstructing and monitoring the G-matrix would therefore be of considerable scientific interest. Doing so would primarily be feasible for species that are closely monitored and pedigreed or for organisms prone to resurrection designs.

Second, we have highlighted the utility of historical samples for retrospective monitoring of molecular markers at decadal scales. A logical next step would involve analysis of ancient DNA, potentially extending time scales by thousands of years. This field has evolved dramatically within the past decade, although studies of ancient DNA still involve formidable tasks in terms of avoiding contamination problems, accounting for DNA damage and estimating the age and verifying the authenticity of samples (Willerslev & Cooper 2005).

Obtaining sufficient sample sizes is also a problem, not least because of the low amounts and quality of DNA in ancient specimens. As an example, Jaenicke-Despres *et al.* (2003) analysed allelic variation at three functionally important nuclear loci in domesticated maize (*Zea mays*) from two archeological sites in Mexico and New Mexico, covering a time span from 4300 to 600 ya. Alleles characteristic of contemporary domesticated maize were already present in the oldest samples, but on the other hand, alleles characteristic of wild maize still remained in 2000-year-old samples, indicating that domestication was not yet complete at that time. Although this study could be characterized as genetic monitoring of adaptive change, the low sample size precluded statistical analysis and did not allow for detailed reconstruction of the domestication process. However, recent technical developments such as massively parallel hybridization capture that allows for retrieving low copy numbers of highly degraded DNA

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could increase the possibilities for obtaining larger ancient DNA sample sizes (Burbano *et al.* 2010).

Finally, technical advances in genomics hold enormous potential for genetic monitoring. During the past five years, population genomics studies of non-model organisms have increased from hundreds to thousands of markers, predominantly SNPs (Namroud *et al.* 2008; Bradbury *et al.* 2010; Hohenlohe *et al.* 2010). With the advent of reduced-representation genome-wide sequencing (Davey *et al.* 2011), it is now feasible to monitor genomes rather than genes, and whole genome resequencing (Li *et al.* 2009) at the level of population samples is a realistic future goal. Although such analysis involves considerable bioinformatics-related effort, monitoring of genomes can provide unprecedented information about the genes involved in adaptive responses to specific environmental changes. Recently, we have even seen an example of whole-genome resequencing based on an archeological ancient DNA sample (Rasmussen *et al.* 2010), potentially making it possible to monitor genomes over centuries or millennia.

Conclusions

In conclusion, our review shows that monitoring adaptive change has already yielded important results demonstrating if and how organisms can adapt to human-altered environments. By proposing a framework of criteria to use in monitoring studies, we hope to further encourage awareness of methodology and experimental designs. With the continuing developments in quantitative genetics, bioinformatics and population genomics, we envisage a bright future for genetic monitoring of adaptive change and foresee that it will not only increase our understanding of contemporary evolution but also provide novel tools for practical conservation of biodiversity.

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References

Allendorf FW, Hard JJ (2009) Human-induced evolution caused by unnatural selection through harvest of wild animals. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 9987–9994.

Allendorf FW, England PR, Luikart G, Ritchie PA, Ryman N (2008) Genetic effects of harvest on wild animal populations. *Trends in Ecology & Evolution*, **23**, 327–337.

Allendorf FW, Hohenlohe PA, Luikart G (2010) Genomics and the future of conservation genetics. *Nature Reviews Genetics*, **11**, 697–709.

Als TD, Hansen MM, Maes GE *et al.* (2011) All roads lead to home: Panmixia of European eel in the Sargasso Sea. *Molecular Ecology*, **20**, 1333–1346.

Anderson S, Sadinski W, Shugart L *et al.* (1994) Genetic and molecular ecotoxicology – a research framework. *Environmental Health Perspectives*, **102**, 3–8.

Arnold SJ, Burger R, Hohenlohe PA, Ajie BC, Jones AG (2008) Understanding the evolution and stability of the G-matrix. *Evolution*, **62**, 2451–2461.

Balanya J, Oller JM, Huey RB, Gilchrist GW, Serra L (2006) Global genetic change tracks global climate warming in *Drosophila subobscura*. *Science*, **313**, 1773–1775.

Balanya J, Oller JM, Huey RB, Gilchrist GW, Serra L (2007) Response to comment on 'Global genetic change tracks global climate warming in *Drosophila subobscura*'. *Science*, **315**, B1497–B1497.

Barbazuk WB, Emrich SJ, Chen HD, Li L, Schnable PS (2007) SNP discovery via 454 transcriptome sequencing. *Plant Journal*, **51**, 910–918.

Bateson W (1900) Collective enquiry as to progressive melanism in moths—memorandum from the Evolution Committee of the Royal Society. *Entomological Records*, **12**, 140.

Beaumont MA, Balding DJ (2004) Identifying adaptive genetic divergence among populations from genome scans. *Molecular Ecology*, **13**, 969–980.

Beaumont MA, Nichols RA (1996) Evaluating loci for use in the genetic analysis of population structure. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **263**, 1619–1626.

Bennington CC, Mcgraw JB, Vavrek MC (1991) Ecological genetic variation in seed banks. 2. Phenotypic and genetic differences between young and old subpopulations of Luzula parviflora. *Journal of Ecology*, **79**, 627–643.

Bernatchez L, Landry C (2003) MHC studies in nonmodel vertebrates: what have we learned about natural selection in 15 years? *Journal of Evolutionary Biology*, **16**, 363–377.

Bouck A, Vision T (2007) The molecular ecologist's guide to expressed sequence tags. *Molecular Ecology*, **16**, 907–924.

Bradbury IR, Hubert S, Higgins B *et al.* (2010) Parallel adaptive evolution of Atlantic cod on both sides of the Atlantic Ocean in response to temperature. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, **277**, 3725–3734.

Bradshaw WE, Holzapfel CM (2001) Genetic shift in photoperiodic response correlated with global warming. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 14509–14511.

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Burbano HA, Hodges E, Green RE *et al.* (2010) Targeted investigation of the Neandertal genome by array-based sequence capture. *Science*, **328**, 723–725.

Burger R, Lynch M (1995) Evolution and extinction in a changing environment – a quantitative genetic analysis. *Evolution*, **49**, 151–163.

Burke MK, Dunham JP, Shahrestani P *et al.* (2010) Genome-wide analysis of a long-term evolution experiment with Drosophila. *Nature*, **467**, 587–U111.

Byars SG, Papst W, Hoffmann AA (2007) Local adaptation and cogradient selection in the alpine plant, *Poa hiemata*, along a narrow altitudinal gradient. *Evolution*, **61**, 2925–2941.

Colosimo PF, Hosemann KE, Balabhadra S *et al.* (2005) Widespread parallel evolution in sticklebacks by repeated fixation of ectodysplasin alleles. *Science*, **307**, 1928–1933.

Coltman DW (2008) Molecular ecological approaches to studying the evolutionary impact of selective harvesting in wildlife. *Molecular Ecology*, **17**, 221–235.

Coltman DW, O'Donoghue P, Jorgenson JT *et al.* (2003) Undesirable evolutionary consequences of trophy hunting. *Nature*, **426**, 655–658.

Conover DO, Munch SB (2002) Sustaining fisheries yields over evolutionary time scales. *Science*, **297**, 94–96.

Coop G, Witonsky D, Di Rienzo A, Pritchard JK (2010) Using environmental correlations to identify loci underlying local adaptation. *Genetics*, **185**, 1411–1423.

Cousyn C, De Meester L, Colbourne JK *et al.* (2001) Rapid, local adaptation of zooplankton behavior to changes in predation pressure in the absence of neutral genetic changes. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 6256–6260.

Czesak ME, Fox CW, Wolf JB (2006) Experimental evolution of phenotypic plasticity: How predictive are cross-environment genetic correlations? *American Naturalist*, **168**, 323–335.

Darimont CT, Carlson SM, Kinnison MT *et al.* (2009) Human predators outpace other agents of trait change in the wild. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 952–954.

Davey JW, Hohenlohe PA, Etter PD *et al.* (2011) Genome-wide genetic marker discovery and genotyping using next-generation sequencing. *Nature Reviews Genetics*, **12**, 499–510.

Decaestecker E, Gaba S, Raeymaekers JAM *et al.* (2007) Host-parasite 'Red Queen' dynamics archived in pond sediment. *Nature*, **450**, 870–U816.

De-Santis C, Jerry DR (2007) Candidate growth genes in finfish – where should we be looking? *Aquaculture*, **272**, 22–38.

Edeline E, Carlson SM, Stige LC *et al.* (2007) Trait changes in a harvested population are driven by a dynamic tug-of-war between natural and harvest selection. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 15799–15804.

Endler JA (1986) *Natural Selection in the Wild*. Princeton University Press, Princeton, NJ.

Falconer DS, McKay TFC (1996) *Introduction to Quantitative Genetics*. Longman, Essex.

Felsenstein J (1971) Biological significance of cost of gene substitution. *American Naturalist*, **105**, 1–11.

Foll M, Gaggiotti O (2008) A genome scan method to identify selected loci appropriate for both dominant and codominant markers: a Bayesian perspective. *Genetics*, **180**, 977–993.

Franks SJ, Sim S, Weis AE (2007) Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 1278–1282.

Garant D, Kruuk LEB (2005) How to use molecular marker data to measure evolutionary parameters in wild populations. *Molecular Ecology*, **14**, 1843–1859.

Gienapp P, Teplitsky C, Alho JS, Mills JA, Merilä J (2008) Climate change and evolution: disentangling environmental and genetic responses. *Molecular Ecology*, **17**, 167–178.

Grant PR, Grant BR (2002) Unpredictable evolution in a 30-year study of Darwin's finches. *Science*, **296**, 707–711.

Haldane JBS (1949) Suggestions as to quantitative measurement of rates of evolution. *Evolution*, **3**, 51–56.

Hansen MM, Meier K, Mensberg KLD (2010) Identifying footprints of selection in stocked brown trout populations: a spatio-temporal approach. *Molecular Ecology*, **19**, 1787–1800.

Hedrick PW (1995) Gene flow and genetic restoration – the Florida panther as a case study. *Conservation Biology*, **9**, 996–1007.

Heino M, Dieckmann U (2008) Detecting fisheries-induced life-history evolution: an overview of the reaction-norm approach. *Bulletin of Marine Science*, **83**, 69–93.

Hemmer-Hansen J, Nielsen EE, Meldrup D, Mittelholzer C (2011) Identification of single nucleotide polymorphisms in candidate genes for growth and reproduction in a nonmodel organism; the Atlantic cod, *Gadus morhua*. *Molecular Ecology Resources*, **11**, 71–80.

Hendry AP, Kinnison MT (1999) Perspective: the pace of modern life: measuring rates of contemporary microevolution. *Evolution*, **53**, 1637–1653.

Hendry AP, Farrugia TJ, Kinnison MT (2008) Human influences on rates of phenotypic change in wild animal populations. *Molecular Ecology*, **17**, 20–29.

Hoekstra HE, Hirschmann RJ, Bundey RA, Insel PA, Crossland JP (2006) A single amino acid mutation contributes to adaptive beach mouse color pattern. *Science*, **313**, 101–104.

van't Hof AE, Edmonds N, Dalikova M, Marec F, Saccheri IJ (2011) Industrial melanism in British peppered moths has a singular and recent mutational origin. *Science*, **332**, 961–963.

Hoffmann AA, Merila J (1999) Heritable variation and evolution under favourable and unfavourable conditions. *Trends in Ecology & Evolution*, **14**, 96–101.

Hoffmann AA, Sgro CM (2011) Climate change and evolutionary adaptation. *Nature*, **470**, 479–485.

Hoffmann AA, Willi Y (2008) Detecting genetic responses to environmental change. *Nature Reviews Genetics*, **9**, 421–432.

Hohenlohe PA, Bassham S, Etter PD *et al.* (2010) Population genomics of parallel adaptation in threespine stickleback using sequenced RAD tags. *Plos Genetics*, **6**, 23.

Ingvarsson PK (2001) Restoration of genetic variation lost – the genetic rescue hypothesis. *Trends in Ecology & Evolution*, **16**, 62–63.

Jaenicke-Despres V, Buckler ES, Smith BD *et al.* (2003) Early allelic selection in maize as revealed by ancient DNA. *Science*, **302**, 1206–1208.

Jensen LF, Hansen MM, Pertoldi C *et al.* (2008) Local adaptation in brown trout early life-history traits: implications for climate change adaptability. *Proceedings of the Royal Society London Series B: Biological Sciences*, **275**, 2859–2868.

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Jimenez S, Reighard GL, Bielenberg DG (2010) Gene expression of DAM5 and DAM6 is suppressed by chilling temperatures and inversely correlated with bud break rate. *Plant Molecular Biology*, **73**, 157–167.

Joost S, Bonin A, Bruford MW *et al.* (2007) A spatial analysis method (SAM) to detect candidate loci for selection: towards a landscape genomics approach to adaptation. *Molecular Ecology*, **16**, 3955–3969.

Jørgensen C, Enberg K, Dunlop ES *et al.* (2007) Managing evolving fish stocks. *Science*, **318**, 1247–1248.

Jump AS, Hunt JM, Martinez-Izquierdo JA, Penuelas J (2006) Natural selection and climate change: temperature-linked spatial and temporal trends in gene frequency in *Fagus sylvatica*. *Molecular Ecology*, **15**, 3469–3480.

Kauer MO, Dieringer D, Schlotterer C (2003) A microsatellite variability screen for positive selection associated with the 'Out of Africa' habitat expansion of *Drosophila melanogaster*. *Genetics*, **165**, 1137–1148.

Kerfoot WC, Robbins JA, Weider LJ (1999) A new approach to historical reconstruction: combining descriptive and experimental paleolimnology. *Limnology and Oceanography*, **44**, 1232–1247.

Kerr RA (2007) Global warming is changing the world. *Science*, **316**, 188–190.

Kettlewell HD (1961) The phenomenon of industrial melanism in Lepidoptera. *Annual Review of Entomology*, **6**, 245–262.

Kruuk LEB (2004) Estimating genetic parameters in natural populations using the 'animal model'. *Philosophical Transactions of the Royal Society of London Series B:Biological Sciences*, **359**, 873–890.

Laikre L, Allendorf FW, Aroner LC *et al.* (2010) Neglect of genetic diversity in implementation of the convention on biological diversity. *Conservation Biology*, **24**, 86–88.

Lande R (1976) Natural selection and random genetic drift in phenotypic evolution. *Evolution*, **30**, 314–334.

Lande R (1977) Statistical tests for natural selection on quantitative traits. *Evolution*, **31**, 442–444.

Lande R (1979) Quantitative genetic analysis of multivariate evolution, applied to brain–body size allometry. *Evolution*, **33**, 402–416.

Lande R (2009) Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. *Journal of Evolutionary Biology*, **22**, 1435–1446.

Lande R, Arnold SJ (1983) The measurement of selection on correlated characters. *Evolution*, **37**, 1210–1226.

Larsson K (1993) Inheritance of body size in the barnacle goose under different environmental conditions. *Journal of Evolutionary Biology*, **6**, 195–208.

Leinonen T, O'Hara RB, Cano JM, Merilä J (2008) Comparative studies of quantitative trait and neutral marker divergence: a meta-analysis. *Journal of Evolutionary Biology*, **21**, 1–17.

Leonard JA (2008) Ancient DNA applications for wildlife conservation. *Molecular Ecology*, **17**, 4186–4196.

Li RQ, Li YR, Fang XD *et al.* (2009) SNP detection for massively parallel whole-genome resequencing. *Genome Research*, **19**, 1124–1132.

Liedvogel M, Szulkin M, Knowles SCL, Wood MJ, Sheldon BC (2009) Phenotypic correlates of Clock gene variation in a wild blue tit population: evidence for a role in seasonal timing of reproduction. *Molecular Ecology*, **18**, 2444–2456.

Lynch M, Lande R (1993) *Evolution and Extinction in Response to Environmental Change*. Sinauer Associates, Sunderland, MA.

Lynch M, Walsh B (1998) *Genetics and Analysis of Quantitative Traits*. Sinnauer Associates, Sunderland, MA.

Mack RN, Simberloff D, Lonsdale WM *et al.* (2000) Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications*, **10**, 689–710.

Mäkinen HS, Shikano T, Cano JM, Merila J (2008) Hitchhiking mapping reveals a candidate genomic region for natural selection in three-spined stickleback chromosome VIII. *Genetics*, **178**, 453–465.

Manel S, Joost S, Epperson BK *et al.* (2010) Perspectives on the use of landscape genetics to detect genetic adaptive variation in the field. *Molecular Ecology*, **19**, 3760–3772.

Margulies M, Egholm M, Altman WE *et al.* (2005) Genome sequencing in microfabricated high-density picolitre reactors. *Nature*, **437**, 376–380.

Marshall JM, Weiss RE (2006) A Bayesian heterogeneous analysis of variance approach to inferring recent selective sweeps. *Genetics*, **173**, 2357–2370.

Maynard Smith J (1978) *The Evolution of Sex*. Cambridge University Press, New York, NY.

McKay JK, Latta RG (2002) Adaptive population divergence: markers, QTL and traits. *Trends in Ecology & Evolution*, **17**, 285–291.

Merilä J, Crnokrak P (2001) Comparison of genetic differentiation at marker loci and quantitative traits. *Journal of Evolutionary Biology*, **14**, 892–903.

Millien V, Lyons SK, Olson L *et al.* (2006) Ecotypic variation in the context of global climate change: revisiting the rules. *Ecology Letters*, **9**, 853–869.

Moss RH, Edmonds JA, Hibbard KA *et al.* (2010) The next generation of scenarios for climate change research and assessment. *Nature*, **463**, 747–756.

Nachman MW, Hoekstra HE, D'Agostino SL (2003) The genetic basis of adaptive melanism in pocket mice. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 5268–5273.

Namroud MC, Beaulieu J, Juge N, Laroche J, Bousquet J (2008) Scanning the genome for gene single nucleotide polymorphisms involved in adaptive population differentiation in white spruce. *Molecular Ecology*, **17**, 3599–3613.

Nielsen R (2005) Molecular signatures of natural selection. *Annual Review of Genetics*, **39**, 197–218.

Nielsen EE, Hansen MM (2008) Waking the dead: the value of population genetic analyses of historical samples. *Fish and Fisheries*, **9**, 450–461.

Nielsen R, Williamson S, Kim Y *et al.* (2005) Genomic scans for selective sweeps using SNP data. *Genome Research*, **15**, 1566–1575.

Nielsen EE, Hemmer-Hansen J, Larsen PF, Bekkevold D (2009a) Population genomics of marine fishes: identifying adaptive variation in space and time. *Molecular Ecology*, **18**, 3128–3150.

Nielsen EE, Hemmer-Hansen J, Poulsen NA *et al.* (2009b) Genomic signatures of local directional selection in a high gene flow marine organism; the Atlantic cod (*Gadus morhua*). *BMC Evolutionary Biology*, **9**, 276.

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Nussle S, Bornand CN, Wedekind C (2009) Fishery-induced selection on an Alpine whitefish: quantifying genetic and environmental effects on individual growth rate. *Evolutionary Applications*, **2**, 200–208.

Olsen EM, Heino M, Lilly GR *et al.* (2004) Maturation trends indicative of rapid evolution preceded the collapse of northern cod. *Nature*, **428**, 932–935.

Ouborg NJ, Pertoldi C, Loeschcke V, Bijlsma R, Hedrick PW (2010) Conservation genetics in transition to conservation genomics. *Trends in Genetics*, **26**, 177–187.

Paetkau D, Slade R, Burden M, Estoup A (2004) Genetic assignment methods for the direct, real-time estimation of migration rate: a simulation-based exploration of accuracy and power. *Molecular Ecology*, **13**, 55–65.

Palumbi SR (2001) Humans as the world's greatest evolutionary force. *Science*, **293**, 1786–1790.

Parker IM, Gilbert GS (2004) The evolutionary ecology of novel plant–pathogen interactions. *Annual Review of Ecology Evolution and Systematics*, **35**, 675–700.

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics*, **37**, 637–669.

Pauwels K, Stoks R, Decaestecker E, De Meester L (2007) Evolution of heat shock protein expression in a natural population of *Daphnia magna*. *American Naturalist*, **170**, 800–805.

Pemberton JM (2008) Wild pedigrees: the way forward. *Proceedings of the Royal Society London Series B: Biological Sciences*, **275**, 613–621.

Phillips BL, Shine R (2004) Adapting to an invasive species: toxic cane toads induce morphological change in Australian snakes. *Proceedings of the National Academy of Sciences of the United States of America*, **101**, 17150–17155.

Pigliucci M, Schlichting CD (1998) Reaction norms of *Arabidopsis*. V. Flowering time controls phenotypic architecture in response to nutrient stress. *Journal of Evolutionary Biology*, **11**, 285–301.

Poncet BN, Herrmann D, Gugerli F *et al.* (2010) Tracking genes of ecological relevance using a genome scan in two independent regional population samples of *Arabis alpina*. *Molecular Ecology*, **19**, 2896–2907.

Pritchard JK, Di Rienzo A (2010) Adaptation – not by sweeps alone. *Nature Reviews Genetics*, **11**, 665–667.

Pritchard JK, Stephens M, Rosenberg NA, Donnelly P (2000) Association mapping in structured populations. *American Journal of Human Genetics*, **67**, 170–181.

Pujol B, Wilson AJ, Ross RIC, Pannell JR (2008) Are Q_{ST}–F_{ST} comparisons for natural populations meaningful? *Molecular Ecology*, **17**, 4782–4785.

Pulido F, Berthold P (2010) Current selection for lower migratory activity will drive the evolution of residency in a migratory bird population. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 7341–7346.

Rasmussen M, Li YR, Lindgreen S *et al.* (2010) Ancient human genome sequence of an extinct Palaeo-Eskimo. *Nature*, **463**, 757–762.

Renaut S, Nolte AW, Bernatchez L (2010) Mining transcriptome sequences towards identifying adaptive single nucleotide polymorphisms in lake whitefish species pairs (*Coregonus* spp. Salmonidae). *Molecular Ecology*, **19**, 115–131.

Reusch TBH, Wood TE (2007) Molecular ecology of global change. *Molecular Ecology*, **16**, 3973–3992.

Riba M, Mayol M, Giles BE *et al.* (2009) Darwin's wind hypothesis: does it work for plant dispersal in fragmented habitats? *New Phytologist*, **183**, 667–677.

Richards CM (2000) Inbreeding depression and genetic rescue in a plant metapopulation. *American Naturalist*, **155**, 383–394.

Rodriguez-Trelles F, Rodriguez MA (2007) Comment on 'Global genetic change tracks global climate warming in *Drosophila subobscura*'. *Science*, **315**, 1497–1497.

Ronce O (2007) How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annual Review of Ecology Evolution and Systematics*, **38**, 231–253.

Rutter C (1904) Natural history of the quinnat salmon. A report on investigations in the Sacramento River, 1886–1901. *Bulletin of the United States Fish Commission*, **22**, 65–141.

Schlotterer C (2002) A microsatellite-based multilocus screen for the identification of local selective sweeps. *Genetics*, **160**, 753–763.

Schwartz MK, Luikart G, Waples RS (2007) Genetic monitoring as a promising tool for conservation and management. *Trends in Ecology & Evolution*, **22**, 25–33.

Sharpe DMT, Hendry AP (2009) Life history change in commercially exploited fish stocks: an analysis of trends across studies. *Evolutionary Applications*, **2**, 260–275.

Smith TB, Bernatchez L (2008) Evolutionary change in human-altered environments. *Molecular Ecology*, **17**, 1–8.

Sørensen JG, Kristensen TN, Loeschcke V (2003) The evolutionary and ecological role of heat shock proteins. *Ecology Letters*, **6**, 1025–1037.

Steppan SJ, Phillips PC, Houle D (2002) Comparative quantitative genetics: evolution of the G matrix. *Trends in Ecology & Evolution*, **17**, 320–327.

Stinchcombe JR, Hoekstra HE (2008) Combining population genomics and quantitative genetics: finding the genes underlying ecologically important traits. *Heredity*, **100**, 158–170.

Stockwell CA, Hendry AP, Kinnison MT (2003) Contemporary evolution meets conservation biology. *Trends in Ecology & Evolution*, **18**, 94–101.

Storz JF (2005) Using genome scans of DNA polymorphism to infer adaptive population divergence. *Molecular Ecology*, **14**, 671–688.

Stranger BE, Stahl EA, Raj T (2011) Progress and promise of genome-wide association studies for human complex trait genetics. *Genetics*, **187**, 367–383.

Tallmon DA, Luikart G, Waples RS (2004) The alluring simplicity and complex reality of genetic rescue. *Trends in Ecology & Evolution*, **19**, 489–496.

Teplitsky C, Mills JA, Alho JS, Yarrall JW, Merila J (2008) Bergmann's rule and climate change revisited: disentangling environmental and genetic responses in a wild bird population. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 13492–13496.

Umina PA, Weeks AR, Kearney MR, McKechnie SW, Hoffmann AA (2005) A rapid shift in a classic clinal pattern in *Drosophila* reflecting climate change. *Science*, **308**, 691–693.

Vasemägi A (2006) The adaptive hypothesis of clinal variation revisited: single-locus clines as a result of spatially restricted gene flow. *Genetics*, **173**, 2411–2414.

Vasemägi A, Primmer CR (2005) Challenges for identifying functionally important genetic variation: the promise of

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combining complementary research strategies. *Molecular Ecology*, **14**, 3623–3642.
Wandeler P, Hoeck PEA, Keller LF (2007) Back to the future: museum specimens in population genetics. *Trends in Ecology & Evolution*, **22**, 634–642.
Weltzien FA, Andersson E, Andersen O, Shalchian-Tabrizi K, Norberg B (2004) The brain–pituitary–gonad axis in male teleosts, with special emphasis on flatfish (pleuronectiformes). *Comparative Biochemistry and Physiology A: Molecular & Integrative Physiology*, **137**, 447–477.
Westemeier RL, Brawn JD, Simpson SA *et al.* (1998) Tracking the long-term decline and recovery of an isolated population. *Science*, **282**, 1695–1698.
Wiehe T, Nolte V, Zivkovic D, Schlotterer C (2007) Identification of selective sweeps using a dynamically adjusted number of linked microsatellites. *Genetics*, **175**, 207–218.
Willerslev E, Cooper A (2005) Ancient DNA. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 3–16.
Williams LM, Oleksiak MF (2011) Ecologically and evolutionarily important SNPs identified in natural populations. *Molecular Biology and Evolution*, **28**, 1817–1826.
Wilson AJ, Reale D, Clements MN *et al.* (2010) An ecologist's guide to the animal model. *Journal of Animal Ecology*, **79**, 13–26.

This paper represents one of the outcomes of the NCEAS/NES-Cent Working Group onGenetic Monitoring (GeM) (PIs F.W. Allendorf and M.K. Schwartz). The authors share a common interest in evolutionary biology and conservation genetics. This specifically includes how to analyze populations repeatedly over time (genetic monitoring) in order to explore the temporal dimension of genetic population structure and to estimate population abundance, demographic parameters and adaptive responses.

Supporting information

Additional supporting information may be found in the online version of this article.

Table S1 Studies employing genetic monitoring of adaptive change, based on molecular markers.

Table S2 Studies employing genetic monitoring of adaptive change, based on quantitative traits.

Fig. S1 Outcomes of studies aimed at detecting adaptive evolutionary response to environmental change by genetic monitoring.

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