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Evolutionary responses to climate change

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By causing changes in abiotic and biotic environmental conditions, climate change generates intense natural selection in populations of many organisms. In order to stay adapted in changing environmental conditions, populations need to respond to this selection, otherwise they will be eventually faced with extinction. The adaptive responses can be of three different kinds. First, populations may restore their fitness by adapting genetically to changed conditions. Second, fitness can be restored without genetic changes through phenotypic plasticity. Third, populations may relocate to favourable environments. All these mechanisms are already at work, but not all populations and species are likely to stay adapted.

There is clear evidence that the globally rising temperatures caused by climate change have had a multitude of impacts on most ecosystems and taxonomic groups. Some of the most commonly observed impacts involve changes in the distribution and phenology of species. Namely, many species, or even entire communities, have shifted their distribution ranges pole-wards. Similarly, many phenological events, such as timing of flowering, breeding, or migration, have advanced in parallel to changes in climatic conditions. There is also evidence for climate change-driven shifts in population means of phenotypes other than phenology, such as frequencies of different colour morphs or mean body size of birds and mammals. All these observations suggest that many organisms and populations are already responding to climate-driven changes in their environment, but most of the time it is not clear whether the responses are ascribable to evolution. This is because

populations can stay adapted to changes in their environment through three distinct ways: (1) by moving to areas where conditions are still favourable to them, (2) by adjustments through phenotypic plasticity, or (3) by adapting genetically via microevolution. Furthermore, these processes are not mutually exclusive, but could be at work simultaneously. However, it is important to note that although all these three ways of responding to climate change are adaptive, only the third mechanism constitutes an *in situ* adaptive evolutionary response.

Differentiating among these three mechanisms of staying adapted under changing environmental conditions is not only of academic interest, but also of practical importance for attempts to predict how populations, species and communities will fare under changing climatic conditions. For instance, phenotypic plasticity may allow populations and species to track changing conditions in the short-term, but there may be limits to what extent plastic

changes are possible before further adjustments through this mechanism are no longer possible. Likewise, relocating to new areas with favourable conditions might not be an option for species with poor dispersal ability, or for populations already occurring at the northern (geophysical) limits of their current distribution ranges. In such situations, the only option for remaining adapted rests on genetically-based evolutionary responses.

How to stay adapted to changes in the environment

While the main focus of our treatment here will be on genetically-based evolutionary responses to climate change mediated selection, it is important to realize that the *process of staying adapted* under climate driven changes to environmental conditions does not necessarily require genetic adaptation. As discussed above, populations can maintain their fitness (i.e. stay adapted) also by relocating to areas where environmental conditions are still favourable to them, or by adjusting their phenotypes (e.g. breeding or emergence times) to changed conditions by plasticity. In the following, we will consider each of these three different mechanisms of staying adapted to changing conditions in more detail. Here, it is also worth noting that although dispersal to new areas and plasticity can essentially be considered as non-genetic responses, they too can have a genetic basis, and hence, evolve in response to climate change mediated selection.

Dispersal

If the local environment changes, populations and species can evade these changes by dispersing to areas where conditions for their persistence are more favourable. However, whether this option is possible or viable depends on whether suitable habitat is present within the typical dispersal distance of the species in question.

As climate change has generally led to an increase in temperatures, climate zones are moving polewards and towards higher elevations. Species are expected to follow these shifts to align their 'bioclimatic envelopes', the abiotic conditions describing their current geographical distributions, with the shifted climate zones. Many species from a variety of taxa and ecosystems have indeed shifted their geographic distributions polewards (Fig. 1). However, for high-altitude species this means that their preferred climate zone may not exist anymore within their current geographic distribution range in the future. As dispersal to different mountain ranges may not be possible, these species cannot evade climate change by dispersal, and this has been identified as a major extinction threat to montane species in the tropics. The same likely applies for many cold adapted species whose distribution is restricted to occupy habitat isolates (e.g. lakes, mountain tops) in the northern hemisphere.

There are also other reasons why dispersal is unlikely to be the 'Holy Grail' for coping with climate change mediated fitness loss in the long-term. Every species is obviously part of a biome, consisting of numerous predator, prey, or competitor species. Dispersal abilities of all species in a biome are, however, highly unlikely to be identical. Consequently, even if a species manages to evade climate change by tracking the shifts in climate zones, it is likely to encounter a changed biome in its new distribution range. The newly encountered predator, prey, or competitor species in the new distribution range can exert novel selection pressures on the species, making the process of staying adapted uncertain. Furthermore, there is evidence to suggest that individuals at the populations' leading edges often have higher dispersal ability than individuals at the core areas. However, these dispersal-prone individuals may not be particularly good competitors due to trade-offs with traits related to their increased dispersal ability (Chuang and Peterson 2016). These considerations also

highlight the point that the greatest evolutionary effects of climate change do not necessarily stem from selection pressures related to changes in abiotic (e.g. temperature) conditions, but perhaps from changes in biotic (e.g. competition, predation) conditions.

All these considerations aside, dispersal to new areas is clearly an important way providing populations and species opportunity mitigate fitness loss due to changing climatic conditions. The fact that latitudinal and altitudinal shifts towards cooler conditions in distribution ranges of many terrestrial and aquatic species are already visible (Fig. 1) testifies to the importance of this mechanism.

presence of a potential predator. Similarly, many species adjust their phenology, the seasonal timing of life-cycle events, to ambient temperatures, with phenology being earlier under warm than in cool conditions. Such phenotypic plasticity in morphology or behaviour has generally evolved as a response to varying environmental conditions and allows individuals or genotypes to adjust their phenotypes so that they can track the varying environmental optimum.

The role of phenotypic plasticity in the context of climate change can be nicely illustrated with the well-studied example of the winter moth-great tit predator-prey system. The development of the caterpillars (mainly winter moth, *Operophtera*

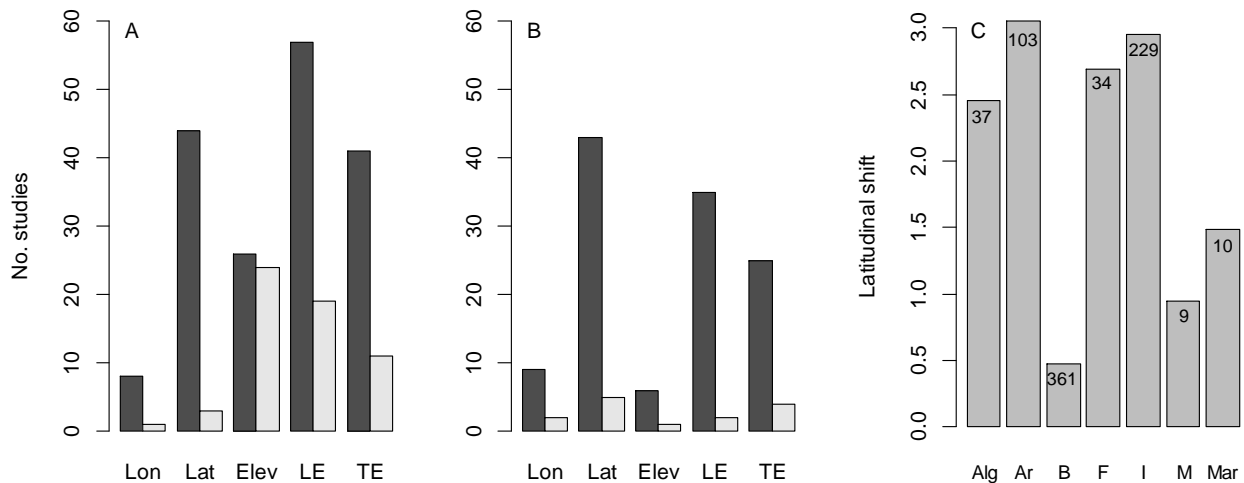


Fig. 1 Dispersal as a response to climate change. Number of studies reporting changes in several aspects of geographic distribution in animals (dark grey bars) and plants (light grey bars) in terrestrial (A) and marine ecosystems (B). Lon: Longitude, Lat: Latitude, Elev: Elevation / depth (for marine ecosystems), LE: Leading edge, TE, Trailing edge. After Lenoir and Svenning (2015). (C) Pole-ward range shifts (km / year) of algae (Alg), arthropods (spiders and millipeds, Ar), birds (B), fish (F), insects (I), mammals (M) and marine invertebrates (Mar). Numbers in bars depict the number of species in each group. Data from Perry et al. (2005) and Chen et al. (2011).

Phenotypic plasticity

Phenotypic plasticity refers to the ability of a genotype to express different phenotypes depending on the environment in which it resides. For example, genetically identical water flea (*Daphnia*) clones can differ in their morphology depending on whether reared in the absence or

brumata), including the timing of egg-hatching, is temperature dependent, which means that the period of highest caterpillar abundance occurs early in years with warm springs. Because these caterpillars constitute an important food source for their nestlings, the great tits (*Parus major*) need to synchronise the nestling period with the time of maximum caterpillar availability, and breed early

in warm springs. This phenotypically plastic response to warmer spring temperatures allows the birds to track the annually variable optimal breeding time.

Climate change has led to increasing spring temperatures and has thereby advanced the timing of maximum caterpillar abundance. However, long-term data collected over the last three decades show that the phenology of the caterpillars has advanced at a faster rate than that of the birds. As such, the question remains why has phenotypic plasticity not (sufficiently) allowed birds to track this climate-induced change in their environment? This is because the environmental variable that determines the breeding time of the birds (here: temperature from mid March to mid April) is not the same as the environmental variable that determines maximum caterpillar peak abundance (temperature from mid March to mid May). Because these two temperatures are not perfectly correlated and the birds cannot therefore 'predict' caterpillar phenology perfectly, it is optimal for the birds to respond slightly less strongly to temperatures than the caterpillars (Gienapp et al. 2014). This means that the phenology of the birds will advance at a slower rate than that of the caterpillars, which explains the observed mismatch in their phenologies.

The situation in which phenotypic plasticity does not allow the environment to be perfectly tracked appears to be a fairly general one. This is because the 'cue' used for trait expression (e.g. temperature during egg laying in the great tit-caterpillar example above) is in most cases an imperfect predictor of conditions at the time when the trait is actually expressed. For example, a *Daphnia* that has perceived the presence of a predator and developed its defensive morphology may not be faced with predation because the predator threat may have disappeared in the meanwhile. This imperfect correlation between the perceived environment (cue) and the environment exerting selection means that tracking on continuously

changing environment will rarely, if ever, be possible (Gienapp et al. 2014). In fact, a large meta-analysis of terrestrial ecosystems shows that the phenology at lower trophic levels has advanced consistently at faster rates than that at higher trophic levels (Thackeray et al. 2010). These mismatches will lead to selection on phenology of the higher trophic level, and staying adapted will require genetically-based microevolutionary responses.

To sum up, rapid phenotypic adjustments via phenotypic plasticity can alleviate immediate negative fitness consequences of environmental changes, but these adjustments are hardly ever perfect as there may be limits and costs to expression of plasticity. Hence, the prevailing consensus is that phenotypic plasticity is an important mechanism providing the first line of defence against fitness loss in changing climatic conditions, but long-term persistence depends critically on populations' ability to adapt through micro-evolutionary responses.

Micro-evolutionary response

In contrast to dispersal and phenotypic plasticity, micro-evolutionary response to climate change mediated selection implicates change in the genetic constitution of populations. Such changes are expected to occur as long as there is directional selection and the traits under selection are heritable. In general, most traits in most populations are known to be heritable, and hence evolutionary responses would be expected even over fairly short time-periods. However, reduced levels of genetic variability in small populations, or depletion of genetic variance due to strong and persistent selection can constrain long-term selection responses. Likewise, the efficiency of natural selection is greatest in large populations, whereas in small populations it can be constrained by the action of genetic drift. However, the rate at which one would expect to see evolutionary responses to climate change occurring depends not

only on levels of genetic variability (heritability) and strength of selection, but also from the species generation time: species with shorter generation intervals are able to respond to selection faster than those with longer ones. Hence, a general expectation is that species with long generation times, such as large and long-lived animals or plants, will adapt slower than small organisms with large population sizes and short generation intervals.

There are several examples where micro-evolutionary responses to climate change mediated selection have been verified by genetic analyses, or otherwise inferred (see below). However, a general interpretational challenge faced by evolutionary studies on climate change responses is to disentangle genetic and environmental (plastic) causes underlying observed phenotypic responses (Merilä & Hendry 2014). Disentangling these two mutually non-exclusive processes is not only of academic interest, but also because the two mechanisms make different predictions about the long-term viability of populations. Namely, as pointed out above, a purely plastic response is highly unlikely to allow perfect tracking of changes in the environment. The resulting ‘mismatch’ between expressed and optimal phenotype will reduce a population’s mean fitness, and ultimately drive it to extinction. In contrast, an evolutionary response, if sufficiently rapid (see *Rates of Evolutionary Change*), would allow populations to persist under changing environmental conditions.

Disentangling plastic and evolutionary responses

Testing directly for genetic changes

The most obvious way to show that an observed phenotypic change is the consequence of evolutionary change is to demonstrate that the population has changed genetically, i.e. allele frequencies at causal loci have changed over time.

However, this requires a good understanding of the genetics of the involved traits, which is still typically lacking when it comes to most ecologically important traits. Currently, there are no studies which would have succeeded to uncover climate change driven genetic changes in loci controlling for phenotypic expression of ecologically important traits. However, there are studies that have uncovered temporal allele frequency changes in some particular genetic loci consistent with the hypothesis that climate mediated selection has been driving these changes.

Quantitative genetic methods provide another way to detect genetic changes over time. By allowing prediction of ‘breeding values’, the summed effects of the genes affecting a given trait, they allow evaluation of genetic changes over time. However, the utility of these methods in natural populations is restricted to systems where pedigrees necessary for estimation of breeding values are available. However, these so-called ‘animal models’ require large amounts of long-term data for evaluation of changes in breeding values over time. Nevertheless, quantitative genetic methods have already been successfully employed in long-term studies of marked bird and mammal populations to provide evidence both for and against the genetic basis of phenotypic responses to climate mediated selection.

Common garden experiments provide another genetic approach to detect genetic changes in quantitative traits over time. By rearing individuals from the same population, collected at different time points, under controlled and identical environmental conditions allows identification of genetic changes: since the influence of phenotypic plasticity on phenotypes is controlled for, any phenotypic changes must be due to genetic changes. While common garden experiments have been typically used to test for genetic differentiation among populations, there are few studies that have conducted such experiments over time, i.e. using individuals from the same

population collected at different time points (e.g., Bradshaw and Holzapfel 2001). In species that produce dormant life-stages, such as seeds, resting eggs or cysts, it may even be possible to perform such studies in retrospect by ‘resurrecting’ dormant life-stages (e.g. from samples taken from aquatic sediments or soil), and testing them in common garden experiments with individuals sampled from contemporary populations. Such work has demonstrated past adaptation and may, in combination with genomic analysis, even allow predicting future adaptation (Orsini et al. 2013). An important consideration in the context of common garden experiments is that they test for genetic differentiation, but they do not differentiate between various causes of such differentiation. Namely, genetic differentiation can be caused both by random genetic drift and natural selection, and differentiating in between these alternatives requires additional tests.

Comparisons of the degree of quantitative trait (Q_{ST}) and neutral genetic differentiation (F_{ST}) provide one straightforward approach to this end. The modern incarnations of these so-called Q_{ST} - F_{ST} comparisons are fairly powerful tools able to identify footprints of natural selection even if only few population samples are available for testing. However, the main challenge for these approaches is that they require fairly elaborate experiments at different time points to be utilized.

Inferring genetic changes indirectly

There are also other more indirect approaches to uncover adaptive genetic changes which do not require a detailed understanding of the genetics of the traits in focus. While these approaches can be helpful and informative, one should nevertheless keep in mind that they are inferential because the genetic change has not been proven.

One indirect approach to disentangle evolutionary and plastic change resides in the realisation that if a trait’s plastic response to the relevant

environmental parameter is well understood (Fig. 2A), then it is possible to predict what would be achievable by plasticity given the observed change in environment over time (Fig. 2B): If an expected plastic response to the observed change in environment can fully explain the observed change in the trait (Fig. 2C), the most parsimonious explanation would be that the observed trend is purely plastic and that no genetic change has occurred.

Alternatively, if the predicted response from the trait’s plasticity is less than the observed phenotypic change, one might conclude that an evolutionary response has taken place because the observed advancement cannot be fully explained by plasticity (Fig. 2D). By the same logic, if the genetic change can be quantified but does not fully explain the observed phenotypic change, one could conclude that the remaining, unexplained change would be due to phenotypic plasticity (Fig. 2E). If both the expected phenotypic change and the genetic change can be quantified, but both together would be unable to fully explain the observed phenotypic change (Fig. 2F), one could conclude that the expected plastic and genetic changes were underestimated. An alternative explanation for the discrepancy could be that the trait may be responding to another environmental variable, and a change in this variable is driving an unidentified plastic response in the observed trait (Fig. 2F). Whether this approach will yield reliable inferences depends crucially on the accuracy of the slope of the reaction norm, which describes the response of the phenotype to the environment. Any underestimation of the reaction norm slope will lead to underestimation of the expected plastic shift and hence, an upwardly biased estimate of evolutionary responses.

The accuracy of the estimated reaction norm depends on several factors. First, it is important to disentangle population-level from individual-level changes, because population-level changes may be a consequence of genetic change, which one aims

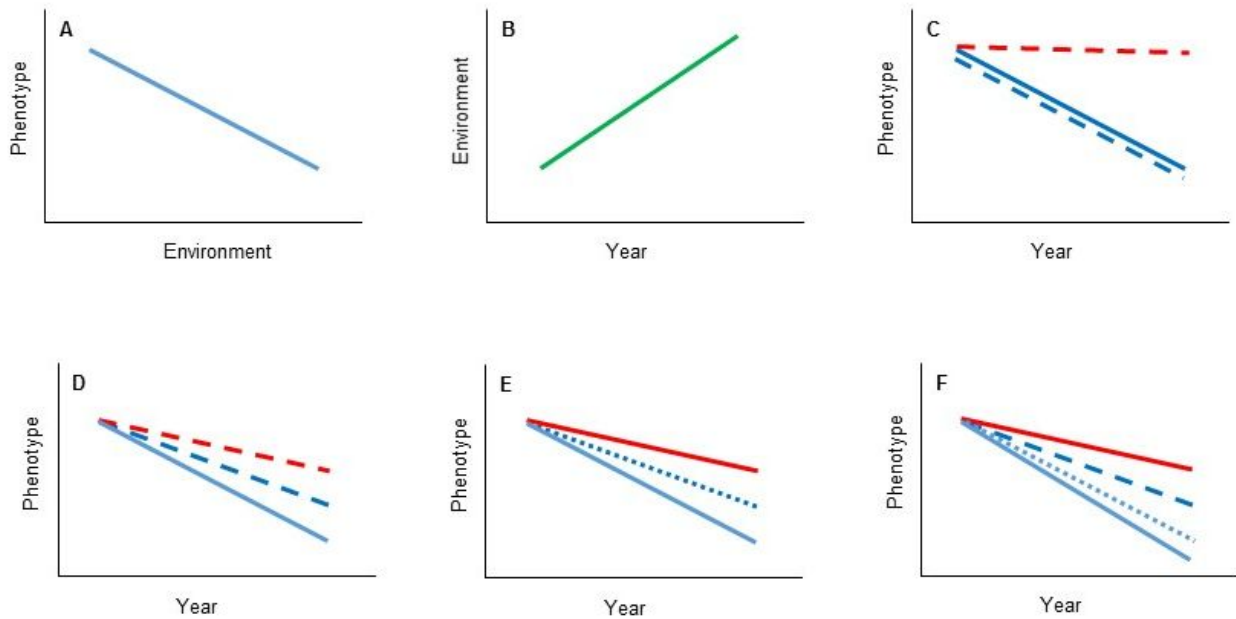


Fig. 2 Schematic illustration how phenotypic change can be partitioned into its genetic and plastic components. (A) Trait as function of the environmental variable, i.e. the trait's reaction norm (blue line). Because the trait is negatively associated with the environmental variable, the trait can be envisioned as a phenological trait and the environmental variable as temperature. (B) Temporal change in the environmental variable (green line) that affects the trait via plasticity. (C) The predicted change from the change in environmental variables and the trait's plasticity (dashed thin blue line) can fully explain the observed phenotypic trend (thick blue line) and one would hence conclude that genotypes (dashed red line) did not change over time. (D) The predicted change from the change in environmental variables and the trait's plasticity (dashed thin blue line) cannot fully explain the observed phenotypic trend (thick blue line). One could hence conclude that a genetic change would have occurred (dashed red line). (E) Here the genetic change was quantified (red line) but it does not fully explain the observed phenotypic trend (blue line). One could hence conclude that an additional plastic change (dotted blue line) would have taken place. (F) Both plastic (dashed blue line) and genetic change (red line) were quantified. However, their combination (dotted blue line) does not add up to the observed trait change (blue line). One possible conclusion is that plastic responses to another, unidentified environmental variable is responsible for the remaining unexplained trait change.

to test, or other processes such as a change in demographic population structure. This can be illustrated by contrasting two studies that tested for both plastic and genetic changes (Fig. 3). The plumage of tawny owls (*Strix aluco*) can vary gradually in colour from brown to grey. A Finnish population of tawny owls became consistently greyer over time and because plumage colour did not change during the individual's lifetime, i.e. plumage colour was not plastic, this change was attributed to a genetic change in the population (Fig. 3A). In contrast, body mass changes in a Finnish population of Siberian jays (*Perisoreus infaustus*) could largely be explained by

individuals becoming increasingly lighter and heavier again, rather than by attributing population-level trends to genetic changes (Fig. 3B). Second, the environmental variable driving plasticity has to be identified correctly, as use of any other variable will bias the estimated reaction norm slope, leading to an over- or under-estimation of the contribution of phenotypic plasticity and consequently, also to a wrongly inferred evolutionary response. Third, a crucial assumption is that the identified environmental variable is the only variable determining the trait. If the trait responds plastically to more than one environmental variable, yet only one has been

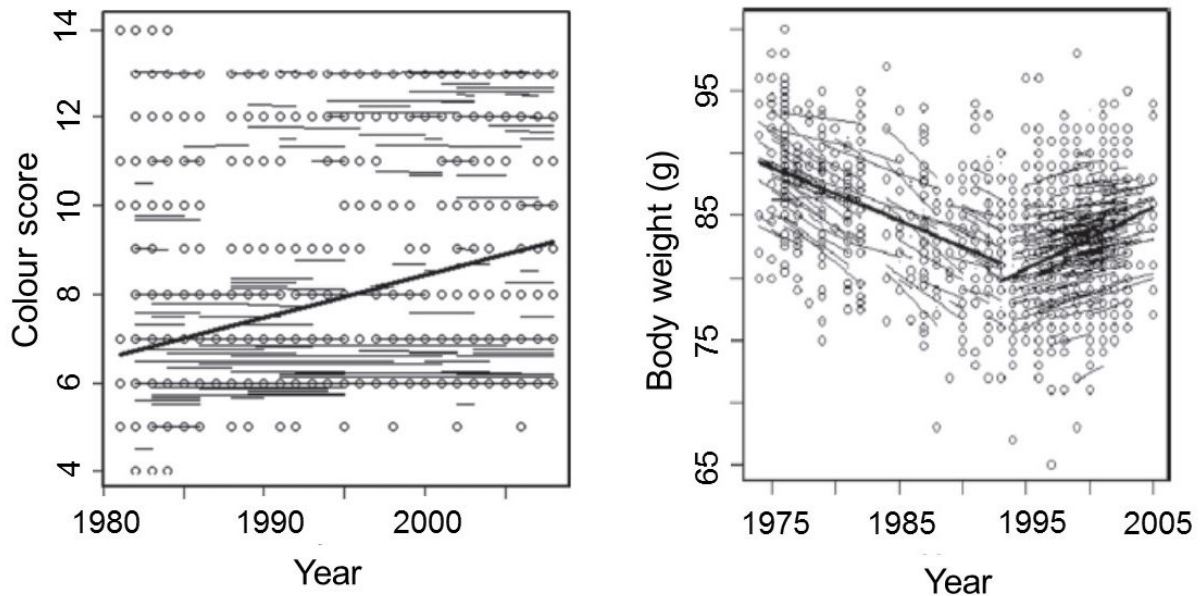


Fig. 3 Population mean trends (thick line) and individual changes (thin lines) in (A) colour morphs of tawny owls (*Strix aluco*) and (B) body weight of Siberian jays (*Perisoreus infaustus*). Individual tawny owls do not change their colour morph over time and change in colour morph in the population could be a genetic change. This population-level change appears to be evolutionary change owing to milder winters favouring survival of the grey morph (Karell et al. 2011). In (B) individual reaction norms (thin lines) are similar to the population mean trends and hence phenotypic plasticity would seem to be the most parsimonious explanation although a small proportion of the body weight decline was actually genetic as shown by animal model analysis (Gienapp & Merilä 2014). Figure re-drawn from Karell et al. (2011) and Gienapp & Merilä (2014).

identified and included in the prediction of plastic changes in the trait, plastic responses to the unidentified variable would be mistaken for genetic change. Hence, predicting plastic changes and comparing them to observed changes (cf. Fig. 2) can be a useful framework for inferring or discounting genetic changes, but careful attention needs to be paid to underlying assumptions.

Other approaches

Most of the variables that are affected by climate change also vary spatially, allowing for what is known as ‘space-for-time’ substitution inference. For instance, under the assumption that spatial variation in a variable will have the same effect on phenotypes as temporal changes, spatial investigation of genetic adaptation and plasticity could substitute investigation of temporal changes.

For example, if individuals originating from populations experiencing different ambient temperature differ in their phenotypes under controlled temperature conditions (e.g. in a common garden experiment), this would be an indication of local adaptation to temperature. An alternative approach without the need of controlled experiments relies on the comparison of within-population responses to annual variation in the environmental variable, with among-population responses to spatial variation in this environmental variable (Phillimore et al. 2010). If the among-population response differs from the plastic within-population response, this difference would be assumed to be a consequence of local adaptation. By inference, observing an equivalent difference in response to changing temperatures due to climate change could be interpreted as an evolutionary response. This conclusion would, however, only be

valid if the compared populations do not show phenotypic plasticity in response to temperature. Otherwise, populations may well be locally adapted to temperature and hence show differentiation in the common garden setting, but the temporal change observed *in situ* could still be plastic. Hence, a space-for-time substitution approach allows one to infer that populations have the *potential* to adapt, but not that they have *actually* adapted.

If it is possible to manipulate an organisms' environment with respect to the environmental variable affected by climate change (e.g. temperature or CO₂ content), one can directly test whether, and how fast, the organism can respond to evolutionary changes in this environmental variable. However, subjecting experimental populations to similar rates of changes as those that have been observed as a consequence of climate change, and testing whether the populations have changed genetically over the duration of the experiment, only demonstrates that an evolutionary change is possible, but not that it has indeed happened in natural populations. Furthermore, this approach is limited to organisms with short generation times, and to those that can be maintained in the laboratory or mesocosms resembling their natural environments.

Evidence for evolutionary responses to climate change

The abovementioned methods can allow disentangling plastic from genetic changes in a trait over time. However, even if evidence is found to show that a trait has changed genetically over time, this does not mean that it is an evolutionary response to climate change unless it is also shown that climate change has actually generated selection on this trait. Theoretically, another environmental variable that is unrelated to climate change could have led to selection on the trait, and hence, be responsible for the observed evolutionary change. To demonstrate that climate

change has led to selection on a trait, it is necessary to first show that the trait is under selection; second, identify the environmental variable that is the real driver of selection; and third, show that this driver of selection has been affected by climate change.

Ideally, selection on a trait is quantified by measuring the covariance between phenotypes and fitness of individuals. This means that it needs to be possible to link offspring to their parents (to measure reproductive success) and to uniquely mark and recapture individuals (to measure survival). As already pointed out above, collecting such individual-level data is difficult or impossible in many species. Replacing reproductive success and survival measures of fitness by proxies, i.e. traits that are known (or can be hypothesised) to be related to them (e.g. number of set seeds or overall physiological condition) is a possible approach to explore whether a trait affects fitness, but formal quantification of the strength of selection will hardly be possible. Theoretically, shifts in population means during episodes of selection can be used to quantify selection, but any dispersal happening at the same time would bias these estimates. Even if selection can be quantified it may be difficult to identify the driver of selection. Given these requirements, i.e. to quantify selection and link it to an ecological driver in addition to showing genetic change, it will be highly challenging to formally demonstrate an evolutionary response to climate change. Nevertheless, even if single links in this 'chain of evidence' are missing, one may accept compelling results as evidence for climate change induced evolution.

Table 1 summarises the findings of several taxon-specific reviews on evolutionary and plastic responses to climate change. The proportion of studies that were able to test for genetic changes varies widely among the taxa. In plants, almost all reviewed studies (92%) were able to test for genetic changes, while the comparable figures in

Table 1. Overview over studies testing for genetic changes in response to climate change in different taxonomic groups. Given is the total number of studies included in the review(s), how many of these had suitable data to test for genetic (vs. plastic) change, how many of the ones that could test for it found evidence for genetic change, and how many of the ones that could test for genetic change also quantified selection on the studied traits. The number of studies listed here differs from those listed in the original reviews for some taxa because we here applied slightly different criteria for inclusion. The table was compiled from the data given in Table 2 in Merilä and Hendry (2014) from where also the references to the original reviews can be found.

Taxon	Total number of studies reviewed	Genetic change tested	Genetic change found	Selection measured (in studies testing for genetic change)
Plants	36	33	33	22
Insects	17	8	8	2
Fish	29	2	2	1
Reptiles ¹	32	4	4	2
Amphibians ¹	26	1	1	0
Birds	23	6	1	6
Mammals	19	3	1	2

¹Here only traits for that a clear link to climate change existed are included to allow a useful comparison to the other reviews.

fish and amphibians were only 7% and 4%, respectively (Table 1). These differences likely reflect differences in methodological constraints imposed by different study systems. For example, in plants common garden and reciprocal transplant experiments are commonly used. Reciprocal transplant experiments are a special form of the common garden experiment where individuals are tested in two (or more) environments representing the environmental conditions at the different origins of the tested populations. In birds or mammals such experimental approaches are logistically far more demanding to implement, if not often simply unfeasible. Hence, nearly all (but very limited) evidence for climate change mediated evolution from animal studies comes from application of ‘animal model’ analyses to long-term datasets of marked birds or mammals.

The two studies in fish, both in Pacific salmon (*Oncorhynchus* sp.), that have demonstrated

genetic responses to climate change used two fairly different approaches. One study showed that the frequency of a molecular marker allele associated with late migration time declined in a population of pink salmon (*Oncorhynchus gorbuscha*) after the beginning of the 1990’s, indicating a genetic shift in the population’s migration time (Kovach et al. 2012). In the other study, Crozier et al. (2011) took an approach based on purely phenotypic data. Because in their study system sockeye salmon (*Oncorhynchus nerka*) were individually marked, it was possible to estimate the relationship between migration time, water temperature and survival, which were then used to predict annual selection differentials for timing of migration. When this predicted selection and plastic drivers of migration time (e.g. river flow or water temperature) were used to model the observed changes in migration time, it was found that inclusion of a genetic response to the selection was needed to explain the observed advancement in the timing of yearly

migration. Although the selection inferred from ecological proxies and the fact that the observed trend could not be explained by plasticity alone, allow the conclusion that a genetic change is likely to have taken place, this is still indirect evidence for climate change-induced evolution as unidentified drivers of plasticity may be responsible for the observed change.

The evidence for climate change driven genetic changes in insects comes from either common garden experiments or from population genetic surveys. For example, by comparing results from common garden experiments done in 1972, 1988, 1993 and 1996 in pitcher-plant mosquitoes (*Wyeomyia smithii*) from different locations along the US East coast, Bradshaw and Holzapfel (2001) were able to show that phenotypic distributions in northern populations had shifted towards Southern ones over time, indicating that the mosquitoes had adapted to northward shifted climate zones. All studies using population genetic inference are based on studies of latitudinal clines in molecular markers in fruit flies (*Drosophila*), such as allele frequencies in alcohol dehydrogenase locus (*Adh*) and chromosomal inversions. They have discovered shifts in the frequency of particular alleles over time in the expected direction under climate change. While this evidence is completely in line with expected changes under climate change driven selection, these studies did not identify the trait under selection. Hence, they merely show that the genetic composition of the populations have changed in an expected direction. In the case of the *Adh* locus, it is even unclear how genetic variation at this locus is linked to individual fitness.

Of the nine studies that tested for genetic change in birds and mammals in the wild, eight are animal model analyses of long-term population studies. Of these, only the one in red squirrels (*Tamiasciurus hudsonicus*) could show that breeding values predicted by the animal model changed in the direction as expected from selection, and that the

remaining trend in phenotypes could be explained by phenotypic plasticity (Réale et al. 2003). While only one out of nine animal studies that tested for genetic change found evidence for it, all of the studies in plants testing for genetic change also found it (Table 1). This illustrates the power of the different approaches for detecting genetic changes, or to disentangle genetic and plastic changes, respectively. The power of animal model analyses depends to a large extent of the structure of the pedigree, which cannot be influenced by the scientist. Experimental approaches, such as common garden studies often employed in plants, are generally powerful, partly because the experimenter can adjust sample sizes to reach sufficient statistical power. A nice illustration of this point is the remaining bird study showing genetic change in migratory behaviour, which was based on a common garden design. Over a period of 14 years hand-raised wild blackcaps (*Sylvia atricapilla*) were tested in the laboratory and their migratory activity declined over time, apparently as an evolutionary response to improved overwintering conditions at northern latitudes caused by climate warming (Pulido & Berthold 2010).

It is also striking that the number of studies actually measuring selection is even smaller than the number of studies testing for genetic change (Table 1). This illustrates the difficulties, as outlined above, to measure the strength of selection, which necessarily has to be done in the wild. It should be noted here that the sizeable proportion of plant studies that quantified selection did this in reciprocal transplants, which actually test whether individuals perform better under 'native' than 'foreign' environmental conditions, but do not formally estimate the strength of selection acting on a particular trait.

Some of the variation in the proportion of studies testing (or being able to test) for genetic change in Table 1 could be due to slightly different criteria used when selecting studies to be reviewed, which can blur patterns arising from different

methodologies. For example, the avian studies listed in Table 1 include only studies that could have had the potential to test for genetic change or for which the original authors claimed to have had the potential. There are far more studies (~60) that have reported changes in avian phenology to climate change, but could not have tested for genetic change because only population-level phenotypic data had been collected. Furthermore, the number of studies that were able to measure selection was consistently lower than the number of studies that could test for genetic change (Table 1). This also reflects the difficulties in collecting the data relevant for documenting climate change driven evolution.

In summary, it can be concluded that thus far we have very little strong evidence for evolutionary responses to on-going climate change. However, this paucity of evidence does not necessarily mean that evolutionary responses are not taking place, but merely that the data of sufficiently high quality to detect these responses is rare. This point is further reinforced by the fact that the little evidence which is available comes mostly from terrestrial and freshwater ecosystems, whereas the examples of climate change mediated evolutionary responses from marine ecosystems are virtually non-existent (Reusch 2014). This is in spite of the fact that many sea-areas have already been strongly affected by climate warming, and the large population sizes of many marine organisms should make them particularly responsive to forces of directional natural selection.

Rates of evolutionary change

As pointed out above, due to the scarcity of suitable high-quality data, direct evidence for climate change driven evolutionary responses is limited. However, given the fact that most traits are heritable and that climate change is likely to impose strong directional selection on many traits, it is likely that the expected evolutionary responses are already taking place. Nevertheless, whether

these responses will be sufficient to keep populations adapted in the long run is unclear. This is because under continuously changing environmental conditions populations' mean fitness is reduced as the majority of individuals will suffer from reduced fitness: a phenomenon known as the demographic load of selection. In populations subject to continuous environmental change, this load can drive them to extinction before adaptation is restored. Why populations faced by climate change may be particularly prone to this problem can be understood by considering that because of changing environmental conditions, the optimal phenotype keeps shifting and the population mean phenotype need to track it through genetic changes. However, because phenotypes are not perfectly inherited from parents to offspring, the shifts in the population mean phenotype will always be smaller than the shifts in the optimum phenotype. If this 'evolutionary lag' becomes too large, the demographic load of selection reduces population fitness to the point where it is driven to extinction.

Whether a population can stay adapted under continuous environmental change depends on a number of factors such as the trait's heritability, the population's growth rate and effective population size, as well as the species generation time. Theoretical models show that there is a 'critical rate of environmental change' that a population can sustain without increased extinction risk, and that this rate is in the order of 0.1 *haldanes* (change expressed in phenotypic standard deviations per generation). In other words, a rate equivalent to ca. 10% of the trait's standard deviation per generation could allow populations to track moving environmental optimum. Yet, many of the observed changes population mean phenotypes attributed climate change exceed 0.1 *haldanes*, raising a concern.

One assumption of these models is that selection indeed leads to a reduction in population mean fitness. This is true for so-called 'hard' selection

where fitness depends only on the individual's trait value. If the strength of selection is, however, density- or frequency-dependent, demographic rates will be unaffected by selection, and selection would not impose any demographic load. Density dependent processes that are unrelated to selection could also 'buffer' populations against the demographic load of selection. For example, if episodes of hard selection on reproduction are followed by density-dependent survival, the latter would increase *per capita* survival rates after episodes of strong selection with therefore reduced mean reproductive success and vice versa so that overall population dynamics are not affected by selection.

A further assumption of these models is that genetic variance is only affected by effective population size. In small populations, random processes increase the rate at which genetic variance is lost, which in turn reduces the populations' ability to respond to selection. However, levels of genetic variation can also be affected by a number of other processes. Gene flow from other populations can increase genetic variability and even bring in 'pre-adapted' genotypes. Especially the latter process could considerably increase the populations' ability to track the changing optimum. Expression of genetic variance can also be increased (or decreased) in novel environmental conditions and also this would also help populations to track changing optimums. Similarly, if a population has shifted its distribution range, it may also come in contact with previously allopatric populations and species, which could lead to hybridisation. This inflow of novel genetic material through introgression can have negative effects because the integrity of a species' gene pool is broken up, but it could also have positive effects through increased genetic variability (Sánchez-Guillén et al. 2016).

To sum up, as limited as the evidence for realised evolutionary responses to on-going climate change is, equally or even more limited is our

understanding as to whether populations will be able to adapt fast enough to climate change to evade extinction. Predicting rates of evolutionary change is possible (e.g. Gienapp et al. 2013), but such predictions rest on a number of assumptions that may or may not hold under changing environmental conditions. However, taking the current estimates of a critical rate of environmental change of about 0.1 *haldanes* as a conservative estimate, and comparing this to the currently observed rates of climate change, substantial concerns about population persistence are warranted. Further concerns arise if one considers that climate-change induced selection may not only act on a single trait, but on several traits at the same time. Genetic correlations among traits under selection can considerably constrain the rate of adaptation if traits are selected in the opposite direction to their genetic correlation. For example, climate change in the US Midwest is predicted to increase drought conditions but adaptation of the annual legume, *Chamaecrista fasciculata*, to increased drought conditions is slowed by genetic correlations among developmental rate, number of leaves and their thickness (Etterson and Shaw 2001). Such 'antagonistic selection' is predicted to break up the constraining genetic correlations, but this process is slow. Genetic correlations among traits under selection clearly have the potential to hamper adaptation to climate change.

Conclusions

The study of evolutionary responses to climate change is a vigorous area of research in contemporary evolutionary biology, with increasing numbers of studies devoted to studying microevolution in response to climate change mediated selection pressures. Although increasing numbers of climate change associated shifts in distribution, phenology and phenotypic appearance of organisms are being reported in scientific literature, the challenges associated with uncovering the genetic basis (or their lack) of these

changes, as well as establishing causality between climate change and the observed genetic shifts, are still often formidable. However, advances in genetic technologies and analytical methods together with the maturing discipline devoted towards the study of climate change mediated evolution do provide promise for accelerating progress towards a better understanding of the

process of evolution in response to climate change. Nevertheless, there is a real concern that current and projected rates of environmental changes may be too high to allow many organisms to stay adapted. If so, the prevalent form of evolutionary response to climate change in the future may not be restoration of the state of adaptedness through genetic changes, but expiration and extinctions.

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