



Introduction to Living with Environmental Change Pilot Review Reports

When establishing a major research programme such as 'Living with Environmental Change' (LWEC) with such clear relevance to the science-policy interface there is a need for identification of priority policy areas, reflection on the current baseline of evidence, exposure of knowledge gaps and hence the design of programmes of research. This need is now addressed, across many sectors, using a formal evidence-based approach. This approach is perhaps most familiar in the health services, social services and education but is now being actively used in environmental management.

The core methodology in evidence-based practice is the systematic review, involving a rigorous and objective assessment of the best available evidence on a question of concern to policy or practice. However, a systematic review is a significant investment of time and resources and, with the limited resources available it is probably not efficient to launch straight into a programme of systematic reviews without some prior estimation of their value. Consequently a funding scheme for pilot reviews was established.

The Pilot Reviews offer the opportunity to scope academic literature and public reports published on specific questions. It was intended that the reports of the reviews would: outline the existing data and highlight the trends and gaps in knowledge, contain details of the search strategy employed, provide critical appraisal of the quality of the sample of the studies and may produce a draft protocol for a full systematic review. It is hoped that the reports will provide a resource for stakeholders and follow the guidelines given for scoping studies on systematic reviews, which can be accessed at:
<http://www.environmentalevidence.org/Authors.htm>

The LWEC partners agreed six strategic objectives that will inform progress towards the design of the programmes of work that will make up LWEC. The first scheme funded the following reports and was in support of **LWEC Objective B - To manage ecosystem services for human well-being and to protect the natural environment in a changing world**. The LWEC partners were keen to support activities that cover both aspects of Objective B. These include the assessment of links and feedbacks between the natural environment, ecosystem services and human well-being; how these might continue to develop within environmental limits in the face of major environmental change; and how decision-making and local and national planning can take account of these links and feedbacks to help in the development of new social, environmental and economic opportunities. Each of the six reports that form the output of this first scheme provides an initial characterisation of the evidence base on their chosen subjects. This provides a

resource with which to judge the potential value of full systematic reviews and the likely need for primary research.

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**Contract no R8/H12/109 – living with environmental change pilot review
scheme – Objective B Scoping Study**

**The biological limits to adaptation:
What is known and not known about genetic and phenotypic
responses to rapid and extreme environmental change**

Pilot review

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SUMMARY

1. Adaptation to environmental change is achieved through multiple different mechanisms, each of which has its own limits in terms of both the rate and amount of change. In the case of natural systems three very different processes: evolutionary change, phenotypic plasticity and dispersal, may individually or in combination determine the persistence of species, ecological communities and ecosystems.
2. The ability of any of these mechanisms to support adaptation will depend upon the history of the population or community, and will vary among species, habitats and geographic areas. Management interventions will need to be different depending on which of these three responses they aim to support, and may conflict with one another.
3. Management plans should therefore be based on an understanding of these different processes, including their likely effectiveness under expected rates of environmental change in specific locations. But there is no synthesis of this information available and the scientific literature is broad, dispersed and has often been undertaken for quite different purposes. This review was designed to assess the extent and quality of the scientific literature in order to design a full systematic review that could produce information directly relevant for policymakers.
4. Using carefully designed search terms we interrogated the research reports in Web of Science and identified an extensive literature that extended back to the 1970s, that was growing exponentially, and that was most commonly focussed on only a single mechanism in relatively uncontrolled conditions. Under these circumstances, experimental designs that distinguish clearly between different processes that could lead to the same outcomes are particularly important. Our methods allowed us to score studies according to the strength of the evidence based on the methodology adopted. Across all studies, but most notably for the genetic studies we found the evidence base was very weak. UK scientists and scientific institutions are relatively active in this area, but there are rather few field-based studies in the UK, and they are not evenly distributed across UK taxa.
5. We conclude that the information is not adequate for a full systematic review. This would be most likely to again reveal the heterogeneous approaches and poor evidence base in the published studies. Instead we recommend a directed research programme that would focus on the following topics:
 1. Studies that clearly identify and quantify the mechanisms in action with an emphasis on ruling out other possible confounding mechanisms.
 2. Studies of the interplay between several mechanisms:
 - Genetic evolution of dispersal/ plasticity.
 - Effects on gene flow of local adaptation in a changing environment.
 - Studies that combine several methodologies
 3. Studies relevant to UK species and habitats

1 INTRODUCTION

1.1 Context

As our understanding of the scale and rate of climate and environmental change grows, policy and decision-makers are increasingly concerned with the way in which natural and societal processes will be affected. Increasingly, attention is focused on how to achieve adaptation with the general goal that people and the environment will be able to cope with environmental change without damaging effects now, or in the future. The general term 'adaptation' is used as shorthand. However it is important to recognise that within are subsumed some very different processes and mechanisms which will all have their own response times, limits and constraints. At the broadest level there include societal responses relating to people and human communities, engineered solutions relating to new physical structures, and natural mechanisms controlling the responses of natural environments and their processes. Policy initiatives need to recognise the major differences in constraints and responses, and incorporate them explicitly into strategies and plans. It is the third area, the response of natural systems which is the starting point for our work.

Natural systems may include species and their habitats, ecological communities and ecosystems. People rely on them for a range of benefits including ecosystem services providing raw material for food, freshwater and energy, regulating functions associated with the control of local and regional climates, floods and protection from disease, and cultural benefits such as aesthetic value and education. Natural systems are not infinitely flexible with respect to environmental changes but neither are they fixed in form or function. In fact, their responses to environmental changes will depend on the extent to which their physiology and ecology will permit them to cope with a new environment or not and, if not, whether they can move to a location where their preferred environment is now found.

In very simple terms, in order to persist under environmental change biological populations must either cope or move (disperse). Coping may be achieved through two fundamentally different mechanisms: one that involves evolutionary change in the genetic composition of the population, and one that does not and entails the species persisting genetically unchanged despite the new environmental conditions. We call these two responses evolutionary adaptation and phenotypic plasticity respectively. If none of the three strategies (dispersal, evolution, plasticity) is achievable then local populations of species will ultimately die out with consequences for the ecological community and ecosystem of which they are a part. The three survival responses depend on very different mechanisms and therefore are likely to exhibit very different constraints according to the rate, extent and nature of environmental change, and this will vary among species, habitats and geographical areas. This review was undertaken with the goal of assessing the extent to which the scientific literature on this topic could be informative about where, when and how natural systems could respond effectively to environmental change.

1.2 Scientific background

An understanding of what is possible for natural systems is essential for designing management interventions. For example, it has been frequently asserted that climate change is too rapid for evolutionary change to allow species to adapt by natural selection (Etterson and Shaw 2001), yet there are many examples of short-term rapid evolution in nature (Carroll et al. 2007). In the case of populations that have been exposed to variable climates we can expect evolutionary responses to be

more effective than those that have persisted in very stable environments. Alternatively, if environmental change is too rapid for evolutionary change or too extreme for phenotypic plasticity, then management might be designed to allow species and habitats to track environmental changes across the landscape through designing dispersal corridors.

Any management intervention will need to take account of the ability of different species and species groups to move over landscapes, to cope with novel habitats and to retain key ecological and environmental interactions. Specific management approaches will be needed in each case; genetic change can be encouraged by maintaining genetic variation within populations, whereas the enhancement of dispersal ability would focus on landscape habitat heterogeneity and the encouragement of phenotypic plasticity would be more likely to be achieved through broadening species ranges across ecological gradients. These different policies may not be mutually compatible.

Evolutionary adaptation, phenotypic plasticity and dispersal are all core elements of basic research in ecology and evolution and the UK has an internationally strong set of researchers in this area. However the context that we describe above is quite new and so many relevant studies are likely to have been undertaken for a different purpose. Hence, although we might be relatively confident that there is a substantial research base from which to draw out conclusions, it was not clear how complete, robust and relevant this would be for the newer set of applied questions. This pilot review was undertaken to evaluate this literature to establish what a full systematic review might be able to achieve.

1.3 Specific focus

The over-arching question we address here is:

What are the biological limits to adaptive change in response to rapid environmental change from different mechanisms, and how strong is the evidence base?

This is addressed through a set of sub-questions that interrogate the published literature:

1. How strong and well-supported is the body of theory and empirical/experimental evidence on phenotypic plasticity?
2. How strong and well supported is the body of theory and empirical/experimental evidence on micro-evolutionary change?
3. How strong and well supported is the body of theory and empirical/experimental evidence on dispersal/range-shifts/migration?
4. How strong is the theory and empirical/experimental evidence on multiple mechanisms, and how is the body of knowledge distributed over time, place and taxa?

2 METHODS

2.1 Literature searches and keywords

All the literature searches were conducted in Web of Science (WoS) using specific keywords. The searches included 'All Years' and specified the Science Citation Index Expanded (SCI- EXPANDED, 1970-present).

2.1.1 General search (overarching question)

For the overarching question of the responses to environmental change, we used the search term: "Environment* chang*" or "climat* chang*". Inverted commas were used to target papers that only included specific phrases in their keywords and not the same words in a possibly different order. The inverted commas were necessary to refine the search and to be able to access the entire catalogue of WoS without any restriction on years due to an excess number of (possibly irrelevant) hits. These particular phrases were deemed appropriate because many papers included the phrase 'climate change' in their keywords, not necessarily 'environmental change'. So although the question we were interested in answering was related to environmental change and not climate change in particular, it was decided that many papers would be missed in our search if we omitted the phrase 'climate change' as a search term. We used asterisks to include any possible extensions of the word asterisked (i.e. chang* would find change, changes, changing, changed etc).

2.1.2 Specific searches (sub-questions)

As seen in the Introduction, the general question can be partitioned into three main sub-questions that relate to the mechanisms by which natural populations can respond to environmental change, namely, evolution through genetic change, phenotypic plasticity or dispersal. To ascertain how many hits we would obtain for each of the sub-questions, we carried out sub-searches within the context of the initial search in WoS (i.e. the main search term was "environment* chang*" or "climat* chang*"). The following terms were run in sub-searches:

- Micro-evolutionary genetic change search terms: evolutionary change* or microevolution* or rapid evolution* or genetic change* or evolutionary rate* AND SUBJECT AREAS=(ECOLOGY OR EVOLUTIONARY BIOLOGY OR GENETICS & HEREDITY OR MULTIDISCIPLINARY SCIENCES)
- Phenotypic plasticity search terms: phenot* plastic* or evol* plastic* or ecol* plastic*
- Range shift by dispersal search terms: species dispersal* or species range* or species migration* or range extension* or range shift* or species movement* AND SUBJECT AREAS= (ECOLOGY OR ENVIRONMENTAL SCIENCES OR BIODIVERSITY CONSERVATION OR MULTIDISCIPLINARY SCIENCES)

To obtain relevant hits for questions on genetic change and dispersal it was necessary to filter the searches by subject category; these naturally differed for each sub-question depending upon the field of study that the sub-question related to. To ensure that general science periodicals such as 'Science' and 'Nature' were included in the searches the category 'MULTIDISCIPLINARY SCIENCES' was also included. Searches on genetic change and dispersal were further focused by asterisking only the second word in each phrase. This was because if these searches were made too general by asterisking all words, then a greater number of non- relevant papers were found. For the search on

plasticity, this was not the case since even asterisking all words as we did produced relatively few hits, and therefore it was important to make this search as wide as possible.

2.1.3 Analysis

The results of each of the searches were exported into Endnote 8 as separate libraries. Articles that appeared in more than one sub-question search ('overlaps' or 'intersects') were found by adding the different libraries together in all possible combinations (genetic change & plasticity, genetic change & dispersal, plasticity & dispersal or all three mechanisms) and identifying duplicates. The duplicates were then cut and pasted into separate libraries and a record of the number of duplicates from each combination was made.

The numbers of articles N for each sub-question were recorded for each year, and the growth rate of the literature over time period t_1 to t_2 was calculated as $[\log(N(t_2)) - \log(N(t_1))]/(t_2 - t_1)$. This was compared to the same calculation for the total number of articles found in searches based on random keywords (namely: 'chairs', 'tables', 'sausages' and 'beans'), in order to control for the general tendency for growth of the literature with time.

We then drew random sub-samples of 100 articles for each sub-question (using the pseudorandom number generator in Microsoft Excel), after removing review articles using the option 'DOCUMENT TYPE= (ARTICLE)' and including only papers in English 'LANGUAGES= (ENGLISH)' in Web of Science. Those articles were then read to assess their content and evaluate their methodology.

2.2 Content of the literature

In order to obtain an overview of the nature of the different studies, where they were based, and the kinds of organisms they studied, we scored each of the 300 papers assessed in detail according to the following classifications:

1. The distribution of theoretical and empirical articles for each sub-question. This distinction is very important in the context of the present study as the response of living organisms to environmental change only makes sense at the level of entire populations, often across several generations. This means that mechanisms of evolutionary/ecological change are often first studied theoretically by means of models, which can then be confirmed or contradicted by empirical evidence. This can then allow the models to be refined for a better understanding of the processes. Hence, a feedback between theory and data is an important feature of research in population biology.

Focusing on empirical work only we classified the studies into three main types:

- Field observation, *i.e.* observation of natural populations in the wild without any kind of manipulation of those populations. This includes mark-recapture of sample individuals (as bird ringing for instance) and monitoring of complete populations, as has been done for some wild mammals. This kind of study has the advantage of realism in that the organisms are studied in their natural habitat, but at the expense of a lack of control: it is difficult in this framework to isolate the effects of particular factors.

- Laboratory experiments. These studies more easily allow the identification of causal relationships. However it is sometimes difficult to know how well results obtained this way may apply a natural context.
- Experimental manipulation in the wild. Some researchers experimentally manipulate living populations in their natural habitats, by modifying either the characteristics of some individuals or their environment. This combines the control of experimental methods with the realism of observation of natural populations.

In practice, which of this three types of empirical studies is conducted depends both on the scientific purpose of the work and on the constraints related to the organism of interest (body size, population size, geographical range, etc...).

2. The type of organism being studied. Here we classified study organisms into Mammals, Birds, Fish, Reptiles and Amphibians, Invertebrates, Plants or Micro-organisms. Plants were placed in a single taxon, unlike animals, because the different subtaxa (angiosperms, gymnosperms, monocotyledons, dicotyledons) did not imply the use of fundamentally different research methodologies.
3. The relevance of the existing literature to the UK. While many studies may allow drawing general conclusions that go beyond the particularities of the studied organism or study site, for applied issues it will be more useful to have data that correspond to species that do occur in the UK and that have been studied there. We scored papers for three measures according to: whether there was a UK-based author, whether it concerned a UK species and whether the study site was in the UK.

2.3 Quality assessment of the literature

We evaluated articles based on predefined criteria of quality for each sub-question, so that the ranking of articles remained objective and scientifically based. Overall, the criteria related to the strength of the evidence for each mechanism, including the extent of control to exclude other possible explanations for observed results.

2.3.1 Micro-evolutionary genetic change

Observed phenotypic change in natural or experimental populations is generally interpreted as being the result of natural selection. However for this to be true, there needs to be not only differential survival and reproduction of some phenotypes, but also heritable genetic variation of those phenotypes. Some authors claim that their studies demonstrate micro-evolution caused by natural selection, yet they fail to demonstrate how selection operates on the phenotype and/or, more importantly, how heritable those phenotypes are. Hence the literature on genetic change caused by natural selection was evaluated based on how well an observed phenotypic change is shown to have resulted from an underlying genetic change. The following ranking was thus applied to all relevant articles (with decreasing quality from 'a' to 'd'):

- (a) Direct measure of the additive genetic variance for traits of interest. This can be done by rearing individuals with different known genotypes in a similar environment ("common garden" experiments).

- (b) An estimate of the heritability of traits under selection by parent-child regression, a pedigree, or of any other kind of information on relatedness.
- (c) Indirect estimation of the genetic variance from the measured response to selection and the selection gradient, which quantifies selection on traits.
- (d) None of the above: there is no demonstration that the phenotypic change is genetically based.

2.3.2 Phenotypic plasticity

Adaptive change at the population level may also be caused by phenotypic change at the individual level, independent of the effects of differential survival or reproduction of those individuals. This is termed phenotypic plasticity, or more precisely for our purposes, adaptive plasticity, since we focus on processes that allow a population to persist in a changing environment. Although the distinction between phenotypic plasticity and genetic change is quite important conceptually and in terms of conservation policies, some studies claim to show phenotypic plasticity without a proper demonstration or quantification of the process. Ideally, to assess the importance of plasticity for one particular trait and population, one needs to find how the phenotype of an individual genotype varies with the environment. Based on this simple argument, we used the following ranking for all relevant articles on plasticity (decreasing quality from 'a' to 'e').

- (a) Clones of the same genotype were placed in different environments at the same life stage.
- (b) The environment changed the phenotypes of individuals with different known genotypes.
- (c) The environment changed the phenotypes of individuals with unknown genotypes.
- (d) A measure of the same individual at several time stages was taken. In this case, phenotypic plasticity might be confounded with ontogeny or, more generally, age-specific trait values/plasticity may be missed.
- (e) No proper way to show that plasticity was involved. This includes studies where a phenotypic change could not be shown to result from a genetic change, and is thus ascribed by default to plasticity.

2.3.3 Range shift through dispersal

Finally, a population may disperse to follow its optimal environment when it moves in time, thus avoiding the need to adapt locally. To demonstrate this process, one needs to show (i) that a range shift actually occurred for a population, as opposed to an apparent range shift that is actually an artefact of the way individuals are sampled; (ii) that this shift is permanent and not a transient or stochastic effect; and (iii) that it has been caused by an environmental change at the right geographical scale. The evaluation was thus partitioned into three questions in this case:

- Q1: Did the study control sampling intensity and its possible changes over time (e.g. apparent range extensions that might simply be previously unobserved occurrences)?
- Q2: Did the study include other information (ecological, lifetime studies or reproductive measures) that could indicate that the dispersal was a long-term response rather than a transient one?

Q3: Did the study include environmental data against which to assess the range change?

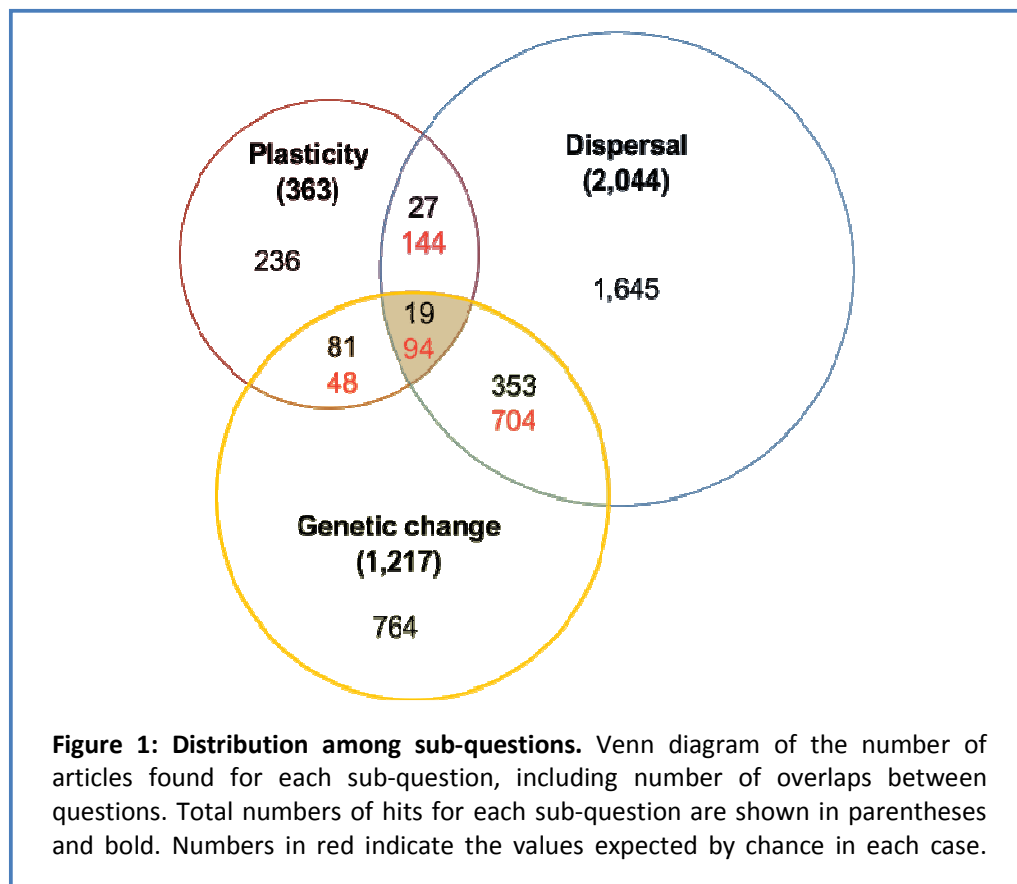
The possible answers to each of these questions (among the articles that were relevant to range shifts by dispersal) were: 'Yes', 'No', and 'Not clear or not applicable'.

3 RESULTS

In this section, we first describe the general properties of the literature found, including its distribution across and between the three mechanisms, over time, scientific fields and taxa before proceeding to the more critical appraisal of the quality of the literature.

3.1 Amount and distribution of literature.

3.1.1 Distribution among sub-questions

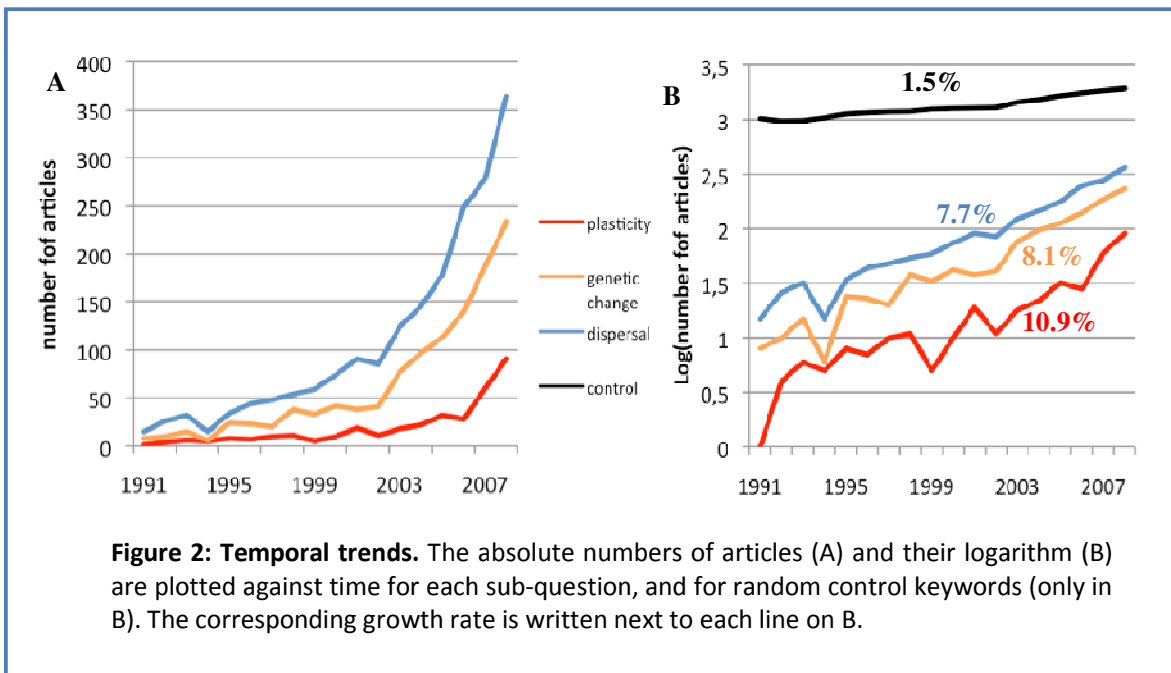


We found 3125 articles relating to our general overarching question on responses to environmental change. The number of articles found for each sub-question is shown in Figure 1. The first salient feature of the search is a great disparity in the volume of literature among the three sub-questions. While there is no *a priori* reason to expect studies of the three main types of responses to environmental change (namely genetic change, plasticity or dispersal) to vary much in quantity, it appears that most literature is devoted to dispersal, then to genetic change, while the literature on plasticity is much more scarce, accounting for only 12% of the total number of articles. A second result is that the literature that aims at understanding the interplay of several factors is generally

less abundant than expected by chance (compare red numbers with black numbers in each intersect). That is, most studies tend to focus on one mechanism of response to environmental change and neglect others, especially across dispersal and plasticity, which are two conceptually closely-related fields of study

3.1.2 Temporal trends

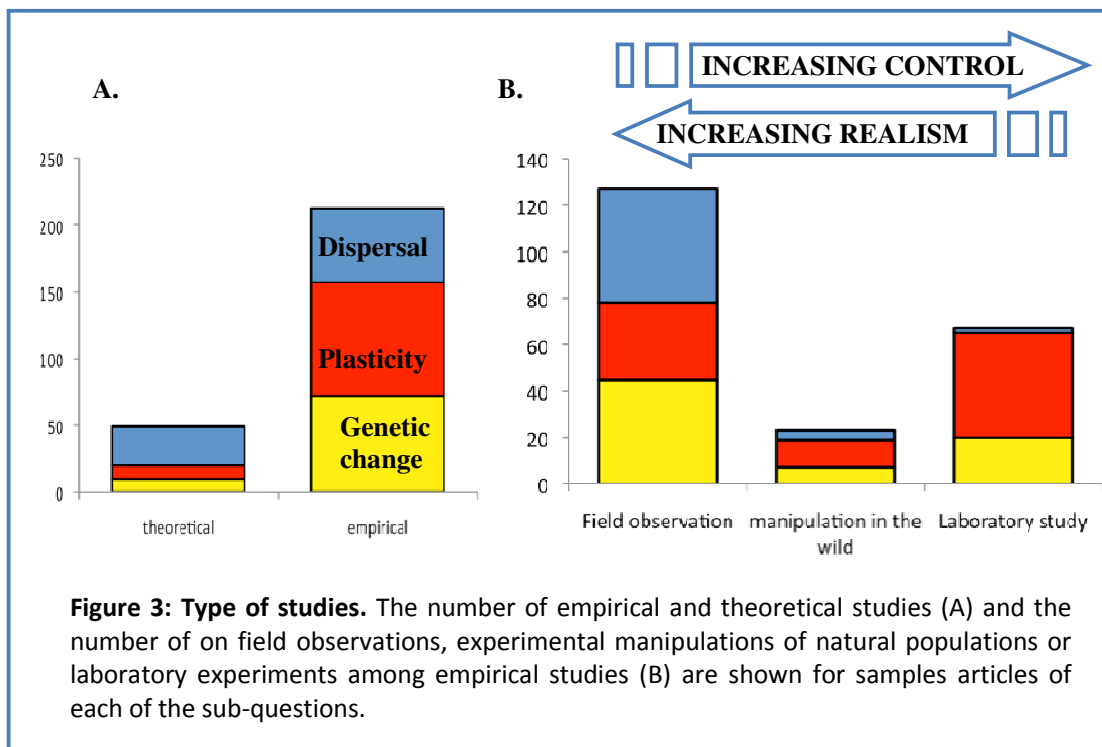
The change in time of the numbers of articles for each of the sub-questions is shown in Figure 2, with a restriction on years where all sub-questions had at least one article. The order of each of the sub-questions in terms of the amount of literature remained consistent with that described in Figure 1 over all the time period considered, with an excess of articles on dispersal, followed by a smaller amount of articles on genetic change, and substantially fewer articles on phenotypic plasticity. Moreover the numbers of articles for all three mechanisms grew exponentially in time. This is more apparent in Figure 2B, which plots the logarithm of the number of articles per year. The quasi-linearity on the log scale is indicative of an exponential increase, and the slope of each line gives the exponential growth rate of the corresponding literature. That the number of articles is increasing exponentially is not surprising *per se*, and reflects a general tendency in the scientific literature. More informative is the comparison with the growth rate of a control literature, based on randomly chosen keywords (see Methods). All three sub-questions exhibit growth rates from 5 to 10 times as high as that of the control. Assuming that the control is indicative of an actual average tendency across all types of literatures, this means that the interest in the questions identified for the present review scoping is increasing particularly fast in the scientific community. It is also interesting to note that the literature on plasticity, although the least important in volume across all years, seems to be the one that is increasing most rapidly.



3.1.3 General overview of the content

Other relevant aspects of the literature could only be assessed by reading through the articles. Since we obviously could not read all the articles, this was performed on samples of 100 articles for each sub-question (see Methods). This also allowed us to assess the accuracy of our search methodology since articles that were clearly irrelevant to the topic were easily identified. The precision of the performed searches was quite high. In all cases, more than 85% of articles accurately addressed the question of interest, and the precision rate reaches 96% for articles on plasticity. The highest error is for articles on genetic change (14%).

The distribution of articles among types of studies is plotted in Figure 3. As Figure 3A shows, the majority of articles are empirical studies for each of the three mechanisms and there are relatively few theoretical studies. Only one article in each sample combined theoretical and empirical approaches (not shown on the graph).



Within the empirical studies, most were field observations (Figure 3B), which seems consistent with the fact that some species cannot be studied easily in the lab. This is all the more true for articles on dispersal, of which the vast majority focus on observations of natural populations; this seems natural by the very nature of the question, since it deals with changes of geographic range in the wild. However, very few studies are based on experimental manipulation in the wild for all three questions (see the middle column in the histogram of Figure 3B). This seems unfortunate, since this kind of study can be expected to lead to more reliable results, by efficiently resolving the trade-off between natural realism and experimental control.

Figure 4 shows how the sample articles were distributed among taxa. The majority of studies are on plants and invertebrates with a very small number addressing more than one taxon.

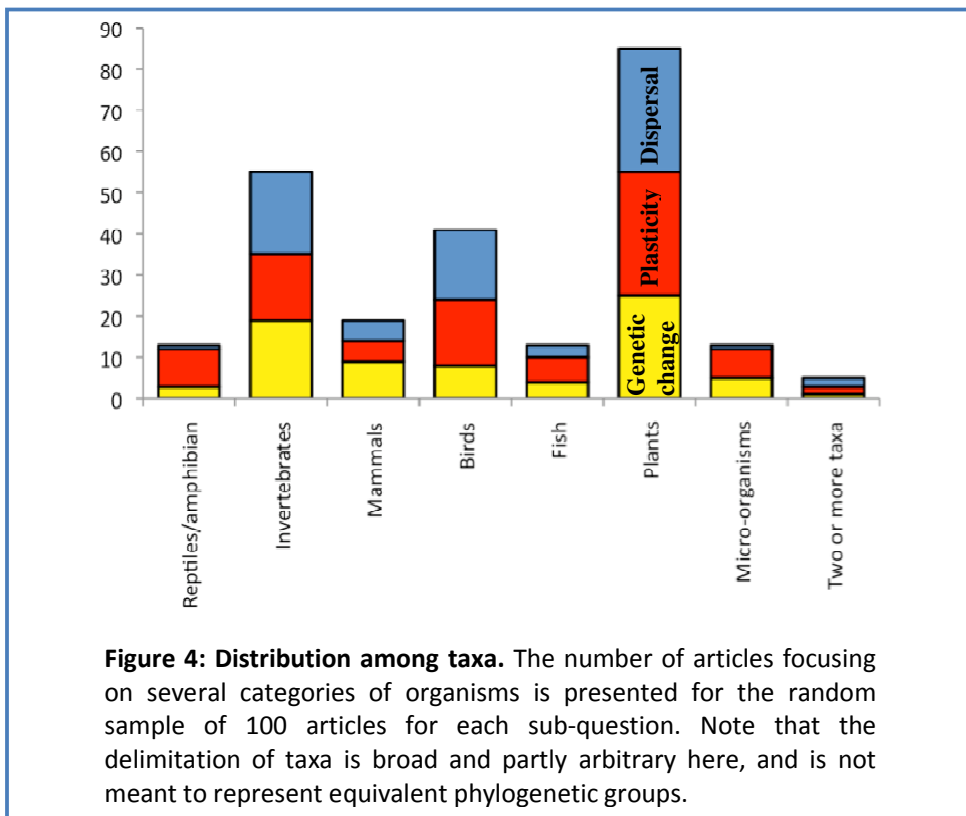
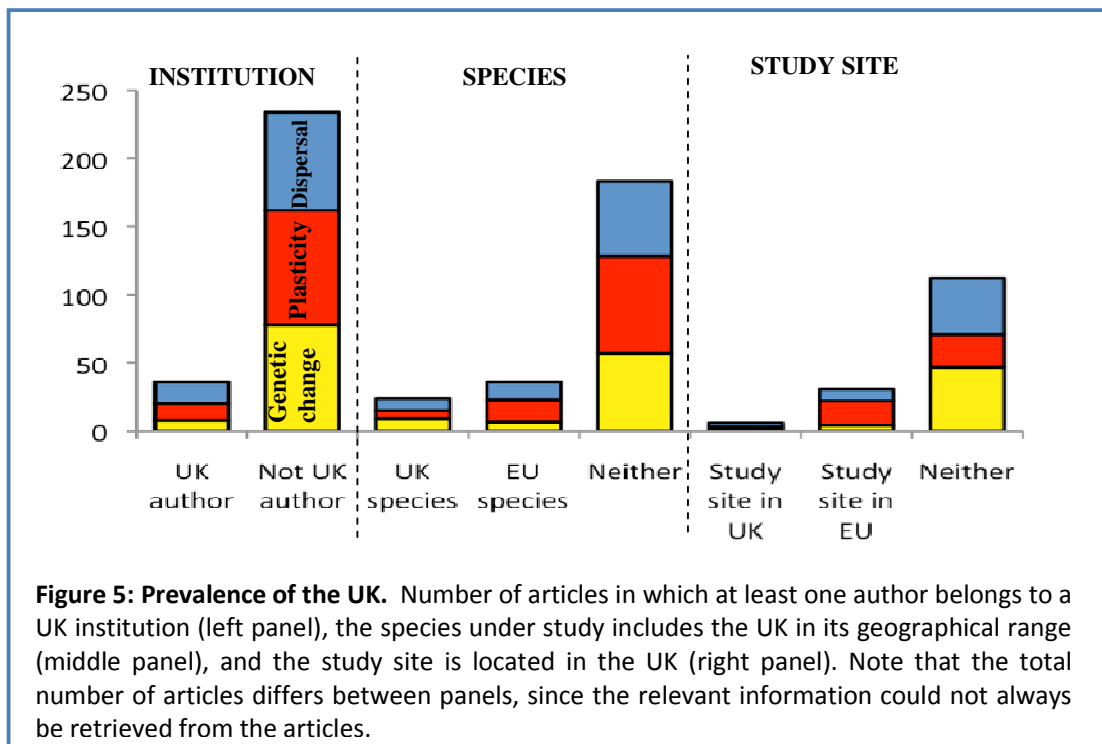


Figure 5 shows the prevalence of the UK in the sampled articles of the literature search. Overall, UK institutions contribute to 36 articles, more than one out of 8, which can be considered a relatively good score. In contrast, only 24 articles (less than 10% of the total) focus on species that are found in the UK, and fewer than 5% of articles have their study site in the UK. In other words, there is an excess of UK institutions that take part to studies that are not conducted on UK species, or in field sites that are not located in the UK. These results must be handled with caution, though, since they may also indicate the involvement of UK institutions in collaborative projects for which the principal



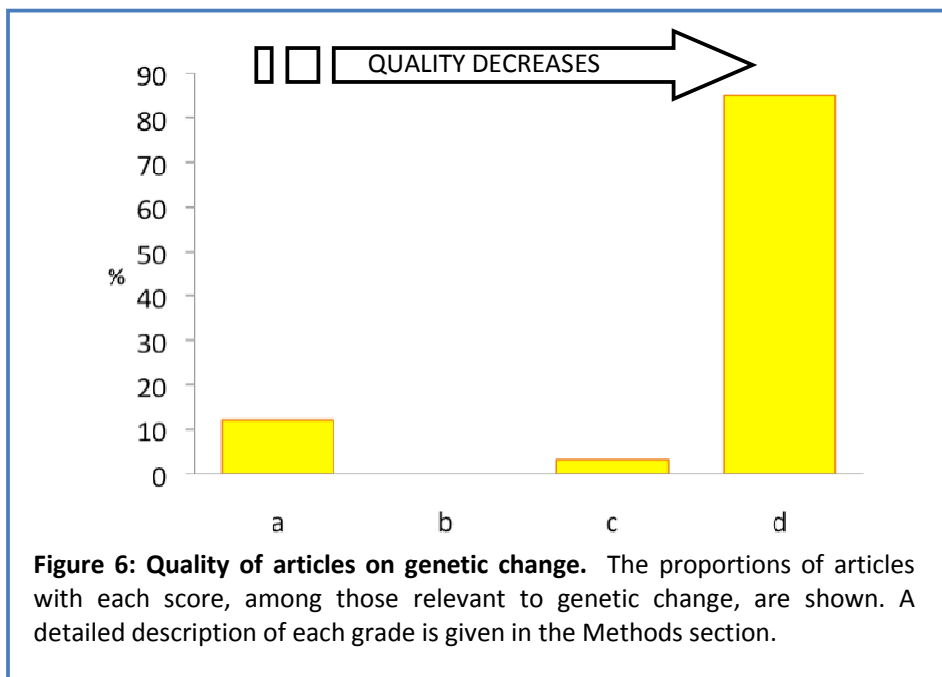
investigator and the main funding source is also abroad.

3.2 Evaluation of the literature

The second step in this work involved assessing the quality of the existing literature on responses to environmental change. The evaluation criteria related to how strong the observations in each study supported any particular mechanism (genetic change, plasticity or dispersal). Good studies were those (i) that relied on proper conceptualization and definition of mechanisms, and (ii) that used an experimental design that efficiently controlled for other possible explanations for observed results (see Methods).

3.2.1 Micro-evolutionary genetic change

The ranking of sample articles on micro-evolutionary genetic change is shown in Figure 6. A first glance at this figure shows that most articles are on the right part of the graph, thus corresponding to poor support for genetic change in response to environmental change. The vast majority of articles are ranked 'd', meaning that, although they do deal with phenotypic responses to environmental change and with genetics, the relationship between the two is not clearly established. Those include: observational studies that fail to estimate genetic variation of phenotypic traits; studies that show phenotypic change together with frequency changes at some genetic markers, but without any correlation between the chosen markers and the phenotype of interest; studies that use genetic markers to infer the demographic history of species (including bottlenecks, biogeography, etc...), possibly related to environmental change, but without identifying relevant adaptive phenotypes and environmental causes.



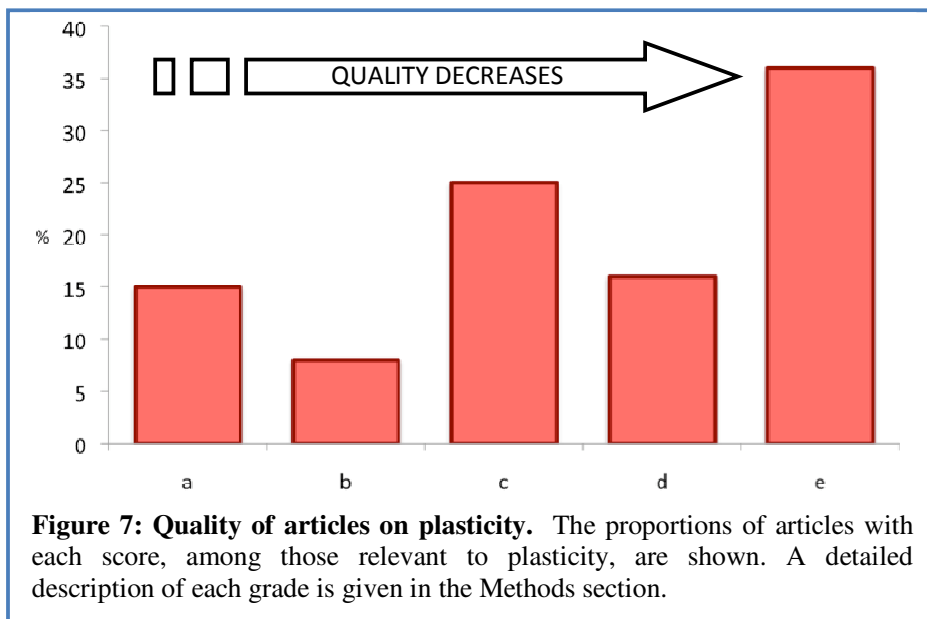
Interestingly in our sample, there are very few articles that estimate genetic variation indirectly from estimates of selection gradients combined with the measured response to selection (labelled 'c'), and no article that uses information on relatedness of natural populations without controlling for the environment (labelled 'b'). Consequently, most articles that actually investigate the heritability of traits are based on the method considered the most efficient here, that is, rearing individuals with

known genotypes in a common environment (labelled 'a'). However, those account for a mere 12% of the total number of studies, so overall our sample of articles includes few studies that could show strong evidence for genetic change caused by environmental change. This does not mean that this mechanism is not important in nature, but rather that the evidence either way is currently lacking.

3.2.2 Plasticity

Figure 7 shows the results for the quality assessment of articles on phenotypic plasticity. The distribution is more uniform than that for genetic change (Figure 6), with relatively fewer articles that are very weak methodologically, and a substantial fraction of intermediate quality articles. Again most articles do not properly show how phenotypic plasticity may have moulded the observed results (36% of 'd' articles). A classic example is the case where a phenotypic change is observed but cannot be firmly ascribed to genetic evolution after testing for heritability, or where no test for heritability is made at all, leading the authors to conclude that the phenotypic change may be plastic. The second most common class is 'c' (24% of articles), which corresponds to situations where an environmental parameter is shown to affect the mean phenotype of a polymorphic collection of genotypes. This case mainly includes laboratory experiments with plants grown in common gardens under various treatments, where a significant environmental effect is found. Studies that also include information about the genotypes of individuals, denoted 'b' (8% of articles), can also uncover genotype by environment (GxE) interactions, which is actually genetic variation in plasticity (see Discussion). Interestingly, a substantial fraction of articles falls into category 'd', which means that the same individual was measured under several environmental conditions. While some of these studies correct for the age of individuals to eliminate the most obvious ontogenic effects (such as growth), they may not be able to account correctly for age-specific plasticity, or for the consequences of plastic response at one life-stage on the response at a later life stage.

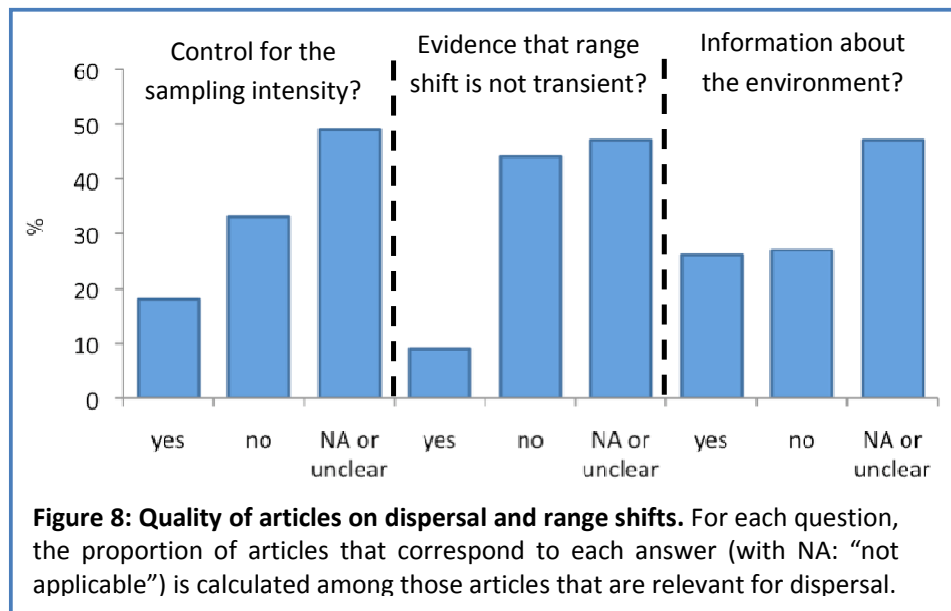
Less than one article out of six corresponds to the strictest definition of plasticity, that is, change in the phenotype of a single genotype with the environment, at a given life-stage ('a'). This type of study requires the use of clones, which often cannot be obtained for organisms that are obligate sexuals, in which case 'b' is the best possible alternative. However, combining 'a' and 'b', only 22% of articles correspond to the best possible evidence of a plastic phenotypic response caused by



environmental change.

3.2.3 Dispersal

The proportions of articles that met each of the three quality criteria defined in Methods for studies on range shifts and dispersal are shown in Figure 8. The tendency is similar to that observed for the other two mechanisms of response to environmental change, in that the vast majority of articles do not meet the best standards of quality. Only 18% of the relevant studies control for changes in sampling intensity over time. This means that in all other cases, finding individuals of a species in a place where they have not been found before may actually trivially indicate that the sampling effort was stronger that year, and not that this species is really more numerous. Similarly, only 9% of the studies gather information on ecology and life history traits, to show that an observed range shift is a permanent response, and not a transient one that may be caused by demographic stochasticity, for instance. Finally, in the context of the present study and in general, it is of the greatest interest to be able to show that the reason why a species changed its geographical range was to track its preferred environment in space. While this is often difficult to show, the first step consists in combining biogeographical data with information about environment. This was done in 26% of the relevant studies, which although a better score than for two other questions, is still a surprisingly low proportion.



4 DISCUSSION

4.1 Accuracy of the searches

Before drawing any general conclusions from the above results, it is important that we ask whether the literature searches effectively addressed the questions that we were interested in. Indeed, there were several less successful attempts of searches before we adopted the search strategy that we report on here, so it seems reasonable to challenge the methodology that was eventually retained.

The proportions of sampled articles that were relevant to each of the sub-questions were reasonably high. About 90% of papers in all three major groupings were of studies relevant to our questions. This quantity can be interpreted statistically as a precision rate (or 'positive predictive value'), that is, the probability that an article that is accepted as relevant by the search method actually *is* relevant. More difficult is the quantification of the power of our searches, that is, the proportion of all relevant articles that were actually found in each search. The balance between precision and power is a classic issue in every statistical problem, and in practice the ratio needs to be adjusted to the specific needs of each work. Here, since we needed to score the quality of articles that were relevant to our questions, we favoured precision over power in our searches: we preferred missing a few relevant articles, but ensuring that the ones we found were indeed relevant. However we can be confident that we did not miss a great quantity of very relevant articles, since we used a collection of words and of their extensions (with the asterisk, see Methods) for each question in order to remain inclusive as far as possible.

We may also wonder whether the relative importance of articles on multiple mechanisms to articles on single mechanisms was well captured by our search methodology. An article that deals with several of our mechanisms of interest would appear in the intersections of the Venn diagram in Figure 1 only if it exhibits the relevant keywords in its title or abstract. Some articles may use a formulation different from the keywords we used for the searches, but there is no reason to think that this occurs more frequently for articles that deal with several mechanisms than for any other one. Hence, the ratio of articles on multiple mechanisms to articles on single mechanisms in Figure 1 can be considered accurate, as well as the difference between the actual and expected number of articles on multiple mechanisms (black and red numbers in the intersects of the Venn diagram in Figure 1).

4.2 Assessment of the literature.

Our work identified several gaps in the literature. The main things that are lacking are: (i) articles with reliable methodologies that allow solid conclusions to be made for each mechanism; (ii) articles that address the interplay of several mechanisms of response to environmental change; (iii) studies that are based on experimentally manipulating wild populations; (iv) UK-based field studies. We will now discuss these gaps and possible explanations for them.

4.2.1 Methodological gaps for each sub-question

Some methodological flaws can be explained simply by intrinsic limitations of the study system. For example, as mentioned earlier, although the most accurate method to study phenotypic plasticity implies placing clones of the same genotype in several environments, this obviously cannot be done for obligate sexual organisms. Similarly, some organisms may not easily be bred in a laboratory and so direct estimation of the genetic variance in a controlled environment cannot be obtained. However this cannot account for all reported low scores in Figures 6-8. Another reason may be that some articles that dealt with the same concepts as those raised in our questions actually had a different research focus that did not coincide with our overarching question. In this case, what would appear to us as a weak methodology could actually have been good for the context in which it was applied. But this explanation cannot account for more than a subset of the papers we identified. Our overarching question and sub-questions were quite general and should have been addressed directly or indirectly in many of the studies. We conclude that the low scores for quality obtained in the evaluation actually reveal a genuine lack of focus and rigour in many studies. Many authors do

not define the mechanism under study properly so as to distinguish it from other mechanisms that could be involved, or do not use experimental designs that can confirm one mechanism and exclude another. More limited reviews have drawn similar conclusions to ours (Gienapp et al. 2007).

4.2.2 Gap in the study of multiple mechanisms

This work also revealed that there is generally a lack of studies that focus on several mechanisms of response to environmental change. All the intersections in the Venn diagram (Figure 1) have lower than expected number of articles, except the one between plasticity and genetic evolution, excluding dispersal (which we discuss at the end of this sub-section). This is partly inherent to the Cartesian reductionism necessary to every scientific study, whereby scientists tend to partition a system into “atomic” units in order to be able to investigate it more easily. However this may also cause scientists to overlook important processes that emerge when interactions are considered, and that cannot be inferred simply by adding the effects of each single mechanism (see some examples in Conclusion). In this case even more than for the study of isolated mechanisms, a proper definition of the process under study is crucial in order to obtain clear results. The lack of articles on interactions may be explained by a lack of clear and simple theoretical predictions to test empirically, or by a failure of empiricists to identify the relevant issues raised in theory that are amenable to empirical study.

The only intersection with more articles than expected by chance is the one between plasticity and genetic evolution. There are probably two main reasons for this. The first one is artefactual: most scientists focusing on phenotypic plasticity tend to explicitly oppose this mechanism to genetic change by natural selection, whose importance is more widely accepted in the neo-Darwinian literature; hence they will mention “genetic change” in their articles and will be found in the corresponding search. The second and more interesting reason may be the long lasting interest in genotype by environment interaction (GxE in the following) effects. These are routinely estimated in experimental designs, but it was only realised fairly recently that they actually quantify genetic polymorphism in plasticity. In other words, GxE are increasingly interpreted as potential for the genetic evolution of plasticity, thereby contributing to the intersection between these two mechanisms.

4.2.3 Little experimental manipulation in the wild

The main reasons for a lack of studies based on experimental manipulation of wild populations are probably technical and financial. First, those studies require continued fieldwork, as opposed to observational studies where scientists gather data from the field once or a few times. Secondly, such studies may also require partially isolating a study population from the rest of the population, which can be a difficult and time-consuming task in practice and require special permission and facilities. However depending on the focus of the study, it may not be necessary to isolate the studied population and mixing of individuals that correspond to the treatment with non-manipulated control individuals may even be more accurate in many cases. Thirdly, this type of approach has a less acknowledged historical lineage than simple field observation in biology, and laboratory experiments in science in general.

4.2.4 Lack of UK studies

That the proportion of studies including authors from UK institutions is higher than the proportion of studies conducted on UK species or in UK field sites can be seen simply as a consequence of

international collaborative projects that involve several institutions, including some from the UK (as mentioned in 3.1.3.3). In such case, it is a rather positive finding, since it implies that the UK is well integrated in international collaborative efforts. However, the actual number of studies that were conducted on UK field sites is very low, which means that it would be very difficult to find any general pattern in them, or even draw any particular conclusion that may influence decisions and policies based on them.

4.2.5 Other biases and gaps in the research literature

We found that most scientific literature focusses on dispersal and least on plasticity although studies on plasticity are growing at a higher rate. Ecologists have long been interested in dispersal but plasticity has become of increased interest in part due to a focus on environmental change, but also with the increased attention paid to ecological versus evolutionary processes contributing to the fitness of individual organisms.

We found a strong bias to empirical studies, with relatively few theoretical studies and a tiny fraction (<1%) that used both. One of the reasons for the excess of empirical papers is that multiple empirical studies are often needed to verify any theoretical hypothesis. Indeed, it is often difficult to test a particular hypothesis based on a particular empirical example in biology, since many species or populations exhibit idiosyncratic properties that prevent generalisations to be made. A second, and perhaps more interesting, reason is that some theoretical principles are eventually confirmed and thus can be used in applied fields, leading to a large number of empirical studies. Despite the general tendency for an excess of empirical articles, the literature on dispersal seems more balanced than the others, which may reflect the technical difficulties in gathering reliable empirical data about changes in geographical ranges of species. Within the empirical studies, there was a strong bias to field-based investigations and relatively few that were lab-based or involved field manipulations. This is an important gap since field-based studies without controls or the ability to investigate the causal pathways will always be less conclusive. This area of study requires careful balancing to maintain both experimental rigour and natural realism and it appears that the current literature is weak on the former.

The majority of studies are on plants and invertebrates. That plants contribute strongly and equivalently for each question can be understood as follows. Plants can easily be grown in a common garden to estimate their genetic variance, such that studies of genetic change in response to selection are common. There is also a long tradition (stemming from agronomy) of studying the effects of various treatments (including the amount of water, minerals, etc...) on plant traits, which now pertains to the literature about phenotypic plasticity. And because they are sessile, plants have evolved many types of pollen and seed dispersal mechanisms that are often amenable to study and can be related to changes of geographical range at the species scale. Bird studies also contribute significantly to the literature on dispersal (in particular for migratory birds) and on plasticity (there were many studies about how laying date is influenced by various environmental parameters). The studies based on microorganisms mainly include experimental evolution in the lab, and focus on plasticity and genetic change. There are relatively few studies on mammals; this may be explained by the practical and financial problems associated with mammalian studies, especially where generation times are long, requiring extended programmes of work that are difficult to maintain.

5 CONCLUSION & RECOMMENDATIONS

The major conclusion of the present work is that, despite the large and growing literature concerning how natural populations respond to environmental change, this literature exhibits important gaps and biases and some methodological weaknesses. It is thus not obvious how firm scientific conclusions – not to say applied policies – could be drawn from this literature. In any case this would necessitate careful selection of the subset of articles for which the methodology and results conform to quality criteria in the line of those that were used here - most probably resulting in a limited number of informative studies.

Therefore while a full systematic review could be undertaken, it can be predicted that it would simply repeat the result here and find that many studies lack strong support for the mechanism under study.

We conclude that what appears most needed is targeted research. Many studies in population biology were not designed for the context in which they are now needed, namely understanding and managing the fate of natural populations under environmental change. Most of the existing literature comes from partially separated fields. As mentioned earlier, one of the reasons why many studies did not meet our quality criteria may be because they lacked the general perspective that comes from unifying evolution, ecology and conservation in the context of global change biology. Based on the identified gaps, we list below some suggestions about what type of research we think should be prioritised.

5.1 Studies that clearly identify and quantify the mechanisms in action

Our work revealed that many studies lack empirical support for the mechanism they intend to study. Besides obvious limitations and difficulties that may arise in each particular case, this also shows that a lot of the published articles were not based on rigorous definitions of the concepts under study. Or at least, that the way the problem was formulated was not useful in terms of understanding what limits the response of natural populations to environmental change. There is thus a need for work in which the mechanism under study is clearly defined from start, and other possible mechanisms at stake are clearly identified, before even designing any experiment (or choosing what to measure in observational studies). For example, observation of a change in the mean phenotype of a wild population over time cannot be considered informative unless it can be shown that this change is caused by genetic evolution, phenotypic plasticity, or even migration from populations with different mean phenotypes. Each of these mechanisms occurs at different temporal and spatial scales, relies on different parameters and can lead to quite different policies when it comes to conservation.

5.2 Studies of the interplay between several mechanisms

There is also a need for a better understanding of the interplay of several mechanisms of response to environmental change. Those are fairly well studied theoretically. What is now necessary is experimental validation of some of the theory, and a development of some of the existing theory in the direction of generating predictions that can be verified with data in the context of environmental change. Below is a brief overview of the fundamental processes that arise when several mechanisms interact, with a focus on unresolved questions that need empirical support.

5.2.1 Genetic evolution of dispersal/ plasticity.

Plasticity and dispersal can themselves evolve genetically as long as they have genetic variance and are under selective pressure.

The evolution of dispersal has been studied theoretically, in particular in the context of an environment that is heterogeneous in space and/or in time (McPeck and Holt 1992). Empirically, the study of the evolution of dispersal involves identifying dispersal traits and quantifying their genetic variance, or even finding specific genes that are modifiers of dispersal. This may be easier for plants with air-borne seeds, for instance, or any organism for which one or few measurable traits are involved in dispersal. Theoretically, it would be interesting to investigate how the evolution of dispersal rate or distance may affect the speed at which a population manages to track its optimum in space, under sustained environmental change.

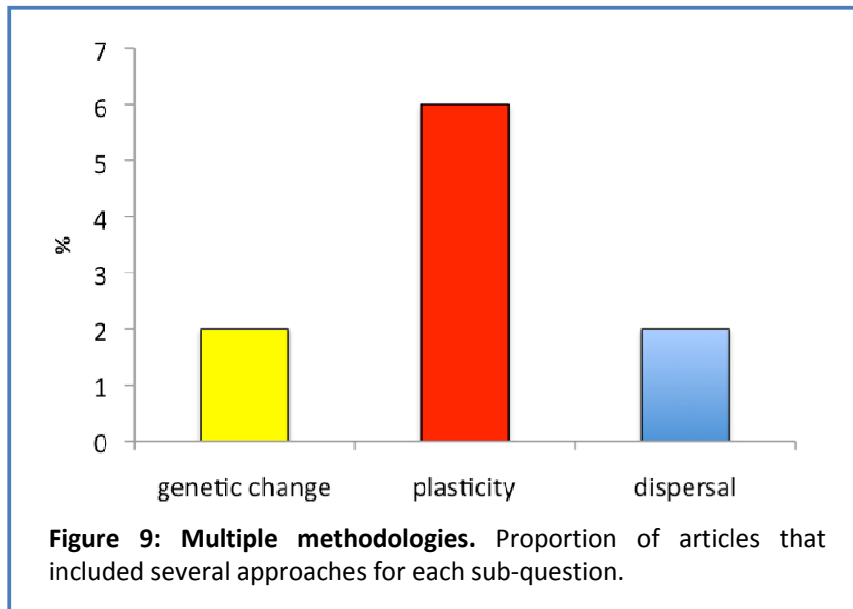
The evolution of plasticity is consistent with the existence of genetic variation in plasticity in many species, apparent in the existence of GxE interactions. It has been investigated theoretically under various assumptions and types of environmental change or heterogeneity. A main result that is consistent across the theoretical literature on the subject is that higher plasticity should evolve under high heterogeneity in the environment and high predictability in the way the environment changes. However, few if any theoretical studies combined the evolution of plasticity with demography to investigate specifically how the evolution of plasticity allows a population to persist in a changing environment. Empirically, studying the evolution of plasticity implies quantifying (i) the genetic variance in plasticity, (ii) patterns of environmental change and their predictability over time scale of the order of the generation time and (iii) possible costs of plasticity. Genetic variance in plasticity is relatively easy to measure, and has been investigated through common garden experiments under variable parameters. The change of the environment in time and its predictability (autocorrelation) can be studied empirically but has rarely been addressed in relation to the evolution of plasticity. As for costs of plasticity, they are now being more intensively studied, but are not always included in studies where their estimation is used to predict the evolution of plasticity.

5.2.2 Effects of gene flow on local adaptation.

Migration can cause maladaptation if the environment is heterogeneous in space. Therefore, gene flow caused by dispersal can be seen as a limiting factor for genetic evolution (Lenormand 2002). However, gene flow can also be beneficial in reversing the depletion of genetic variation in small populations. The effect of gene flow on local adaptation (and on local maladaptation, caused by so-called 'outbreeding depression') has been quite well studied in constant environments, but for the current purpose this work, needs expanding to incorporate the effects of environmental change. This has been studied in a few theoretical papers to date (Pease et al. 1989) but empirical support is lacking. One of the central question that needs to be addressed is notably: under which conditions does the advantage of dispersal – in allowing each population to track its preferred environment in space – overcome the negative impact of dispersal for local adaptation – gene flow from neighbouring populations causing local maladaptation?

5.3 Studies that combine several methodologies

Finally, it seems important to promote studies that combine several methodologies (i.e., theory and experiment, field observation and laboratory experiments). In our samples, only one article for each question combined theoretical and empirical approaches. More generally, the studies that combined several approaches (including within purely empirical articles) represented a very small proportion of the entire number of articles, between 2 and 6% (Figure 9). Moreover, most of them correspond to articles that include several studies on different organisms. Ideally, studies should include several



approaches to a particular question in one study organism. For instance, making a model that yields theoretical predictions that can be tested empirically, or combining field observations with lab experiments to exclude confounding factors in the field but still retain realism and thereby reach more solid conclusions. Where multiple approaches cannot be combined easily, it would be useful to promote studies that experimentally manipulate populations in their natural habitat, since this approach combines the control of experimental protocols with the realism of the observation of natural populations.

5.4 Studies relevant to UK species and habitats

For LWEC the UK species and habitats are a prime concern and while good studies in other places may be helpful and informative, it would be preferable to have some strong studies in the UK. One possibility would be to focus on particular habitats of concern and design studies that can include different taxa and habitat types, preferably supporting *in situ* studies with theoretical modelling or experimental work. A reasonable large-scale and integrated study of this sort would not only provide directly relevant results, but would also have the side-benefit of supporting the growth of a research community using strong methods to tackle internationally relevant questions.

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