Biodiversity Climate Change impacts report card technical paper

15. Implications of climate change for genetic diversity and evolvability in the UK

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What's changed?

Since 2013 there have been a number of studies that:

1. demonstrate the potential for genetic diversity to facilitate species/population survival and mitigate the impacts of climate change, termed 'evolutionary rescue'.
2. document changes in the organisation of genetic diversity, primarily its loss, or demographic changes predicted to alter the amounts of genetic diversity as a result of climate change;
3. synthesise the evolutionary genetic changes documented in response to climate change in a range of species

In general, this new information strengthens the conclusions drawn in 2013; highlighting the importance of genetic diversity in ameliorating the effects of climate change. Critically, recent studies show that some widespread species are more susceptible to climate change than previously thought, due to restricted gene flow between locally adapted populations. This new information adds further support for previous recommendations that restoring and maintaining gene flow between populations is critical to reducing extinction risk under changing climatic conditions. While the evidence available has increased in general this has not been sufficient to substantially alter confidence categories, particularly for UK species/populations and habitats, where data is still limited.

Executive summary

- Intraspecific genetic diversity is a recognised component of overall biological diversity and requires effective management to prevent its loss. This intraspecific diversity:

    o Underpins the fitness of individuals, and hence the persistence of populations, the ecosystem services and functions these provide, and, ultimately, long term species viability [*High agreement; Robust evidence*]

    o Allows evolutionary responses that facilitate long-term persistence through environmental change [*High agreement; Limited evidence*]

    o Contributes to community diversity and dynamics, as well as resistance and resilience to environmental change. [*Moderate agreement; Limited evidence*]

- The amount and distribution of genetic diversity in the landscape has already been altered (often negatively) by habitat loss and fragmentation [*High agreement; Robust evidence*]. Climate-driven environmental changes will *virtually certainly* have further impacts on genetic diversity and gene flow, via changes in species distributions, population sizes and selection pressures, with consequences for other components of biodiversity [*High agreement; Limited evidence*].

- The negative impacts of climate change on biodiversity may, in part, be ameliorated by evolutionary adaptation [*Moderate agreement; Limited evidence*]. The potential for these evolutionary responses is known as evolvability.

- The likelihood and rate of evolutionary change is influenced by multiple demographic, genetic, and biological factors. Species with low evolvability, and so high risk of extinction, are likely to be those with small population sizes, low levels of gene flow, low reproductive output, long generation times, narrow ecological niches or with low levels of phenotypic plasticity [*Moderate agreement; Limited evidence*].

- Active management to prevent the loss of genetic diversity is likely to be the most effective means to facilitate adaptive evolutionary responses to climate-driven changes. If management is in response to the loss of diversity, adaptive potential will have already been reduced. Proactive management involves maximising population sizes and health, and connecting populations to facilitate the movement of genes/individuals in the landscape. This management will also buffer sub-populations against extinction and facilitate other responses, such as range shifts.

- Large-scale monitoring of genetic change in relation to environmental and ecological alterations will be crucial to understanding and contextualising climatic impacts acting on, or mediated through, genetic diversity.

1. What is genetic diversity?

Biodiversity is typically recognised at three levels: genetic diversity, species diversity and ecosystem diversity (CBD 1992). Genetic diversity is the variation in DNA sequence that is heritable from generation to generation and is manifested as variation in organismal form and function. Its loss reduces individual fitness, population viability and species persistence in the short term that can compromise ecosystem function. In the longer term, reduced genetic diversity limits the potential for adaptation to environmental change, including climate change and climatic fluctuations. Genetic diversity is the raw material on which natural selection acts to adapt populations to their environment, and hence genetic diversity is critical for population persistence during climate change.

Genetic variants are classified according to the effects they have on the phenotype of the organism possessing them. Specifically, they may be adaptive, deleterious or neutral. Adaptive and deleterious genetic variants influence the fitness of the individual possessing them. In contrast, neutral diversity confers no advantage or disadvantage. This neutral variation may provide a proxy for adaptive variation and a means for monitoring gene flow and other demographic processes. It is important to note that the benefits derived from adaptive variation are context dependent: phenotypes that are advantageous at a given place or time may not be useful in other situations. Given the unknown suite of changes likely to be driven by climate change, it is impossible to predict which variants may confer advantages in future environments (Jump *et al.* 2009). Furthermore, in most cases adaptive genetic responses are based on changes in many genes of small effect (and hence difficult to detect) rather than a few genes of large effect (Rockman 2012). These considerations together suggest that evolutionary potential is better predicted by overall genetic diversity than by a focus on individual genes.

2. Impacts of climate change on genetic diversity

The impacts of climate change on genetic diversity are not as obvious as many other changes, such as the phenological and distributional shifts already apparent in the UK (Thackeray *et al,* 2010; Thackeray *et al*, 2013; Pateman 2015; Sparks and Crick 2015; Garcia *et al.* 2014). Yet, multiple studies demonstrate climate change *is impacting* on the amounts and distribution of genetic diversity, potentially compounding changes caused by human-mediated landscape modifications, such as habitat loss and fragmentation (Pauls *et al.* 2013). Changes in genetic diversity are primarily driven by changes in:

Population size: A reduction in population size will lead to the loss of genetic diversity and increased inbreeding within populations (Frankham 1996; Leimu *et al.* 2006; Honnay & Jacquemyn 2007). In populations that remain small, further genetic diversity is lost, and deleterious genetic variants accumulate, due to the magnified effects of genetic drift (Ellstrand & Elam 1993; Young *et al.* 1996). The loss of genetic diversity due to small population size is typically greater in species with outcrossing mating systems compared with those reproducing via self-fertilisation (Leimu *et al.* 2006; Honnay & Jacquemyn 2007).

Connectivity: Geographical isolation in the landscape typically restricts gene flow leading to a reduction in genetic diversity within populations and increasing the differences between them (Honnay & Jacquemyn 2007; Aguilar *et al.* 2008). This

is because interconnected populations act as a single larger population from a genetic perspective, where each population has access to the standing genetic variation and the new variants generated by mutation in *all* the populations in the network. Thus, even in small populations, where genetic diversity is typically low, gene flow can replenish lost diversity and provide access to potentially adaptive genetic variants contained in populations elsewhere in the range. In contrast, isolated populations only have access to the standing genetic variation and new mutations they contain. The greatest risk of genetic diversity being lost due to isolation is in species with outcrossing mating systems and those with a history of large population size, even if they have recently become rare (Honnay & Jacquemyn 2007; Aguilar *et al.* 2008).

Conversely any increase in connectivity among populations of the same or closely related species may allow genetic exchange resulting in a *reduction* in genetic differentiation. In general, gene flow is expected to increase diversity by creating interconnected networks of populations, as outlined above. However, the precise effects of connectivity will be context-specific and depend on the extent of genetic or ecological differences between populations. In some situations it may lead to diversity loss and/or the "swamping" of locally adapted genetic variants.

Distributions: The levels of genetic diversity across a species' distribution will be influenced by climate-driven changes in the distributional area (i.e. expansions, reductions and range shifts). A reduction in area is expected to lead to the loss of genetic diversity, such as that observed in the garden tiger moth (*Arctia caja*; Anderson *et al*, 2008). It is important to note that genetic diversity is often unevenly distributed within the range, and hence it may be eroded more quickly than the distributional area itself (Balint *et al.* 2011; Provan & Maggs 2011; e.g. Dubey *et al.* 2013; Bystriakova *et al.* 2014). Even where new populations are established during range expansion or shifts, these populations may contain less diversity than populations at the core of the previous range. This is expected to occur where the number of individuals founding the new populations is low, and subsequent gene flow is restricted (Eckert *et al.* 2008; Excoffier *et al.* 2009; Uller & Leimu 2011). In these new populations genetic drift can also result in the random fixation of genetic variants, even where these may be highly deleterious or maladapted (Travis *et al.* 2007, 2010; Van Bocxlaer *et al.* 2010; Lehe *et al.* 2012; Bocedi *et al.* 2013). Overall genetic diversity is predicted to be lost if (formerly) core populations no longer in the viable range become extinct before gene flow restores diversity in newly established populations (Atkins & Travis 2010; Arenas *et al.* 2012). Recent projections for plants with northerly distributions indicate that many of these species will lose genetic diversity as a result of shifts in the distribution of suitable conditions (Alsos *et al.* 2012).

Selection pressures: Changes in environmental conditions and community composition will alter selection pressures. The effects of selection will often be localised within the genome, altering the amount and type (i.e. beneficial or deleterious) of diversity at given set of loci (Buckley & Bridle 2014). These changes can enable populations to adapt to the new conditions and ameliorate the impacts of climate change. Spatial variation in the environment can lead to selection pressures that vary from population to population, leading to increased differentiation of adaptive genetic variants between populations (Phillimore *et al.*

2010, 2012; Hangartner *et al.* 2012; Kremer *et al.* 2014). In some instances selection pressures may also lead to genome-wide changes in the levels of diversity. For example, a reduction in pollinator abundance may lead to selection favouring self-fertilisation in plant populations, leading to a decrease in genetic diversity (Eckert *et al.* 2010; Bodbyl Roels & Kelly 2011). Likewise, very strong selection can result in genome-wide diversity loss if only a few individuals survive to contribute to subsequent generations (Bell & Gonzalez 2009).

3. Consequences of changes in genetic diversity for biodiversity

Climatically (and anthropogenically) driven alterations in population size, connectivity, species' distributions and selection pressures can lead to the loss of genetic diversity within populations and changes in genetic differentiation between populations. These genetic changes may impact on populations, species and communities in several ways.

Loss of diversity: Many of the observed and predicted environmental changes are likely to lead to the loss of genetic diversity and this is relevant in four main ways.

Intrinsic value: Genetic diversity is a measurable component of biodiversity and hence it possesses an intrinsic value. The loss of refugial populations, for instance, may equate to the loss of unique, highly divergent intraspecific lineages, and irreplaceable genetic variants. Many British populations represent a genetic subset derived from larger European populations. However, there is increasing evidence for the occurrence of unique genetic lineages/refugial populations at high northern latitudes (e.g. Parducci *et al.* 2012). Indeed, studies on patterns of post-glacial phylogeography of UK fauna frequently resolve cryptic genetic discontinuities associated with multiple recolonisation events and routes following the retreat of the Pleistocene ice sheet. These represent separate evolutionary significant units that can be viewed as important components of UK biodiversity and as local evolutionary heritage (e.g. Searle *et al.* 2009). In addition, some genetic variation may have clear commercial/economic value; for instance, the diversity contained within the wild relatives of domestic species is a well recognised resource for enhancing food production and sustainability (e.g. drought tolerance, disease/pathogen resistance; Dempewolf et al. 2014; Ford-Lloyd et al. 2011).

Inbreeding depression: The loss of genetic diversity in small populations can reduce their short-term persistence. This is because under these conditions mating amongst relatives (inbreeding) is more likely, allowing the expression of deleterious genetic variants, and leading to offspring with lower fitness (i.e. inbreeding depression; Angeloni *et al*, 2011; Keller and Waller, 2002; Leimu *et al*, 2006; Reed and Frankham, 2003). Further reduction in population size resulting from the loss of fitness may exacerbate the effects of inbreeding. This positive feedback of reduced population size on fitness loss is known as an extinction vortex (Frankham *et al.* 2010). O'Grady et al (2006) showed inbreeding depression and ecological stressors both significantly increase the risk of extinction. The fitness costs associated with inbreeding depression also limit responses to stress and changes in environmental conditions (Bijlsma and

Loeschcke, 2012; Dierks *et al*, 2012; Fox and Reed, 2011; Ketola and Kotiaho, 2009).

Evolvability: In the longer term, persistence of populations will typically involve responding to altered selection pressures arising from changes in the environment. The loss genetic variation will constrain the ability of a population to respond to these changes. Selection acts on standing genetic variation to adapt populations to the prevailing conditions as individuals possessing beneficial genetic variants survive and reproduce to pass these beneficial variants onto the next generation. These evolutionary changes enable a population to persist *in situ* under changing conditions. This issue is critical in understanding biodiversity responses to climate change. On the one hand, climate change may lead to the loss of genetic diversity and the associated problems, such as inbreeding depression. On the other, evolutionary changes underpinned by genetic diversity may ameliorate the impacts of climate change on biodiversity. The role of evolutionary change is dealt with in detail in section 4.

Impacts on communities: The levels of genetic diversity and evolutionary changes within one population can alter ecological processes, dynamics and higher-order community structure. Climate driven changes in community composition and/or environmental conditions will generate feedback loops between ecology and evolution. Evolutionary response may dampen or amplify these effects, as changes in one species driven changes in others (Becks *et al.* 2010; Schoener 2011; Walsh *et al.* 2012; Chevin *et al.* 2013; Northfield & Ives 2013; Bailey *et al.* 2014). Adaptive genetic diversity can influence, and is correlated with community-level structure and species diversity (Whitlock 2014). Booth and Grime (2003) have shown that genetically diverse grassland communities tend to lose species diversity at a lower rate than genetically impoverished communities. This is due to direct effects of genetic composition on species abundance, but also interspecific interactions that depend on plant genotype (Fridley *et al.* 2007; Whitlock *et al.* 2011). In addition, higher levels of genetic diversity are associated with increased resistance and resilience to stressful environments, reducing the likely impact of changing environments on communities and ecosystems (Hughes & Stachowicz 2004, 2009; Reusch *et al.* 2005; Ravenscroft *et al.* 2014). Consequently, the amount of genetic variation may impact on ecosystem productivity and functioning, particularly where this variation exists within dominant or keystone species (Johnson *et al.* 2006; Bailey *et al.* 2009; Fischer *et al.* 2013).

Increased genetic differentiation among populations: Differential adaptation among populations may occur in response to local differences in selection pressures. Local adaptation can be countered by the homogenising effects of gene flow, such that some level of isolation can enhance a population's ability to diverge from its neighbours and adapt to local conditions. However, *on balance, genetic isolation is expected to have a negative effect on population persistence.* This is because isolated populations behave as independent genetic units and are more susceptible to the loss of genetic diversity due to random drift and have reduced opportunities for the replacement of lost diversity via gene flow. This undermines the ability of small populations to become locally adapted (Leimu & Fischer 2008). In addition, populations will be unable to receive an influx of

potentially adaptive variants from other populations, further limiting future evolvability.

Decreased genetic differentiation among populations: The consequences of increased genetic exchange between previously isolated populations or taxa (decreased differentiation) are expected to depend on the extent of their genetic divergence. *In most cases this process is expected to be benign or beneficial for individual fitness and population persistence* (Whitlock *et al.* 2013; Frankham, 2015). Increased movement of genetic variants between populations is beneficial because it counteracts inbreeding problems and increases evolvability by replacing lost diversity and introducing novel variants (Reed 2004; Thompson *et al.* 2010; Whiteley *et al.* 2014). In the context of climate change, gene flow from populations currently inhabiting conditions similar to the predicted changes may introduce adaptive genetic variants. For instance, long-distance dispersal in trees may allow the movement of adaptive genes over scales greater than the predicted habitat shifts due to climate change (Kremer *et al.* 2012). In addition, mixing may lead to the generation of beneficial combinations of genes not previously present in either population, enhancing adaptation to the prevailing environment conditions (Rieseberg *et al.* 2003; Hegarty *et al.* 2008).

Set against the potential benefits of an influx of diversity is the risk of outbreeding depression. This refers to the reduction in the individual fitness of hybrids derived from the mixing of previously isolated and genetically differentiated populations. For instance, the repeated introduction of maladapted variants may move the population away from the locally optimal phenotype, opposing selection and potentially leading to declines in density and the associated loss of diversity and genetic problems (Bridle *et al.* 2009, 2010). Even where populations inhabit similar environments, outbreeding depression may arise due to intrinsic genetic incompatibilities, sometimes referred to as the break-up of co-adapted gene complexes (Edmands 2007; Edmands *et al.* 2009). Although gene flow will sometimes result in outbreeding depression, the situations where this is most likely to occur can be predicted by considering the demographic and environmental contexts of the populations exchanging genes (Frankham *et al.* 2011; Whitlock *et al.* 2013; Frankham 2015). It is also worth noting that local adaptations can be maintained in the face of gene flow, provided that gene flow is not too high relative to selection (Gonzalo-Turpin & Hazard 2009; Nuismer *et al.* 2012).

An extension to the concept of decreased population differentiation is decreased taxonomic differentiation. If species' ranges are altered due to climate change then it will be possible for previously geographically isolated species to co-occur in novel communities. Hybridisation between these species may lead to the loss of unique genetic and/or species diversity due to genetic swamping or replacement, particularly where invasive species hybridise with native species (e.g. Muhlfeld *et al.* 2014). For instance, hybridisation between the introduced ruddy duck (*Oxyura jamaicensis*) and the white-headed duck (*Oxyura leucocephala*) threatens the genetic/species integrity of the latter, which may in turn lead to its extinction (Muñoz-Fuentes *et al.* 2013). This may have implications for species interactions and community dynamics. The greatest risks of extinction-by-hybridisation are associated with populations that have short

generation times, no local competitive advantage, low numbers and outcrossing mating systems (Currat *et al.* 2008).

Table 1: *Summary of the causes and consequences of genetic changes relevant to climate perturbation, and an indication of whether the consequences are positive (+ve) or negative (-ve) for the maintenance of biodiversity.*

Genetic changes	Cause	Consequences
Loss of genetic diversity	Reduced/small population size	Inbreeding depression (-ve)
	Changed selection pressure(s)	Reduced evolvability (-ve)
	Fragmentation reducing gene flow	Reduced community diversity and ecosystem function, resistance and resilience (-ve)
Increased genetic differentiation of populations	Differential selection pressures	Increased risk of intrinsic genetic problems (inbreeding depression) (-ve)
	Increased genetic drift in small populations	Populations unable to replace lost diversity or receive useful adaptive variants from other populations (-ve)
	Fragmentation reducing gene flow	May promote adaption to local conditions in some circumstances (+ve)
Decreased genetic differentiation of populations	Anthropogenic movement, range shifts, habitat changes leading to mixing of previously isolated taxa/populations	Increased access to standing genetic variation (replacing lost diversity and alleviating inbreeding depression) and beneficial variants in other populations (+ve)
		Generation of novel gene combinations that may enhance adaptation (+ve)
		Outbreeding depression (destruction of novel gene combinations)/loss of local adaptation (-ve)
		Extinction-by-hybridisation/replacement (-ve)

4. Evolutionary responses to climate change

Evolutionary or genetic changes can adapt populations to the prevailing conditions through selection acting on phenotypes that are underpinned by heritable genetic variation. In the face of changing environmental conditions these changes can enable populations to persist *in situ*. This effect is often referred to as 'evolutionary rescue'. In addition to evolutionary change, populations may tolerate the changed conditions or migrate to more suitable areas. These mechanisms may buffer populations in the short term but there are limitations associated with both (but see the following sub-section; Chevin *et al.* 2010, Kovach-Orr & Fussmann 2012). This means that in the longer-term, populations must ultimately evolve to persist, as

sustained maladaptation can lead to extinction (Gonzalez *et al.* 2013; Kopp & Matuszewski 2014; Gienapp *et al.* 2014).

Evidence for historical genetic changes adapting populations to their environment is abundant in natural and domestic populations. Adaptation to climatic and environmental conditions that vary *spatially* is widespread, as demonstrated by common garden and transplant experiments (Leimu & Fischer 2008). Not surprisingly, there are fewer studies documenting *temporal* evolutionary change, particularly in response to climate-driven changes, although the evidence is rapidly increasing (see Table 2 for examples in UK species; Charmantier & Gienapp 2014; Urban et al. 2014; Franks et al. 2014; Schilthuizen & Kellermann 2014; Boutin & Lane 2014). Franks *et al.* (2007) for example revealed a rapid genetic shift in flowering time in response to drought conditions in *Brassica rapa*. Furthermore, recent climate change in the UK has led to changes in habitat use in brown argus butterflies (*Aricia agestis*), which in turn enabled a poleward range expansion (Thomas *et al.* 2001). These phenotypic changes are based on selection acting on heritable genetic variation for host preference that existed within the pre-expansion distribution (Buckley *et al.* 2010, 2012).

In comparison to the number of documented cases of distributional, phenological and morphological changes, the number where evolutionary genetic changes in response to recent climate change can be conclusively demonstrated is limited. There are several (non-mutually exclusive) reasons for this apparent lack of empirical evidence, including constraints on evolutionary responses (Table 3), biological phenomena and methodological limitations. The majority of studies investigating responses to recent climate change focus on phenotypic responses and are unable to distinguish plastic from evolutionary genetic responses (Gienapp *et al.* 2008; Merilä & Hendry 2014). In fact only a small proportion of studies/datasets appear capable of effectively disentangling these types of adaptive responses. In addition, many datasets only encompass a small number of generations, limiting the detection of genetic responses to selection (Gienapp *et al.* 2008; Merilä & Hendry 2014). Models and experimental findings suggest that evolutionary responses are typically due to large numbers of small-effect genes, which may be undetectable individually (Rockman 2012). Hence, while genetic responses may have occurred, current approaches may fail to detect the signal (Postma 2006) and/or separate it from environmental noise (Björklund *et al.* 2009; Merilä 2012; Merilä & Hendry 2014). The monitoring of adaptive responses using genomic techniques, which enable many genes to be investigated and improved experimental designs, particularly those that facilitate measurement of changes over time (e.g. longitudinal studies) will be a valuable tool in the identification of populations that may be unable to respond adequately to climate change (Hansen *et al.* 2012; Pauls *et al.* 2013; Hoban *et al.* 2014). In addition to methodological limitations, the absence of genetic responses to current climate change may be due to evolutionary time lags. Although the rate of evolutionary change may be rapid, matching ecological time scales where selection pressures are strong, it may also be slow, particularly in species with long generation times (Kuparinen *et al.* 2010). It is possible that phenotypic plasticity may buffer populations from selection pressures in the short term. For example, behavioural thermoregulation in ectothermic species may be sufficient for populations to tolerate changes in temperature, thus limiting evolutionary responses (Kearney *et al.* 2009; Gienapp *et al.* 2013). However physiological adaptation to temperature based on

genetic change may be necessary for survival as temperatures continue to change (e.g. Dixon *et al.* 2009).

Evolutionary change enhancing plastic and migratory responses to climate change

Evolutionary change is not the only mechanism that can facilitate persistence through climate change, many species will also respond via the migration of individuals to more suitable areas and/or tolerance of the changing environment *in situ* through phenotypic plasticity. The relative importance of these responses is likely to vary depending on the timescale considered, the rate and extent of environmental changes, the availability of suitable alternative habitat within dispersal distance and the life history of the organism (Gienapp *et al*, 2008). In many cases, persistence will involve a combination of responses. However, limitations associated with plasticity and movement suggest that evolutionary responses via selection on standing genetic diversity are likely to be required for long-term survival of species, particularly towards their warm range margin (Gienapp *et al.* 2014)

Movement: Many species have undergone shifts in range distribution as they take advantage of newly suitable areas, or track moving resources in response to climate change (Pateman 2015; Chen *et al,* 2011; Hickling *et al.* 2006). This may act as an immediate buffer to climate change, enabling persistence in the short term. However, movement will be limited by dispersal ability and the presence of suitable habitat within dispersal range (e.g. Willis *et al.* 2009). In some cases, dispersal ability itself will exhibit a heritable genetic component and, hence be responsive to selection, allowing evolutionary changes in dispersal ability. For instance, a climate-driven range expansion in bush crickets (*Conocephalus discolour* and *Metrioptera roeselii*) has been facilitated by an increase in wing length, which is genetically determined (Simmons & Thomas 2004). In addition, range shifts will lead to species encountering environments that are novel in ways unrelated to the climate, and to which adaptation may be necessary.

Plasticity: Phenotypic plasticity occurs where the phenotype expressed by a given genotype alters in response to an environmental change (Pigliucci 2005). Several studies demonstrate the importance of plasticity in acclimating populations to novel conditions, and indicate that it might be more important than genetic changes, at least in the short term (Hoffmann *et al.* 2005; Ozgul *et al.* 2010; Franks *et al.* 2014; Schilthuizen & Kellermann 2014; Urban *et al.* 2014; Charmantier & Gienapp 2014). For instance, common frog (*Rana temporaria*) exhibit plasticity that allows populations to cope with some temporal variation in conditions but the presence of local adaptations between populations indicates limitations to these plastic responses (Phillimore *et al.* 2010, 2012). Plastic responses may be constrained by species-wide adaptations in life-history strategy, limitations to resource allocation, the reliability of environmental cues and the ability to generate extreme phenotypes (Auld *et al.* 2010; Chevin *et al.* 2010). Where phenotypic plasticity is underpinned by heritable genetic variation, it will be responsive to selection, leading to evolutionary change (Pigliucci 2005). Climatic selection acting in a Dutch population of great tit (*Parus major*) has led to an evolutionary increase in individual plasticity. In this system, more plastic females were better able to provide for their offspring following a climate-induced mismatch between the timing of reproduction and the peak availability of their caterpillar prey (Nussey *et al.* 2005, 2007). Recent theoretical work has also highlighted the potential for phenotypic plasticity to facilitate and even

accelerate evolutionary responses (Lande 2009; Chevin & Lande 2011). Where the direction of adaptive plastic responses are favoured by natural selection, they may be genetically assimilated (i.e. evolution will converge with the new optimal phenotype generated by plasticity; Aubret & Shine 2010).

Predicting evolutionary change

Studies of evolutionary changes in natural and experimental populations, as well as theoretical models, indicate that not all species/populations are equally likely to exhibit evolutionary change. For instance, evolutionary response was influenced by the rate of environmental change, dispersal, population size and genetic variation in experimental populations of yeast exposed to environmental stress (e.g. Bell & Gonzalez 2009, 2011). The ability to predict evolutionary responses would be useful for the identification of populations, species or communities that might be threatened by climate change. This is not straightforward but a combination of empirical evidence and model simulations enables some predictions to be made (Table 3).

Multiple factors influence evolutionary changes, these are associated with the rate of change/turnover (e.g. generation time) and the presence of suitable genetic diversity on which selection can act (e.g. Kroiss & HilleRisLambers 2014; Alberto et al. 2013; Valladares et al. 2014; Cochrane et al. 2015; Boeye et al. 2012). Evolutionary responses are expected to be constrained where the amount of genetic variation is low. A lack of climatically-relevant variation may represent an intrinsic limitation to adaptation, such that a species cannot evolve beyond certain physiological limits (e.g. Hoffmann *et al.* 2003; Huey *et al.* 2009; Kellermann *et al.* 2009; Davis *et al.* 2014). Typically, diversity is measured at neutral markers, which provide only an indirect indication of adaptive variation (Reed & Frankham 2001). Although the rate of loss may differ, adaptive variation is expected to be lost alongside neutral variation (Willi *et al.* 2006). Hence, neutral makers, although not ideal, can provide an indication of low adaptive potential. Predictions from theoretical and empirical studies suggest populations containing fewer than 1000-5000 reproducing individuals are likely to suffer reduced evolvability as they cannot maintain variation in the long term (Franklin & Frankham 1998; Lynch & Lande 1998; Frankham *et al.* 2014). This may be offset by connectivity to other populations, which may replace lost variation and enhance adaptive variation locally. A counter point to this is that antagonistic gene flow (i.e. against the direction of selection) may hamper selection by retarding divergence. However, the benefits of increased genetic variance outweigh these antagonistic effects in most circumstances (Bridle *et al.* 2009, 2010; Frankham, 2015).

Table 2: Examples of UK species where evolutionary responses to climate change have been observed or are predicted.

	Species	Trait type	Adaptive?	Study type	Drivers	References
Insects	Brown argus butterfly* (*Aricia agestis*)	Host shift, Dispersal traits	+	FO	Habitat availability; Dispersal distance	Thomas *et al.* 2001; Buckley *et al.* 2012
	Comma butterfly* (*Polygonia c-album*)	Host shift	N/A	FO	Habitat availability	Hill *et al.* 2011
	Map butterfly (*Araschnia levana*)	Dispersal traits	+	FO	Dispersal distance	Mitikka & Hanski 2010
	Speckled wood butterfly (*Pararge aegeria*)	Dispersal traits	N/A	FO	Dispersal distance	Hill *et al.* 1999
	Silver-spotted skipper* (*Hesperia comma*)	Dispersal traits	N/A	MD	Dispersal distance	Hill *et al.* 1999
	Garden tiger moth* (*Arctia caja*)	Dispersal traits	+	FO	Dispersal distance	Anderson *et al.* 2008; Hill *et al.* 2011
	Winter moth (*Operophtera brumata*)	Phenology	+	FO	Trophic interactions /temperature	van Asch *et al.* 2012
	Banded Demoiselle (*Calopteryx splendens*)	Dispersal traits	N/A	FO	Dispersal distance	Hassall *et al.* 2009; Hill *et al.* 2011
	Long-winged cone-head* (*Conocephalus discolour*)	Dispersal traits	+	FO	Dispersal distance	Thomas *et al.* 2001; Simmons & Thomas 2004
	Roesel's bush cricket* (*Metrioptera roeselii*)	Dispersal traits	+	FO	Dispersal distance	Thomas *et al.* 2001; Simmons & Thomas 2004
	Two-spotted ladybird (*Adalia bipunctata*)	Coloration	+	FO; EX	Temperature	de Jong *et al.* 2010; Brakefield & de Jong 2011
	Fruitfly (*Drosophila melanogaster*)	Anonymous trait (allele frequencies)	N/A	FO	Not specified	Anderson *et al.* 2005; Umina *et al.* 2005
	Fruitfly (*Drosophila subobscura*)	Anonymous trait (allele frequencies)	N/A	FO	Temperature	Balanyá *et al.* 2006
	Waterflea (*Dapnia*)	Thermal tolerance	+	EX; RS	Temperature	Geerts *et al*, 2015
Snails	Grove snail* (*Cepaea nemoralis*)	Coloration	+	FO; EX	Temperature	Ożgo & Schilthuizen 2012; Cameron *et al.* 2013
	White-lipped snail* (*Cepaea hortensis*)	Coloration	+	FO	Temperature	Cameron & Pokryszko 2008

	White garden snail (*Theba pisana*)	Coloration	+	FO	Temperature	Johnson 2011, 2012; Scheil *et al.* 2012
Birds	Blackcap (*Sylvia atricapilla*)	Phenology (migration)	+	FO; EX	Temperature	Berthold *et al.* 1992; Pulido & Berthold 2010
	Great tit *[1] (*Parus major*)	Phenology (laying date)	+	FO	Trophic interactions/ temperature	Nussey *et al.* 2005; Charmantier *et al.* 2008
	Tawny owl (*Strix aluco*)	Coloration	+	FO	Habitat/Temperature	Karell *et al.* 2011
Amphibians	Common frog* (*Rana temporaria*)	Spawning date	+	FO	Temperature	Phillimore *et al.* 2010
Plants	Field Mustard (*Brassica rapa*)	Phenology, Physiology,	+	RS	Drought	Franks *et al.* 2007; Franks & Weis 2008; Franks 2011
	Mediterranean wild thyme (*Thymus vulgaris*)	phenotypes/physiology	+	FO	Temperature (freezing)	Thompson *et al.* 2007, 2013
	Downy Birch (*Betula pubescens*)	Phenology	+[†]	EX	Temperature	Billington & Pelham 1991
	Silver birch* (*Betula pendula*)	Phenology; Anonymous trait (allele frequencies)	+[†]/ N/A	EX; DO	Temperature	Billington & Pelham 1991; Kelly *et al.* 2003
	Thale cress (*Arabidopsis thaliana*)	Phenology	0	EX	Temperature	Springate *et al.* 2011
	Mustard (*Brassica juncea*)	Phenology; Growth	0	EX	CO_2; Temperature	Potvin & Tousignant 1996
	European beech (*Fagus silvatica*);	Phenology; Anonymous traits (allele frequencies)	N/A	EX; DO	Temperature	Jump *et al.* 2006; Vitasse *et al.* 2010
	Sessile oak (*Quercus petraea*)	Phenology	N/A	EX	Temperature	Vitasse *et al.* 2010
	Cork oak (*Quercus suber*)	Physiology; Growth	Y	EX	Water availability	Ramírez-Valiente *et al.* 2010
	27 Alpine plant species	Anonymous traits (allele frequencies)	N/A	MD	N/A	Alsos *et al.* 2012
	Scots pine (*Pinus sylvestris*)	Phenology; Physiology; Anonymous traits (allele frequencies)	0/+[†]	MD	Temperature; Frost; Drought	Savolainen *et al.* 2004, 2007, 2011

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* UK study populations; [1]no evidence of genetic changes in UK populations; For adaptive: + indicates change is adaptive, - is maladaptive, 0: neither adaptive nor maladaptive; NT: not tested; † Not predicted to keep pace with climate change. For study type: FO: Field observations; EX: greenhouse/field experiment; RS: resurrection study; DO: dendrochronology (tree-ring data); MD: modelled.

Table 3. Summary of factors influencing evolvability

Factor	Influence on evolvability	High risk traits/ attributes	References
Population size	A reduction in population size is expected to reduce evolvability. This is because population size will influence the amount of standing variation contained within the population, and the relative impacts of genetic drift (random change) versus selection (adaptive change). It also influences the likelihood of genetic problems (inbreeding depression) which may act as an intrinsic fitness limitation restricting responses to selection.	Small populations, populations with low levels of genetic diversity [*High agreement; Limited evidence*]	Frankham 1996; Franklin & Frankham 1998; Leimu *et al.* 2006; Leimu & Fischer 2008; Lanfear *et al.* 2014
Gene flow	Increased gene flow is expected to enhance evolvability by providing access to standing genetic variation in other populations. A counter point to this is that evolvability will be reduced when gene flow contains maladapted variants, or causes the break-up of sets of co-adapted genes.	Low gene flow, high frequency influx of maladapted alleles or genetically diverged individuals [*Moderate agreement; Limited evidence*]	Bell & Collins 2008; Bell & Gonzalez 2009, 2011; Bridle *et al.* 2010; Kremer *et al.* 2012; Schiffers *et al.* 2013; Bourne *et al.* 2014; Cochrane *et al.* 2015
Physiological limitations	Intrinsic organismal constraints (frequently associated with a lack of heritable genetic variation) represent ceilings to adaptive change and potential evolvability. Closely related species often possess similar limitations (i.e. they are phylogenetically correlated)	Near limits of tolerance for a given condition [*Low agreement; Limited evidence*]	Deutsch *et al.* 2008; Willis *et al.* 2008; Kellermann *et al.* 2009, 2012; Somero 2010; Thuiller *et al.* 2011

Genetic correlations among traits	Different traits can have a shared genetic basis. Thus selection on one trait results in correlated responses in the other. Where selection on one trait results in a maladaptive response in a second, then the overall evolutionary response can be retarded, and evolvability reduced	Antagonistic trait interactions (negative genetic correlations) [*Low agreement; Limited evidence*]	Etterson & Shaw 2001; Etterson 2004; Sgro & Hoffmann 2004
Mode of reproduction	The way in which a species reproduces influences the amount of standing genetic variation and opportunities for recombination and genetic exchange. Where variation and/or genetic exchange is infrequent evolvability will be reduced	Predominantly asexually reproducing or self-fertilising species [*Moderate agreement; Limited evidence*]	Honnay & Jacquemyn 2008
Ploidy	The number of sets of chromosomes will influence the amount of genetic diversity contained within an individual. In some cases this increased diversity may enhance evolvability	Low ploidy level species (e.g. diploid/haploid) [*Low agreement; Limited evidence*]	Comai 2005; Pandit *et al.* 2011
Ecological amplitude	The range of environmental conditions inhabited may reflect levels of (adaptive) genetic variation (or tolerance), and thus potential evolvability	Specialist/narrow niche [*Low agreement; Limited evidence*]	Hoffmann *et al.* 2003; Kellermann *et al.* 2009, 2012; Merilä 2009; Berger *et al.* 2014; van Heerwaarden & Sgrò 2014; Valladares *et al.* 2014; Bridle *et al.* 2014
Reproductive output	The number of offspring produced per generation will influence the number of individuals (and potential beneficial genotypic combinations) on which selection can act.	Low reproductive output; species with high variance in reproductive success (reducing genetically effective population size) [*Moderate agreement; Limited evidence*]	Frankham 1995; Rice & Emery 2003
Generation time	The time to first reproduction will influence the ability to cycle through generations, and hence rate of evolutionary change/ evolvability	Long generation time/slow to reach 1st reproduction, (but also influenced by reproductive output, see above) [*Low agreement; Limited evidence*]	Rice & Emery 2003; Alberto *et al.* 2013

| Overlapping generations | Species whose individuals have become established over multiple years and have experienced different environmental conditions across life stages are expected to maintain more genetic variation (and greater evolvability) than short lived species with highly synchronised birth-reproduction-death cycles. | Species with highly synchronised birth-death cycles, (also, more rarely, in long lived species if a particular cohort of adults regularly introduce maladapted variation) [*Low agreement; Limited evidence*] | Petit & Hampe 2006; Kuparinen *et al.* 2010 |

5. Managing evolutionary potential and responses

There is a need for proactive management that aims to maximise the potential for species to respond adaptively to changing climatic conditions. In many cases, early interventions (as outlined below) are likely to be the most effective means to allow adaptive responses to climate change. This is because responses to selection depend upon pre-existing genetic variation. If management is reactive, genetic diversity may already have been eroded and evolvability reduced, limiting the ability of populations to persist through climate change. There is increasing recognition of the need to incorporate evolutionary processes into conservation planning to maximise the ability of populations/taxa to persist in the current conditions and undergo evolutionary responses to cope with changing environmental conditions (Lawton *et al.* 2010; Hannah 2011; Shoo *et al.* 2013). In addition, as outlined below, such programmes are also expected to enhance other adaptive responses, such as range shifts. Despite this, examples of conservation practice that are guided by evolutionary principles are still rare (Hannah 2011).

Maximising evolvability within populations/taxa

There are two key components to promoting evolutionary responses: maintaining population size and fostering genetic exchange. To prevent the loss of genetic diversity and evolutionary potential, current information suggests population sizes of approximately 1000-5000 breeding individuals may be necessary (Franklin & Frankham 1998; Lynch & Lande 1998; Frankham *et al.* 2014). It is important to note that the effective population size may be increased through the establishment of (genetic) connectivity in the landscape as well as by maximising size within individual populations. This is because networks of interconnected population act as a single unit genetically, since each population has access to the standing genetic variation in other populations. The facilitation of effective genetic exchange and turnover in some predominantly asexual plant species may require active enhancement of sexual reproduction (i.e. flowering). Genetic exchange between populations also facilitates the movement of adaptive genetic variants through population networks. In the context of climate change, the most important influx of diversity may be from populations inhabiting conditions closer to those expected under future climate regimes.

Prioritising populations/areas for protection

Protected areas, such as Sites of Special Scientific Interest and National Nature Reserves will continue to have an important role in conservation under climate change. However, typically site selection has neglected intraspecific diversity, which will influence evolvability and hence species and community persistence (Laikre 2010; Laikre et al 2010). Conservation management should include a focus on populations containing high diversity and local adaptations, aiming for the maintenance of populations in the broadest possible range of environmental conditions. Conversely, reactive management directed towards populations where genetic erosion has already occurred is less likely to be effective at maintaining evolvability. Key populations for maximising the conservation of genetic diversity and hence evolutionary potential have maintained large population size (i.e. have not undergone population bottlenecks). Evolutionary refugia represent sites where species have persisted when excluded from much of their range during past climate

change and as a result typically contain higher levels of genetic variation, despite only representing a small portion of the total range. Thus protection of refugia is important as they represent stores of genetic diversity (Keppel *et al.* 2012; MacLean *et al,* 2014; Suggitt *et al,* 2014). Refugia may be identified based on ecological criteria, such as mountain tops or areas of high environmental heterogeneity, which may enable species persistence, or by phylogeographic analysis (Moritz 2002; Emerson & Hewitt 2005). Many populations are adapted to the local conditions and contain unique genetic diversity, particularly where they occur across divergent environmental conditions (Leimu & Fischer 2008). Populations towards the edge of the range, for example, may contain unique diversity that may be important in facilitating future adaptation, such as range shifts (Buckley *et al.* 2010).

The protection of key sites alone, however, is unlikely to be sufficient to enable persistence during climate change.   Even where a species is widespread, populations may contain local adaptations and a lack of gene flow between these populations will hamper evolutionary responses, meaning these species may be susceptible to range loss and extinction (Schiffers *et al.* 2013; Bourne *et al.* 2014). Hence it is essential that management focuses on the maintenance or establishment of connectivity across the landscape, between new and existing protected areas (Lawton *et al.* 2010). This will enable the movement of individuals and genes, and so promote adaptation via evolutionary change and/or tracking of the viable range.

Translocations

Translocations are human-mediated movements of individuals in the landscape. They include movement between established populations (reinforcement), movement within the native range but into unoccupied sites (reintroduction or range restoration), or to locations outside the known native range (conservation introductions). In order to enhance the potential for evolutionary responses to climate change, translocations will need to be broadened beyond the currently dominant approach of moving individuals over small geographic scales (e.g. only from local donor populations to neighbouring areas).

Conservation introductions to locations predicted to be more suitable under anticipated climate-change may reduce climate-mediated extinction risk in species that possess low evolvability, limited dispersal ability, low phenotypic plasticity or narrow climate niche. However, the need for, and effectiveness of this strategy continues to be the focus of debate (Hoegh-Guldberg *et al.* 2008; Ricciardi & Simberloff 2009; Richardson *et al.* 2009; Schwartz *et al.* 2009; Vitt *et al.* 2009; Loss *et al.* 2011). A key limitation in the use of conservation introductions may arise from invasive species policies, which would not permit such movements or recognise the conservation status of species outside their known native range (IUCN 2012; National Species Reintroduction Forum 2014a; b).

Reinforcements have been an effective conservation tool to alleviate genetic problems arising from the loss of genetic diversity following the disruption of natural gene flow by habitat fragmentation (Bouzat *et al.* 2009; Hedrick & Fredrickson 2010; Whiteley *et al.* 2014). Moving beyond the use of reinforcement in response to existing problems, these same principles may also be applied to maximise evolvability and prevent genetic problems arising (Hedrick 2005; Whiteley *et al.* 2014). For instance, the introduction of a single individual per generation may be

employed to mitigate potential genetic problems (i.e. inbreeding depression and reduced evolvability) where natural dispersal has been disrupted (Newman & Tallmon 2001; Wang 2004; Weeks *et al.* 2011; Whiteley *et al.* 2014). This low level of gene flow is unlikely to disrupt local adaptation. In addition, translocations may be employed to introduce potentially adaptive diversity in the predicted direction of change (i.e. predictive provenancing), such as from warm-adapted populations, although the effectiveness of such a strategy is still uncertain (Jones *et al.* 2011; Sgrò *et al.* 2011; Weeks *et al.* 2011; Aitken & Whitlock 2013). Composite provenancing aims to maximise evolvability by mimicking natural gene flow dynamics by utilising mixed donor stock consisting of decreasing proportions of individuals with increasing distance from the recipient site (Broadhurst *et al.* 2008; Sgrò *et al.* 2011). The active use of such strategies to generate evolutionarily resilient populations and communities may minimise the need for ongoing and future intervention.

Outbreeding depression has been a major conservation concern and a limitation to adoption of conservation practices that result in population admixture. However, as previously noted, recent evidence suggests that situations where there is a high risk of outbreeding depression can be predicted, and this may allow avoidance of the genetic risks posed by outbreeding (Frankham *et al.* 2011; Whitlock *et al.* 2013). The greatest risks of outbreeding depression are associated with mixing populations which have been separated for 100s of generations and/or inhabit highly divergent habitats (Frankham *et al.* 2011).

6. Evidence base and Knowledge Gaps

Defining strategies to effectively manage genetic resources such that species are retained as self-sustaining entities capable of dealing with any scenario of environmental change is challenging. This is due to a limited understanding of the genetic basis of traits of ecological importance and an unknown suite of selection pressures that will result from a climate change scenario that itself cannot be accurately predicted. That said, the evidence on which this review is based is underpinned by well-established theory backed by varying amounts of empirical data. Collectively, this information enables some broad generalisations to be made, although knowledge gaps exist as outlined below.

Impact of climate change on distribution of genetic diversity and its effects on biodiversity:

Conclusions concerning the factors influencing genetic diversity and its subsequent impact on other levels of biodiversity come from a large evidence base, in which several aspects have been summarised by formal meta-analysis, providing a high level of certainty. There are, however, still aspects underpinned by a weaker evidence base.

We have a broad general understanding of:

- The factors influencing the movement of genes in the landscape and the spatial scale over which genetic differentiation can occur [*High agreement; Robust evidence*]
- The circumstances leading to the loss of genetic diversity [*High agreement; Moderate evidence*]

- The life history traits that influence the levels and distribution of genetic diversity. [*Moderate agreement; Moderate evidence*]
- The fitness consequences of inbreeding [*Moderate agreement; Robust evidence*]
- The situations where genetic problems (inbreeding and outbreeding depression) are most likely to arise [*Moderate agreement; Moderate evidence*]
- The impact of the amount of genetic diversity on community diversity, structure and ecosystem function [*Moderate agreement; Limited evidence*]

Detailed information is limited/lacking on:

- The way in which specific landscapes/environments interact with life history strategies to cause genetic isolation, or the inability to colonise new sites.
- The impact of climate change, land management practices and their interaction on the movement of genes in the landscape
- The circumstances and life history traits that will influence how the amounts and distribution of genetic diversity will alter during range shifts
- The mechanisms by which intraspecific genetic diversity influences community diversity, resistance and resilience, ecosystem functioning and service provision.

Evolvability and persistence in the face of climate change

The evidence base for evolutionary change in response to recent climate change is comparatively small and hence there is a higher degree of uncertainty due to knowledge gaps.

We have a broad general understanding of*:*

- The role of genetic change in adapting populations to the prevailing conditions [*High agreement; Moderate evidence*]
- The life history traits that will limit evolutionary responses and the rate of change [*Moderate agreement; Moderate evidence*]

Detailed information is limited/lacking on:

- The ability of evolutionary changes to keep pace with rapid climate change, and the relative roles of movement and plasticity in buffering populations in the short-term
- Detailed information on the circumstances in which species with different life history traits are likely to respond adequately to changing conditions, or fail to do so
- The relative contributions of plasticity and genetic change to *in-situ* adaptive responses to changing conditions.
- The effects of species interactions and ecological processes on the rate of evolutionary change
- The impact of inbreeding on evolutionary and plastic responses to climate change

- The selection of donor populations containing adaptive diversity that will enable/enhance the persistence of threatened populations under future environmental conditions

7. Recommended actions
- Continue and enhance existing dialogue to improve integration of evolutionary/genetic thinking within conservation management, particularly regarding the relative costs and benefits of the movement of individuals.
- Encourage proactive management, which aims to maximise the ability of populations to respond to changing environmental conditions, including climate change.
- Utilise existing information (e.g. long-term datasets in natural systems and ecological experiments) to understand the potential for evolutionary responses to climate change and provide information on vulnerable species/habitats to assist in the development of appropriate management programmes.
- Undertake long-term large scale ecological and genetic monitoring of natural and translocated populations with the aim of investigating the impacts of climate change and management interventions.

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