

REVIEWS AND
SYNTHESESRunning to stand still: adaptation and the response
of plants to rapid climate change

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Abstract

Climate is a potent selective force in natural populations, yet the importance of adaptation in the response of plant species to past climate change has been questioned. As many species are unlikely to migrate fast enough to track the rapidly changing climate of the future, adaptation must play an increasingly important role in their response. In this paper we review recent work that has documented climate-related genetic diversity within populations or on the microgeographical scale. We then describe studies that have looked at the potential evolutionary responses of plant populations to future climate change. We argue that in fragmented landscapes, rapid climate change has the potential to overwhelm the capacity for adaptation in many plant populations and dramatically alter their genetic composition. The consequences are likely to include unpredictable changes in the presence and abundance of species within communities and a reduction in their ability to resist and recover from further environmental perturbations, such as pest and disease outbreaks and extreme climatic events. Overall, a range-wide increase in extinction risk is likely to result. We call for further research into understanding the causes and consequences of the maintenance and loss of climate-related genetic diversity within populations.

Keywords

Adaptation, climate change, conservation, decreased fitness, extinction risk, gene flow, genetic diversity, habitat fragmentation, migration, plant populations.

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INTRODUCTION

The 20th century experienced the strongest warming trend of the last millennium with average temperatures rising by about 0.6 °C (Jones *et al.* 2001). Future temperature rises are likely to exceed this with a predicted rise of between 0.1 °C and 0.4 °C per decade across Europe (IPCC 2001) – a rate that is unparalleled in recent history (Huntley 1991). One of the predicted consequences of climate change is the movement of plant species to higher elevations and latitudes as the climate to which they are adapted is displaced. There is now considerable evidence that such changes in plant distribution are occurring (Walther *et al.* 2002; Parmesan & Yohe 2003; Walther 2003). Significant elevational rises have been reported in Alaska (Lloyd & Fastie 2003) Scandinavia (Kullman 2002), the Alps (Grabherr *et al.* 1994) and the Mediterranean region (Peñuelas & Boada 2003; Sanz-Elorza *et al.* 2003), as well as a latitudinal advance of arctic shrub cover (Sturm *et al.* 2001).

When compared with reported rates of past migrations of plant species, the rapid rate of current climate change has the potential to render many species unable to track the climate to which they are currently adapted (Huntley 1991; Davis & Shaw 2001); an effect that will be exacerbated by habitat fragmentation because of human activity (Halpin 1997; Honnay *et al.* 2002). A rapid, worldwide increase in extinction risk is likely to result (Thomas *et al.* 2004). Realized migration rates will differ greatly between different plant species and consequently we may see the formation of novel plant communities in response to climate change (Pacala & Hurtt 1993; Walther *et al.* 2002; Walther 2003). Such communities are evident in the fossil record as species assemblages with no modern analogue. These communities are believed to result from differential migration rates during past climatic changes (Huntley 1990, 1991). Based on the similarity of species relationships with climate in their past and present distributions, it has been suggested that adaptation has played only a minor role in the response of

plants to changing climate (Bradshaw 1991; Huntley 1991). However, the frequent differentiation of populations with respect to climate demonstrates that climate asserts strong selective pressure on natural populations (Turesson 1925; Clausen *et al.* 1940; Linhart & Grant 1996; Joshi *et al.* 2001; Etterson 2004a) and thus the role of adaptation in response to past and future climatic changes may well have been underestimated (Davis & Shaw 2001).

Interannual variability in climate is a normal occurrence, even in the absence of long-term climatic changes. Most species tolerate such short-term variability through phenotypic plasticity. However, beyond the point at which individuals (and therefore species) are able to tolerate changes in climate, distributional and evolutionary changes are inevitable (Lynch & Lande 1993). The accumulating evidence of plant migrations indicates that this point has already been passed for many species.

As plant species move towards higher latitudes and altitudes, populations at the leading edge of the species range are expected to expand and occupy new territory, with a concomitant reduction in population sizes and increase in population extinction at the contracting edge. The links between climate and plant reproduction and vegetative survival are well understood (Woodward 1987), providing a clear mechanism for expansion of a species at its leading edge. For those species where geographical limits are described by climate, poor reproduction and survival at the poleward and upper altitudinal limits of distribution are likely to be ameliorated by increasing temperatures. At the equatorial and lower altitudinal limit of its range, a species may be replaced through competitive exclusion (Woodward 1987), most likely influenced by both water availability (Pigott & Pigott 1993) and higher temperatures (Conolly & Dahl 1970). Changes in climate are however likely to differ between continental and oceanic environments, possibly leading to lack of range expansion or even range reductions in some northern regions (Crawford & Jeffree 2005). A review of current evidence for changes in plant distribution and community composition is presented by Walther (2003).

In this paper we review literature that demonstrates within-population genetic differentiation of individuals with respect to climate and those studies that have investigated the adaptive response of genetically variable populations to simulated climatic warming. We discuss how rapid climate change may act as a potent agent of natural selection within populations and its likely interaction with habitat fragmentation in altering population genetic structure (Fig. 1). In the final section of the paper we discuss some of the consequences of reduction of genetic diversity in plant populations and communities and their possible ramifications for the persistence of individual species. Climate change is multidimensional and simultaneous changes may occur in a number of variables such as temperature,

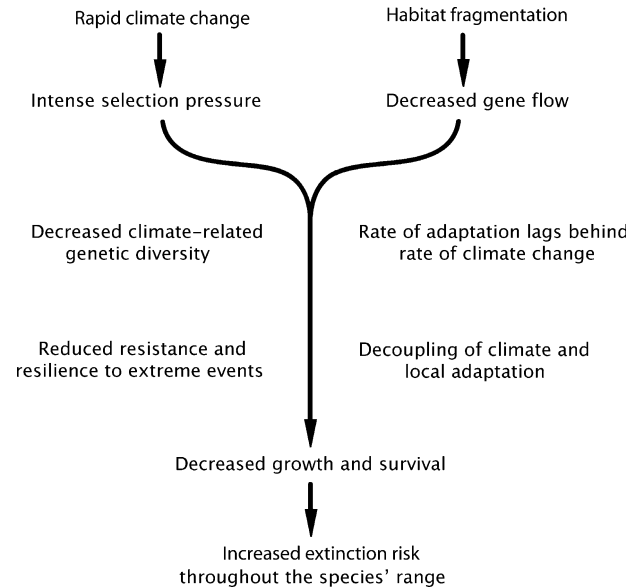


Figure 1 The interaction of rapid climate change and habitat fragmentation within populations leading to a range-wide increase in extinction risk. This can occur in the absence of habitat fragmentation if climate change occurs at a rate faster than the maximum rate of gene flow between populations.

precipitation, growing season length and changes in day length during latitudinal range changes. Although we focus primarily on the effects of climatic warming, the arguments we present are equally applicable to rapid changes in other variables.

CLIMATE-RELATED GENETIC VARIABILITY WITHIN POPULATIONS

Local adaptation of populations to climate has been demonstrated often since the pioneering work of Turesson (1925) and Clausen *et al.* (1940). However, differential responses to climate occur not only between populations throughout a species range, but also between co-occurring individuals within a population. Li *et al.* (1999, 2000, 2001) report significant microgeographical genetic differentiation of populations of *Triticum dicoccoides* (wild emmer wheat) in response to climate (solar radiation, temperature and aridity stress) over distances of several metres within a habitat mosaic. A similar pattern has been reported in *Hordeum spontaneum* (wild barley) (Owuor *et al.* 1997; Huang *et al.* 2002) (Table 1). In both species significant segregation of individuals occurs between adjacent microsites with differing climatic conditions, such that particular genotypes are confined to, or occur preferentially in, different sites. This within-population differentiation was detected using both microsatellite, randomly amplified polymorphic DNA and allozyme molecular markers and is repeated across spatial

Table 1 Climatic factors correlated with microgeographical genetic differentiation and the molecular markers with which it was detected

Species	Climatic factors correlated with differentiation	Molecular marker	Reference
<i>Avena barbata</i>	Temperature, water availability	Allozymes	Hamrick & Allard (1972), Hamrick & Holden (1979)
<i>Hordeum spontaneum</i>	Temperature, water availability	RAPD, microsatellites	Owuor <i>et al.</i> (1997), Huang <i>et al.</i> (2002)
<i>Triticum dicoccoides</i>	Temperature, water availability	Allozymes, RAPD, microsatellites	Li <i>et al.</i> (1999, 2000, 2001)
<i>Betula pendula</i>	Temperature	AFLP	Kelly <i>et al.</i> (2003)
<i>Picea engelmannii</i>	Water availability	Allozymes	Stutz & Mitton (1988), Mitton <i>et al.</i> (1989)
<i>Pinus edulis</i>	Water availability	Allozymes	Cobb <i>et al.</i> (1994), Mitton & Duran (2004)
<i>Pinus ponderosa</i>	Water availability	Allozymes	Beckman & Mitton (1984)

scales ranging from <10 m to up to 1 km. A comparable pattern of microgeographical allozyme differentiation is seen in *Avena barbata* (slender oat) across sites varying in temperature and soil moisture status (Hamrick & Allard 1972; Hamrick & Holden 1979), where microgeographical patterns of differentiation are also repeated at a range wide scale. Although population differentiation will be promoted by the low rates of outcrossing in these species, gene flow (by seed transfer) has been demonstrated between microsites. Critically, the differentiation of populations varies with climate over both space and time as a consequence of natural selection operating on seedling establishment.

Kelly *et al.* (2003) report a parallel example based on analysis of amplified fragment length polymorphism loci in a natural population of *Betula pendula* (European white birch). In this outcrossing, wind-pollinated tree, co-occurring individuals demonstrate genetic segregation related to mean temperature in the early years of seedling establishment. The evidence presented by Kelly *et al.* (2003) suggests different genotypes establish preferentially in warm and cool years. These 'cool year' and 'warm year' genotypes are intermixed within the same population, despite presumably high levels of gene flow between neighbouring trees.

Further examples of microgeographical adaptive differentiation of tree species with respect to climate are found in *Picea engelmannii* (Engelmann spruce) (Stutz & Mitton 1988; Mitton *et al.* 1989), *Pinus edulis* (piñon pine) (Cobb *et al.* 1994; Mitton & Duran 2004) and *Pinus ponderosa* (ponderosa pine) (Beckman & Mitton 1984) (Table 1). All of these species show significant association of different allozyme markers in adjacent or nearby sites that differ in their severity of moisture stress. These patterns of differentiation are repeated at local and range wide scales. In *P. edulis*, different *Gly* genotypes show differences in fitness when growing on dry soils, with the genotype most commonly found on dry soils having the highest growth and viability (Mitton & Duran 2004). Genetic isolation by distance,

genetic drift and restricted gene flow cannot adequately explain the observed patterns of climate-related genetic differentiation, as these patterns are repeated across a variety of different spatial scales both within and between species. In all these studies the most parsimonious explanation is the action of natural selection during plant establishment (Linhart & Grant 1996; Ennos 2001).

These examples use a population genomic approach to indicate local adaptation without prior identification of the adaptive traits concerned (Luikart *et al.* 2003). The trait variation that underlies the genetic differentiation in these studies merits further research. In future studies, data analysis with newly emerging population genomic methods (see Luikart *et al.* 2003) will strengthen the conclusion that such differentiation results from the effects of natural selection.

Given a sufficiently strong selective pressure, adaptive differentiation of populations is possible even in the presence of high levels of gene flow (Jain & Bradshaw 1966; Antonovics 1968; Ennos 2001). The studies outlined above demonstrate that differentiation may occur within populations in response to selection pressures that show variability over time (e.g. climate) in addition to those that vary over space (e.g. soil type).

EVOLUTIONARY RESPONSE TO SIMULATED CLIMATE CHANGE

Although there is evidence that considerable climate-related genetic variation may be present in many natural populations, this does not necessarily indicate that adaptation to new climatic conditions will occur, or that the rate of any adaptation will match the forecast rate of climate change. Billington & Pelham (1991) assessed the degree of genetic variation in date of budburst in *Betula pendula* and *B. pubescens* – a trait that will be critical in these species ability to exploit a lengthening growing season as the climate warms. They found that although some of the

Table 2 Studies assessing evolutionary change in species subject to global warming

Species	Trait	Heritability (h^2)* of traits	Conclusion	Reference
<i>Betula pendula</i> , <i>B. pubescens</i>	Budburst	0.00–0.65	Rate of evolution unable to match predicted rate of warming even in the most variable population.	Billington & Pelham (1991)
<i>Pinus sylvestris</i>	Bud set, frost hardiness	0.20–0.67	Rate of evolution likely to be slower than rate of climate change.	Savolainen <i>et al.</i> (2004)
<i>Chamaecrista fasciculata</i>	Seed production, leaf number and thickness, development rate	0.00–0.48	Response critically slow due to requirement for simultaneous evolution of several traits. Rate of evolutionary response much slower than predicted rate of climate change.	Etterson & Shaw (2001); Etterson 2004b
<i>Brassica juncea</i>	14 traits including, seed, leaf and stem number and mass	0.15–0.55 (values for silique biomass only)	No genetic or phenotypic response in fitness-related traits. Little or no adaptive response in other traits.	Potvin & Tousignant (1996)
<i>Drosophila birchii</i>	Desiccation resistance	0.00	No response to selection. Little potential for adaptation in response to climate change.	Hoffmann <i>et al.</i> (2003)

*Narrow sense heritability (the proportion of the total phenotypic variance in a trait that is due to the additive effects of genes), summarized as a range covering all of the traits assessed. With the exception of Potvin & Tousignant (1996), values for all individual traits are given in the original publication.

populations contained considerable levels of heritable variation for budburst date (Table 2), the levels were inadequate to allow date of budburst to track forecast changes in climate, even in the most variable population investigated. Similar findings are reported by Savolainen *et al.* (2004) in an investigation of variation of bud set and frost hardiness in *Pinus sylvestris*. Again they found that although genetic variation for these traits is high, the rapid rate at which warming is predicted to occur will outstrip the potential rate of adaptive evolution in this species.

Adaptation to future climates may require the simultaneous evolution of a number of different traits that may be constrained by correlations between them (Lynch & Lande 1993; Etterson & Shaw 2001). Etterson & Shaw (2001) and Etterson (2004b) found that the annual legume *Chamaecrista fasciculata* was unable to respond fast enough to track predicted conditions, despite the existence of significant levels of variation for the quantitative traits investigated. In this case the simultaneous evolution of the suite of traits required for an adaptive response in this species was critically slow. The most northern population of this species was at a greater disadvantage under simulated climate change, because of a combination of lower genetic variability, reduced heritability of traits and reduced fecundity when compared with other populations (Etterson 2004a,b). In the case of *Brassica juncea* – a short-lived outcrossing annual – experimental populations failed to respond either genetically or phenotypically to simulated climate change in any of five fitness-related traits, again despite sufficient relevant variation for these traits in the source population (Potvin & Tousignant 1996). Failure of

B. juncea to respond to the intense selection pressure of the simulated changes in climate was believed to result from the high levels of inbreeding that this caused. Further reports of a failure to respond to simulated climate change come from *Drosophila birchii* (Hoffmann *et al.* 2003) collected from natural populations. *Drosophila birchii* was selected for increased desiccation resistance and the lack of response is believed to result from a lack of heritable variation for this trait. In *D. birchii* such variation is likely to be critical to enable populations to respond to the changes in its environment that are predicted to result from global warming.

The potential for a population to adapt to changes in climate will in part be governed by the average lifespan of individuals and the age at which they reach reproductive maturity. If all other things are held equal, annual plants will adapt faster to a changing environment because of their short generation time. The lag of adaptation in those species with a long generation time and long lifespan will be significantly larger for several reasons. Delayed reproductive maturity will reduce the number of generations that can establish during any given period of time, whilst long lifespan (and hence low turnover) of individuals will reduce the opportunities for establishment of new genotypes within existing populations (Savolainen *et al.* 2004). The experimental studies of Potvin & Tousignant (1996), Etterson & Shaw (2001) and Etterson (2004a,b) were necessarily conducted on species with a short generation time.

For populations that show little potential for an *in situ* adaptive response to climate change, gene flow from populations in warmer areas of the species range will be

of critical importance in permitting adaptation to their new conditions (Billington & Pelham 1991). For many species however, gene flow between populations may be critically low because of the effects of habitat fragmentation; thus in these species, adaptation to the changing climate may be even more restricted (Savolainen *et al.* (2004).

MIGRATION, GENE FLOW AND HABITAT FRAGMENTATION

In populations subject to climate change, the most rapid response of established individuals is likely to be phenotypic (Bradshaw 1965). In subsequent generations, natural selection acting primarily during plant establishment will lead to some degree of adaptation, assuming that genetic variation for the traits under selection exists within the population (Lande 1988; Bradshaw 1991). Considering adaptation as primarily dependent on extant variation (Bradshaw 1991), the migration of plant species in response to rapid climatic warming will frequently be slower than phenotypic and adaptive genetic changes, largely because of the uncertainties of population establishment (see below).

Migration involves the physical dispersal of propagules (i.e. seeds, plant fragments) and successful establishment of new populations in previously unoccupied territory. Natural selection will act on the diversity of arriving propagules to filter out those that are less well adapted to the conditions of the new site (Lande 1988; Davis & Shaw 2001). The process of population establishment demonstrates that adaptation to local conditions is often inherent in migration, the evidence of this has been documented for many years (Turesson 1925; Clausen *et al.* 1940). As the climate warms, individuals from populations throughout the species range are likely to establish at higher altitudes and latitudes in response to the movement of their climatic optimum. Thus migration will occur throughout the species range in the form of both propagule and pollen dispersal, not simply as a result of expansion and contraction at the range margins (Davis & Shaw 2001). However, for a plant species to migrate across a landscape, its habitat patches must be sufficiently well connected to allow gene flow (by pollen and propagule dispersal) between populations. In the heavily fragmented landscapes that have resulted from the activities of humankind this may not always be possible, leading to the fragmentation of the range of many species and increased genetic isolation of their populations (Young *et al.* 1996; Aldrich *et al.* 1998; Knutsen *et al.* 2000; Williams *et al.* 2003).

Habitat fragmentation poses specific threats to populations through genetic factors such as increases in genetic drift and inbreeding, together with a potential reduction in gene flow from neighbouring populations (Young *et al.*

1996). These combine with demographic factors such as altered mating systems and changes in pollinator behaviour, resulting in a reduction of individual fitness and an increased risk of population extinction (Lande 1988; Ellstrand & Elam 1993; Young *et al.* 1996). The effects of habitat fragmentation are compounded by demographic stochasticity and the inherently poor dispersal of many species. The probability of population establishment therefore declines rapidly with increasing distance between habitat patches (Clark *et al.* 2001; Honnay *et al.* 2002; Skov & Svenning 2004).

Population isolation is also a feature of many communities that occur in natural habitat islands – such as high alpine ecosystems, where migration between populations is absent or extremely restricted (Krajick 2004). Habitat fragmentation and consequent population isolation poses particular problems for species subject to rapid climatic changes, as isolated populations throughout a species range may be left outside of their optimum climate space. Experimental evidence from work on the climate response of the tree species *Pinus contorta* and *P. sylvestris* suggests that this decoupling of climate and local adaptation may significantly decrease both growth and survival of individuals (Rehfeldt *et al.* 1999, 2002).

THE CONTRIBUTION OF PHENOTYPIC PLASTICITY

Although so far we have concentrated largely on the genetic response of populations to climatic variability, phenotypic plasticity is an essential component of plants' response to an ever-changing environment. We use the term 'phenotypic plasticity' to describe the differences in an organism's physiology, morphology and development that arise in response to changes in its environment, thereby encompassing reversible (acclimatory) and non-reversible phenotypic changes (Bradshaw 1965; Callahan *et al.* 1997). Plants may respond to changes in their environment over several generations via genetic changes, however when environmental variation occurs on a timescale shorter than the life of the plant any response must be in terms of a plastic phenotype (Bradshaw 1965). If the possession of a plastic phenotype buffers individuals against short-term environmental fluctuation, then it might be expected that phenotypic plasticity could buffer individuals against the long-term effects of climate change. This would reduce the genetic and distributional changes that we might expect based on the species typical climate response (Loehle & LeBlanc 1996; de Jong 2005).

In future climate scenarios it is not only an increase in global mean temperatures that is predicted, but also an increase in the frequency of extreme climatic events. Under such conditions, plant species will be called upon to tolerate an increase in frequency of extreme weather events around a

directionally changing norm (in this example, rising mean temperatures). This would require individuals to possess near 'perfect' plasticity – tolerating all changes in climate with no apparent fitness costs (DeWitt *et al.* 1998). Ongoing distributional changes and reports of climate-related forest dieback demonstrate that such widespread plastic tolerance of the changing climate is not typical (Peñuelas *et al.* 2001; Gutschick & BassiriRad 2003; Peñuelas & Boada 2003; Walther 2003).

Both the occurrence and magnitude of phenotypic plasticity for any trait are themselves characteristics that are under genetic control, with levels varying between traits, individuals and populations (Pigliucci 1996; DeWitt *et al.* 1998; Schlichting & Smith 2002; de Jong 2005). Although a plastic phenotype will allow plants to respond to climate fluctuations over the lifetime of the individual, the capacity for a plastic response to an event weakens for events of greater extremes experienced at longer time scales (Janzen 1967; Gutschick & BassiriRad 2003). Thus for both individuals and species, the capacity to respond to environmental change by phenotypic plasticity has its limits (Bradshaw 1965; Bradshaw & McNeilly 1991; DeWitt *et al.* 1998; de Jong 2005).

An increase in the frequency of extreme climatic events may be even more important in determining the species response than changing mean conditions (Loehle & LeBlanc 1996; Gutschick & BassiriRad 2003). Consequently, there will be selection pressure on many plants for an increased plastic response to future climate (Janzen 1967; Gutschick & BassiriRad 2003). Phenotypic plasticity can respond to selection (Bradshaw 1965; Pigliucci 1996; Schlichting & Smith 2002; de Jong 2005), but in the context of climatic warming it cannot be relied upon to reduce the distributional and genetic response of species to increased temperatures. In this scenario, phenotypic plasticity should be viewed as another character that is likely to be under strong directional selection in many species.

RAPID CLIMATE CHANGE AND ADAPTATION

Both phenotypic plasticity and the existence of high levels of climate-related variation within plant populations may present a number of complications for forecasting species and population responses to climate change. Kelly *et al.* (2003) calculated that the difference in mean temperature of the year of establishment for their 'cool year' and 'warm year' genotypes is close to 1 °C – equal to the temperature increase predicted for 35–55 years, hence according to the 'business as usual' scenario (Watson & Team 2001). They argue that if this is a general response in forest trees it could call into question the magnitude of species migrations that should be expected in response to rising temperatures. This conclusion is consistent with the view that the role of

adaptation has been largely overlooked in response to future climate change (Davis & Shaw 2001). However, whereas Davis & Shaw (2001) propose that populations may adapt to rising temperatures through the arrival of 'pre-adapted' individuals from warmer areas of the species range; Kelly *et al.* (2003) propose that these individuals are already present within the population and would therefore need only to increase in frequency.

Given the divergent life-history traits of birch, pines and the wild cereals mentioned above (Table 1), it is likely that climatic differentiation within populations is a more general pattern. These studies indicate that populations may contain considerable climate-related variation and should therefore have a broader climatic optimum than has previously been recognized (Davis & Shaw 2001). Loehle & LeBlanc (1996) discuss this point at length. As Loehle & LeBlanc (1996) and Kelly *et al.* (2003) suggest, in the short-term this could reduce the impact of climate change on the population. The invasibility of such climatically diverse natural populations may not immediately increase as the climate warms, as 'pre-adapted' individuals within the population could reduce the temperature-based advantage of invading species. However, this is unlikely to reduce the likelihood or magnitude of range changes as, given the opportunistic nature of plant establishment, 'cool year' genotypes at the leading edge of a species geographical range will still be in a position to effect a range expansion as the climate warms.

For relatively contiguous populations, adaptation to a warming climate will be aided by gene flow from populations in already warmer areas of the species range; for isolated populations, gene flow from neighbouring populations will be limited. The response of isolated populations to changing climate will depend on the level of climate-related variability already contained within the population. If the population contains considerable variability for the traits that determine the species response to climate (whether genetic or plastic), the population is likely to show a greater tolerance of changes in climate (in terms of plant fitness; Lynch & Lande 1993; Rehfeldt *et al.* 1999) than if it were genetically less variable. The response of such populations to changing climate would be an increase in the proportion of individuals that are 'pre-adapted' to the new conditions. As an example, if a population subject to rapid warming contains Kelly *et al.*'s 'warm year' and 'cool year' genotypes, the 'warm year' genotypes should be strongly favoured by natural selection.

As the 'warm year' genotypes spread throughout the population in a climatically variable population, no depression in growth or survival of individuals may be evident. However, without gene flow from neighbouring populations, there will be little supply of new variation (Ellstrand & Elam 1993; Young *et al.* 1996; Davis & Shaw 2001). Therefore rapid warming could lead to a reduction in the climate-related variability of populations as 'cool year'

genotypes are lost from the population. By acting as a potent agent of natural selection, rapid climatic warming has the potential to dramatically reduce levels of climate-related genetic variation in natural populations. Once such relevant variation has been exhausted this will effectively render these populations unable to adapt to any further changes [see Bradshaw (1991) for discussion of rate of supply of relevant new variation by mutation]. Beyond the point at which populations may adapt to climate, their fitness is likely to decline, as Rehfeldt *et al.* (1999, 2002) demonstrate. The action of rapid warming in causing such a 'selective sweep' in natural populations has the potential to decrease the variability of loci physically linked to those controlling the climate response (Maynard Smith & Haigh 1974; Kaplan *et al.* 1989), an effect that is likely to be most severe in inbreeding and apomictic species (Ennos 2001; Schlotterer 2003). Both theoretical and experimental studies of plant adaptation to rapid warming show that the strong selection pressure that this imposes may also result in high levels of inbreeding and steep declines in plant fitness (Billington & Pelham 1991; Lynch & Lande 1993; Potvin & Tousignant 1996; Etterson & Shaw 2001; Etterson 2004a,b). Investigation of the effect of rapid warming on a population of *Drosophila subobscura* derived from the wild has shown the loss of approximately 18% of chromosomal diversity over a period of 16 years (Rodríguez-Trelles & Rodríguez 1998). It is possible therefore that rapid warming will decrease genetic diversity within populations beyond those loci directly involved in determining the species response to climate.

DIVERSITY, STABILITY AND PERSISTENCE

The potential for rapid warming to induce a selective sweep in natural populations is likely to be greatest in, although not restricted to, isolated populations, where new variation is unlikely to be supplied by gene flow from neighbouring populations (Lande 1988). However, if throughout the species range, climatic warming causes the displacement of a population's climatic optimum to occur at a rate that exceeds the maximum rate of gene flow between populations (Lynch & Lande 1993; Davis & Shaw 2001) the effect will be felt range-wide. This would involve not only a potential range-wide reduction in population fitness, growth and survival (Lynch & Lande 1993; Potvin & Tousignant 1996; Rehfeldt *et al.* 1999, 2002; Etterson & Shaw 2001; Etterson 2004a,b), but also a reduction in genetic variation both determining and linked to the species climate response. The action of rapid climate change in decoupling locally adapted populations from their typical climate may significantly increase population extinction risk throughout the species range. Using a species-based 'climate envelope' approach for predicting extinction risk (e.g. Thomas *et al.* 2004) may therefore lead to underestimation, as populations

throughout the species range will be left outside their typical climate, not just those populations at the range margins.

Maintenance of genetic diversity within populations is a key conservation aim, as it will enhance their ability to adapt to future environmental changes (Frankel *et al.* 1995; Freeman & Herron 1998). Different genotypes may show different responses to competitive interactions with other genotypes (Taylor & Aarssen 1990; Reusch *et al.* 2005) and variation in their susceptibility to attack by pests and diseases (Burdon & Thrall 2001; Chen *et al.* 2001). Reduction of genetic diversity within populations may significantly reduce the ability of the population to resist and recover from perturbations such as pest and disease outbreaks (Burdon & Thrall 2001; Altizer *et al.* 2003) or extreme weather events (McLaughlin *et al.* 2002; Reusch *et al.* 2005) and may increase their risk of extinction *per se* (Newman & Pilon 1997). Reusch *et al.* (2005) found that genetically diverse experimental populations of the seagrass *Zostera marina* showed faster recovery after a natural extreme warming event when compared with populations that were genetically depauperate. This effect was because of complementarity of different genotypes in the more genetically diverse populations. The studies reported by Burdon & Thrall (2001) show that populations with reduced genetic diversity may be more susceptible to pest and disease outbreaks because of lower occurrence of resistant individuals within the population. Although the consequences of reduced genetic diversity will vary between species and populations, decreased climate-related diversity is likely to reduce a population's ability to withstand and recover from future climatic perturbations.

Species-specific reductions in fitness and diversity will change community dynamics by altering species competitive abilities. This will contribute to the expected changes in both the occurrence and relative abundance of individual species in plant communities (Huntley 1991; Peñuelas *et al.* 2002; Booth & Grime 2003). As Booth & Grime (2003) discovered by manipulating the genetic diversity of experimental grassland communities, reduced genetic diversity may lead to changes in species abundance and reduced community diversity. Working on the same experimental communities, Whitlock (2004) found striking differences between genotypes of several species in terms of their size and abundance within communities. Whitlock suggests that it is these differences between genotypes that are likely to have determined community structure in the earlier study of Booth & Grime (2003). A supplemental finding is that mortality of individual *Campanula rotundifolia* genotypes increased in low diversity communities, suggesting a direct effect of reduced genetic diversity on the stability of community composition. As Whitlock (2004) demonstrates however, the effect of reducing genetic diversity within communities differs between species, therefore although

community stability may decrease, the effect on individual species is not readily predictable.

In species with widespread distributions and well-connected populations, a reduction of genetic diversity within populations is likely to contribute to population extinctions, but is less likely to threaten the existence of the species. The consequences for rare species and those occurring in isolated habitats (e.g. high alpine species) are likely to be more severe, because their populations are likely to be less numerous and may be less well connected or occur over narrow geographical regions. For many such species, even where efforts are made to manage population sizes, a reduction in fitness may result from the effects of changing climate alone (Lynch & Lande 1993). The combination of reduced fitness interacting with a potential reduction in diversity may be catastrophic (Shaffer & Samson 1985; Gilpin & Soulé 1986) and lead to local or widespread population extinctions.

CONCLUSIONS

When considering the potential responses of species to past climatic changes, the role of adaptation may well have been underestimated. The most visible response of species is one of migration, yet climate is a key factor in determining species distributions and many studies provide evidence of local adaptation to current climatic conditions. As the rate of future climate change is predicted to outstrip the potential of many species to migrate and thereby track the climate to which they are adapted, the pressure upon them to adapt to their new conditions will be intense. Although levels of climate-related genetic variation in natural populations may be high, they are not inexhaustible in the face of intense directional selection that will result from rapid climate change. Habitat fragmentation will amplify the effect of intense selection by reducing the supply of new genetic variation by gene flow from neighbouring populations. It is likely therefore that in many cases plant adaptation will fail to match the pace or magnitude of predicted changes in climate. The decoupling of climate and local adaptation is liable to have negative consequences for plant fitness and survival throughout a species range. Consequences will include unpredictable changes in the presence and abundance of species within communities and a potential reduction in their ability to respond to environmental perturbations such as pest and disease outbreaks and extreme weather events. A range-wide increase in population extinction risk is likely to result.

Despite an abundance of evidence demonstrating adaptation of many populations to their current conditions, we know very little about how local adaptation of populations will interact with future changes in climate, or how this is likely to contribute to the extinction risk of individual species. Given the rapid rate at which climate change is

predicted to occur, we should consider climate as a key selective force in driving genetic change within populations. Directing research effort at understanding the potential effects of climate change on genetic diversity within populations will allow us to predict, with better accuracy, the changes that are likely to take place and possibly to prepare for some of their more extreme effects.

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REFERENCES

- Aldrich, P.R., Hamrick, J.L., Chavarriaga, P. & Kochert, G. (1998). Microsatellite analysis of demographic genetic structure in fragmented populations of the tropical tree *Symphonia globulifera*. *Mol. Ecol.*, **7**, 933–944.
- Altizer, S., Harvell, D. & Friedle, E. (2003). Rapid evolutionary dynamics and disease threats to biodiversity. *Trends Ecol. Evol.*, **18**, 589–596.
- Antonovics, J. (1968). Evolution in closely adjacent plant populations VI. Manifold effects of gene flow. *Heredity*, **23**, 507–524.
- Beckman, J.S. & Mitton, J.B. (1984). Peroxidase allozyme differentiation among successional stands of ponderosa pine. *Am. Midl. Nat.*, **112**, 43–49.
- Billington, H.L. & Pelham, J. (1991). Genetic variation in the date of budburst in Scottish birch populations: Implications for climate change. *Funct. Ecol.*, **5**, 403–409.
- Booth, R.E. & Grime, J.P. (2003). Effects of genetic impoverishment on plant community diversity. *J. Ecol.*, **91**, 721–730.
- Bradshaw, A.D. (1965). Evolutionary significance of phenotypic plasticity in plants. *Adv. Genet.*, **13**, 115–155.
- Bradshaw, A.D. (1991). Genostasis and the limits to evolution. *Philos. Trans. R. Soc. Lond.*, **333**, 289–305.
- Bradshaw, A. & McNeilly, T. (1991). Evolutionary response to global climate change. *Ann. Bot. (Lond.)*, **67**, 5–14.
- Burdon, J.J. & Thrall, P.H. (2001). The demography and genetics of host-pathogen interactions. In: *Integrating Ecology and Evolution in a Spatial Context* (eds Silvertown, J. & Antonovics, J.). Blackwell Science Ltd, London, pp. 197–217.
- Callahan, H.S., Pigliucci, P. & Schlichting, C.D. (1997). Developmental phenotypic plasticity: where ecology and evolution meet molecular biology. *Bioessays*, **19**, 519–525.
- Chen, Z., Kolb, T.E., Clancy, K.M., Hipkins, V.D. & DeWald, L.E. (2001). Allozyme variation in interior douglas-fir: association with growth and resistance to western spruce budworm herbivory. *Can. J. For. Res.*, **31**, 1691–1700.

- Clark, J.S., Lewis, M. & Horvath, L. (2001). Invasion by extremes: population spread with variation in dispersal and reproduction. *Am. Nat.*, 157, 537–554.
- Clausen, J.D., Keck, D. & Hiesey, W.M. (1940). *Experimental Studies on the Nature of Species. I. Effect of Varied Environments on Western North American Plants*. Carnegie Institute of Washington, Washington, DC.
- Cobb, N., Mitton, J.B. & Whitham, T.G. (1994). Genetic variation associated with chronic water and nutrient stress in piñon pine. *Am. J. Bot.*, 81, 936–940.
- Conolly, A.P. & Dahl, E. (1970). Maximum summer temperature in relation to the modern and quaternary distributions of certain arctic-montane species in the British Isles. In: *Studies in the Vegetational History of the British Isles* (eds Walker, D. & West, R.G.). Cambridge University Press, Cambridge, pp. 159–223.
- Crawford, R.M.M. & Jeffrey, C.E. (2005). Northern climates and woody plant distribution. In: *Environmental Challenges in Arctic-alpine Regions* (eds Ørbæk, J.B., Kallenborn, R. & Tombre, I.M.). Springer Verlag, Berlin, in press.
- Davis, M.B. & Shaw, R.G. (2001). Range shifts and adaptive responses to quaternary climate change. *Science*, 292, 673–679.
- DeWitt, T.J., Sih, A. & Wilson, D.S. (1998). Costs and limits of phenotypic plasticity. *Trends Ecol. Evol.*, 13, 77–81.
- Ellstrand, N.C. & Elam, D.R. (1993). Population genetic consequences of small population size: implications for plant conservation. *Annu. Rev. Ecol. Syst.*, 24, 217–242.
- Ennos, R.A. (2001). Inferences about spatial patterns in plant populations from the analysis of molecular markers. In: *Integrating Ecology and Evolution in a Spatial Context* (eds Silvertown, J. & Antonovics, J.). Blackwell Science Ltd, London, pp. 45–71.
- Etterson, J.R. (2004a). Evolutionary potential of *Chamaecrista fasciculata* in relation to climate change. I. Clinal patterns of selection along an environmental gradient in the Great Plains. *Evolution*, 58, 1446–1458.
- Etterson, J.R. (2004b). Evolutionary potential of *Chamaecrista fasciculata* in relation to climate change. II. Genetic architecture of three populations reciprocally planted along an environmental gradient in the Great Plains. *Evolution*, 58, 1459–1471.
- Etterson, J.R. & Shaw, R.G. (2001). Constraint to adaptive evolution in response to global warming. *Science*, 294, 151–154.
- Frankel, O.H., Brown, A.H.D. & Burdon, J.J. (1995). *The Conservation of Plant Biodiversity*. Cambridge University Press, Cambridge.
- Freeman, S. & Herron, J.C. (1998). *Evolutionary Analysis*. Prentice Hall, Upper Saddle River, NJ.
- Gilpin, M.E. & Soulé, M.E. (1986). Minimum viable populations: the processes of species extinctions. In: *Conservation Biology: The Science of Scarcity and Diversity* (ed. Soulé, M.E.). Sinauer Associates, Sunderland, MA, pp. 19–34.
- Grabherr, G., Gottfried, M. & Pauli, H. (1994). Climate effects on mountain plants. *Nature*, 369, 448.
- Gutschick, V.P. & BassiriRad, H. (2003). Extreme events as shaping physiology, ecology, and evolution of plants: toward a unified definition and evaluation of their consequences. *New Phytol.*, 160, 21–42.
- Halpin, P.N. (1997). Global climate change and natural-area protection: management responses and research directions. *Ecol. Appl.*, 7, 828–843.
- Hamrick, J.L. & Allard, R.W. (1972). Microgeographical variation in allozyme frequencies in *Avena barbata*. *Proc. Natl Acad. Sci. USA*, 69, 2100–2104.
- Hamrick, J.L. & Holden, L.R. (1979). Influence of microhabitat heterogeneity on gene frequency distribution and gametic phase disequilibrium in *Avena barbata*. *Evolution*, 33, 521–533.
- Hoffmann, A.A., Hallas, R.J., Dean, J.A. & Schiffer, M. (2003). Low potential for climatic stress adaptation in a rainforest *Drosophila* species. *Science*, 301, 100–102.
- Honnay, O., Verheyen, K., Butaye, J., Jacquemyn, H., Bossuyt, B. & Hermy, M. (2002). Possible effects of habitat fragmentation and climate change on the range of forest plant species. *Ecol. Lett.*, 5, 525–530.
- Huang, Q.Y., Beharav, A., Youchun, U.C., Kirzhner, V. & Nevo, E. (2002). Mosaic microecological differential stress causes adaptive microsatellite divergence in wild barley, *Hordeum spontaneum*, at Neve Yaar, Israel. *Genome*, 45, 1216–1229.
- Huntley, B. (1990). Dissimilarity mapping between fossil and contemporary pollen spectra in Europe for the past 13,000 years. *Quatern. Res.*, 33, 360–376.
- Huntley, B. (1991). How plants respond to climate change – migration rates, individualism and the consequences for plant communities. *Ann. Bot. (Lond.)*, 67, 15–22.
- IPCC (2001). *Climate Change 2001: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.
- Jain, S.K. & Bradshaw, A.D. (1966). Evolutionary divergence among adjacent plant populations. I. The evidence and its theoretical analysis. *Heredity*, 21, 407–441.
- Janzen, D.H. (1967). Why mountain passes are higher in the tropics. *Am. Nat.*, 101, 233–249.
- Jones, P.D., Osborn, T.J. & Briffa, K.R. (2001). The evolution of climate over the last millennium. *Science*, 292, 662–667.
- de Jong, G. (2005). Evolution of phenotypic plasticity: patterns of plasticity and the emergence of ecotypes. *New Phytol.*, 166, 101–118.
- Joshi, J., Schmid, B., Caldeira, M.C., Dimitrakopoulos, P.G., Good, J., Harris, R. *et al.* (2001). Local adaptation enhances performance of common plant species. *Ecol. Lett.*, 4, 536–544.
- Kaplan, N.L., Hudson, R.R. & Langley, C.H. (1989). The “hitchhiking effect” revisited. *Genetics*, 123, 887–899.
- Kelly, C.K., Chase, M.W., de Bruijn, A., Fay, M.F. & Woodward, F.I. (2003). Temperature-based population segregation in birch. *Ecol. Lett.*, 6, 1–3.
- Knutsen, H., Rukke, B.A., Jorde, P.E. & Ims, R.A. (2000). Genetic differentiation among populations of the beetle *Bolitophagus reticulatus* (Coleoptera: Tenebrionidae) in a fragmented and a continuous landscape. *Heredity*, 84, 667–676.
- Krajick, K. (2004). All downhill from here? *Science*, 303, 1600–1602.
- Kullman, L. (2002). Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *J. Ecol.*, 90, 68–77.
- Lande, R. (1988). Genetics and demography in biological conservation. *Science*, 241, 1455–1459.
- Li, Y.C., Fahima, T., Beiles, A., Korol, A.B. & Nevo, E. (1999). Microclimatic stress and adaptive DNA differentiation in wild emmer wheat, *Triticum dicoccoides*. *Theor. Appl. Genet.*, 98, 873–883.
- Li, Y.C., Fahima, T., Krugman, T., Beiles, A., Röder, M.S., Korol, A.B. *et al.* (2000). Parallel microgeographic patterns of genetic diversity and divergence revealed by allozyme, RAPD, and microsatellites in *Triticum dicoccoides* at Ammiad, Israel. *Conserv. Genet.*, 1, 191–207.

- Li, Y.C., Krugman, T., Fahima, T., Beiles, A., Korol, A.B. & Nevo, E. (2001). Spatiotemporal allozyme divergence caused by aridity stress in a natural population of wild wheat, *Triticum dicoccoides*, at the Ammiad microsite, Israel. *Theor. Appl. Genet.*, 102, 853–864.
- Linhart, Y.B. & Grant, M.C. (1996). Evolutionary significance of local genetic differentiation in plants. *Annu. Rev. Ecol. Syst.*, 27, 237–277.
- Lloyd, A.H. & Fastie, C.L. (2003). Recent changes in treeline forest distribution and structure in interior Alaska. *Ecoscience*, 10, 176–185.
- Loehle, C. & LeBlanc, D. (1996). Model-based assessments of climate change effects on forests: a critical review. *Ecol. Model.*, 90, 1–31.
- Luikart, G., England, P.R., Tallmon, D., Jordan, S. & Taberlet, P. (2003). The power and promise of population genomics: from genotyping to genome typing. *Nat. Rev. Genet.*, 4, 981–994.
- Lynch, M. & Lande, R. (1993). Evolution and extinction in response to environmental change. In: *Biotic Interactions and Global Change* (eds Kareiva, P.M. & Kingsolver, J.). Sinauer Associates Inc., Sunderland, MA, USA, pp. 234–250.
- Maynard Smith, J. & Haigh, J. (1974). The hitch-hiking effect of a favorable gene. *Genet. Res.*, 23, 23–35.
- McLaughlin, J.F., Hellmann, J.J., Boggs, C.L. & Ehrlich, P.R. (2002). Climate change hastens population extinctions. *Proc. Natl Acad. Sci. USA*, 99, 6070–6074.
- Mitton, J.B. & Duran, K.L. (2004). Genetic variation in piñon pine, *Pinus edulis*, associated with summer precipitation. *Mol. Ecol.*, 13, 1259–1264.
- Mitton, J.B., Stutz, H.P., Schuster, W.S.F. & Shea, K.L. (1989). Genotypic differentiation at PGM in Engelmann spruce from wet and dry sites. *Silvae Genet.*, 38, 217–221.
- Newman, D. & Pilson, D. (1997). Increased probability of extinction due to decreased genetic effective population size: experimental populations of *Clarkia pulchella*. *Evolution*, 51, 354–362.
- Owuor, E.D., Fahima, T., Beiles, A., Korol, A. & Nevo, E. (1997). Population genetic response to microsite ecological stress in wild barley, *Hordeum spontaneum*. *Mol. Ecol.*, 6, 1177–1187.
- Pacala, S.W. & Hurtt, G.C. (1993). Terrestrial vegetation and climate change: integrating models and experiments. In: *Biotic Interactions and Global Change* (eds Kareiva, P.M. & Kingsolver, J.). Sinauer Associates Inc., Sunderland, MA, USA, pp. 57–74.
- Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421, 37–42.
- Peñuelas, J. & Boada, M. (2003). A global change-induced biome shift in the Montseny Mountains (NE Spain). *Global Change Biol.*, 9, 131–140.
- Peñuelas, J., Lloret, F. & Montoya, R. (2001). Severe drought effects on Mediterranean woody flora in Spain. *For. Sci.*, 47, 214–218.
- Peñuelas, J., Filella, I. & Comas, P. (2002). Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Global Change Biol.*, 8, 531–544.
- Pigliucci, M. (1996). How organisms respond to environmental changes: from phenotypes to molecules (and vice versa). *Trends Ecol. Evol.*, 11, 168–173.
- Pigott, C.D. & Pigott, S. (1993). Water as a determinant of the distribution of trees at the boundary of the Mediterranean zone. *J. Ecol.*, 81, 557–566.
- Potvin, C. & Tousignant, D. (1996). Evolutionary consequences of simulated global change: genetic adaptation or adaptive phenotypic plasticity. *Oecologia*, 108, 683–693.
- Rehfeldt, G.E., Ying, C.C. & Hamilton, D.A. (1999). Genetic responses to climate in *Pinus contorta*: Niche breadth, climate change, and reforestation. *Ecol. Monogr.*, 69, 375–407.
- Rehfeldt, G.E., Tchebakova, N.M., Parfenova, Y.I., Wykoff, W.R., Kuzmina, N.A. & Milyutin, L.I. (2002). Intraspecific responses to climate in *Pinus sylvestris*. *Global Change Biol.*, 8, 912–929.
- Reusch, T.B.H., Ehlers, A., Hämmerli, A. & Worm, B. (2005). Ecosystem recovery after climatic extremes enhanced by genetic diversity. *Proc. Natl Acad. Sci. USA*, 102, 2826–2831.
- Rodríguez-Trelles, F. & Rodríguez, M.A. (1998). Rapid microevolution and loss of chromosomal diversity in *Drosophila* in response to climate warming. *Evol. Ecol.*, 12, 829–838.
- Sanz-Elorza, M., Dana, E.D., Gonzalez, A. & Sobrino, E. (2003). Changes in the high-mountain vegetation of the central Iberian Peninsula as a probable sign of global warming. *Ann. Bot. (Lond.)*, 92, 273–280.
- Savolainen, O., Bokma, F., Garcia-Gil, R., Komulainen, P. & Repo, T. (2004). Genetic variation in cessation of growth and frost hardiness and consequences for adaptation of *Pinus sylvestris* to climatic changes. *For. Ecol. Manag.*, 197, 79–89.
- Schlichting, C.D. & Smith, H. (2002). Phenotypic plasticity: linking molecular mechanisms with evolutionary outcomes. *Evol. Ecol.*, 16, 189–211.
- Schlotterer, C. (2003). Hitchhiking mapping – functional genomics from the population genetics perspective. *Trends Genet.*, 19, 32–38.
- Shaffer, M.L. & Samson, F.B. (1985). Population size and extinction: a note on determining critical population sizes. *Am. Nat.*, 125, 144–152.
- Skov, F. & Svenning, J.-C. (2004). Potential impact of climate change on the distribution of forest herbs in Europe. *Ecography*, 27, 366–380.
- Sturm, M., Racine, C. & Tape, K. (2001). Climate change: increasing shrub abundance in the arctic. *Nature*, 411, 546–547.
- Stutz, H.P. & Mitton, J.B. (1988). Genetic variation in Engelmann spruce associated with soil moisture. *Arctic Alpine Res.*, 20, 461–465.
- Taylor, D.R. & Aarssen, L.W. (1990). Complex competitive relationships among genotypes of 3 perennial grasses – implications for species coexistence. *Am. Nat.*, 136, 305–327.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C. *et al.* (2004). Extinction risk from climate change. *Nature*, 427, 145–148.
- Turesson, G. (1925). The plant species in relation to habitat and climate. *Hereditas*, 6, 147–236.
- Walther, G.R. (2003). Plants in a warmer world. *Perspect. Plant. Ecol.*, 6, 169–185.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C. *et al.* (2002). Ecological responses to recent climate change. *Nature*, 416, 389–395.
- Watson, R.T. & Team, C.W. (2001). *Climate Change 2001: Synthesis Report. A Contribution of Working Groups I, II, and III to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.
- Whitlock, R. (2004). The consequences of genetic impoverishment for plant community structure and function. PhD thesis. The University of Sheffield, Sheffield, UK.

- Williams, B.L., Brawn, J.D. & Paige, K.N. (2003). Landscape scale genetic effects of habitat fragmentation on a high gene flow species: *Speyeria idalia* (Nymphalidae). *Mol. Ecol.*, 12, 11–20.
- Woodward, F.I. (1987). *Climate and Plant Distribution*. Cambridge University Press, Cambridge.
- Young, A., Boyle, T. & Brown, T. (1996). The population genetic consequences of habitat fragmentation for plants. *Trends Ecol. Evol.*, 11, 413–418.

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