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Rapid climate change and the rate of adaptation: insight from experimental quantitative genetics

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Summary

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Evolution proceeds unceasingly in all biological populations. It is clear that climate-driven evolution has molded plants in deep time and within extant populations. However, it is less certain whether adaptive evolution can proceed sufficiently rapidly to maintain the fitness and demographic stability of populations subjected to exceptionally rapid contemporary climate change. Here, we consider this question, drawing on current evidence on the rate of plant range shifts and the potential for an adaptive evolutionary response. We emphasize advances in understanding based on theoretical studies that model interacting evolutionary processes, and we provide an overview of quantitative genetic approaches that can parameterize these models to provide more meaningful predictions of the dynamic interplay between genetics, demography and evolution. We outline further research that can clarify both the adaptive potential of plant populations as climate continues to change and the role played by ongoing adaptation in their persistence.

I. Introduction

Over >4 billion years, biological evolution has proceeded through periods of considerable change in climate, atmospheric composition and many other aspects of environment. Plants have evolved in response to these changes, as reflected in

macroevolutionary patterns of divergence that are congruent with climate change (e.g. Edwards *et al.*, 2010; Franks *et al.*, 2012) and in predictable relationships between biogeography and plant functional traits (Reu *et al.*, 2011). Such evidence illuminates climate-influenced evolution in deep time, with changes in climate greater and more rapid during some periods than in

others (Jansen *et al.*, 2007). Plant response to climate has involved change in both geographic distributions and the genetic composition of taxa. Geographic shifts have been documented in paleobotanical studies that show the reinvasion of plant species into available habitats with climate warming since the last glacial maximum (Davis, 1981). Population differentiation with respect to climate tolerance provides evidence of adaptive evolution in response to spatial gradients in climate across contemporary ranges (Rehfeldt *et al.*, 1999).

Projected changes in global mean temperature over the next century (Meehl *et al.*, 2007) are similar in magnitude to the change over 5000 yr following the last glacial maximum, but are expected to occur 50 times faster (Jansen *et al.*, 2007, p. 465). As emphasized in earlier reviews (e.g. Geber & Dawson, 1993; Hoffman & Sgro, 2011), responses of the biota to climate changing dramatically and erratically will, without doubt, include the interrelated processes of evolutionary change and shifts in geographic range, as well as extinction, as in the remote past. However, the relative role of each process is far from clear.

Although there is abundant evidence of the past evolution of plants in response to climate, a critical outstanding question of our time is the extent to which adaptive evolution will ameliorate the detrimental effects of rapid contemporary climate change on the biota. This question has broad societal implications, but is vexingly difficult to address, because it lies at the interface of complex and dynamic phenomena, namely climate change, demography and evolution. In this review, we aim to highlight current progress towards addressing this knotty issue by drawing on theoretical and empirical research in the field of plant quantitative genetics. Most importantly, we link advances in theoretical modeling of interacting evolutionary processes to recommendations for future empirical work. A central thrust of these recommendations is a focus on the estimation of the mean fitness of populations across spatial and temporal gradients, as well as the genetic variance of fitness within populations. We also emphasize the importance of conducting research in natural or semi-natural conditions that allow interacting evolutionary processes to proceed, and thus provide a realistic context for inferences that are relevant to natural populations. Finally, we highlight a new seed banking initiative, Project Baseline, which will provide an unparalleled genetic resource to dissect the architecture of future evolutionary change in natural populations.

Variation in fitness and the traits associated with it is typically attributable to many genes, as well as environmental conditions (reviewed in Hill, 2010; Rockman, 2012). Accordingly, we focus on studies that employ the approaches of quantitative genetics (Falconer & Mackay, 1996; Lynch & Walsh, 1998), because they can address directly the key questions concerning the nature of ongoing selection, the availability of genetic variation on which response to selection depends and the rates of response to selection. This approach accounts for the expression of all genes collectively, in contrast with studies that identify genes of major effect and tend to overlook genes of individually small, but evolutionarily consequential, effect (Hoffman & Willi, 2008; Box 1; Rockman, 2012). Although advances in the understanding of the

molecular underpinnings of climate response have been achieved, this is beyond the scope of this paper and is reviewed elsewhere (Mitchell-Olds & Schmitt, 2006; Bergelson & Roux, 2010).

We begin this review by underscoring the potential importance of plant evolutionary responses to contemporary climate change by, first, evaluating whether range expansion by itself is likely to dominate plant responses and, second, by examining evidence that adaptive evolution can proceed at rates that are relevant to contemporary climate change. Next, we present a case for evaluating fitness across geographic gradients and through time. There are few examples of these key kinds of empirical evidence, even though they would valuably inform theoretical models that examine feedbacks among evolutionary processes and their influence on adaptive evolutionary change. Finally, we provide an overview of studies of evolutionary processes in relation to climate change, emphasizing the limits of inference of each approach and recommendations for modifying the designs of future studies. We conclude by outlining a research agenda that we believe will expand the capacity to integrate theoretical models and empirical evidence through measurements of population fitness, the crucial link between demography and evolution.

II. Will migration be enough?

Because the paleorecord documents shifts of geographic range following the retreat of the glaciers (Davis, 1981; Huntley, 1991), considerable attention has focused on poleward or elevational range shifts as a potentially important biotic response to ongoing change in climate. Ackerly (2003) has suggested that such geographic 'tracking of climate' would largely eliminate the dependence of a population's persistence on its adaptive evolution, and Parmesan (2006) has also emphasized the role of range shifts over evolutionary response. However, rates at which ranges shift, relative to the rate of climate change, are crucial.

Over the 20 millennia following the last glacial retreat, the rate of advance of the northern range limit of the predominant species of forest trees was initially inferred to have exceeded 100 m yr^{-1} for many species. For example, Davis (1981) indicated a rate of *c.* 200 m yr^{-1} for *Acer* species, a rate that implies an important role of rare, long-distance dispersal. Recently, documented evidence for beech and red maple that small populations persisted much closer to the glacial margin suggests more modest rates of northward range expansion: $< 100 \text{ m yr}^{-1}$ (McLachlan *et al.*, 2005). As emphasized by Bradshaw (1972), the sedentary habit of plants, with passive, leptokurtic dispersal of individuals only at the seed stage, restricts the large majority of offspring to growth in close proximity to the maternal parent. This severely limits the rates of range expansion over tens of generations, and this limitation is exacerbated by anthropogenic fragmentation of landscapes, which impedes seed dispersal. Nevertheless, as pointed out by Cain *et al.* (2000), it is extremely difficult to quantify the extent and importance of rare long-distance migrants, and more research on this issue is warranted.

Recent poleward and elevational range shifts of numerous animals have been recorded, but evidence of such shifts has been obtained for considerably fewer plants (Parmesan & Yohe, 2003;

Hickling *et al.*, 2006; Parmesan, 2006), and the prediction of the tendency of a species to shift range based on its traits has not been proven to be tractable (Angert *et al.*, 2011). Beckage *et al.* (2008) reported a shift upslope of the mean abundance of hardwood species into boreal forests in the mountains of Vermont USA, and Kelly & Goulden (2008) reported an increased mean elevation of the dominant species of the Santa Rosa Mountains in southern California. Yet, a change in elevation of mean abundance does not imply population expansion beyond previous upper elevational limits. Indeed, Zhu *et al.* (2012) have found that the present-day spatial distribution of seedlings and saplings relative to adult trees indicates range contraction at both latitudinal extremes for nearly 60% of 92 species of the USDA Forest Inventory and Analysis; only 20% of species show expansion of these juvenile stages in the poleward direction, implying a shift in geographic range in the direction that would putatively be favored. Bertrand *et al.* (2011) have inferred lags in community composition, particularly of lowland areas, in response to changing temperatures from 1985 to 2006. These findings undermine confidence that natural dispersal will allow contemporary plant populations to track climatic conditions to which they are adapted by shifting geographic range. This concern has prompted calls to consider the relative risks and benefits of human assistance of dispersal (Richardson *et al.*, 2009).

Dispersal capacity itself could evolve in ways that enhance or inhibit range expansion, as explored in a large body of theory (e.g. Olivieri *et al.*, 1995; Ronce *et al.*, 2000). On the one hand, selection in temporally varying environments at the periphery of the range may favor greater dispersal capacity (Travis & Dytham, 1999; Cadet *et al.*, 2003; Levin *et al.*, 2003), as suggested by observations made in central and marginal populations for one dune species (Darling *et al.*, 2008). Selection for increased dispersal may be reinforced as founding individuals encounter suitable conditions (Travis & Dytham, 2002; Dytham, 2009; Travis *et al.*, 2010), as suggested by a study of *Pinus contorta* (Cwynar & MacDonald, 1987). We emphasize that these models identify evolutionarily stable dispersal rates; evolutionary response to attain these rates will depend on the availability of genetic variation in traits that affect dispersal capacity. Alternatively, selection may favor reduced dispersal in populations isolated by habitat fragmentation, because establishment outside of the confines of the habitat patch may fail. The evolutionary dynamics of populations in a matrix of unsuitable agricultural and urban environments may be akin to that in island populations where dispersal capacity has been found to decline in 5–10 yr (Cody & Overton, 1996). Empirical studies that examine the evolution of dispersal in the context of climate change have yet to be conducted, and so this evolutionary potential remains uncertain; nor is it clear whether these dynamics would ameliorate, exacerbate or be overwhelmed by other effects of climate change.

III. Can adaptation proceed fast enough?

It is now well documented that adaptation to dramatically altered environments can proceed rapidly, within dozens of generations (throughout, we use 'adaptation' in the evolutionary sense). An

early, thoroughly documented example is the adaptation of the grass species, *Anthoxanthum odoratum* and *Agrostis tenuis*, to soils contaminated with heavy metals by mining over a period of c. 100 yr (McNeilly, 1968; Antonovics & Bradshaw, 1970; Antonovics, 2006). Rates of mortality and recruitment from seed (Antonovics, 1972) indicate that this period corresponds to 50 generations at most, and perhaps as few as 20. As another example of rapid adaptation, evolved resistance to agricultural herbicides has been documented in 200 angiosperm species (Weedscience.org, 1993). This includes resistance to glyphosate, introduced in the mid-1970s.

These and other examples of adaptation to a radically altered environment demonstrate the potential, in principle, for adaptation to abrupt environmental changes. However, as noted by Bradshaw (1991), many more species in pasture adjacent to metal-contaminated mine tailings have not adapted to the change in environment (than the short list of cases that have), and a similar observation would apply to other instances of rapid environmental change. Thus, if a change in environment reduces fitness below replacement, a capacity for adaptive evolution does not guarantee evolutionary rescue. That is, the rate of adaptation may nevertheless be inadequate to ensure persistence in the current range, or at all (Gomulkiewicz *et al.*, 2010).

Some have questioned the role of evolution in response to ongoing climate change on the grounds that the paleorecord does not indicate changes in form in conjunction with past climate change (e.g. Parmesan, 2006). However, changes in morphology of plant macrofossils do coincide with major environmental shifts, but such changes could reflect either evolutionary change or direct effects of environment. For example, stomatal guard cell size has fluctuated in parallel with atmospheric CO₂ concentration over the last 400 Myr (Franks *et al.*, 2012). By contrast, the fossil pollen record does not provide information on questions about evolutionary change within species; it is not even possible to distinguish fossil pollen of congeneric species, which often differ greatly in geographic range. Moreover, as also noted by Travis & Futuyma (1993), many organismal traits that often reflect local adaptation, such as those of physiology and phenology, are not recorded in fossils. Well-documented examples of rapid adaptive evolution (e.g. metal tolerance and herbicide resistance) would not leave evidence in the macrofossil or fossil pollen record. Although examples above indicate the possibility of rapid adaptation to drastic environmental change, the current rate of climate change far surpasses that of earlier eras (Jansen *et al.*, 2007, p. 465), and it is unclear whether adaptation of many plant populations will keep pace with the change in conditions.

Others have emphasized the importance of phenotypic plasticity, the direct dependence of trait expression on environmental conditions. Plasticity is ubiquitous, although it varies widely in magnitude, as well as in direction. Consequently, plasticity may be nonadaptive or even maladaptive (Bradshaw, 1965, 2006; de Jong, 2005; van Kleunen & Fischer, 2005; Maherali *et al.*, 2010) and may obscure evolutionary divergence (Conover & Schultz, 1995). However, to the extent that plasticity is adaptive, enhancing fitness in the specific environments under consideration, it can contribute substantially to overall fitness. Moreover, to the

extent that a population harbors genetic variation in plasticity (i.e. it expresses interaction between genotype and environments to which it is exposed), plasticity itself can evolve (Via & Lande, 1985; Scheiner, 1993; Tufto, 2000). Long-term monitoring alone (e.g. Gordo & Sanz, 2010) cannot disentangle genetic responses from plasticity. Experimental approaches are required to definitively distinguish the roles of genetic and plastic responses in observed changes in traits and fitness.

IV. Fitness links demographic and evolutionary processes

For a population persisting in a particular habitat, its mean absolute fitness must be adequate for it to replace itself over generations. A radical change in conditions can drastically reduce survival and reproduction, including to the point that it begins to decline and tend towards extinction. In conjunction with this ecological effect on mean fitness, novel environments can expose genetic variation in fitness, on which response to natural selection depends. The additive genetic variance in fitness ($V_A(w)$) determines the rate of adaptation (i.e. the increase of a population's mean fitness) over generations (Fisher, 1930; Ewens, 2004). For traits that are genetically associated with fitness, their means are expected to change as adaptation proceeds. To the extent that populations express $V_A(w)$ as climate changes, they display the potential to adapt to it. Nevertheless, the environment may change at a rate that exceeds the rate of adaptation. In this case, a population may adapt to some degree, without regaining fitness to the point that individuals replace themselves; the consequently declining population would then dwindle to extinction.

1. Evolutionary processes that influence $V_A(w)$

Although natural selection alone accounts for adaptation, other evolutionary processes strongly modulate rates of adaptation. Mutation is the ultimate source of genetic variation, on which response to selection depends. Recombination, by generating novel gametic combinations of alleles, is also a key process contributing to genetic variation for traits and fitness. However, random genetic sampling results in a change in allele frequency that is as likely to oppose selection as to contribute to it. Although the direction of allele frequency change is random, the general tendency of this process of genetic drift is to reduce genetic variance at a rate that is inversely related to the size of the population. The smaller the population, the more likely it is that rare alleles will be lost altogether, including those that enhance fitness. Consequently, genetic drift tends to reduce adaptive potential. The increasing fragmentation of once widespread populations is expected to exacerbate the role of drift and its consequences (Lopez *et al.*, 2009).

Quantitative genetic models of the change in selection on a quantitative trait as environment changes, as well as mutation, genetic drift and density dependence, confirm the intuition that populations are more prone to extinction at higher rates of environmental change (Burger & Lynch, 1995; Lande & Shannon, 1996). These models also show that stochasticity

superimposed on a directional change in environment can exacerbate extinction risk. However, for a sink population coupled to a source by gene flow, Holt *et al.* (2004) have found that a moderate degree of stochasticity in the environment can weakly enhance the probability of adaptation and persistence. Thus, numerous ecological and evolutionary processes influence rates of adaptation. It is not straightforward to understand the interplay of these processes, nor to make precise evolutionary predictions.

2. The role of gene flow

It is important to realize that dispersal is not limited to the leading edge of a migration front, but occurs throughout a species' range. An isolated population within the range could, in principle, shift its geographic location without a change in its genetic composition. However, genetic differentiation on relatively fine spatial scales implies that dispersal, whether of pollen or seed, introduces genetically distinctive immigrants into neighboring populations. As a result, dispersal and evolution are intimately connected (Davis *et al.*, 2005).

Gene flow within a species' range can alleviate inbreeding depression and thereby enhance fitness (e.g. Richards, 2000; Sexton *et al.*, 2011), and modeling shows that this is particularly likely when the populations exchanging genes are adapted to similar conditions (Lopez *et al.*, 2009). Moreover, when the environment is changing directionally through time and space, this mixing not only enhances the genetic variation of the recipient population, and thereby its capacity to adapt, but may increase directly the population's adaptation, whether by alleviating inbreeding depression or by introducing alleles that are newly adaptive in the recipient population. For example, in *Chamaecrista fasciculata*, the positive effect of directional gene flow from a southern population into a northern recipient population has been documented based on the superior fitness of F1, F2 and F3 hybrids compared with northern parental plants in a site that mimicked future climate change (Etterson, 2008).

Conversely, gene flow can compromise fitness if the populations that are exchanging genes are adapted to temporally stable environments that are selectively distinct (Antonovics *et al.*, 1988). In this case, alleles that are adaptive in one habitat may be maladaptive in the other. The severity of outbreeding depression, whether from this scenario of interbreeding between populations adapted to abruptly differing habitats or from intrinsic causes, such as chromosomal rearrangements, varies widely (Frankham *et al.*, 2011) and is of uncertain duration (Erickson & Fenster, 2006; Ronce *et al.*, 2009). This facet of migration has long been considered an important evolutionary basis for limits of species' geographic ranges (Bradshaw, 1972; Antonovics, 1976).

Kirkpatrick & Barton (1997), considering an environment that varies spatially, but is temporally fixed, modeled the effects of gene flow on adaptation through the effect of a quantitative trait on fitness and the consequent demographic effects. They found that gene flow limits range expansion under particular parameter combinations, although Barton (2001) then showed that this result depends critically on the assumption that genetic variance remains

constant. When stochastic effects are included in models with similar structure, marginal populations fail to become established for a broader range of parameter values, especially when the carrying capacity is low (Bridle *et al.*, 2010). Lavergne *et al.* (2010) have noted that evidence for the role of gene flow from the center to the margin of a species range, as a constraint on evolutionary expansion of the range, is, to date, limited.

3. Numeric and genetic dynamics in a changing environment

A substantial body of theoretical work has grappled with the challenges of jointly modeling the dynamics of changes in genetic composition and in numerical abundance as environments change through time. These models approach the problem of adaptation to changing environment by considering fitness as dependent on a single quantitative trait subject to stabilizing selection, with the optimum of the trait shifting through time as a consequence of spatial and temporal changes in environment. Pease *et al.* (1989) first modeled adaptation and migration in response to changing conditions and concluded that increased genetic variance in a population improves its chance of persistence as climate changes, and that movement of populations plays a critical role.

Polechova *et al.* (2009) investigated this scenario further, taking density-dependent population regulation into account, and identified the conditions that permit adaptation throughout the range and through time vs those that limit adaptation and result in eventual extinction. Duputié *et al.* (2012) have extended these results by accounting for selection jointly on multiple characters. They showed that rates of adaptation are expected to be greatest when migration is intermediate and when the trait combinations for which stabilizing selection is weakest align with the direction of change in the environment. Considering the question of the circumstances under which a population is likely to adapt too slowly to evade extinction, Gomulkiewicz & Houle (2009) have determined minimal values of the additive genetic variance of a fitness-determining trait consistent with the population persisting and adapting. They have generalized this result to allow for multiple traits that determine fitness via joint stabilizing selection.

These models focusing on fitness mediated by one or more quantitative traits have, for simplicity, tended to ignore phenotypic plasticity. Chevin & Lande (2010) explored the effect of adaptive plasticity and its evolution on population persistence in a changing environment. For an isolated population undergoing density-independent selection and density-dependent population growth, they found that adaptive phenotypic plasticity initially buffers population fitness against abrupt environmental change. Over the longer term, ongoing evolution of plasticity increases population fitness and population persistence as long as the cost of plasticity is much lower than its benefit.

Another simplification of most of the relevant theory is to ignore the biotic context in which any single focal organism will respond evolutionarily to changing climate. Yet competitors, natural enemies and mutualists can strongly influence the numerical

dynamics of any plant of interest, as well as its evolution (Antonovics, 1992; Neuhauser *et al.*, 2003; Lavergne *et al.*, 2010). Recent extensions of models to account for such effects of biotic context on adaptation to environment changing temporally (Johansson, 2008) or spatially (Price & Kirkpatrick, 2009) indicate that competition can substantially impede a focal organism's adaptation.

These modeling efforts underscore the potential for adaptation as climate changes, but do not lead directly to the prediction of how many or which populations can be expected to adapt and evade extinction, because values of the critical parameters are not known (Gomulkiewicz & Shaw, 2012). Moreover, the traits on which adaptation to climate change critically depends are also not known or readily determined with confidence. Observations of changes in traits in conjunction with climate warming (Miller-Rushing & Primack, 2008; Gordo & Sanz, 2010) may reflect evolutionary change, but phenotypic plasticity could account for much of the phenotypic change, or for all of it. Consequently, the assessment of the evolutionary response requires experimental evaluation.

V. Experimental studies: what do they tell us and how can we improve them?

The complexities of both evolution and climate make the prediction of evolution in response to changing climate enormously challenging. As noted previously, evolution results from the four basic processes, natural selection, genetic drift, mutation and gene flow, all operating concurrently. Likewise complex, climate encompasses temperature, moisture and insolation, among other aspects, throughout diurnal, annual and longer cycles. Attention to changing climate tends to focus on increasing temperature, but striking changes in precipitation, atmospheric circulation and other components of climate are also under way (Trenberth *et al.*, 2007). Moreover, rates of warming vary strongly with latitude, and changes in precipitation vary regionally in both direction and degree. Still further, climatic variability is increasing together with the general warming trend (Trenberth *et al.*, 2007, pp. 265, 308). The high dimensionality of climate, together with correlations among its components, makes the prediction of rates of climate change imprecise. Bewildering as these manifold complexities are, the inexorability of changing climate and the threats it poses to the biota have galvanized researchers to evaluate the capacity for adaptation to changing climate.

To advance fundamental understanding of rates of evolutionary change in response to extremely rapidly changing environment, as well as limits to adaptation, further research is sorely needed. New empirical research can parameterize models and test model assumptions, while also informing conservation practice in the face of changing climate (Hufford & Mazer, 2003; Hoffman & Sgro, 2011). The approaches we propose will help fill gaps in our understanding of the role of ongoing evolution in maintaining populations as climate changes, including questions posed in Box 1.

Quantitative genetics and evolutionary ecology offer powerful approaches for addressing these questions. In the following, we

Box 1 Outstanding empirical questions concerning evolution in response to climate change

- To what extent will adaptive plasticity mitigate the effects of changing climate on plant fitness; conversely, to what extent is plasticity maladaptive?
- If maladaptive plasticity is common, will proximate or eventual climate conditions tend to compromise fitness to the extent that a population of interest loses the capacity to maintain itself?
- At what rate does a population have the capacity to adapt as climate changes, and how does this rate compare with the rate of change in climate?
- In view of the prediction that climate variation will become increasingly erratic, how will fluctuations and extremes of climate affect evolutionary rates?
- Given that the generation time must importantly influence the rate of biotic response, via a passive shift in range or adaptation, whether *in situ* or during the course of a range shift, does this effect largely account for differences among species in rates of adaptation to climate?
- Warming climate may directly accelerate development and hence the turnover of perennial populations, and may also select for earlier reproduction; to what extent is decreasing generation time likely to enhance evolutionary rates in relation to absolute time?
- Beyond the change in natural selection caused by the changing abiotic environment, how will associated plants, herbivores and mutualists affect rates of evolution in response to climate?

provide an overview of research to examine facets of evolutionary process in response to climate change, and we recommend improvements and expansions of the approaches. We start by reviewing studies that estimate genetic variation for traits that are considered to be likely to be important in a changed climate, and selection on those traits. Second, we discuss the less frequently employed chronosequence approach, in which spatial variation in climate is used as an approximation for climatic change anticipated in the future. Third, we review the rare instances in which ancestors have been compared directly with descendants by resurrecting viable buried or stored seeds. We describe a new seed banking initiative, Project Baseline, which will greatly expand the opportunities to employ this approach in the future. Finally, we advocate for studies that assess genetic variation in absolute fitness as the most direct basis for the evaluation of both the tendency of a population to grow or decline and its adaptive potential.

VI. Predicting evolutionary change based on genetic variation and natural selection

Efforts to predict the evolutionary responses of plants as climate continues to change have, in some cases, evaluated the genetic variation of traits on which changing climate seems likely to impose selection. Some of these studies have been conducted in conditions, whether in the glasshouse or field, not intended to represent future climate. For example, in a study of genetic variation with respect to physiological traits of *Lobelia*, Caruso *et al.* (2005) studied one population sampled from each of two species, *Lobelia siphilitica* and *L. cardinalis*. They employed a crossing design of full-sibs nested within paternal half-sibs (Falconer & Mackay, 1996, p. 166f) and detected significant genetic variation in photosynthetic rate and efficiency, specific leaf area (SLA) and chlorophyll content, as well as rosette size, for each population. The *L. siphilitica* population also harbored significant narrow-sense heritability (h^2) in stomatal conductance and water-use efficiency (WUE). This latter trait was found to be negatively genetically correlated with rosette size, implying that selection for both larger size and greater WUE would lead to slower response than for either trait alone (see Geber & Griffin, 2003 for a more complete review of inheritance of plant traits).

Burgess *et al.* (2007) carried out divergent artificial selection on flowering time of *Campanulastrum americanum*. By three generations, they had obtained appreciable changes of *c.* 15 d in mean flowering time in both directions, reflecting substantial h^2 (20–30%). Although the flowering phenology of this population shows a clear capacity to respond to selection, these investigators noted that correlated responses of other traits to selection for earlier flowering may be maladaptive. For example, earlier flowering plants produced fewer, smaller flowers than controls or lines selected for later flowering. Differences in flowering phenology were maintained in field conditions and influenced other life-history attributes, such as the timing of seed dispersal and germination (Galloway & Burgess, 2012).

Selection and genetic variation under simulated changes in climatic components

Further efforts have evaluated adaptive potential under conditions manipulated along one or more dimensions of climate. For example, to elucidate how physiological traits may be subject to selection in drought, Sherrard & Maherali (2006) studied recombinant inbred lines (RILs) produced from a cross between plants representing xeric and mesic ecotypes of wild oat (*Avena barbata*). They grew plants in both well-watered and drought conditions, and evaluated relationships between fitness and traits. They detected highly significant selection for earlier flowering, as well as selection towards reduced photosynthetic capacity and increased chlorophyll content. The direction of selection in the well-watered treatment matched that in the drought conditions, but the strength of selection for greater photosynthetic capacity was greater in drought, whereas selection for increased chlorophyll content was weaker. No selection on stomatal conductance was detected.

Sherrard *et al.* (2009) found that the broad-sense heritabilities (H^2) of the physiological traits tended to be greater in drought than in well-watered conditions, and there was a similar tendency for the genetic correlations between physiological traits. In well-watered conditions, these lines exhibited appreciable H^2 for hydraulic conductivity (33%), photosynthetic rate (23%) and flowering time (62%), but negligible H^2 for stomatal conductance (Maherali *et al.*, 2008). Many physiological

traits exhibited plasticity in response to drought. However, adaptive plasticity did not appear to be common and, for three traits (flowering date, stomatal density, maximum velocity of carboxylation of Rubisco), the plasticity was maladaptive (Maherali *et al.*, 2010).

Likewise focusing on physiological traits, Agrawal *et al.* (2008) evaluated the strength and direction of natural selection, as well as genetic variation and plasticity, of a population of *Asclepias incarnata* planted into ambient conditions in nature. They detected phenotypic selection favoring increasing numbers of trichomes and reduced SLA (thicker leaves). Of these, only the latter showed significant genetic variation, with H^2 estimated as 14%. In addition to this, the ratio of carbon to nitrogen in leaves and WUE (measured as $\Delta^{13}\text{C}$) were also significantly heritable (33% and 16%, respectively). In a subsequent growth chamber experiment, the plasticity of these traits in response to drought was relatively slight, although SLA increased somewhat, suggesting a maladaptive plastic response.

Over two dozen studies have evaluated the evolutionary potential of plants in relation to increasing atmospheric concentration of CO_2 , a major contributor to climate warming, and thus a possible agent of natural selection which is expected to correlate closely with a change in climate. Of these, a small proportion have detected significant interactions between genotype and CO_2 level affecting fitness, and thus the potential for an evolutionary increase in fitness in response to elevated CO_2 itself (reviewed in Lau *et al.*, 2007; but see discussion of Ward & Kelly, 2004). In a selection experiment, Ward *et al.* (2000) obtained suggestive evidence of increased seed production of *Arabidopsis thaliana* in response to selection on this trait in elevated CO_2 , and also observed correlated responses towards earlier flowering and reduced biomass. Collins & Bell (2006) detected no evolutionary change in the fitness of populations of the green alga *Chlamydomonas reinhardtii* following 1000 generations of evolution at elevated CO_2 , whereas the photosynthetic efficiency declined.

The evolution of competitive interactions may depend on the atmospheric concentration of CO_2 , but no clear generalizations have emerged from the smaller set of studies that have considered this issue. Of these, several were severely limited in the scope of inferences because very few genotypes were sampled (Bazzaz *et al.*, 1995; Andalo *et al.*, 2000). Steinger *et al.* (2007), studying 31 clonally propagated genotypes of *Bromus erectus* in a Swiss grassland, detected greater H^2 in the number of flowering culms when the grass was growing in multispecies communities at ambient relative to elevated levels of CO_2 . Analogously, J. A. Lau *et al.* (unpublished), studying a set of 58 RILs of *A. thaliana*, found that competition increased the predicted response to natural selection favoring earlier flowering, but to a lesser extent, in elevated relative to ambient CO_2 environments, reinforcing a similar finding in a comparison of 19 accessions of *A. thaliana* (Lau *et al.*, 2010).

Thus, insight into the potential for adaptive evolution has been gained by evaluating genetic variation in traits that are likely to be the targets of selection in a changing climate. However, genotypic effects and environmental conditions commonly interact in

their effects on the expression of traits and fitness. Consequently, it is evident that genetic variation in traits in the current climate or in environments with one dimension experimentally altered in the direction of expected change may inaccurately represent genetic variation that will be exhibited with changing climate. It is possible to manipulate one or a few dimensions of climate, but it is not feasible to experimentally impose climates closely representative of future conditions. Feasibility aside, there is considerable uncertainty about the details of future climates in specific locations. The complexity of climate and the uncertainties of climate prediction undermine evolutionary prediction for actual future climates, but geographic variation in climatic conditions can be used to inform an understanding of potential evolutionary responses.

VII. The chronosequence approach

Etterson (2004a,b), in her study of the North American native annual plant, *Chamaecrista fasciculata*, assessed selection and genetic variation in populations in the context of a chronosequence, the method of substituting space for time. She treated the latitudinal gradation in climate in North America as a proxy for the projected temporal sequence of climate, choosing populations and sites in Minnesota (MN), Kansas (KS) and Oklahoma (OK) (45, 39 and 35°N latitude, respectively), according to climate predictions for MN that temperatures would approach those of KS by 2050, and that temperatures in KS would, by that time, be similar to those in OK. By reciprocally planting seedlings obtained from formal genetic crosses (full-sib groups nested within paternal half-sib groups) within each population into each of the sites, Etterson (2004a) evaluated the plasticity of traits in response to the climatic differences among locations, as well as selection and genetic variation in each population in each site (Etterson, 2004b).

This work indicated that the average fitness of plants declined strikingly in each southward transfer (Etterson, 2004a). Although the plasticity of traits was most often in an adaptive direction, as indicated by the direction of selection on them, it was not sufficient to maintain fitness across environments. This study further revealed substantial genetic variation of traits under selection (reproductive stage, leaf number and leaf thickness) within each population growing at each location (table 1 in Etterson, 2004b), as well as genetic variation in fitness (obtained as an estimate of the number of seeds produced), in most of the combinations of population and site. An especially intriguing result was that the southernmost population exhibited the greatest genetic variation in fitness, including in its home location. These findings clearly indicate the potential of these populations to adapt in response to changed climate conditions. However, of the three cases of a population transferred to a warmer, drier climate (MN to KS and OK; KS to OK), only one (MN to KS) exhibited significant genetic variation in fitness, associated with significant prediction of selection response (Etterson & Shaw, 2001). Genetic correlations between traits opposing the joint direction of selection also contributed to the predictions of hindered response to selection in these cases.

As noted in the original papers, this chronosequence approach has limitations of its own. First, in addition to the aspects of climate that distinguish the sites, they differ in many other respects. This important issue necessitates efforts to eliminate, to the extent possible, the confounding of climatic differences with other factors likely to differ among sites. Etterson (2004a) minimized biotic differences among the sites by planting into bare soil, rather than into existing vegetation, which differed in ways that probably would not reflect future community composition. She also inoculated at each site with the same strain of the plant's rhizobial symbiont and excluded deer, a major herbivore. Despite such efforts, differences unrelated to climate, for example, photoperiod, distinguished the experimental sites, as will generally be the case. Glasshouse experiments (Etterson, 2000) demonstrating that the populations differed in traits, as well as their performance under drought, in ways consistent with findings from the field experiment, provided important confirmation of the key role of climatic conditions.

A second issue is that the choice of locations did not mimic a gradual change in climate but, rather, an abrupt shift coinciding with about three decades of predicted climate change. By contrast, populations of an annual plant will undergo selection in the changing climate and, consequently, will change in genetic composition, year by year. For longer lived plants, or where seed dormancy is substantial (in contrast with *C. fasciculata*; Fenster, 1991), generations overlap, and the expression of fitness of a single individual spans multiple years, with variation in fitness accumulating over multiple annual bouts of survival and reproduction, likely to depend on continually varying climatic conditions. Thus, studies of selection, and the genetic variation in response to it, in climates that differ more subtly from those at the origin (e.g. Rehfeldt *et al.*, 1999) can make important contributions. We emphasize, however, that the trend in changing climate has been accompanied by an increase in variability in climatic conditions, including higher frequency of extremes of drought and rainfall (Trenberth *et al.*, 2007, p. 308). Indeed, in 1998, when Etterson conducted her experiment, drought in OK was exceptional.

Expansion and modifications to the chronosequence approach

We strongly advocate the implementation of experimental designs that employ chronosequences in natural conditions. Even recognizing that future climates may have no close analogues in the present, as has been inferred of past climates from species assemblages in fossil pollen (e.g. Williams *et al.*, 2001), it seems likely that this approach better represents multidimensional climatic differences than does the manipulation of a single aspect, such as temperature or water input. It also allows for realistic inclusion of natural environmental variation within sites.

To avoid the drawback that, among sites, all other differences in environment are confounded with differences in climate, future studies building on this approach could employ locations that represent climatic differences predicted for a focal population, but that lie in distinct directions from it. For

example, the present-day gradient of soil moisture declining towards the west in MN encompasses levels similar to those of both the KS and OK site used by Etterson (2004a). Stanton-Geddes *et al.* (2012) transplanted *C. fasciculata* into a western MN site, beyond the species' current range, and found that, although some plants survived to reproduce, the mean absolute fitness of the study population was nearly zero. Eckhart *et al.* (2010) showed how effects of precipitation on plant water status can be distinguished from effects of soil characteristics. Furthermore, sites within the chronosequence may be positioned to more finely sample climate gradients and could be replicated across years. The biotic environment could also be experimentally varied to evaluate its effect on adaptation to changing climate.

Moreover, to make clear the generality of inferences, it is essential that studies evaluate the potential to adapt to changing climate of a range of populations and species, and findings are likely to differ among them. The inherent sampling variation of estimates of the key properties of populations demands that studies be as large in scale as feasible, in order that the differences detected are interpretable. For example, returning to Etterson's experiment on *C. fasciculata*, it comprised, at the outset, *c.* 10 000 seedlings, representing 45–50 paternal half-sib families per population. It is likewise important that studies employ approaches to data analysis that are statistically rigorous. For example, the use of estimates of breeding values in subsequent analyses to infer genetic selection can seriously mislead (Hadfield *et al.*, 2010; Morrissey *et al.*, 2010). Direct estimation of the genetic covariance between fitness and traits (as in Etterson & Shaw, 2001) yields valid predictions of response to natural selection (Robertson, 1966; Price, 1970).

VIII. Resurrection of ancestral propagules

The accumulation of climate records clearly documents warming since *c.* 1985 (Trenberth *et al.*, 2007). We are not aware of research that has anticipated the onset of this trend by establishing experimental studies designed to yield evolutionary comparisons of populations subject to novel conditions with ancestral populations before the onset of climate change. However, in a few cases, direct demonstration of the nature of contemporary change in wild populations has been possible because propagules (e.g. stored seeds, seeds preserved in tundra soils or eggs in lake sediments) have been fortuitously available in a condition to be revived and grown side-by-side with their contemporary descendants, or have been recovered from soils or sediments (Bennington *et al.*, 1991; Vavrek *et al.*, 1991; Hairston *et al.*, 1999; Kerfoot *et al.*, 1999; Franks *et al.*, 2007; Franks, 2011). This 'resurrection approach' has permitted the phenotypic and genetic comparison of populations representing different time periods.

The power of this approach is illustrated by the work of Franks *et al.* (2007), who took advantage of stored seeds of *Brassica rapa* collected in 1997 in advance of a drought in southern California from 2000 to 2004. They grew progeny collected before and after the drought in a glasshouse for one generation and then produced hybrid progeny by crossing between these ancestors and descendants. When offspring of the 1997 and 2004 cohorts and their

hybrids were grown under common conditions, the post-drought descendants bloomed earlier than the ancestral populations, such that seeds would mature before the onset of the seasonally driest conditions. The production of a generation in the glasshouse before crossing and the contemporaneous comparison of the populations grown in common conditions eliminated phenotypic plasticity as a source of trait differences within or between generations, and thus justified the inference that genetically based evolution in flowering time had occurred (see also Franks, 2011). Moreover, the direction and degree of difference in the trait between samples before and after the drought accorded quantitatively with predictions based on estimates of selection and heritability in one population, although the difference was considerably less than predicted in the second.

To date, the application of this approach has depended on the fortuitous preservation of ancestral material. A new initiative, called Project Baseline, has begun to systematically collect and archive seeds of present-day populations, so that they will be available to biologists for future studies of evolutionary responses to anthropogenic and natural changes in the environment that will occur in the coming decades (Franks *et al.*, 2008; Etterson *et al.*, 2012). This seed-banking effort encompasses *c.* 100 species with diverse life-history attributes. Collections within each species will include 20 populations in different habitats and climates across the species' geographic range and from *c.* 100–200 individuals per population (Fig. 1). This sampling plan will capture genetic variation among differentiating populations and also within populations. Seeds will be stored to maximize viability at the USDA National Center for Genetic Resources Preservation, a world-renowned germplasm repository.

Over the anticipated 50-yr lifetime of this collection, seeds will be made available to researchers to study evolutionary change through direct comparison of plants grown from

archived materials with individuals newly sampled from nature. With such a resource secured, evolutionary biologists will be able to grow out genetic material representing populations from the past and compare them with later assemblages utilizing long-established and new genetic approaches, as well as those yet to be developed, to dissect the underlying mechanisms of evolutionary change.

IX. The mean and variance in fitness, a link between genetics and demography

We outline here an approach that builds on those exemplified by the studies reviewed above and that we envision as particularly illuminating. It builds on the premise that the mean absolute fitness (\bar{W}) of a population, that is, the average number of seeds produced per individual seed over the complete lifespan, reflects the population's tendency to maintain itself, grow or decline. A population whose mean absolute fitness falls and remains below unity is in decline towards extinction. Further, as noted above, additive genetic variance in absolute fitness [$V_A(w)$] implies a population's capacity to evolve towards higher mean absolute fitness; it indicates the maximal rate of adaptation. Thus, the mean and the additive genetic variance of fitness most directly reflect a population's capacity for persistence and adaptation in the near future.

To our knowledge, these quantities have never been jointly estimated for any population in nature, perhaps largely because of the challenges of doing so. The evaluation of absolute fitness requires the complete accounting of survival and reproduction throughout the lifespan; consequently, the feasibility of obtaining the requisite data declines as the longevity of the focal organism increases. Even with complete data, precise, accurate inference about fitness has, until recently, been stymied by the idiosyncratic nature of fitness distributions, which

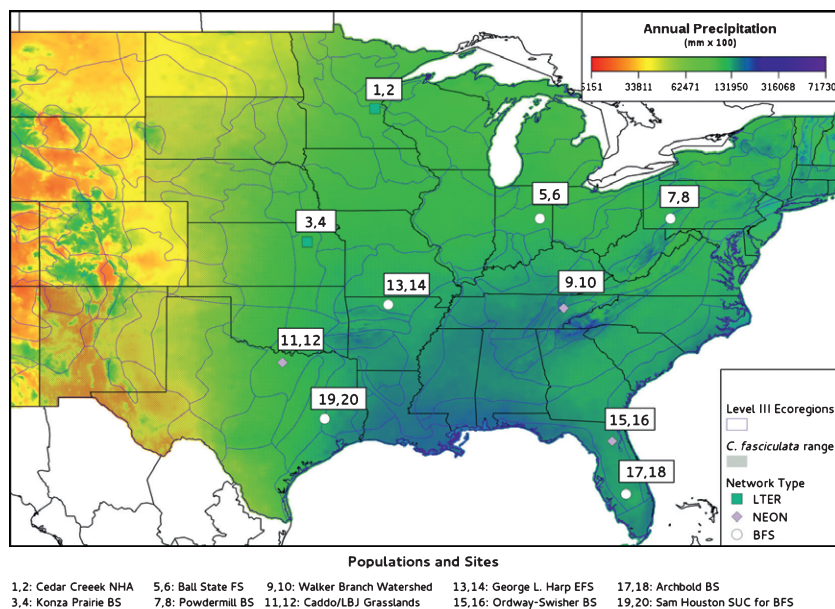


Fig. 1 Population selection for Project Baseline. Sites that are likely to be preserved into the future are identified (e.g. LTER, NEON, BFS). Ten sites (20 populations) are identified for seed collection based on the distribution of a target species (e.g. *Chamaecrista fasciculata*). Additional co-occurring species at these sites are also collected (e.g. *Asclepias tuberosa*, *Dalea purpurea*, *Schizachyrium scoparium* and *Heliopsis helianthoides*).

are not well approximated by classic probability distributions that are the usual basis for parametric statistical analyses (see, for example, Fig. 4 of Wagenius *et al.*, 2010). This is because the distribution of fitness reflects the compounding of episodes of survival and components of fecundity throughout the lifetime. Formal statistical modeling of the compound nature of fitness has recently been accomplished through the use of graphical models for the dependence of components of fitness (Fig. 2) in an approach dubbed ‘aster modeling’ (Geyer *et al.*, 2007; Shaw *et al.*, 2008). Implementation of aster to model random effects, as required for quantitative genetic analysis to infer $V_A(w)$, makes possible the estimation of the distribution of additive genetic effects on fitness (Fig. 3), together with $V_A(w)$ (C. Geyer *et al.* unpublished).

The power of measuring the mean and variance of fitness in a chronosequence

Studies that yield estimates of the mean absolute fitness of focal populations, as well as $V_A(w)$, would establish the foundation for predicting their persistence and immediate adaptive potential. Such studies for a population in its home site would yield these predictions under current conditions. Expansion of this approach

spatially, in different sites representing a chronosequence, as exemplified above, is dependent on population persistence in conditions approximating climates of the future, as well as the capacity for adaptation and the rate of adaptation to these conditions. Experiments that employ locations differing to a finer degree than the sites of Etterson (2004a,b) would elucidate nearer term climatic effects on genetic distributions of fitness. In addition to assaying absolute fitness, such studies may include the consideration of traits deemed likely to relate to fitness as climate changes. We note, however, that many traits, not all feasibly measured on large numbers of individuals, probably contribute jointly to fitness, and it is highly problematic, in its own right, to identify traits on which fitness depends most directly and crucially (Shaw & Geyer, 2010). Fortunately, the prediction of rates of adaptation does not depend on a knowledge of the traits that contribute to fitness. We propose that it is more urgent to evaluate adaptive capacity and its evolution than to clarify the nature of selection on traits or to determine the genes underlying them, either of which is a tremendously challenging task.

Beyond spatial replication, an experiment that is replicated over years would reveal the stability or variability of the distribution of genetic effects on fitness over environmental

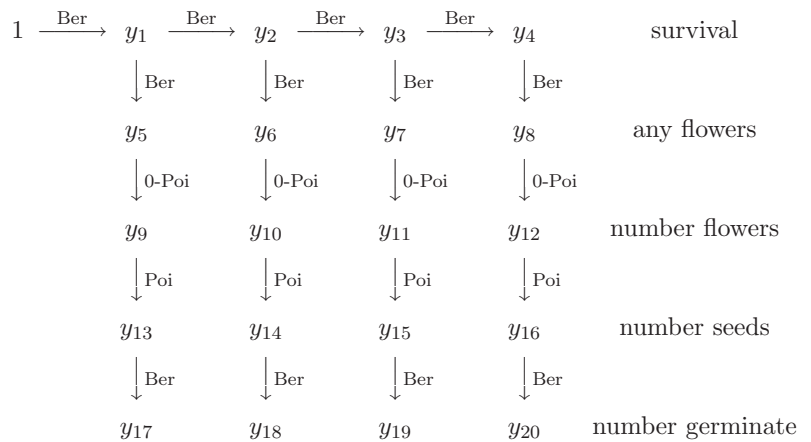


Fig. 2 An example of a graphical model for fitness for an organism that lives up to 4 yr. ‘1’ represents an individual at the start of its life, for example, seed. Thereafter, the variables y_1 – y_{20} represent observations of its components of fitness, including survival to the next year, whether or not it flowered in a given year, the number of flowers it produced in that year given that it flowered, the corresponding number of seeds it produced and the number that germinated from that cohort. Probability distributions appropriate for each of the components are specified: Ber, Bernoulli; Poi, Poisson; 0-Poi, zero-truncated Poisson. (Reproduced from Shaw & Geyer (2010)).

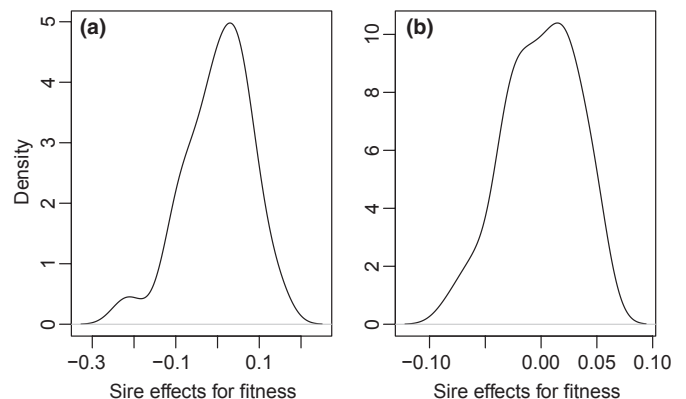


Fig. 3 Estimates of the distribution of breeding values for fitness for a population of *Chamaecrista fasciculata* sampled at Konza Prairie, KS, USA in 1997 and grown in Konza Prairie, KS (a) and at Pontotoc Ridge OK (b) in 1998 (data from Etterson, 2004a,b). Fitness, estimated via aster modeling, takes into account survival, flowering and the number of fruits for each individual; thus, values indicate the expected number of fruits per seedling planted.

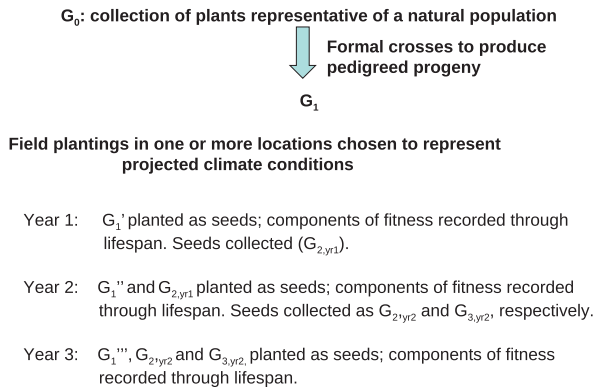


Fig. 4 Diagram of an experimental scheme to evaluate the distribution of additive genetic effects on fitness, including $V_A(w)$, its variability over the years and the realized change in mean fitness between generations. All descendant generations were planted within the same location in successive years; the design could be planted in multiple locations, as a chronosequence. Comparison of G_1 , G_1 ' and G_1 '' indicates variation in the fitness distribution over successive years. Genetic correlation between fitness expressed in different years indicates the degree to which selection favors the same or different genotypes through time. Comparison of G_1 '' with $G_{2,yr1}$ indicates the change in mean fitness as a result of selection in G_1 '. This assessment of adaptation is replicated in the following year by comparison of G_1 '' with $G_{2,yr2}$ and of $G_{2,yr2}$ with $G_{3,yr2}$.

conditions as they vary temporally. Predicted changes in climate include more erratic variability, and it is not at all clear how fitness will respond to climate extremes. Likewise unknown is the effect of erratic climate variation on the capacity to adapt to an overall trend in climate. Just as growing sets of individuals from the same pedigrees in multiple sites provides a basis for estimating genetic correlations between site-specific fitnesses (Table 3 in Etterson, 2004b; Fig. 3), an experiment that employs the same genetic material (e.g. full-sib and half-sib groups) in multiple years will yield estimates of additive genetic correlations between fitnesses as expressed in different years. Importantly, this will reveal the extent to which genetic selection differs in different years, a condition that will impede ongoing adaptation. In each successive year, the experiment could also include the offspring of the previous year's field-grown individuals; the difference between the mean fitness of these progeny and the mean fitness of plants of the previous generation would reflect the response to natural selection in the previous season (Fig. 4).

Experiments of this kind would yield predictions of rates of adaptation to the conditions that prevail in the locations and years in which they are conducted. To the extent that selection is similar in each generation, quantitative genetic predictions of response to selection can be expected to hold for one or two dozen generations. When the population size is large, selection moderate and many loci contribute to variation, a steady response to selection may persist much longer (Weber, 1990; Weber & Diggins, 1990; Dudley & Lambert, 2004). As climate becomes more erratic, it seems unlikely that selection will remain consistent, and it may often be severe. We urge efforts to evaluate the temporal variation in genetic selection both over

short periods of a few generations and over longer periods of several decades.

X. Conclusions

Adaptive evolution in relation to spatial and temporal variation in climate in the past is well documented, as are shifts in geographic ranges of species in conjunction with changing climate. However, current rates of change in climate far exceed those of the past. The evaluation of a population's adaptive capacity is a major empirical challenge. Experimental approaches to assess genetic variation in absolute fitness require intensive effort and substantial resources, but address directly the pressing problem of how readily plants can adapt to changing climate.

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