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Environmental change and the option value of genetic diversity

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Rapid anthropogenic environmental change is altering selection pressures on natural plant populations. However, it is difficult to predict easily the novel selection pressures to which populations will be exposed. There is heavy reliance on plant genetic diversity for future crop security in agriculture and industry, but the implications of genetic diversity for natural populations receives less attention. Here, we examine the links between the genetic diversity of natural populations and aspects of plant performance and fitness. We argue that accumulating evidence demonstrates the future benefit or 'option value' of genetic diversity within natural populations when subject to anthropogenic environmental changes. Consequently, the loss of that diversity will hinder their ability to adapt to changing environments and is, therefore, of serious concern.

The 'option value' of genetic diversity in natural plant populations

In striving to slow or halt the loss of biodiversity, the conservation of diversity within species has been recognized as fundamentally important. The value of such intraspecific genetic diversity is evident from the often deleterious impacts of its loss on populations through effects such as increased inbreeding and genetic drift [1–3]. Likewise, genetic diversity has a fundamental role in both the evolutionary history and future evolutionary trajectory of a species [4–6]. As the magnitude of anthropogenic impacts on the biosphere becomes increasingly evident, it is important to understand how, and indeed whether, populations can adapt to current anthropogenic environmental changes [7]. Consequently, the conservation of genetic diversity has become a renewed focus under the expectation that its loss could render populations and species less able to adapt to ongoing environmental changes [1,5,8,9].

The assumption that genetic diversity is of fundamental importance for the adaptation of species to future environmental changes is a reasonable one [7,9,10]. Genetic diversity is the raw material for evolution, and all species have arisen via an evolutionary walk where each step depends on the variation present at the last [11]. Although not every genetic variant is potentially adaptive, a proportion will be, even if most of the genetic variation within a population

remains of indifferent value throughout its lifetime [12]. When subject to environmental change, genetic diversity therefore has a value that is likely to be proportional to its amount [12]. However, as we are unable to predict the future beyond the extrapolation of current trends, we are unable to determine the evolutionary direction that any species will take. Consequently, we cannot identify which genetic variants will be valuable for the persistence of a species in the natural environment but must assume that all genetic variation is valuable *per se* [13].

There is a more developed understanding of the links between genetic diversity and the productivity and stability of plant species cultivated for agriculture, forestry and industry than for non-crop species [14,15]. Furthermore, wild-sourced genes are used to 'improve' cultivated plant species and varieties, demonstrating that intraspecific diversity can have high economic value in our exploitation of these biological resources [15–19]. The importance of conserving genetic resources in wild relatives of cultivated plants can, therefore, be argued on the grounds of their 'option value' [13], that is, that the potential exists for the future exploitation of this diversity even if its economic value is currently unrecognized [1]. However, actual quantification of this option value is rare [18]. To assume that, when exposed to rapid environmental change, all genetic variation in natural populations is inherently valuable is an essential extension of this concept.

Until recently, there was little supporting evidence from non-crop species to link genetic diversity to population persistence in a rapidly changing environment, and the application of relevant information from agricultural systems to natural populations was limited. However, increasing evidence shows that maintaining genetic diversity within natural populations can maximize their potential to withstand and adapt to biotic and abiotic environmental changes. Here, we highlight key examples of this evidence, with specific reference to the links between genetic diversity and pest and disease resistance, tolerance of climatic change and population productivity and fitness.

Pest and disease susceptibility
Resistance diversity in crops
Much of the interest in the impacts of reduced diversity on pest and disease susceptibility comes from the agricultural sector, because decreased yields due to related crop damage have profound and direct societal and economic

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impacts [17]. Two recent reviews discuss the value of genetic diversity in agricultural systems in some detail [16,17]. For example, the devastating outbreak of southern corn leaf blight that swept the maize crop in the USA in 1970 is one of the worst plant disease epidemics ever recorded, inflicting damage that would be valued in excess of US$5 billion in 2008 when adjusted for inflation [17]. The blight outbreak was due to the rapid evolution of a new race (Race T) of the pathogen *Cochliobolus heterostrophus.* A particular gene, *T-cms*, that rendered individuals highly susceptible to this strain had become nearly ubiquitous during breeding programmes that led to the production of the dominant maize cultivars planted by 1970. Thus, the rapid spread of Race T, and the severe damage it caused, was facilitated by widespread lack of genetic variability for its resistance.
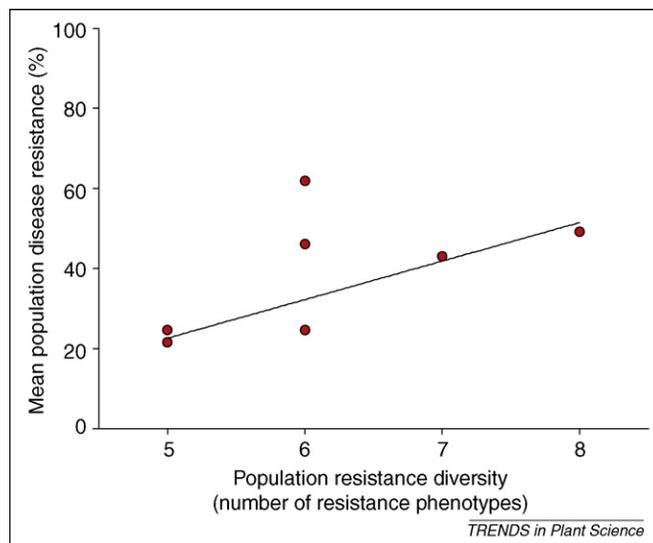
Resistance diversity in natural populations
In contrast to agricultural systems, host resistance structure and its implications for disease dynamics have been less well studied in natural populations [20,21]. However, there is now abundant evidence of genetic polymorphism for pathogen resistance in natural populations [20–25]. In the case of ribwort plantain, *Plantago lanceolata,* 16 phenotypes resistant to strains of the powdery mildew fungus *Podosphaera plantaginis* were identified from a sample of 64 individuals taken locally from natural populations [21]. These phenotypes were predominantly genetically determined. Populations varied in their composition from a minimum of five phenotypes per population to one population in which every individual sampled represented a different resistance phenotype. Non-infected populations showed significantly higher mean levels of resistance than did infected populations, and individuals that were resistant to all strains of the pathogen occurred only in non-infected populations.

Further examples of genetic diversity for disease resistance in natural populations come from the morning glory *Ipomoea purpurea* in response to the rust pathogen *Coleosporium ipomoeae* [25] and the legume *Amphicarpaea bracteata* in response to *Synchytrium decipiens* [23], as well as the interaction of the flaxes *Linum marginale* [26] and *Hesperolinon californicum* [20] with the rust pathogen *Melampsora lini*. Genetic diversity for resistance to insect pests has also been identified, as in the example of the Douglas fir *Pseudotsuga menziesii,* which displays phenotypes that are either resistant or susceptible to herbivory by the western spruce budworm (*Choristoneura occidentalis*) [27].

Implications of reduced resistance diversity
The factors determining the genotypic composition of populations in response to different pest and pathogen strains are complex and currently the subject of intense study [28,29]. However, a highly diverse resistance structure is emerging as a common characteristic of natural plant–pathogen systems [20,21,28,29]. Within populations, resistance diversity reduces the probability of pathogen establishment by decreasing the chances of pathogen propagules coming into contact with a compatible host. If a pathogen establishes, its subsequent spread is inhibited by the diversity of resistance phenotypes that it encounters,

Figure 1. The relationship between resistance to the pathogen *Podosphaera plantaginis* and the resistance diversity of natural populations of *Plantago lanceolata*. The positive impact of resistance diversity on reducing disease occurrence is indicated by the trend line, which highlights the significant correlation between the two variables (r_s = 0.747, $P_{one\ tailed}$ = 0.017, Spearman rank correlation, corrected for ties). Figure and analysis are derived from data presented in Ref. [21].

thereby also decreasing propagule dispersal to new populations [21]. Thus genetic diversity for resistance has a fundamental role in preventing the outbreak of pests and diseases in natural systems, limiting the severity of outbreaks when they occur and limiting the speed with which they spread [14,16,17,21] (Figure 1). The loss of quantitative genetic diversity associated with resistance in natural populations is, therefore, likely to increase their vulnerability to attack.

On a longer timescale, the importance of genetic diversity is equally clear as a basic resource in the co-evolutionary 'arms-race' between a pest or pathogen and its host [28,29]. Even in a highly studied system where present disease dynamics are well understood, we cannot predict the characteristics of novel strains of a pathogen that are yet to evolve. Consequently, we are unable to identify the value of any given genotype until its 'hour of need' arrives – a problem exemplified by the devastating southern corn leaf blight epidemic detailed earlier.

Response to climatic variation
Pioneering studies detailing ecotypic differentiation between populations subject to contrasting environmental conditions provided an early indication of the existence of genetic variability associated with climatic variation at the species level [30,31]. At the within-population, or microgeographic scale, initial evidence for the genetic differentiation of individuals in response to climatic variation began to accumulate from studies investigating the environmental correlates of enzyme polymorphisms within populations (see Ref. [8] for a recent review). With the spectre of rapid climatic changes looming, this area of research has seen renewed interest.

Climate–genotype associations
Much of the work that has reported climate-linked genetic variability within populations is based on the association

or correlation of the frequency of different molecular marker alleles with particular climatic variables. A large body of evidence comes from studies conducted on the wild cereals slender oat (*Avena barbata*), wild emmer wheat (*Triticum dicoccoides*) and wild barley (*Hordeum spontaneum*). Work on these species has detected significant microgeographic genetic differentiation in response to environmental factors, including solar radiation, temperature and aridity stress (detailed in [8]). Analogous findings have been reported for the trees Engelmann spruce (*Picea engelmannii*), pinyon pine (*Pinus edulis*) and ponderosa pine (*Pinus ponderosa*), with water availability being a common factor in explaining the patterns of genetic differentiation identified [8].

The approach of correlating allele frequency with environment (on which the previous examples are based) is hampered by the high likelihood of detecting false positive results [32]. This problem of a high type 1 error rate has been reduced by the application of more stringent population genomic analyses [33], but, ultimately, the adaptive value of any genetic differentiation detected must be demonstrated experimentally [32,34,35]. Population genomic analyses can, however, provide a useful first step in identifying ecologically important genetic variation linked to climate or other selection pressures [35–37].

Climate change and natural selection
In a recent population genomic analysis in the maritime pine (*Pinus pinaster*), genetic variation linked to the drought response of this species was identified by analysing variation in the frequency of polymorphisms located in candidate genes [38]. Variation among individuals in their ability to establish in elevated drought conditions was also indicated in the Mediterranean shrub *Fumana thymifolia* from an analysis of amplified fragment length polymorphism (AFLP) data [39]. Rapid evolution of drought avoidance was demonstrated directly in field mustard (*Brassica rapa*), where genotypes sampled after a multiyear drought showed significantly earlier flowering than did pre-drought individuals sampled from the same population [40]. Similarly rapid genetic change is indicated in the European beech (*Fagus sylvatica*), in which a population genomic analysis identified an AFLP locus where allele frequency varied predictably according to establishment temperature [32]. Furthermore, rapidly rising temperatures linked to global climate change have driven predictable changes in allele frequency at this locus over the latter half of the 20th century.

Assessment of climate-linked genetic variation in non-model species is complicated by the fact that it commonly focuses on the analysis of molecular genetic variation rather than variation for known quantitative traits (Box 1). However, in combination, the above examples demonstrate not only that climate-linked variation exists but also that, in some cases at least, it can also respond to selection on a timescale relevant to current rapid anthropogenic environmental changes [7,41].

Productivity and fitness
Effects of genetic diversity on plant productivity can arise as a consequence of the combined effects of genotypic

Box 1. Neutral marker and quantitative trait diversity

Here, we have, by necessity, considered studies that have assessed diversity impacts based on investigating genotypes with known differences in quantitative traits, alongside those that have assessed more general impacts of molecular genetic diversity measured at marker loci that are typically assumed to be selectively neutral. A question raised by this approach is, how comparable are patterns based on these two types of genetic diversity?

A recent review [72] demonstrates that levels of molecular genetic variation at molecular marker loci might be poor indicators of diversity for quantitative traits. However, the correlation of levels of differentiation between populations for quantitative traits (Q_{ST}) and neutral molecular markers (F_{ST}), although weak, remains generally significant [73], suggesting that neutral markers can be cautiously applied to predict genetic differentiation for quantitative traits in natural populations [73]. Further results from Q_{ST} vs F_{ST} meta-analyses indicate that divergence due to natural selection and local adaptation is widespread and that the direction and magnitude of selection varies among local populations [73,74].

In assessing correlations between neutral and quantitative genetic diversity, Reed and Frankham [72] state that 'allozymes or other forms of neutral molecular markers are unlikely to provide conservation or evolutionary biologists with reliable information on a population's evolutionary potential or to accurately reflect population differentiation and local adaptation'. Using neutral variation as a surrogate is not ideal, but given the findings of Ref. [73] described above, the degree to which this lack of accuracy or reliability must be tolerated remains an open question.

Considerable spatial and temporal variation in selection pressures, and consequently the selective value of associated quantitative traits, occurs in natural populations. Anthropogenic environmental changes serve to alter selection pressures further [56,75]. Local adaptation and rapid contemporary evolution can be taken as evidence for the existence of the underlying genetic diversity on which the selection response is based – and of its fundamental importance for the adaptation of populations to environmental changes [7,41,56,76]. Although non-ideal, so long as molecular genetic diversity remains the most rapidly and easily assessable measure of diversity in natural populations, it will remain our best estimate of the adaptive potential of these populations in an uncertain environment.

replacement (selection) or complementarity. Assuming that different genotypes of a species differ in their productivity, as the number of genotypes within a population increases, so does the probability that the population will include a genotype that is unusually productive. If highly productive genotypes are better competitors within a mixture, then increased genetic diversity can lead to increased productivity through this sampling effect and subsequent selection for increased abundance of the most productive genotype.

Genotypic replacement
This replacement process is illustrated in an experimental manipulation of mixtures of different genotypes of the alga *Chlamydomonas reindhartii* [42]. Mixtures of genotypes were consistently more productive than were monocultures, and the productivity of each genotype in a mixture was strongly correlated with its productivity in monoculture. By analysing the genotypic composition at the end of the experiment, it was found that the most productive genotypes had come to dominate each mixture [42]. Although genotypic replacement will lower the diversity of the population over time in a stable environment, gene flow and environment-dependent differences in fitness between genotypes interact with fluctuating selection

pressures in a heterogeneous environment to maintain diversity [43,44]. Loss of diversity will therefore reduce the capacity of a population to respond to environmental change, because a reduction in mean fitness over time will occur owing to the loss of potentially highly productive genotypes from the population.

Genotypic complementarity

Under complementarity, a mixture of different genotypes is able to exploit available resources more fully and might therefore show greater productivity compared with that of component genotypes occurring in isolation. A simple illustration of this principle is provided by work on genotypes taken from a natural population of white clover (*Trifolium repens*) [45]. Individuals within the source population were found to have genetically determined differences in root growth, with some exploiting deeper and some shallower soil layers. When water availability is low, long-root plants accumulate greater biomass than do short-root plants owing to the greater availability of water in deeper soil layers. However, a mixture of the two genotypes was even more productive as a consequence of greater exploitation of the soil profile together with decreased belowground competition at any particular depth.

Further evidence of increased productivity in high diversity populations comes from work conducted on the seagrass *Zostera marina* [46] and the goldenrod *Solidago altissima* [47]. In both studies, experimental populations were constructed from differing numbers of genotypes taken from a natural population, and diversity was positively correlated with biomass production. In *Z. marina,* this seems to result from genotypic complementarity because selection effects were negative, that is, genotypes producing high biomass in monocultures performed poorly in mixtures. However, only a weak link between complementarity and diversity was identified in *S. altissima* [47].

Genetic diversity and population fitness

Increased productivity is cited as evidence of higher fitness in high diversity populations of plants, including primrose (*Primula vulgaris*) [48] and small scabious (*Scabiosa columbaria*) [49], that show a positive correlation between biomass and reproductive output [49]. However, direct assessment of fitness requires assessment of reproductive success over several generations, such as that performed in a classic multigeneration study into the effects of decreased genetic diversity on fitness in pinkfairies (*Clarkia pulchella*) [50]. In *C. pulchella,* populations with a lower genetically effective population size showed decreased fitness owing to significantly reduced germination and seedling survival. This decline ultimately translated into a higher extinction rate of low diversity populations. The positive relationship between genetic diversity and plant fitness indicated by these studies has been confirmed as a general pattern based on recent meta-analyses [51,52] and can extend below the population level to diversity within individuals (Box 2).

It is not only productivity itself that is positively linked to genetic diversity within natural populations but also productivity stability, which has been found to be greater in more diverse populations. In experimental plots manipulating the genotypic diversity of calcareous grassland

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Box 2. Diversity within individuals

Here, we discuss the positive contribution that genetic diversity makes to the productivity, stability and fitness of natural populations. In many ways, the effects described at the intra-population level are mirrored by those at the intra-individual level. Essentially, this is the notion of heterozygote advantage [77,78], where, in its simplest definition, the fitness of an individual having two different alleles at a given locus (heterozygote) is higher than the fitnesses of individuals with two copies of either allele (homozygotes).

In examples analogous to those described for the population level, a significant positive relationship has been reported between the mean heterozygosity of individuals and fitness in marsh gentian (*Gentiana pneumonanthe*) [79,80] and Tatarian orache (*Atriplex tatarica*) [81], with higher fitness assumed from elevated vegetative and reproductive productivity. Individual-level heterozygosity has also been positively linked to growth rate in quaking aspen (*Populus tremuloides*) [82], and there is a strong indication that high heterozygosity can be particularly important in enabling individuals to respond to environmental change [27]. In several *Pinus* species, increased heterozygosity has been linked to a decrease in growth rate variability rather than to growth rate itself [82]. This decrease in growth variability with increasing heterozygosity parallels an increased developmental stability of heterozygotes in *G. pneumonanthe and A. tatarica* and compares directly with the population-level diversity–stability effects that we describe in the main text.

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species, an increase in the variability of productivity was reported if genotypic diversity was severely reduced [53], an effect that was also reported for *Z. marina* [46], *P. vulgaris* [48] and *S. columbaria* [49]. Diversity–stability effects can also extend to other areas of population function. In *Solidago altissima,* increased diversity was also linked to decreased invasibility of the experimental populations [54]. However, in thale cress (*Arabidopsis thaliana*) populations differing in their genotypic diversity, it was suggested that a decrease in invasibility was solely a consequence of increased plant density, rather than an effect of diversity itself [55]. Further work is necessary to resolve this issue because genetic complementarity can naturally increase the density of plants within a high diversity population [46,54].

Pre-existing genetic diversity and environmental change

Continual fluctuations in the biotic and abiotic environment of a species provide a background of continuously changing selection pressures to which the species must respond. Thus, temporal and spatial environmental heterogeneity, by constantly altering the selective value of traits or their combinations, is a powerful force for maintaining genetic diversity within natural populations [28,43,44]. Although direct fitness effects of environmental change are assessed in only a few of the studies described earlier, these studies do provide clear examples of how the relative fitness of different genotypes might differ in different biotic or abiotic environments. Alongside phenotypic plasticity [8], selection on standing (pre-existing) genetic variation within natural populations is, therefore, a primary mechanism that enables them to adapt to environmental fluctuations [7,9,44].

Natural selection during extreme events

Environment-dependent fitness differences between genotypes can drive fluctuation in allele frequencies in response

to 'normal' environmental variation [8,44]. However, whether via continuous changes in current conditions, such as atmospheric gas concentrations or ambient temperature, or via abrupt changes, such as the introduction of novel pathogens, predators and competitors, rapid anthropogenic environmental change is altering selection pressures on most, if not all, natural populations. It might be during such periods of rapid environmental change that the value of high genetic diversity within populations becomes particularly clear. Indeed, it has been proposed that selection is all but absent except during these extreme events [44].

In addition to heterozygote advantage and fitness trade-offs between linked traits, alternating selection over time might cancel out periods of directional selection such that effective selective neutrality of trait variation is maintained over time when integrated over periods of normal environmental fluctuation [44]. However, during extreme events, this balancing effect does not occur, leading to rapid, directional changes in allele frequency within the population [7,8,41,44,56].

This mechanism was invoked to explain the maintenance of the temperature-linked polymorphism in *F. sylvatica* and its subsequent selection response to rising temperatures [32]. In this scenario, it is only during periods of rapid environmental change that the selective value of genotypes pre-adapted to the novel environmental conditions becomes clear [57]. This might be an important factor in studies such as that of sticky catchfly (*Lychnis viscaria*) [58], where, despite theoretical expectations, no fitness impacts of substantial diversity reduction have been reported; it should also caution against assuming that normal fitness of reduced diversity populations will be maintained far into the future [41].

Several examples illustrating the hypothesized elevated value of diversity during extreme events can be identified from the studies cited above. In the plant–pathogen interaction of Ref. [21], genetic diversity of *P. lanceolata* for resistance to *P. plantaginis* had a key role in reducing mortality linked to severe drought. Although population densities declined in all populations, the decline was steepest in those populations where infection was prevalent. In *T. repens*, the relative fitness of different root-length genotypes became evident during a period of drought, as evidenced by the productivity differences described in Ref. [45]. *Zostera marina* provides a further example: in this species, the positive association between genotypic diversity and biomass accumulation and recovery became evident after a period of exceptionally high temperature [46]. Likewise, high genotypic diversity increased the resistance of *Z. marina* to disturbance, but no differences between diversity treatments were measured under 'normal' (non-disturbed) conditions [59].

A parallel source of evidence demonstrating the value of genetic diversity in species challenged with novel environments comes from study of biological invasions. Although not a prerequisite, enhanced genetic diversity owing to hybridization, polyploidization or multiple introduction events can enable a species to colonize a greater range of habitats, leading to a substantial increase in its invasiveness [10,60–63].

The option value of genetic diversity for population persistence

Diversity loss is likely to elevate the genetic vulnerability of populations to rapid environmental change, whether through the direct loss of potentially adaptive alleles [14,16,17,28,41] or via the more general increase in extinction vulnerability owing to increased selective load interacting with decreased genetically effective population size [2,9,48,50,51] (Figure 2). In the former scenario, alleles that are of future benefit but confer no current fitness advantage are likely to be at low frequency within the population relative to those that are currently selectively advantageous [7,28]. It is these low-frequency alleles that are most likely to be lost during any reduction in population size [64]. Maintaining genetic diversity within natural populations is thus a key element of maximizing their chances of survival in a future of rapid environmental change. Avoiding the loss of genetic diversity from populations cannot, however, guarantee their survival if selection pressures overwhelm the demographic potential of the population [9] or where interactions between traits cause
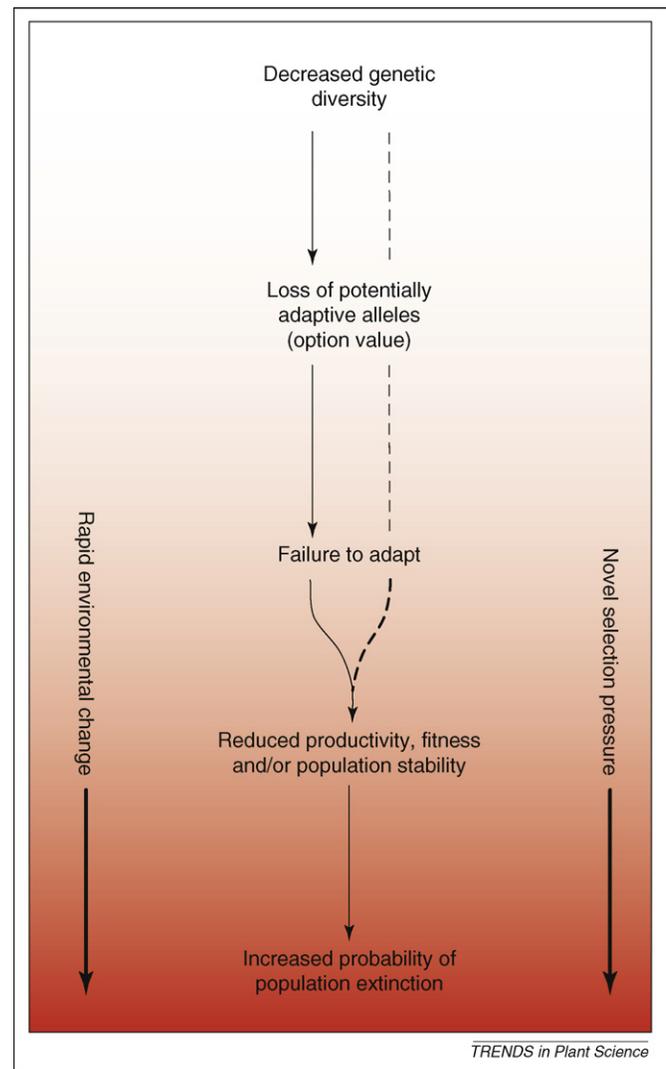
Figure 2. Increased genetic vulnerability to environmental change resulting from the loss of population genetic diversity and its option value for the species adaptation to future conditions. Elevated extinction risk results from the direct loss of alleles of future adaptive value (bold arrows) and/or the negative impact of reduced diversity on plant fitness and demographic stability (broken arrow).

any selection response to be too slow to enable individuals to adapt [65].

Given the case studies referred to above, it is evident that reduction in the genetic diversity of populations is likely to have both long-term implications for their future evolution and negative impacts on their ability to tolerate rapid environmental changes. Considering the latter scenario, the implications are likely to vary with the life-history characteristics of the species. Those species with long lifespan and delayed reproductive maturity might be most at risk due to lower turnover of individuals within populations (low establishment probability) and the lag between establishment of individuals and their subsequent reproduction, during which the environment might have changed markedly [8]. A failure to consider the potential value of genetic diversity within populations, and therefore to maximize its conservation, is likely to be storing up substantial problems in such species. It is surprising, therefore, that even in forest trees, with their considerable ecological, economical and cultural importance, the value of genetic diversity in maximizing their probability of persistence remains largely ignored [66].

Future research

Much of the current evidence linking diversity to persistence is derived from the impact of environmental change on the genetic diversity of natural populations, rather than on the role of genetic diversity in the ability of the population to persist. Consequently, we need to determine how differing levels of genetic diversity interact with novel environmental conditions to impact plant fitness. Such work needs to challenge populations with relevant changes in conditions, such as temperature, drought, novel competitors and predators, pests and diseases, and in soil and atmospheric chemistry. Experiments need to be conducted over multiple generations and need to consider the impact of environmental change on species with different natural levels of population genetic variation, life histories and geographic distributions to identify suites of traits that render species most at risk. Furthermore, we should examine different levels of population genetic diversity for both quantitative diversity and neutral markers in parallel. This last point raises a further question of how we measure relevant quantitative genetic variation. When selecting quantitative traits for study, we must aim to choose those that will be important in the novel environment. Thus, we are forced to attempt a 'plants-eye-view' of its environment, which is not straightforward.

Ecosystem-level implications

Given the ubiquitous nature of anthropogenic population extinctions and habitat fragmentation, to which even common and widespread species are known to be susceptible [64,67], all genetically highly variable populations should be considered valuable [48]. However, the importance of lower-diversity populations should not be automatically discounted, because some might also harbour important adaptations to their current environment. Conservation of genetic diversity should, therefore, consider variability at the species level and must maintain mechanisms for its movement via seed and pollen dispersal. Strong parallels exist between processes influencing levels of diversity within species and ecosystems [68]. Genetic diversity within populations and species diversity within communities can have comparable implications for their sustainability during periods of environmental change [69]. Positive impacts of genetic diversity within populations extend beyond the short-term fate of populations in an uncertain environment; via cascade effects, these impacts can cross trophic levels to affect the structure and function of whole ecosystems [43,46,47,54,69,70].

Conclusion

To maximize our capacity to adapt to environmental change, we must maintain the capacity of natural systems to also adapt to changing conditions [71]. Our exploitation of crop species highlights the reality that all countries rely on the option value of genetic diversity for food security and stability in an uncertain environment [16], as well as for the development of future bioenergy resources [19]. It is time that we recognized the degree of environmental uncertainty that we now face and apply the same principle to natural populations, understanding that if we are to maximize their chances of persistence, the loss of genetic diversity, including both known and unknown genetic functions, can no longer be overlooked.

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Plant Science Conferences in 2009

Plant Dormancy
4th International Symposium
8–11 June 2009
Fargo, North Dakota, USA
http://www.plantdormancy.com/

2009 Medicago truncatula Model Legume Congress
12–16 June 2009
Asilomar Conference Grounds, Pacific Grove, CA, USA

The 8th International Symposium on the Plant Hormone Ethylene
21–25 June 2009
Cornell University in Ithaca, New York, USA

20th International Conference on Arabidopsis Research
30 June–4 July 2009
Edinburgh, Scotland
http://arabidopsis2009.com/

Plant ROS 2009
8–10 July 2009
Helsinki, Finland
http://pog2009.org/