REVIEW

Climate change and evolutionary adaptation

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Evolutionary adaptation can be rapid and potentially help species counter stressful conditions or realize ecological opportunities arising from climate change. The challenges are to understand when evolution will occur and to identify potential evolutionary winners as well as losers, such as species lacking adaptive capacity living near physiological limits. Evolutionary processes also need to be incorporated into management programmes designed to minimize biodiversity loss under rapid climate change. These challenges can be met through realistic models of evolutionary change linked to experimental data across a range of taxa.

Natural populations are responding to global climate change by shifting their geographical distribution and timing of growth and reproduction, and these changes are, in turn, altering the composition of communities and the nature of species interactions[1]. However, the responses of many populations are likely to be inadequate to counter the speed and magnitude of climate change, leaving groups such as lizards vulnerable to decline and extinction[2]. Extinction can be avoided if populations move to favourable habitats, organisms successfully overcome stressful conditions via plastic changes, or populations undergo evolutionary adaptation[3].

Recent studies have highlighted that evolutionary change can be rapid in a number of taxa[4], including in species that have invaded new areas[5] and in native species responding to biotic invasions[6]. This indicates that evolutionary adaptation could be an important way for natural populations to counter rapid climate change, and that predicted colonization patterns and distribution shifts are markedly affected by the inclusion of evolution[7,8]. Evolutionary adaptation might be the only way that threatened species can persist if they are unable to disperse naturally or through human-mediated translocation to climatically suitable habitats. This process might also be essential for the ongoing health of keystone species facing threats arising from climate change, as in the case of dominant conifers being attacked by bark beetle populations benefiting from warming conditions[9]. Adaptive changes are likely to influence the ability of species to take advantage of potentially favourable conditions arising from climate change, including the effects of CO_2 enrichment on growth rate[10] and the extension of favourable seasonal conditions[11]. However, with few exceptions, the importance of evolution tends to be ignored both in broader discussions about the effects of climate change on biodiversity and in models for predicting species responses to climate change.

Rapid climate change is likely to produce a range of new selection pressures on populations. Increasing periods of thermal stress and drought will produce directional selection for resistance, particularly in species close to physiological limits such as warm-adapted porcelain crabs[12] and tropical lizards[13] existing close to upper thermal thresholds that are likely to be exceeded in the next few decades. Warmer conditions will select for earlier emergence from winter diapause[11] and for dispersal to new environments[14] as species take advantage of conditions that have become newly favourable. Not all selection pressures arising from climate change will be directional; stabilizing selection is likely to occur on hatching/breeding times in birds colonizing new areas where food supply and breeding times coincide[15].

Climate change is occurring at a time when natural environments are becoming increasingly fragmented through habitat destruction, and when species are being moved inadvertently or deliberately around the globe at ever faster rates[16,17]. This means that the effects of climate change are occurring at a time when many populations are already under pressure from invading species and disturbances. Fragmentation and invasions also affect evolutionary processes by changing the way genes move around landscapes and by introducing novel genotypes into populations through hybridization.

This review considers the likelihood that evolutionary changes within species can contribute to species adapting to global climate change. Evidence for and against recent evolutionary adaptation is briefly discussed, along with the relevant evolutionary approaches and models that predict future evolutionary potential. Impacts of evolution on predicted changes in species distributions are discussed, as well as management practices that might facilitate evolutionary adaptation essential for long-term species persistence.

Plastic versus genetic change in time and space

The evolutionary potential of populations can be assessed in several ways (Table 1). Longitudinal studies of single populations help determine whether changes in traits have evolved (are genetic) or instead have occurred through plasticity (determined by the environment) (Table 1). Quantitative genetic models are often used to isolate genetic effects but these have been applied incorrectly in several longitudinal studies, resulting in phenotypic changes due to environmental effects being interpreted as genetic changes[18].

Where genetic and plastic contributions have been separated successfully, the latter often seem to be more important. This pattern has been noted for changes in bird population breeding dates[19] and for an increase in adult body size in marmots driven by early emergence from hibernation rather than genetic changes[20]. Also, a decrease in body size in a Soay sheep population was caused by environmental effects that decreased the growth rate of lambs, despite the presence of heritable variation for size[21] and selection favouring larger size.

On the other hand, there is abundant evidence for genetic adaptation to climatic conditions varying in space rather than time, particularly in cases where transplant/common garden experiments have been carried out along environmental gradients (Table 1). Transplants have been widely used in plants to demonstrate genetic adaptation to climatic changes involving altered aridity and thermal conditions[22,23]. Common

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Table 1 | Approaches for predicting and describing evolutionary responses to recent climate change in natural populations

Approach	Outcome	Limitation	Example references
Longitudinal studies testing for genetic changes in populations	Where relationships among individuals are available or genotypes can be repeatedly sampled and tested in a common environment, changes can be partitioned into genetic and environmental components.	Requires longitudinal and relatedness data or common environment comparisons, only possible for some populations.	21,85
Spatial studies across climatic gradients involving transplants or common garden experiments	Indicates the relative importance of plastic and genetic contributions to variation along a gradient. Can be used to identify patterns of selection.	May not indicate the speed at which adaptation occurs, patterns of local adaptation will depend on gene flow, transplants only possible for plants/relatively sessile organisms unless these can be confined.	24,43
Standing quantitative genetic variation estimates within populations	Heritable variation reflects evolutionary potential.	Only possible for subset of species, evolutionary costs of adaptation are not commonly measured.	26,86
Quantitative genetic variation estimated through selection experiments	Species/populations with genetic variation respond to selection, others do not.	Can be slow, requires multiple generation selection experiments, only possible for a subset of species, intense artificial selection and laboratory adaptation may mean results are not reflective of processes in natural populations.	28,37
Experimental evolution in simulated environments	Populations exposed to conditions relevant to climate change indicate potential for selection, may include biotic interactions.	Can be slow across multiple generations, may reflect genetic variation in direction of selection, but target of selection can be unclear.	87,88
Evidence of loss of function of candidate gene/protein	Where function has been lost, may indicate fundamental limits and loss of evolutionary potential.	Depends on understanding the biochemical/molecular basis of key ecological traits.	67
Genetic variation in candidate genes for traits pointing to potential for evolution	Where candidate genes control a substantial amount of the phenotypic variance in traits associated with climate adaptation, these might be directly assessed to indicate evolutionary potential.	Requires important candidates to be identified, applicable where phenotypic variation is controlled by major genes or their expression.	89,90

garden experiments have been applied to animal as well as plant populations to assess the relative importance of plastic and genetic effects. For instance, in common garden experiments with *Drosophila melanogaster,* environmental rearing conditions—which have a large impact on thermal resistance[24]—contribute around one-and-a-half times more than genetic factors to clinal variation in resistance[25]. Plastic responses themselves can evolve and contribute to climatic adaptation, as in the case of cabbage white butterfly populations, which differ in their plastic responses to temperature[26].

In an attempt to demonstrate evolutionary responses to climate change, genetic differences in space have been compared over time in a few cases (that is, combining the first two approaches listed in Table 1). These have provided the strongest evidence for evolutionary responses in traits related to the timing of activity or reproduction, including shifts in diapause patterns in mosquitoes[11], flowering time in plants[27] and migration patterns in birds[28]. Changes in spatial patterns can only be established when experimental investigations are repeated across years or when stored material such as seed is available[27], and when the direction of selection imposed through climate change is clear[28].

Indirect evidence can point to evolution as a probable explanation for longitudinal changes in trait patterns across gradients. For instance, several species of passerine birds from the east coast of Australia show a latitudinal cline for body size (smaller in tropical localities); this cline has undergone a shift over the last 100 years equivalent to 7.8° in latitude, and this is probably due to evolution because nutrition has not changed[29]. However, definitive evidence of longitudinal changes requires genetic effects to be clearly separated from environmental effects[19]. This may require repeated common garden experiments, whereas morphological or phenological data are normally only collected at the phenotypic level.

It has been suggested that climate change adaptation is more likely to involve altered timing of life history traits rather than evolved physiological responses[11], but this assertion seems premature. In pitcher-plant mosquitoes in which environmental diapause triggers have evolved, selection for phenological changes is strong[30] but selection for tolerance is weak[31], which may account for a lack of physiological evolution. Evolved tolerance changes will be more difficult to demonstrate than evolved timing changes because of the low repeatability of physiological assays. Nevertheless, evolved shifts in physiological limits will be critical in avoiding extinction if populations living close to their physiological limits are to persist under increasingly stressful conditions[2,12]. This might be achieved through evolving increased resistance within a life-cycle stage or through evolving a way of evading stressful conditions by entering an inactive stage such as diapause resistant to stressful conditions[32].

The absence of genetic adaptation to recent climate change now documented in some populations raises questions about the conditions under which evolution might be expected. Which factors might constrain or promote evolutionary responses? When they occur, will these responses be sufficient to keep up with rapid climate change?

Predicting evolution within populations

The evolutionary potential of populations to selection pressures associated with climate change can be measured through family studies and selection experiments in laboratory and field populations (Table 1). A simple model for interpreting the results of these experiments involves the breeder's equation, which predicts the size of the selection response given a certain selection pressure and trait heritability (Box 1 and Table 2). This equation applies across a single generation, although it has also been applied across multiple generations on the assumption that heritability and selection intensity remain constant. It can help highlight cases where a selection response is not possible owing to a low level of heritable variation[33] and/or rapid environmental changes and strong selection pressures[2].

A low genetic variance is usually regarded as unlikely to account for a poor selection response because most traits have quite high levels of genetic variation[34]. Widespread species often have abundant genetic variation for numerous traits likely to be involved in climatic adaptation including seasonal timing[11,35], morphological variation affecting thermal responses[36], and resistance to stressful climatic conditions both in insects[37] and in plants[38]. Genetic variation allows for local adaptation to climatic conditions in fitness-related traits[22] including traits potentially related to physiological limits as well as phenological timing[23,39]. On the other hand, some traits do lack genetic variation; the heritability of morphological traits and the timing of breeding can be very low in field populations[40,41]. Moreover, the heritability of desiccation resistance and cold resistance is very low in sensitive *Drosophila* species restricted to the wet tropics, in sharp contrast to their more climatically widespread (and more resistant) relatives[42]. A low heritability in one trait might reflect a lack of genetic variation generally due to low population size, but this is not the case in sensitive *Drosophila* species[42].

BOX 1

Population persistence models

Several models have been used to predict the response of traits to selection under climate change and to determine whether populations can successfully evolve through key traits to keep up with the rate of climate change. In the simplest case, the response to selection (R) (change in mean of a trait) is given by the breeder's equation, $R = h^2S$, where h^2 is heritability and S is selection differential, expressed as difference in selected mean versus mean of base population. This equation can be used to predict the response of a population to climate change across a generation and to test whether the response is adequate, assuming that one trait has overriding importance in population survival[2].

When multiple traits are considered, the multivariate equivalent of the breeder's equation is used, where $\Delta \mathbf{z} = \mathbf{G}\boldsymbol{\beta}$, relating a vector of changes in trait means ($\Delta \mathbf{z}$) to the genetic variance–covariance ($\mathbf{G}$) matrix and to the vector of linear selection gradients ($\boldsymbol{\beta}$). There is ongoing debate about how long the genetic variance–covariance matrix stays the same under multiple generations of selection. Where multiple traits influence fitness, the response to selection can depend on how interactions among traits influence fitness. Several ways of assessing the predicted changes in traits can then be applied[43], such as the change in trait means, $\Delta \bar{\mathbf{z}}$, through $\Delta \bar{\mathbf{z}} = \text{covA}[W, \mathbf{z}]$, where covA is the additive genetic covariance between all pairs of traits, w is individual relative fitness and $\mathbf{z}$ is the vector of traits.

Over multiple generations, the ability of a population to counter the effects of climate change will depend on population size. The critical rate of environmental change where population growth rate is maintained to be greater than 0 (k_c) is given by

$$k_c = \frac{V_A}{\sqrt{V_W}} \sqrt{2r_{max} - \frac{V_P}{V_W} - \frac{1}{2N_E}}$$

where N_E is the effective population size, V_W the width of the selection function, V_P the phenotypic variance, V_A the additive genetic variance, r_{max} the maximum growth without selection[47]. Other models incorporating demographic factors have also been developed[51].

Alternative formulations for critical environmental rate incorporating plasticity have also been developed, such as

$$k_c = \sqrt{\frac{2r_{max}V_W}{T}} \frac{h^2 V_P}{|B - b|}$$

where T is the generation time, B measures how environmental changes influence the optimal phenotype, and b measures plasticity[50]. A cost to plasticity can be included in formulations of these models.

A different class of models considers the ability of mutations to rescue asexual populations from extinction after climate change. Rescue only occurs when the fraction of rescue mutations (ϕ) as a proportion of the overall genome mutation rate (U) is defined as $\phi > -[r_0/(r_{0-r_1})][\ln(1-P)]/(2N_0U)$, where r_0 is the growth rate due to the stress, r_1 is the growth rate of the rescue mutations, N_0 is the initial carrying capacity and P is the probability of spread of the beneficial mutation[10].

Evolutionary changes take place in a multivariate space, where both genetic interactions between traits and the direction of selection across multiple traits dictate the potential for selection responses (Table 2). These factors can markedly slow rates of evolutionary adaptation[34], as demonstrated in some plants responding to rapid climate change[43]. Trait interactions may restrict shifts in breeding time in birds[44] as well as thermal adaptation in insects because genes increasing resistance to thermal stresses can have relatively lower fitness under favourable conditions in the laboratory and in nature[45,46]. Genetic interactions between traits may slow selection responses owing to tradeoffs or when there is a low genetic variance for traits in the direction of selection[34]. Strong constraining interactions or a low level of genetic variance can therefore provide an indication of whether rapid evolutionary adaptation is likely, but this is difficult to measure in practice.

Incorporating demographics and gene flow

Some models that predict evolutionary responses to climate change include details about population size and shifting patterns of stabilizing selection on populations (Table 2), emphasizing the importance of demographic factors in limiting adaptive responses in populations[47,48]. Large effective population sizes are required for maintaining genetic variation and evolutionary potential—typically a thousand rather than a hundred breeding individuals are required[47,49]. These models have recently been extended to include plasticity; this relaxes the conditions under which extinction is inevitable unless the costs of plasticity are high[50]. At small population sizes, demographic and environmental stochasticity will have a much larger impact on extinction probabilities than genetic variation[49], and demographic factors may lead to extinction even when populations have the requisite genetic variation to evolve[51].

Demographic factors have been emphasized in models of asexual populations where mutational input enables adaptive responses and beneficial mutations (already present in populations or newly arisen) increase in frequency to rescue populations by providing new genetic variation (Table 2). To avoid extinction, mutation rate and population size need to be sufficient to maintain beneficial mutations and counter demographic effects[10,52]. Populations need to consist of several hundred individuals for rescue through the introduction of new genetic variants to be effective when there is a sudden decrease in population size[53].

Gene flow among populations also influences the potential for evolutionary responses (Table 2), particularly at species margins that often represent sinks for dispersers from within the centre of species ranges. These dispersers may be maladapted to the conditions experienced at range margins, resulting in a fitness cost that prevents adaptation[54,55]. This might constrain evolutionary responses, as recently suggested for barnacles[56]. Gene flow may act in combination with other factors like trait interactions[57] and demographic effects[55] to constrain evolution.

Both demographic factors and gene flow can be incorporated into individual-based models of selection (Table 2). When these models are applied to elevation gradients in birch and Scots pine, they indicate that evolution is expected to keep up with a rapid rate of environmental change much more effectively when there is high mortality in established birch and pine trees, regardless of gene flow differences between the tree species[58]. Given sufficient knowledge about patterns of selection, dispersal and population size, individual-based models can provide detailed predictions about the ability of species to track environmental change through evolution.

Lastly, statistical models help predict the likelihood of evolution on the basis of the rates at which phenotypic changes in traits have evolved in the past (Table 2). Phenotypic changes can be dissected into genetic and non-genetic components according to formulations of the Price equation[21]; the strength of any evolutionary shifts can then be used to predict evolutionary adaptation into the future.

Adaptation and the rate of environmental change

The single population models in Table 2 predict that extinction rather than evolution is likely if environmental conditions change too quickly. Evolutionary responses might only be sufficient to allow changes of a few per cent per generation[47] unless there are also plastic effects acting alongside evolution[50], whereas bird breeding dates have shifted almost 20% in the last few years[19]. This raises the question of whether long-lived organisms in particular can evolve to keep up with rapid climate change.

As a lag develops between environmental conditions and the optimum values of a trait[47], the intensity of directional selection on the trait will increase. This could theoretically lead to a faster evolutionary response. Using the breeder's equation (Box 1), stronger directional selection should increase the rate of response across a generation because the selection differential will increase if heritability remains constant.

Table 2 | Models applied to understand evolutionary responses (or lack of these responses) and distribution shifts under climate change

Trait, population	Model	Nature of constraints	Limitations
One trait, one population	Breeder's equation (Box 1), where the directional response to selection across a generation depends on the heritability of a trait and intensity of selection.	Arise when heritability (h^2) is low in the environment where selection occurs[37] and/or selection is too strong[2].	Only applicable to one generation, although often applied to several generations. No interactions among traits, no stochasticity in demography or environment, indicates extent to which mean of trait can be changed under constant selection, h^2.
Multiple traits, one population	Multivariate equivalent of breeder's equation (Box 1), where continuous directional selection affects the vector of linear selection gradients and also the genetic variance–covariance matrix if this changes with the environment.	Constraints to selection responses can be detected through a combination of approaches[34] and occur when there is no genetic variance in the direction of selection, even in the absence of strong negative genetic correlations among traits.	Stochasticity in demography or environment not considered, limits only identified if relevant traits are included in variance–covariance matrix, which may alter across generations.
Multiple traits, one population	Various equations for describing how selection results in changes in traits that are connected to fitness (Box 1).	Link multiple traits to fitness, and then assess changes in traits when selection and interactions with other traits are taken into account[43].	As for multiple traits, one population.
One trait, one population (varying in size)	Models involving stabilizing selection with a shifting peak where fitness is normally distributed about a changing optimum value shifting at different rates (Box 1)[47], may include stochasticity[51].	Indicates the rate of environmental change that can be countered through evolution, also highlights effects of a decrease in population size in limiting evolutionary change.	Depends on traits being under stabilizing selection, as for other single trait models.
One trait (showing plasticity), one population	Stabilizing selection with a shifting peak where fitness is normally distributed about a changing optimum value and plasticity occurs (Box 1), which may have a cost[50].	Alternative formulation for critical environmental rate that can be countered through evolution, highlights potential effects of plasticity on countering extinction unless there are large costs associated with these responses.	As for one trait, one population (varying size).
Beneficial mutation influences fitness, one population	Model of sudden decrease in growth rate of population following stress, countered by evolutionary rescue through beneficial mutation (Box 1)[10].	Rescue depends on having a sufficiently high genomic mutation rate, population growth rate and population size.	Model is applicable to asexual microbial populations where model parameters can be estimated.
Marginal population and source population, unidirectional gene flow	Various models and simulations[54,55] of directional selection in marginal populations that predict potential for adaptation at margins under different levels of gene flow.	Intermediate levels of gene flow favour adaptation, ensuring presence of genetic variation but ensuring that dispersal load is not too high. Small population size and increasing fluctuations at margins make adaptation less likely[55].	Only applicable to a population spreading from periphery but constrained by migration load.
One trait (limiting fitness), multiple populations along gradient	Individual-based model on the basis of a mechanistic model of growth along an environmental gradient, with directional selection on trait depending on position along gradient[58].	Successful adaptation depends on patterns of dispersal and selection, whereas demographic factors influence efficiency of selection.	Only allows relative importance of dispersal and demographic factors to be considered when there is enough information on trait responses along gradients.
One trait, one population in the past	Price equation describing whether changes in trait values under climate change are due to selection or other factors including plastic responses to the environment[21]. Changes in average value of a trait over generations, decomposed into components due to selection and other factors, in particular environmental values.	The change in mean phenotypic trait value across a generation is given by $\Delta\bar{z} = \mathrm{cov}(W/\bar{W}, z) + E[(W/\bar{W})\delta z]$, where the first term is the covariance between trait value (z) and relative fitness ($W/\bar{W}$), and reflects the effects of trait selection, whereas the second term reflects the change in a trait arising from a lack of fidelity of transmission across generations, with δz being the discrepancy between an individual and offspring trait. Constraints arise when there is a large discrepancy and the effects of selection are not passed on across generations.	Statistical model for describing changes rather than predicting evolutionary responses where parameter values are known.
One trait (limiting distributions), multiple populations across landscape	Mechanistic model that is spatially explicit with threshold evolutionary model based on breeder's equation (Box 1), and climate variables that set selection intensity varying geographically[7].	Indicates potential of evolution to influence shifts in distribution under climate change, tests whether evolution has an impact on distribution and whether abundance shifts under climate change.	As for one trait, one population (limiting fitness), does not consider changes in population size or gene flow.

However, genetic variability available to selection might decrease rapidly under directional selection, particularly in small populations.

Under intense selection, trait changes are more likely to be due to genes with large effects, but major genes are often associated with deleterious effects[59], as illustrated by populations of the alga *Chlamydomonas reinhardtii* exposed to stressful conditions for 200 generations[60]. These populations had lower growth rates when more intense selection favoured genes with larger effects on traits, whereas slower rates of evolution reduced the cost of adaptation. It is not clear how often intense selection through rapid climate change will be constrained by the pleiotropic effects of major genes (when the same gene(s) influence two or more traits). In nature, selection will fluctuate from generation to generation[61], and selection responses will depend not only on the intensity of selection but also on the way environmental fluctuations are correlated[62].

Experimental evolution and phylogenetic constraints

Experimental evolution (Table 1) is a popular approach for monitoring adaptive potential in populations, particularly in microbes. In these experiments species or communities are exposed to simulated conditions likely to be encountered in the future. Examples of this approach include populations of *Chlamydomonas* exposed to increasing concentrations of ambient CO_2 for several hundred generations[63] and experimental populations of the bacterium *Escherichia coli* exposed for 20,000 generations to intermediate or high temperatures[64]. The *Chlamydomonas* experiments showed that increased CO_2 levels did not necessarily increase algal growth and carbon uptake, which are important for mitigation. The *E. coli* experiments showed that populations at 37 °C had improved performance in the range 27–39 °C, but decreased performance at lower and higher temperatures, indicating that at least some lines are likely to show

tradeoffs across different thermal conditions[65]. These types of experiments can be used to test specific predictions about evolutionary constraints, which might arise owing to pleiotropy or DNA decay (accumulation of mutations in genes leading to loss of gene function). Pleiotropy probably contributed to the decline in performance of *E. coli* at thermal extremes, whereas genes underlying mechanisms for concentrating carbon may have decayed in *Chlamydomonas* under high CO_2.

If genetic limits in species and populations arise because of DNA decay or pleiotropy, both processes could reduce genetic variation, which in turn might provide a surrogate measure for evolutionary potential. *Drosophila* climate specialists from wet tropical rainforests lack genetic variance for desiccation and cold resistance presumably because alleles required have been lost through decay or pleiotropic selection, even though the species have genetic variation for other traits and neutral markers[42]. An understanding of the mechanisms that underlie physiological constraints—such as oxygen limitation in marine organisms—can point to reasons for evolutionary limits[66], and the presence of decay in the genes underlying these mechanisms could reflect a low evolutionary potential. For example, some marine organisms adapted to stable, cold and well-oxygenated environments lack functional genes coding for proteins and regulatory systems for dealing with warmer conditions[67]. A fraction of climatically restricted species might never be able to adapt owing to such genetic limits. As information emerges on genes controlling variation in adaptive traits, genetic limits might eventually be identifiable from comparisons of species genomes[33] (Table 1).

Where phylogenetic information is available, evolutionary constraints can be studied across lineages. Related plant species including anemones, buttercups and mints that have been more prone to extinction in Thoreau's woods, Massachusetts, seem to lack variability in flowering time[68]; this might reflect a low genetic variance for flowering time or its plasticity. Conversely, the flowering time of invasive species has been responsive to temperature, potentially contributing to their expansion under recent climate change[69].

Hybridization

As some populations and species spread under favourable climatic conditions, new contact zones arise between related lineages, leading to interspecific competition but also an increased likelihood of hybridization between taxa[70]. Hybridization is often regarded as a negative outcome for conservation, both because diversity is lost when a species' genome is replaced, and because fitness declines following admixture[71]. Genome replacement is particularly likely in populations that are becoming small and peripheral under climate change, as in the case of peripheral wintergreen (*Pyrola minor*) populations facing extinction due to hybridization with more abundant *P. grandiflora*[72].

However, hybridization can also facilitate evolutionary adaptation. Molecular evidence indicates that the expansion of species' climatic ranges can be a consequence of past hybridization[73]. Moreover, hybridization can increase the evolutionary potential of populations by introducing genetic variation, as in Darwin's finches where interspecies hybridization has provided most of the genetic variance in morphology for adapting to changing conditions[74]. Lastly, hybridization may facilitate adaptation to new environments when hybridizing species are initially adapted to different conditions[75]. As species distributions shift under climate change and the incidence of hybridization increases, there may be some unexpected evolutionary consequences and even benefits when new variation is introduced into populations lacking adaptive potential.

Evolution in distribution modelling

With an increasing number of studies demonstrating the potential for evolutionary changes in populations (Table 1) and documenting its effects in natural populations through comparisons of traits or genetic markers[11], it seems appropriate to incorporate evolution into models that predict shifts in the distribution and abundance of species. This applies particularly to species with short generation times and large population sizes (that is, with the potential to evolve rapidly and maintain genetic

variation). At present, correlative distribution models, which have become particularly popular for predicting distribution shifts[76], consider correlations between species distributions and current climatic variables. These only include evolutionary potential to the extent that adaptive geographical variation affects the climate niche of species. However, the geographical ranges of introduced species commonly cover climate space outside areas in the native range, pointing to the importance of factors such as rapid evolution and species interactions in driving range expansion[77].

Evolutionary changes in traits should be incorporated into mechanistic models of species distributions. These models of energy and mass transfer for organisms and their microclimates start from first principles to identify the traits that limit distributions[78], which can then be allowed to evolve (Table 2). An example of this approach (Fig. 1) predicts changes in the distribution of the mosquito *Aedes aegypti* as a consequence of evolution in egg desiccation resistance[7]. In this model, evolution allows the species to become established in the city of Darwin under climate change, where it could then potentially transmit dengue fever. Without evolution, the species would fail to establish in Darwin. Mechanistic models have also been used to predict adaptive dynamics in plant populations[58].

Evolutionary components could be routinely built into mechanistic models to explore the potential impact of evolution on distribution shifts. Estimates of heritable variation, selection intensity and even demographic effects on genetic variance could be incorporated into these models.

Managing evolution

Because evolutionary processes are potentially important in dealing with climate change, evolutionary criteria should be considered in biodiversity management strategies[3,50]. DNA decay in genes that are functionally important, low levels of genetic variation, or phyletic conservatism may point to groups of species being particularly susceptible to climate change because of a limited capacity for adaptation. These species groups should receive particular attention in conservation programs.

Many populations of threatened species are confined to habitat fragments with limited options for dispersal under climate change. The adaptive potential of these populations is probably already low if they are small and have inherently low levels of genetic variance for traits limiting their distribution. For these populations, managers should consider any process that might increase their evolutionary potential,
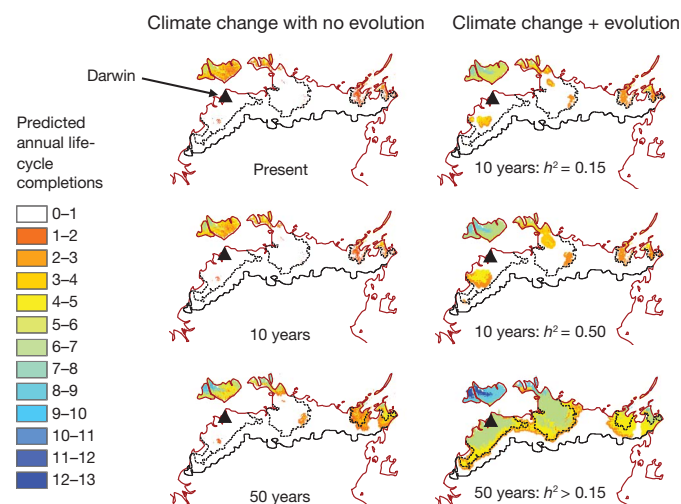

Figure 1 | Potential effect of evolution in egg desiccation resistance on life-cycle completions of the mosquito *Aedes aegypti* in the region around Darwin, Australia. Predictions are based on a mechanistic model of mosquito development with egg desiccation resistance evolving as a threshold trait determined by the length of time that eggs are exposed to air after water in breeding sites has evaporated. Modified with permission from ref. 7.

including improving connectedness with other populations even in the face of evidence for genetic distinctiveness[79].

Evolutionary potential could be used to identify populations and species that might be threatened in the future. Criteria based on patterns of local adaptation to climate gradients, probable levels of genetic variance now and into the future, and exposure to ongoing climate selection could all be used to identify species at risk. Models that incorporate the effects of climate change with evolutionary adaptation, demographics and stochastic variation could be developed to predict the likelihood of adaptation or extinction of populations[58]. Gene flow among populations in fragments may need to be maintained at intermediate levels to maximize local adaptation[55].

By considering evolution, the likelihood that key plant and animal species will persist within landscapes under climate change can be increased. For revegetation projects, seed of key species could be sourced from climatically diverse areas to increase the future speed of adaptation[80,81], although there is a risk that this might increase disease transmission and in some cases produce outbreeding depression (where the fitness of genotypes from population crosses is low). Where these problems are minor, seed and pollen could be deliberately exchanged between populations as a way of ensuring that some genotypes adapted to future climatic conditions exist in populations[80]. The genetic breadth of stock used in nurseries for propagating plants, fish and other groups could be expanded to capture evolutionary diversity in populations, including sourcing material from different climates.

When designating areas for reserves, areas containing high genetic variation across multiple species should be prioritized[82]. Areas for conservation should include climatic gradients where selection varies over small geographical areas, ensuring that genotypes adapted to different conditions are maintained[83]. Environmental heterogeneity also provides a way of ensuring that phenotypic variability is maintained in species[84], increasing the adaptedness of populations as conditions change. Reserves could be designed or modified to maximize evolutionary processes, by connecting areas to enable gene flow, and allowing for ongoing selection in response to fire, drought, thermal stresses and changing species interactions.

Future directions

The literature is now replete with examples illustrating the power of evolution to generate rapid phenotypic changes and influence community dynamics. However, empirical and theoretical studies indicate that some populations will have difficulty in adapting to climate change because of low trait heritability, overriding environmental effects on phenotypes, and strong but fluctuating selection pressures. Far more empirical data are needed to test evolutionary potential across groups of species, including those sensitive to thermal extremes and intermittently dry conditions. Evolutionary models of climate change responses need to be extended to incorporate stochastic climatic conditions. Individual-based models can provide precise predictions about the level of environmental change to which populations might adapt and the evolutionary processes that facilitate adaptation, but these models require detailed information only available in a few cases. In the absence of such information for the majority of species and in light of the complex selection pressures likely to arise from climate change, it seems prudent to incorporate evolutionary considerations in predictive modelling, and to take a precautionary approach when conserving sensitive species with a low adaptive potential.

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