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Species may respond to climate change by shifting in abundance and distribution, by going extinct, or by evolving. Predicting which will occur is difficult. Climate change may lead to alterations in both abiotic and biotic components of selection. Although there is evidence that abundant genetic variation exists in some species which can respond to such selection, other species seem to have little genetic variation for key characters determining distribution and abundance. Moreover, climate change can affect nonselective components of microevolution, such as genetic variances and covariances, and the magnitudes of drift, mutation and gene flow. There is almost no species for which we know enough relevant ecology, physiology and genetics to predict its evolutionary response to climate change.

A fundamental theme of ecology and biogeography is that climate is an important determinant, either directly or indirectly, of species' distributions and abundances¹⁻³. Species can respond to rapid climate change by: (1) changing distribution and abundance, without evolving; (2) extinction; or (3) evolving, perhaps coupled with an altered distribution or abundance.

Because species respond individually to the environment, there will be no typical evolutionary response to climate change. Moreover, all populations have tolerance limits to physical factors, beyond which extinction quickly occurs. Worrying about microevolution is moot when climate change is so extreme as to force rapid extinction. For the survivors, climate change could in principle influence all the driving forces of microevolution^{4,5}. In this commentary, I examine with broad brushstrokes those issues on the interface between ecology and microevolution that must be better

understood before we can predict the microevolutionary consequences of climate change.

The ecological context of microevolution

A perennial ecological problem is to disentangle the relative importance of biotic and abiotic factors in population dynamics⁶. Likewise, understanding how climate affects microevolution requires assessment of the relative significance of abiotic and biotic selective factors. The effective dimensionality of the selective regime - which is related to the dimensionality of the niche and adaptation - varies among species, and among populations within species.

Direct effects of climate are overwhelmingly important in the dynamics of some populations. In other populations, an altered biotic environment may be the principal consequence of climate change. The strength of interspecific interactions often depends on climate; for example, ladybird predation on aphids increases with temperature⁷. The strength of selection acting on both the predator and its prey will surely also vary with temperature. Our ability to predict the evolutionary effects of climate change is limited by a scarcity of mechanistic models that relate morphological, physiological and behavioral traits to demographic rates as functions of climate variables⁷.

If multiple abiotic and biotic factors influence demographic rates selection is likely to affect many characters simultaneously. Most evolutionary theory addresses single loci or characters, but adaptation to even a simple environ-

mental change may require changes in many characters. This increases the selective load and makes the direction of selection harder to predict, in part because of our insufficient understanding of community structure. Suppose that species A is reduced in density because of thermal stress; to predict the net effect on species B, in addition to any direct effect of A on B, one must account for the indirect effects cascading through chains of species linking the two species. Yodzis⁸ examined such 'press perturbations' in systems where all direct interactions between species were known to within an order of magnitude, and concluded that the sign and magnitude of net effects on abundance are highly indeterminate. This problem is aggravated by strongly nonlinear interactions⁹. It may be difficult to predict with any precision how biotic dimensions of the selective regime will be altered by climate change.

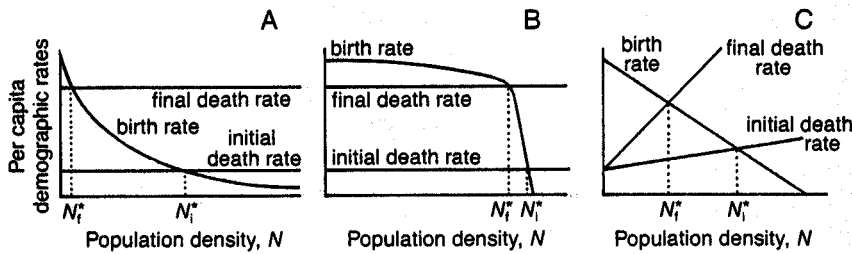
Unfortunately, few empirical studies simultaneously examine natural selection and population regulation¹⁰. In theory, climate change may alter selection without changing population size; conversely, population size can be depressed without changing selection (Box 1). In small populations, evolutionary rates can be limited by the amount of genetic variation maintained in the face of drift or generated *de novo* by mutation^{11,12}. Compensatory density dependence permits a larger effective population size in a deteriorating environment (Box Fig. B). Species with weak density dependence near carrying capacity (Box Fig. A)

The Microevolutionary Consequences of Climate Change

Robert D. Holt

Box 1. Population dynamics and natural selection

Graphical models depicting birth and death rates as a function of density are useful tools for analysing the interplay of density dependence and density independence in population dynamics⁶. The figures below illustrate several distinct ways in which a climatic shift can affect the equilibrium size of a population.



In each of the three figures, per capita birth and death rates are plotted against population density, N . The equilibrium population size is determined by that density at which birth rates match death rates (i.e. the carrying capacity, N^*). In each case shown, the effect of climate change is to increase the death rate, and thereby reduce equilibrium density from N_i^* to N_f^* . But the magnitude of the reduction depends on how density dependence operates.

In the populations shown in Figs A and B, birth rates are density dependent, but death rates are density independent. Assume that a change in climate increases average death rate in a density-independent manner. With a weakly density-dependent birth rate (Fig. A), an increase in mortality greatly depresses population size; with strong, compensatory density dependence (Fig. B), the same amount of environmental deterioration has a minor effect on population size. Compensatory density dependence permits a larger effective population size following climate change, which enhances the potential for adaptive modification.

If climate change induces density-independent viability selection in each population (e.g. by altering a physiological optimum), selection acts to decrease the average death rate. In Fig. A this increases population size; in Fig. B population size does not change markedly, despite the improvement in viability. Thus the effect of selection on population size in a changing environment depends on how a population is regulated.

Moreover, a change in population size will alter the selective environment only if there is a concomitant re-shuffling of the rank-ordering of fitnesses of alternative phenotypes and genotypes. For the population shown in Fig. C, there is density dependence in both births and deaths, and climate change intensifies the density dependence in deaths. If this density-dependent mortality arises from direct competition for suitable territories, and climate change simply reduces the number of suitable territory sites, the phenotype that is competitively superior before climate change may also ensure superiority after it. In this case, climate change will reduce population size without influencing the direction of selection.

that survive climatic modification may experience severe, sustained bottlenecks (compared to species with compensatory density dependence), and so are less likely to show substantial adaptive modification. Ironically, the populations that most 'need' to increase in density following a change in climate may be those least able to do so.

The impact of climate change on evolution in closed populations

With current rates of habitat fragmentation, an increasingly large fraction of Earth's biota is becoming restricted to island-like situations; for these, the question of evolutionary responses to climate change will be particularly acute.

In considering the likely responses of isolated populations, two straightforward approaches are: (1) start with known genetic polymorphisms (e.g. allozymes) and elucidate climatic influences on selection, and (2) analyse pheno-

typic responses to abiotic stresses using quantitative genetics. Studies in a wide range of species suggest that polymorphisms at many loci are correlated with climatic variables, particularly climatic extremes^{5,13}. Direct evidence that thermal stress is a selective agent at polymorphic loci comes from organisms as diverse as violets, mussels and ladybirds⁹ (see Parsons, this issue). Of the 121 species in Endler's survey of natural-selection studies¹⁴, 26 cases implicated climate in selection. Climate change should alter selection coefficients in these systems, leading to rapid genetic change.

The quantitative genetic approach to tolerance limits is exemplified by a study of Hoffmann and Parsons¹⁵, who selected for desiccation tolerance in *Drosophila melanogaster* (see Parsons, this issue). They observed a rapid response – with a high realized heritability – and several correlated responses, including increased re-

sistance to heat shock and starvation. They hypothesize that the selective response involves a general stress-resistance mechanism (allowing increased heat and cold tolerance) coupled with a lower metabolic rate. They suggest that this may be a general feature of physiological adaptation to climatic stress (see also Ref. 16). Species with such a response may become 'weedier', capable of exploiting a wider range of environments.

The selective impact of climate change via altered abundances of resources, natural enemies and mutualists may often outweigh direct physiological effects. Darwin's finches provide instructive examples of climate change leading to microevolution because of reduced resource availabilities¹⁷. The medium ground finch (*Geospiza fortis*) consumes a wide range of seed sizes; when seeds are abundant, all birds feed on soft, small seeds. During droughts these preferred seeds become rarer, and birds increasingly depend on large, hard seeds, which are more effectively exploited by large-billed birds. Increased small-seed availability during wet years reverses the direction of selection. Oscillatory changes in seed availability induce oscillatory microevolutionary responses¹⁸. The cactus finch (*G. scandens*) also experiences heavy mortality during droughts. Yet relative to its congener it has highly specialized feeding behavior, and the main effect of drought is to tighten stabilizing selection on body size¹⁷. Closely related species can thus show disparate evolutionary responses to climate change.

The conventional wisdom is that most characters in natural populations show high levels of genetic variation¹⁹. Direct evidence supporting this for traits that are demonstrably important in determining distribution and abundance is rather scant. Even in *Drosophila melanogaster*, selection experiments show that widening the tolerance limits to high temperature is difficult⁵. Although most traits are heritable, so that there will be some evolution following climate change, there are likely to be limits on the extent of the response. Some authors^{10,20,21} have argued that many species are depauperate for genetic

variation related to distribution and abundance – a condition termed *genostasis* by Bradshaw²¹. For instance, Huntley *et al.*² found that the distribution and abundance of beech (*Fagus*) in Europe and in North America can be described by very similar climate-response surfaces (though these lineages have been separated for millions of years), and they concluded that 'the physiological characteristics determining the species' distributions are presumably evolutionarily conservative'.

Strong directional selection induced by climate change may push populations to selection limits, analogous to those observed in artificial selection. In directional selection experiments, populations typically reach response plateaus by 10–20 generations²², though plateaus may later be transcended because of recombination or mutation. The response may cease because selection consumes the additive genetic variance for the selected trait; or because of countervailing selection on other, pleiotropically linked characters; or because in small populations, drift depletes variation²³. For outbred species, inbreeding depression in small populations further aggravates fitness reductions caused by environmental deterioration. Larger populations permit greater final responses to a given intensity of selection, as they are more likely to harbor alleles without deleterious pleiotropic effects²³. Overall, rarer species are less likely to show significant adaptive responses to climate change.

Adaptive evolution involving major mutations seems most prevalent in severely disturbed populations; strong selection is needed to overcome the deleterious pleiotropic effects associated with major mutations²⁴. A given secular change in climate is experienced as a severe deterioration in the environment by organisms with long generations, but as a gradual worsening by organisms with short generations. All else being equal, selective responses in the latter are more likely to involve polygenic responses.

If a novel selective pressure depresses effective population size, drift will reduce additive genetic variance. This may be partially off-

set by other processes. If the original population has nonadditive (epistatic) genetic variance in fitness, a moderate-sized bottleneck persisting for several generations can convert this into additive genetic variance²⁵. In *Drosophila* and other organisms, rates of recombination and mutation increase in stressed populations^{4,26}; this may increase additive genetic variation in fitness, but in the short run it also depresses mean fitness. Parsons⁴ has argued that additive variance for characters related to fitness increases in stressful environments, because fitness differences among genotypes are accentuated in stressful circumstances; however, in some cases heritabilities are reduced in suboptimal conditions²³.

To estimate short-term selective responses, one must know the additive genetic variances and covariances of selected traits^{22,23}. Measuring these quantities prior to climate change may not be very useful for predicting the direction of evolution subsequent to the change, simply because the phenotypic expression of genotypes depends on the environment; the novel environment may alter the elements of the genetic variance-covariance matrix²³. A number of experiments show that genetic covariances among traits change as a function of temperature²⁷. In general, genotype-environment interactions hamper our ability to predict selective responses to changing environments²³.

The impact of climate change on continental populations

In a closed, island-like population, one can assume that conspecifics largely experience similar selective pressures. In widespread continental species, by contrast, climate change will be experienced differently by different populations along gradients. For several reasons, the evolutionary consequences of climate change are likely to be qualitatively different on continents than on island-like systems.

First, more species are available to invade and supplant a given continental species at a site following climate change. Relative physiological tolerances are an important, albeit neglected, component of competitive ability (J. Travis, pers.

commun.). The classic experiments by Park²⁸ with *Tribolium* demonstrate that the outcome of interspecific competition varies sensitively with climatic conditions. Climatic shifts can lead to rapid alterations in community structure because of reversals in competitive dominance. A species might in principle be able to adapt to a local climate change, but before recombination and selection have sufficient time to generate the locally optimal genotype, other species (competitors, predators) that are already well adapted to the novel environment could invade and exclude it.

Second, dispersal permits a species to shift its range and persist, often without evolution. Habitat selection permits organisms to restrict their activities to habitats to which they are already well adapted¹²; the selective environment experienced by a species may not change even though climate does.

Third, individualistic species' responses to physical gradients imply that the constellation of species comprising the biotic selective environment will vary, kaleidoscope-like, across space²⁹. Directional changes resulting from selection are likely to be ephemeral, and in different directions in different places. Without speciation, as populations move about in space they will meet and merge, tending to wash out local adaptive modifications³⁰.

Finally, gene flow between high- and low-density populations hampers selection in the latter³¹, particularly when selection acts independently on multiple characters¹. Dispersal allows a species to track the environment to which it is best adapted, but also constrains adaptive improvement in less well-adapted, low-density populations. An additional complication is that climate change will change population structure, via changes in local abundance and dispersal patterns, and evolution may proceed differently in structured than in unstructured populations.

When does natural selection retard extinction?

Most evolutionists agree that the direction of selection is independent of the effect of such selection upon the likelihood of species

Box 2. A model relating population persistence to dispersal and evolution

To examine quantitatively the effect of evolution on population persistence, one must develop models that simultaneously describe changes in population size and genetic composition. Most models of population persistence ignore evolution and assume that there is no secular trend in environmental conditions. In a recent paper, Pease, Lande and Bull³⁶ relax these assumptions, by allowing the environment to move smoothly across a landscape, and by permitting the population to evolve toward the optimal mean phenotype at each point in space.

Their model assumes that a species is distributed across an environmental gradient, with density $n(x,t)$ at location x at time t . Subpopulations at different points on the gradient are coupled by dispersal. At any point in time, the mean fitness $\bar{W}(x,\bar{z},t)$ of a subpopulation is a function of its position on the gradient and of its mean phenotype, \bar{z} . It is assumed that in an unchanging environment without dispersal, the population grows exponentially with an intrinsic rate of growth equal to $\ln \bar{W}$, and that there is a constant amount (G) of additive genetic variance for the character. The model consists of two coupled partial differential equations (for simplicity, $n(x,t)$ is denoted by n):

$$\frac{\partial n}{\partial t} = n \ln \bar{W} + \frac{\sigma^2}{2} \frac{\partial^2 n}{\partial x^2}$$

(population growth) = (in situ growth) + (net dispersal)

$$\frac{\partial \bar{z}}{\partial t} = G \frac{\partial \ln \bar{W}}{\partial \bar{z}} + \frac{\sigma^2}{2} \frac{\partial^2 \bar{z}}{\partial x^2} + \sigma^2 \frac{\partial \ln n}{\partial x} \frac{\partial \bar{z}}{\partial x}$$

(rate of evolution in \bar{z}) = (local selection) + (simple mixing) + (source-sink flows)

where σ^2 is the mean-squared distance that individuals move per generation, assuming random dispersal. In this model, dispersal may permit a population to track a varying environment, but it also precludes precise, local adaptation. The model is completed by specifying $\bar{W}(x,\bar{z},t)$. Pease *et al.* assume that mean fitness is a bivariate gaussian function of mean phenotype and spatial position. The spatial position at which the population has a maximal growth rate moves at a constant rate across space. When the population persists, it settles into a gaussian spatial distribution in abundance, with a linear character cline. The modal population density lags behind the most favorable environmental position, and nearly all subpopulations are to a degree maladapted to local conditions. Above a threshold rate of environmental movement, the population goes extinct. A larger value for G permits the population to persist at higher rates of environmental movement.

To see the connection with the Fundamental Theorem, consider an island population with a low dispersal rate (i.e. $\sigma^2 = 0$). This decouples evolution from population dynamics; the rate of population growth depends upon phenotypic evolution, but not the converse. For simplicity, assume that a simple linear function describes the effect of environmental deterioration after a sharp climatic change (e.g. hard, directional selection): $\ln \bar{W} = r - vt + a\bar{z}$, where r is a basic population growth rate, v is the rate of environmental deterioration, and the quantity a defines a linear relation between the mean character state and fitness. If $d(\ln \bar{W})/dt = a^2G - v > 0$, the population will eventually have a positive growth rate, and so (deterministically) persist. If we measure the character in units of fitness ($a = 1$), the persistence condition is merely $G > v$. For the population to persist, the additive genetic variance in fitness must exceed the average rate of environmental deterioration in fitness.

Although one might quibble about various features of this model (e.g. the assumption that genetic variance in fitness is constant, even though the environment and population size are constantly changing), it represents an important advance toward understanding more precisely how evolution and environmental change influence population persistence.

extinction³². Let's say that the environment changes from state E to E' , that because of this environmental change a species evolves from phenotype P to P' , and that had the species not evolved (i.e. had it stayed at P) it would have gone extinct. Surely it is fair to say that in such cases evolution prevents extinction, even if the avoidance of extinction does not itself cause evolution. It is important to identify circumstances in which microevolution, as a happy by-product, enhances population persistence.

There is surprisingly little direct evidence on this. For instance, one datum omitted from most reports of artificial selection experiments is the frequency with which selected lines have gone extinct during the experiment, as a function of selec-

tion intensity. If climate change forces the mean absolute fitness of a population below 1.0, even after density-dependent responses are accounted for, then in the absence of evolution extinction is inevitable.

Selection prevents or at least retards extinction only if natural selection increases mean absolute fitness. This occurs when Fisher's Fundamental Theorem of Natural Selection is at least approximately true. The Fundamental Theorem in its usual interpretation states that the rate of change in mean fitness is proportional to the additive genetic variance in fitness. Some authors³³ are dubious about the utility of the Fundamental Theorem because of the restricted circumstances in which it is valid. However, for our purposes these restrictions usefully

delimit those conditions in which selection fosters population persistence.

Imagine that an island population was in approximate evolutionary equilibrium prior to climate change. In the new environment, previously hidden variability is released via recombination or genotype-environment interactions. If individual viability is determined by variation at a single major locus, or by alleles of small effect at many weakly linked loci, and fitnesses are frequency independent, selection increases mean fitness³⁴. Mean fitness can decrease during selection if viability depends on several linked loci with epistasis, or if selection acts at levels other than the individual (e.g. fertility selection), or if fitnesses are frequency dependent³⁴. Some sources of frequency-dependent selection (e.g. predator switching) may become less important as population numbers decline. If this is generally true, populations driven to low densities by climate change may better fit the assumptions of Fisher's theorem than do abundant populations, and selection will tend to enhance population persistence, to the limit allowed by genetic variation.

Pease, Lande and Bull³⁵ have recently developed a model that examines how selection may permit a species to survive in a changing environment (Box 2). Their model, which couples an equation for evolution of a quantitative character with a population dynamic equation by means of mean population fitness, is in some ways a concrete application of Fisher's theorem. Their results suggest that an increase in genetic variance does indeed enhance population persistence.

Conclusion

The problem of predicting the microevolutionary consequences of climate change for even a single species is dauntingly complex. There are many gaps in our current understanding. Some are mainly genetical, such as predicting how genetic variance-covariance matrices will be affected by changing physical environments. Some are mainly ecological, such as ascertaining how the indirect effects of abiotic stresses percolate through

communities of interacting species. Others lie squarely on the interface of genetics and ecology, such as measuring extant genetic variation for key traits determining distribution and abundance.

A disturbing theme that emerges from the literature is that species expected to have substantial adaptive responses to climate change that can promote their persistence—i.e. those with high abundances, wide geographical distributions, short generation lengths, high dispersal rates, etc. — are just those species least at risk of extinction in any case. In contemplating the biological consequences of climate change, maybe we should worry most about those species that do not evolve.

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