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Evolutionary aspects of climate-induced changes and the need for multidisciplinarity

C. Pertoldi[a,b,*], L.A. Bach[c]

[a]Department of Ecology and Genetics, University of Aarhus, Building 540, Ny Munkegade, DK-8000 Aarhus C, Denmark
[b]Department of Wildlife Ecology and Biodiversity, National Environmental Research, Institute, Kalø Grenåvej 14, DK-8410 Rønde, Denmark
[c]Department of Theoretical Ecology, Ecology Building Sölvegatan, Lund University, SE-223 62 Lund, Sweden

Abstract

An integrated view on the possible effects of global climate change is provided while taking into account that not only the rising average temperature is likely to impact natural populations but also that increased variation around the mean and higher frequency of extreme events will be important. We propose that complex genetic effects in concert with demographic patterns may affect how focal populations react to the environmental challenge in an adaptive way (if they can). In order to aim for an inclusive picture of the ongoing environmental change we argue for a synthesis of knowledge from a range of 'classical' disciplines such as quantitative genetics, conservation genetics and population ecology. A hereto little exposed concern is the importance of the increase in amplitude of environmental fluctuations and how the corresponding evolutionary and ecological reactions are expected to occur. Due to the complex interactions between the ecological and genetic mechanisms in the response to climate-induced impacts interdisciplinary approaches are the most promising path in seeking knowledge about the present and future changes in the biosphere.

Keywords: Climate change; Genetic diversity; Fluctuating population size; Environmental variability; Adaptive potential

1. Introduction

1.1. Known consequences of the increasing average temperature

1.1.1. Temperature increases and future projections

The climate changes with regard to several variables (e.g. temperature and precipitation) and measures (e.g. averages and extremes), of which, change in average temperature is the most frequently monitored. The global environment is currently affected by temperatures changing with a speed surpassing estimates of the past 10,000 years. The average global temperature has increased by 0.7° over the past century and future projections show a substantial acceleration (Walther et al., 2002). According to the intergovernmental panel of climate change (IPCC) emission scenarios predict the Earth's mean surface temperature to rise from 1.4° to 5.8° by the end of the 21st century (IPCC; http://www.ipcc.ch).

1.1.2. Effects of temperature increases on biodiversity

Most studies focus on the consequences of climate-induced environmental changes (CIEC) for biodiversity at various scales including: distributional range of species, phenology, community structure and species interactions (Walther et al., 2002; Cleland et al., 2006). Of a total of 47 invertebrates, 10 mammals, 59 plants, 29 amphibians and reptiles and 388 birds species and approximately 80% of analysed species showed changes in the biological parameters measured in the manner expected with global warming. Not only increasing temperatures but also prolonged and more frequent extreme events are thought to affect biodiversity at various levels (IPCC; http://www.ipcc.ch).

A reduction in species diversity as well as retrogression to opportunistic species and shifts to smaller-sized species are expected phenomena in stressed communities as previously documented by Forbes and Forbes (1993).

*Corresponding author. Department of Ecology and Genetics, University of Aarhus, Building 1540, Ny Munkegade, DK-8000 Aarhus C, Denmark.
E-mail address: biocp@nf.au.dk (C. Pertoldi).

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Under climate change, the ability of communities to respond rapidly changing conditions is of particular interest. The biodiversity in grazing lands can maintain productivity in response to stressors such as pests (Altieri, 1999) and drought (Tilman and Downing, 1994). The net effect on communities is, however, a complex balance between immigrating species and the emigrating indigenous species. This immigration–emigration phenomenon becomes evident as recent findings suggest global warming to shift the species' spatial distributions on average 6.1 km per decade towards the poles (IPCC; http://www.ipcc.ch).

1.1.3. Effects of temperature increases on genetic variability

The immigration–emigration spatiotemporal dynamics has profound consequences for the population genetic structure (Kaitala et al., 2006), and since migration itself can evolve due to environmental stochasticity and genetic relatedness the consequences may be hard to predict (Gandon and Michalakis, 1999; Bach et al., 2006). Increased gene-flow typically increase the genetic variability of populations while simultaneously reducing their local adaptation (Holt and Gomulkiewicz, 1997; Lenormand, 2002). In a population, the actual degree of adaptation is the residual effect of the dynamic interaction between the selective pressure acting on the population and gene flow. Hence, high levels of gene flow can reduce or impede the capacity of adaptation to a stressor (Comins, 1977; Taylor and Georghiou, 1979; Roush and McKenzie, 1987) or may introduce essential new genes for future adaptation or increase the tolerance of the populations (Slatkin, 1987; Caprio and Tabashnik, 1992; Orrock, 2005, Swindell and Bouzat 2006). The importance of gene flow as a force for the maintenance of genetic diversity and avoidance of inbreeding depression is therefore quite evident (Guillaume and Perrin, 2006). However, high levels of gene flow also have the potential to introduce poorly adapted genes (outbreeding depression) that can reduce viability of the population (Andersen et al., 2002). A shift in distribution range due to climate change reducing the area available for a species can decrease the effective populations size (N_e). This may render the patches isolated and vulnerable to stochastic environmental extinction and/or inbreeding depression (Bijlsma et al., 2000). The obvious example of a direct impact of increased average temperature is the 'summit trap phenomenon'; species inhabiting mountain summits are forced to move to higher altitudes when temperatures increase. They have no escape route and may become locally extinct and even if the population do persist the restriction of the suitable habitat reduces the carrying capacity, which in turn depresses the N_e. Limited habitat ranges due to increase temperature are furthermore accelerated by human-induced habitat fragmentation, which may reduce the exchange of individuals (and consequently gene flow) between populations. In addition, the spatiotemporal patterns of autocorrelation and synchronicity of demographical and environmental origin (Lundberg et al., 2000; Ranta et al., 2006) may strongly affect N_e in itself, but may also interact with the effects of habitat deterioration. The rate of loss of genetic variability is related to the N_e which is a valuable predictor of a population's capacity to survive in a changing environment and more reliable than the census size. Small populations are dominated by random genetic processes (genetic drift) leading to loss of genetic variability, which may depress the evolutionary potential and thereby the ability to respond to changing environments (Bijlsma et al., 2000; Pertoldi et al., 2006). Ultimately, populations only persist if the rate of adaptive evolution at least matches the rate of environmental change (Bürger and Lynch, 1995). A requirement for any evolutionary response of quantitative traits to selection is the presence of heritable variation as phenotypic response to selection is the product of additive genetic variance (σ_a^2) times the selection differential or standardized intensity of selection coefficient. (Lynch and Walsh, 1998).

Firstly, with accelerating environmental changes the demand for rapid adaptation becomes pronounced as the selection differential increase, as in the simplest case, where a optimum mean trait value shifts as a result of e.g. a rise in mean temperature. This requires a 'standing crop' of genetic variation in order for the population to track the moving optimum. Studies have observed evolutionary responses to the current directional climate change (Rodriguez-Trellis and Rodriguez, 1998; Bradshaw and Holzapfel, 2001; Pulido and Berthold, 2004). However, the response of a single trait to selection may be inhibited by antagonistic selection on a genetically correlated trait (Lynch and Walsh, 1998) and genetic correlations have been found to be sufficiently large to limit the potential response to climate change (Etterson and Shaw, 2001).

Quantitative genetic models of wild populations have investigated whether they will adapt or go extinct in response to continuous environmental change (Bürger and Lynch, 1995; Lande and Shannon, 1996). Gomulkiewicz and Holt (1995) concluded that only large populations experiencing relatively small environmental changes are likely to be rescued by evolution. If the population becomes very small, the selective pressures should be overwhelmed by genetic drift effects, making all traits and genes effectively selectively neutral and the population become unable to react in a adaptive way to a selective pressure despite the presence of genetic variability. The existing analytical models in population genetics do not directly include environmental and demographic stochasticity. This is a serious omission because these stochastic effects may cause the extinction of a population even if its mean intrinsic capacity for increase is positive (May, 2001).

1.2. Less known consequences of temperature increases due to increased temperature fluctuations

1.2.1. Empirical and theoretical evidences for increased environmental variability

Theoretical studies have established that both statistical and biological mechanisms have the potential to influence