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Tracking the genetic effects of global warming: *Drosophila* and other model systems

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ABSTRACT

Current efforts to study the biological effects of global change have focused on ecological responses, particularly shifts in species ranges. Mostly ignored are microevolutionary changes. Genetic changes may be at least as important as ecological ones in determining species' responses. In addition, such changes may be a sensitive indicator of global changes that will provide different information than that provided by range shifts. We discuss potential candidate systems to use in such monitoring programs. Studies of *Drosophila subobscura* suggest that its chromosomal inversion polymorphisms are responding to global warming. *Drosophila* inversion polymorphisms can be useful indicators of the effects of climate change on populations and ecosystems. Other species also hold the potential to become important indicators of global change. Such studies might significantly influence ecosystem conservation policies and research priorities.

KEY WORDS: biodiversity conservation, biological indicator, chromosomal inversion polymorphism, climate change, evolutionary ecology, genetic diversity, global warming, microevolution.

GENERAL ISSUES

The current greenhouse–induced increase in world temperatures is exceedingly rapid compared with prehistoric climate changes of similar magnitude (Vitousek 1992, Schneider 1993). In the face of such global environmental change, adaptive evolution may be the only route to many species' long–term survival (Travis and Futuyma 1993, Lande and Shannon 1996). In spite of their potential relevance, microevolutionary responses have, however, been largely neglected in detecting biological consequences of global warming. Most studies assume that worldwide climate amelioration will lead primarily to shifts in species' geographic boundaries (Schneider 1993), and have correspondingly focused on tracking population movements at species borders (Parmesan 1997),

with little or no interest in genetic analyses. Although some already claim that climate warming is affecting species' distributions (Parmesan 1997), we know little about microevolutionary responses, which may occur instead of, or in conjunction with, boundary shifts. Because species differ in their ability and rate of migration (Davis 1981), both demographic and evolutionary processes need to be studied.

At least some species have the potential to experience substantial adaptive responses to climate warming. In turn, these rapid adaptive responses might affect genetic or chromosomal diversity at some localities. Such responses are scarcely surprising, given the many examples in plants and animals that document rapid adaptation to environmental change (Endler 1986, Travis and Futuyma 1993). However, because of the recent emphasis on boundary shifts, the potential importance of genetic change seems to have been forgotten.

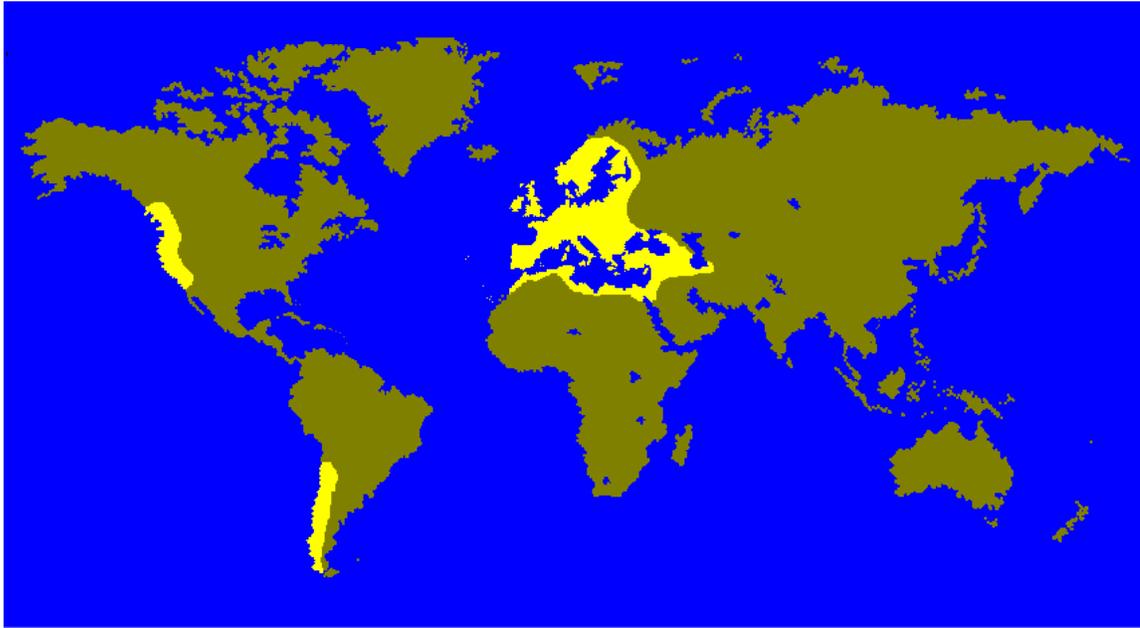
Identifying sensitive and reliable indicators for assessing levels of environmental change is a priority for population and community research on global change (Kingsolver et al. 1993, Bella et al. 1994). However, solely monitoring species dynamics is insufficient if we are to understand biotic responses to global change. Efforts must take into account variation within and among populations. For example, population dynamics are responsive to changes in gene frequencies (e.g., Richardson 1974, Kingsolver and Watt 1983, Watt et al. 1983, Hilbish and Koehn 1985, Templeton et al. 1990). Thus, the ultimate responses of the world's species to global change will depend on levels of genetic variation.

In this paper, we examine the issue of monitoring microevolutionary change as a way of studying the effects of global change. We look at this issue at several levels. At the most detailed level, we consider recent data on *Drosophila subobscura*. Changes in chromosomal inversion frequencies in this species present the clearest evidence to date of a microevolutionary response to global change (Rodríguez-Trelles and Rodríguez 1998). This species also holds great promise as a model system for such studies over much of the world. At a more general level, we examine the potential for the genus *Drosophila* to serve as a broad-scale indicator group. Finally, we suggest other well-studied species that might also be monitored or measured.

MICROEVOLUTION IN *D. SUBOBSCURA*

Since the discovery of variation in the polytene chromosomes of *Drosophila* (Sturtevant and Dobzhansky 1936), inversion polymorphism studies have revealed some of the intricacies of evolutionary change. In most cases, climate-related variables have been invoked as the major factors that determine the frequency of inversions in natural populations. The Palearctic species *D. subobscura* provides the most conclusive evidence that this is indeed the case (Fig. 1). There are well-established latitudinal clines in the original populations of this species for its five large, acrocentric chromosomes (Krimbas 1992). The clines have also independently evolved in the recently colonized areas of North and South America (Prevosti et al. 1988), strongly suggesting that temperature is the most important variable.

Fig. 1. Worldwide range of *Drosophila subobscura*. Originally an Old-World species, it has recently colonized North and South America.



Extensive research makes *Drosophila* chromosomal inversion polymorphisms one of the best known genetic systems (Krimbas and Powell 1992). In the particular case of chromosome *O* of *D. subobscura*, more than 30 different inversions have been described (Krimbas 1992), many of them showing spatiotemporal heterogeneous distributions (Menozzi and Krimbas 1992) as well as seasonal cyclic variation (Rodríguez-Trelles et al. 1996). These studies strongly suggest that different inversions carry alleles that are differentially favored in warm and cold climates. Studies of the geographical distribution of its chromosomal polymorphisms in the Palearctic date back to the mid-1950s (Krimbas 1992; see [Appendix](#)). About 140 different populations have been investigated throughout this region. From this information, one could build detailed maps of the spatial distribution of the species and its inversions (Krimbas and Loukas 1980, Krimbas 1992, Menozzi and Krimbas 1992).

Long-term monitoring of inversion frequencies in a Spanish population found seasonal variation that fits expectations based on the latitudinal clines (Rodríguez-Trelles et al. 1996). The seasonal variation is coupled with a long-term decline in the frequency of those inversions presumably carrying alleles associated with adaptation to colder temperatures. We (Rodríguez-Trelles and Rodríguez 1998) observed an 18.3% decrease in inversion diversity of chromosome *O* during the period 1976 -1991. This decline is strongly correlated with the climate-warming that has affected the northern hemisphere since the mid-1970s. Thus, these results conform to projected scenarios on the effect of climate-warming.

We can use this genetic information to better predict the fate of *D. subobscura* in Iberia and Europe. The key is several inversions that differ in the sensitivity of their alleles to temperature: *OST*, whose carriers perform better in colder environments, and *O₃₊₄*, among others, which predominate in warmer environments. Extrapolating from available temporal data in the Iberian peninsula, it appears that the *OST* inversion, with its alleles that improve performance in the cold, is being replaced there by the inversions that improve warm-temperature performance. This replacement insures the persistence of the species in the Iberian peninsula for now. This adaptive process could not be detected solely by tracking population numbers.

This information also provides insight into species' range changes, as such shifts may be due to microevolutionary changes. In Europe, *D. subobscura* has shifted toward northern latitudes (Saura 1994). Presumably, shifts in the species' range resulted from flies carrying the *OST* gene arrangement. Thus, rather than a mere local change in population density or range expansion, the advance of *D. subobscura* to the north may

reflect differences among genotypes in their ability to cope with the new environment. Knowledge of these responses will be critical in understanding the evolutionary potential of species' responses to global warming. Gathering genetic information (e.g., inversion frequencies) along with demographic data may reveal adaptive responses. We emphasize that genetic studies cannot replace demographic and range data, rather that they are a vital complement to them.

Direct, long-term monitoring of some representative populations, with an emphasis on species boundaries, could produce, in the near future, critical information on how climate warming is affecting the spatial distribution of inversions and their rates of change. *Drosophila subobscura* recently colonized North and South America. The newly occupied territories provide abiotic environments that replicate those in the Palearctic (Prevosti et al. 1988). In addition, several potentially important traits, such as body size and developmental rate, are associated with some gene arrangements in this species (Misra and Reeve 1964, Prevosti 1966). Recording quantitative variation, in conjunction with inversion data, can provide insights on phenotypic responses to climate change. The genetic architecture of responsive quantitative traits could be explored subsequently in the laboratory, using techniques such as QTL mapping. By mapping this variation to different gene arrangements (e.g., *Ost* vs. *O₃₊₄*, evolutionary changes in important life history traits can be easily tracked.

Additional efforts can focus on relevant major loci. Candidate genes for these analyses are the *Hsp70* family. These genes are expressed in response to multiple harmful situations, including abnormally high temperatures. The resulting proteins enhance the probability of survival by increasing resistance to stress. Studies in *D. melanogaster* showed that differences in the number of *Hsp70* gene copies imply dramatic differences in viability to heat shock treatment in the lab (Feder et al. 1996). In *D. subobscura*, this gene family controls the principal inducible heat-shock protein, and is located on the *O₃₊₄* inversion region (89A and 90A loci; Moltó et al. 1992). A challenging hypothesis, yet unexplored, is that observed spatiotemporal patterns of chromosomal polymorphisms reflect differences in the number of heat shock gene copies among inversions. Indeed, differences in copy number have already been found associated with inversions in other gene families (e.g., the *amylase* region in *D. pseudoobscura*; Aquadro et al. 1991). Besides the heat shock genes, the clock gene period (*per*) has recently become a focus for studies of microevolutionary effects of climate warming. In *D. melanogaster*, the major length variants of the *per* gene exhibit a clinal distribution in Europe and North Africa that is causally related to the flies' ability to maintain a circadian period at different temperatures (Sawyer et al. 1997). Progress at identifying chromosomal homologies in the *Drosophila* genome project will no doubt provide extremely valuable information for these studies.

THE GENUS *DROSOPHILA* AS A MODEL SYSTEM

Owing to their relatively narrow physical limits for resource utilization, *Drosophila* species have been recognized as potentially useful candidates for assessing levels of environmental change (Parsons 1991). Because chromosomal inversions can have large fitness effects (Wright and Dobzhansky 1946, Dobzhansky 1947), they are extremely valuable in monitoring genetic variation for stress-response. In addition, in contrast to single-locus approaches (e.g., allozyme markers), inverted blocks of genes contain multiple loci with linkage and epistatic interactions, thereby providing a more realistic basis for exploring phenotypic responses in potentially key ecological traits.

Comprehensive data on chromosomal inversion polymorphisms exist for a number of *Drosophila* species, including the closely related nearctic *D. pseudoobscura*, the nearctic *D. robusta*, and *D. repleta*; the neotropical *D. willistoni*; the cosmopolitan *D. melanogaster*; and the subcosmopolitan *D. buzzatii*. Detailed information on some of these species can be found in Krimbas (1992). For exhaustive lists of published literature on *Drosophila*, see [Flybase Home Page](#), and [The Drosophila Virtual Home Page](#).

On the technical side, use of *Drosophila* chromosomal polymorphisms could benefit from methods for fly sampling, and chromosomal isolation and identification, fly marker stock availability, techniques for

chromosomal staining, and maps of chromosomal inversions, which are easy to carry out and are already optimized and standardized across laboratories. This standardization simplifies comparisons among research groups.

Besides its potential advantages, using chromosomal inversion polymorphisms to monitor the biological consequences of climate change also faces some limitations. The most serious are current limits on our understanding of the ecology of *Drosophila* and how it is connected to evolutionary processes. Measuring gene flow among populations and the capacity to colonize new habitats are examples of this concern. These aspects can critically affect population structure and the ability of a species to exploit its total genetic variation to respond to novel conditions (Travis and Futuyma 1993). We still need to determine which key ecological factors limit species' distributions, and which phenotypic traits determine survival under rapid environmental change

OTHER SPECIES

We have emphasized the genus *Drosophila* because it is such a well-studied system worldwide. Other groups, however, have much the same potential. We describe a few here to indicate potential research avenues. In general, any such group should have the following properties: (1) a relatively well-studied genome and ecology; (2) easily monitored genetic markers; and (3) a relatively short generation time, so that microevolutionary responses are likely to be observed.

Among insects, grasshoppers are both important ecologically and well-studied genetically. In particular, White's (1978) extensive studies of cytogenetic patterns in Australia might provide a system similar to that we have just described for easy monitoring of genetic changes. A number of small rodents, particularly in the genera *Mus* and *Peromyscus*, are well-studied both ecologically and genetically in both Europe and North America (see [the Virtual Library of Genetics Home Page](#), and [the Peromyscus Database Home Page](#)). Among plants, the genus *Arabidopsis* is a prime candidate. *Arabidopsis thaliana* has one of the best characterized genomes among plant species (see [the Arabidopsis Home Page](#) for data on the genetics, ecology, and distribution of *Arabidopsis*). It has become a cosmopolitan weed, although its extreme southern and northern distribution limits, predicted to be more sensitive to global warming, remain to be determined (Dr. Robert Price, *personal communication*). Other members of the genus are distributed across the northern hemisphere. Among aquatic species, the genus *Daphnia* is particularly promising (Peters and De Bernardi 1987). Ecologically, it is a keystone genus. Its genetics has been extensively studied in both North America and Eurasia. This list is not exhaustive. Rather, it indicates the large potential for the approach described here. In some cases, current information is sufficient that population monitoring could begin immediately. In other cases, very little additional information would be needed to make these groups suitable candidates. What is most important is that we recognize the need to monitor genetic changes within species.

CONCLUSIONS

In situations in which a species cannot avoid an increasingly stressful environment by shifting its geographic distribution, adaptation or extinction will rely decisively upon its ability to mobilize sufficient genetic variation to track the environmental change (Travis and Futuyma 1993, Lande and Shannon 1996). The potential for adaptive responses to strong, directional selection imposed by climate change may be limited, either because additive genetic variance for the selected traits becomes exhausted, or because it is counterbalanced by genetically correlated responses in other characters (Holt 1990, Travis and Futuyma 1993). Accordingly, taking into account that the probability of fixation of deleterious pleiotropic alleles declines as population size increases (Crow and Kimura 1970), larger populations are expected to have greater responses to climate warming than do smaller populations, which are prone to accumulate a greater mutational load (Holt 1990, Travis and Futuyma 1993,

Lynch et al. 1995). This implies that intensities of directional selection capable of inducing microevolutionary responses in a generalist species like *D. subobscura*, with large population numbers, wide geographic distribution, and high dispersal rates (Krimbas 1992), may ultimately drive to extinction many rarer, specialist, and noncolonist species. Therefore, conservation strategies and efforts by taxonomists to record extant biodiversity in the face of the ongoing climate warming, should be urgently directed to these species and their potential habitats.

The approach outlined here could further provide a potentially fertile experimental link between microevolutionary responses and the dynamics of ecosystems (Holt 1995). Insects are important contributors to nutrient and carbon cycling, to energy flow, and to biomass decomposition (Schowalter et al. 1986). Consequently, changes in insect species' genetic composition induced by climate warming may have profound consequences on ecosystem processes through their influence on population growth rates, phenology, and colonization ability. Experimental results in *D. subobscura* showed that flies carrying gene arrangements that prevail in southern populations exhibited higher developmental rates than those carrying gene arrangements that are common in northern populations (Krimbas 1992). Genetic differences for this and other life history traits are doubtless being filtered by current levels of climate warming in other insect species as well. For instance, changes like these already may be altering threshold disturbance regimes, perhaps as outbreaks of insect pests.

Species do not exist in isolation, but in dynamic relationships with competitors, predators, pathogens, and parasites; these interactions, particularly competition, are all sensitive to temperature (Jenkinson et al. 1996, Davis et al. 1998). Studies of the drosophilid fauna in Chile show that, coinciding with the recent expansion of *D. subobscura* into the area, the relative abundance of other species (e.g., *D. pavani* and *D. immigrans*) has dramatically declined, presumably outcompeted by the new colonist (Brncic 1994). Similarly, the presumptive climate-mediated displacement of *D. subobscura* northward in Europe is expected to alter the structure of local communities.

Evolutionary biologists can provide a unique perspective to the examination of how climate change will affect the earth's biota. It is increasingly recognized that, without the contribution of evolutionary biology, ecological predictions of the effects of global change can be naive (Travis and Futuyma 1993). The information base and the expertise currently exist to apply evolutionary knowledge to global change concerns. With this paper, we hope to stimulate efforts in that direction.

RESPONSES TO THIS ARTICLE

Responses to this article are invited. If accepted for publication, your response will be hyperlinked to the article. To submit a comment, follow [this link](#). To read comments already accepted, follow [this link](#).

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APPENDIX 1

List of the studies containing frequency data of *Drosophila subobscura* chromosomal inversion polymorphisms in natural populations throughout the Palearctic.

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