

hard work, but it will probably be worth it!

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Department of Genetics, University of Leicester, University Road, Leicester, UK.
E-mail: maj4@leicester.ac.uk

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Global Warming: Fly Populations Are Responding Rapidly to Climate Change

New studies on chromosome inversion polymorphisms in *Drosophila* species show that the genetic constitution of populations is responding to recent climate change and that widespread species may have the potential to undergo adaptive shifts. Genetic markers in widespread species can act as indicators of climate change on natural populations.

Belinda van Heerwaarden
and Ary A. Hoffmann

The global surface temperature has increased by an unprecedented 0.8°C over the past 100 years and by 0.2°C per decade in the last 30 years [1], demonstrating that the climate around the world is changing rapidly. Observed changes in phenotypic traits of organisms, such as the timing of life history traits [2,3] and geographical shifts in species ranges [4], indicate that natural populations are responding to this change. For instance, data from a study over a 25 year period found that 20 species of birds in the UK began laying eggs around nine days earlier [2] and a global meta-analysis found that 84% of species analysed either showed a range shift towards the poles or mean advancement of spring events [4].

With few exceptions [5,6], it is not clear whether these biological responses are due to phenotypic plasticity — a single genotype

altering its phenotype in response to environmental conditions — or adaptation. If selection and adaptation are occurring, there is the potential for evolutionary shifts that ameliorate the impact of climate change. The contraction of the distribution of threatened species might then be less severe than predicted from ecophysiological models. Adaptation in species predicted to expand their range might also allow them to move well beyond their current distribution [7].

A recent study by Balanyá *et al.* [8] has shown that shifts in the genetic composition of natural populations of a widespread species can be linked to climate change. The cosmopolitan species, *Drosophila subobscura*, is a native of the old world and recent invader of South and North America. The species has a number of chromosomes with inversion polymorphisms that vary clinally with latitude across these continents. Chromosome inversions are regions of the

chromosome where the arrangement of genes is reversed, and populations can be polymorphic for the inverted or non-inverted ('standard') arrangements, recognized by looping patterns in salivary gland chromosomes (Figure 1). Although there is high gene flow between *D. subobscura* populations on each continent, the clinal patterns exhibited by chromosome polymorphisms suggest the

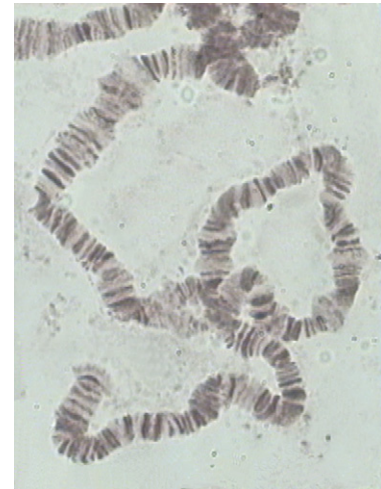


Figure 1. A typical inversion loop seen in a *Drosophila* polytene chromosome produced by pairing of an inverted and non-inverted chromosome arrangement. The loop depicted involves the left arm of chromosome 2 from *D. serrata*. Inversion frequencies in populations are scored by looking for loops in crosses to marker strains or by diagnostic molecular markers that involve the breakpoint region of the inversion. (Photo: Ann Stocker.)

operation of natural selection and adaptation to environmental factors such as mean temperature that vary with latitude. Chromosome polymorphisms were one of the first types of genetic marker to be characterized at the population level, and historic frequencies in populations dating as far back as the 1940s are available in several *Drosophila* species.

To examine whether global climate warming has already influenced the frequency of chromosome arrangements, Balanyá *et al.* [8] contrasted the historic frequencies of over 21 chromosome inversion polymorphisms, gathered over an average of 24 years, to contemporary frequencies. They then compared these with monthly mean temperature records during this time period. Consistent with predictions of climatic natural selection on these markers, there was a highly significant correlation between the indices used for chromosomes and for climate across all three continents. As expected from global warming, temperature had increased at 22 of the 26 sites examined across the three continents. Among these 22 sites, the chromosome frequencies had shifted towards a more low-latitude pattern in all but one population. In fact, when the magnitude of these shifts was rescaled in terms of equivalent degrees of latitude, it is comparable to moving the historical population approximately 1° of latitude closer to the equator. The shift is most clearly seen in European populations monitored at many sites, particularly at higher latitudes (Figure 2).

It appears that, on a very short evolutionary time scale of only two decades, populations of *D. subobscura* on three separate continents have evolved, in parallel, genetic changes in response to global warming. This may reflect the effects of selection on chromosomal arrangements, or movement of flies with particular arrangements. These results build on initial studies with *D. subobscura* in Europe [9,10] and support other recent findings

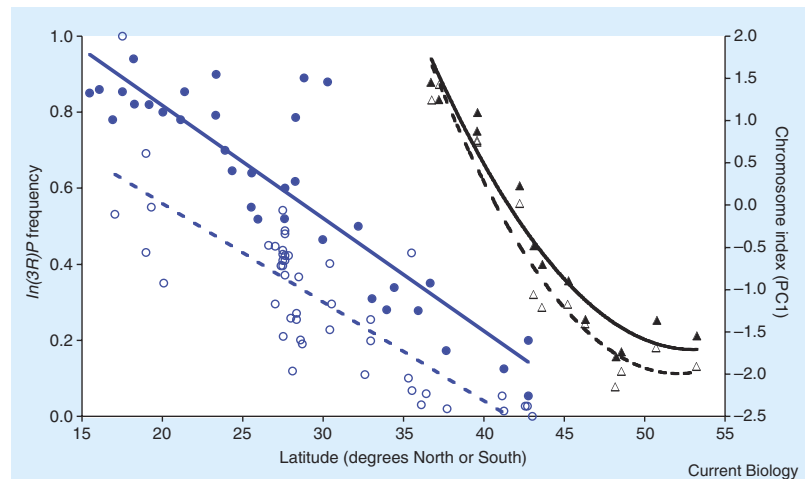


Figure 2. Changes in clinal patterns of chromosome inversion polymorphisms across latitudes.

Blue/circles, frequencies of the *In(3R)Payne* chromosome inversion of *D. melanogaster* at different latitudes in eastern Australia (modified from [11]); black/triangles, chromosome index (Ch_{PC1}) of *D. subobscura* at different latitudes in Europe (modified from [8]). Open symbols and dashed lines indicate historic data points; solid symbols and solid lines indicate contemporary data points.

indicating that rapid genetic changes are occurring in generalist species in response to climate change. Substantial changes in linear clinal patterns corresponding to several degrees in latitude have been observed for one of the inversion polymorphisms of *D. melanogaster* collected along the east coast of Australia (Figure 2) [11]. Changes in chromosomal arrangement frequencies of *D. robusta* from North America have also been linked recently to shifts in minimum temperature since the 1970s [12].

Chromosome inversion polymorphisms are useful markers to track climate change because historic frequency data are often available and many inversion arrangements rapidly form clines latitudinally, indicative of climatic adaptation. When recombination occurs between inverted and non-inverted chromosomes, gametes are inviable unless a double recombination event takes place within the inverted region. This causes alleles of loci within some regions of the inversion to be inherited together, particularly near inversion breakpoints. As numerous loci are located within *Drosophila* inversions, it is difficult to tease out the particular genes under

selection and responsible for clinal patterns, although some progress has been made in identifying clinally varying regions of the *In(3R)P* inversion of *D. melanogaster* [13]. Inversions may evolve by locking up particular combinations of alleles beneficial in a population which might normally be split up due to recombination. Recent theory [14] suggests that inversions can also evolve and spread by locking up alleles that are both favoured independently in populations rather than interacting to influence fitness. The fact that inversion polymorphisms in several species have now been linked to climate change over several decades suggests that the allelic content of inversions within a population changes relatively slowly.

Eventually it should be possible to link shifts in allele frequency at specific genes to climate change. One gene known to be under climatic selection and to have responded to climate change is the polymorphic alcohol dehydrogenase (*Adh*) locus in *D. melanogaster*. This polymorphism shows latitudinal clines on several continents, and responds to temperature-related factors both in the field and in the laboratory. Umina *et al.* [11] contrasted historic and

contemporary allele frequencies at the *Adh* locus along the east coast of Australia. Although the slope of the cline did not change over the 20 year study period, there was a shift equivalent to 4° in latitude in the *Adh* cline, with the southern high-latitude populations now having the genetic constitution of more northerly populations. Maximum daily temperature measures had increased and both humidity and rainfall had decreased over this period.

These findings show the power of latitudinally varying genetic markers to reveal the effects of climate change on natural populations. Widespread generalist species such as *D. melanogaster* and *D. subobscura*, which have short generation times and rapidly form phenotypic and genotypic clines, appear to be excellent candidates for sensitive indicators. The marker changes also illustrate the adaptive potential that exists in widespread species with short generation times. But species with long generation times [15], or restricted species with low additive genetic variance for climatic stress traits [16] may show very different patterns and evolutionary potential. Studies of genetic changes in a variety of species should shed light on the variation in rates and magnitudes of evolution in response to climate change in different species.

Ongoing work in *D. melanogaster* and other model organisms is leading to the identification of candidate genes responsible for climatic adaptation. As candidate genes emerge, they offer new prospects for linking climate change to evolutionary shifts in populations. When markers have not been historically characterized in populations, museum specimens may provide samples for longitudinal studies, as demonstrated in the case of insecticide resistance [17]. For now, rapid changes in inversion polymorphisms such as those found in *D. subobscura*, provide evidence for genetic responses to climate change over broad geographic regions.

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Centre for Environmental Stress and Adaptation Research, Department of Genetics, The University of Melbourne, Victoria 3010, Australia.
E-mail: ary@unimelb.edu.au

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Microtubule Modification: Acetylation Speeds Anterograde Traffic Flow

Microtubules in neurites undergo multiple post-translational modifications. Recent work shows that neurites enriched in acetylated microtubules selectively support kinesin-mediated transport of the JNK regulator JIP-1 to growth cones.

J. Chloë Bulinski

Back in the 1970s, a subset of tubulin molecules in the vertebrate brain was shown to undergo an enzyme-mediated, RNA-independent incorporation of tyrosine into the carboxyl terminus of its α -subunit [1]. Ever since this observation, researchers have speculated on how this so-called tyrosination/detyrosination modification — as well as other, subsequently discovered but equally intriguing,

post-translational modifications such as acetylation [2], and poly-glutamylolation [3] — could affect the function of the microtubule polymers in which the modified tubulin subunits are found [4]. Like tyrosination/detyrosination [5], acetylation and poly-glutamylolation were shown to be reversible, with the primary modification occurring on the microtubules, such that modified tubulin subunits accumulate in more stable, i.e., long-lived, populations of microtubules [6] that are localized