

Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change

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Summary

1. Most predictions of species distribution and abundance changes in response to global warming relate the individual requirements of a single isolated species to climate variables through some form of climate mapping. This method fails to account for the effects of species dispersal and species interactions, both of which may strongly affect distribution and abundance.

2. We therefore examined the effects of dispersal and species interactions on the distribution and abundance of three *Drosophila* species in a laboratory system that mimicked a latitudinal cline of 15 °C. We then investigated how species distribution and abundance in this system responded to simulated global warming.

3. Dispersal allowed populations to persist at non-optimum temperatures, overriding physiologically imposed range limits.

4. Temperature determined the outcome of competition. In pairwise interactions, *Drosophila subobscura* eliminated *D. melanogaster* or *D. simulans* at low temperatures but was itself eliminated at high temperatures.

5. Competitive interactions changed abundance and range sizes thus shifting the position of species optima. These changes depended on both the number and the identity of the competing species.

6. Enemy–victim interactions altered range and abundance. Adding the parasitoid *Leptopilina boulardi* affected the host assemblage directly at high temperatures where the parasitoid was present, and indirectly (mediated by dispersal) at low temperatures where it was scarce or absent. Host species coexisted for longer at low temperatures in clines when parasitoids were present than when they were absent.

7. Simulated global warming produced complex, counter-intuitive effects on distribution and abundance, including the reversal of species' relative abundance at some temperatures.

8. Because dispersal and species interactions strongly influenced both range and abundance (sometimes in unexpected ways) current species distributions are no guide to what they might be under global climate change. Furthermore, since both these factors are missing from climate envelope models of range and abundance change, their predictions are, at best, incomplete.

Key-words: abundance, climate change, cline, range, temperature.

Journal of Animal Ecology (1998) **67**, 600–612

Introduction

Almost all attempts to predict the effect of global warming on species' ranges and abundance make use of 'climate mapping' (Sutherland & Maywald 1985; Nix

1986; Kohlmann, Nix & Shaw 1988; Rogers & Randolph 1993; Porter 1995; Jeffree & Jeffree 1996). This is the venerable (Latreille 1819) and attractively simple idea that range and abundance are determined by the individual organism's physiological response to

climate, particularly temperature. It remains influential (Hoffmann & Blows 1994) and has been widely used in ecoclimatics (Rogers 1979; Caughley *et al.* 1987; Parry 1990; Sutherst 1990; Carter, Parry & Porter 1991; Porter, Parry & Carter 1991; Scott & Poynter 1991; Beerling 1993; Jeffree & Jeffree 1994). If it were true, species ranges would simply follow shifts in their characteristic climate envelopes and changes due to global warming could be predicted easily, given adequate models of future climate. Populations of organisms are, however, affected by a multitude of additional factors which complicate this simple view (Lawton 1995), especially those that produce horizontal and vertical integration of populations. Predictions from climate mapping ignore the potentially most potent of these: species dispersal and the multitude of complex species interactions, themselves affected by climate (Kingsolver 1989) and already known to influence range and abundance (Connell 1961; Paine 1966; Lawton & Hassell 1984; Price 1992).

The importance of dispersal is that it disrupts the dependence of populations on locally acting climate, allowing local presence and abundance to be influenced by other, distant populations. This, in the real world, creates networks of interdependent populations that influence each other. In metapopulations (Gilpin & Hanski 1991; Hanski & Gilpin 1997) and central-marginal populations (Boorman & Levitt 1973; Brussard 1984) with source-sink dynamics (Pulliam 1988), local presence and abundance are strongly influenced by dispersal between populations. Many sink populations may only persist if they receive sustained immigration from sources elsewhere in the range (Watkinson 1985; Rodriguez, Jordano & Fernandez Haegar 1994). Under such conditions, widespread in nature, dispersal will alter ranges and abundance predicted from the physiological responses of individual species.

Similarly, both horizontal (competition) and vertical (enemy-victim) interactions will affect species ranges and distributions, because these interactions are unlikely to remain unchanged under global warming. If species are differentially affected by climate change, as climate mapping sometimes predicts (Jeffree & Jeffree 1996), their interactions may be significantly altered or even totally disrupted (Peters 1992; Walter & Patterson 1994) leading to the dissociation of current species assemblages and the formation of new ones. That such fracture has been produced by individual species' responses to climate change in the past is supported by an increasing amount of evidence for both animals (Graham 1992; Valentine & Jablonski 1993; Coope 1995) and plants (Davis 1981, 1986; Overpeck, Webb & Webb 1992; Brubaker & McLachlan 1996). It is likely, therefore, that climate change will produce, not replicates of current assemblages, but new constellations of species (Walter & Patterson 1994), 'non-analogue' associations absent from the current biota (Roy *et al.* 1996).

It is unlikely that the effects of these interactions will be confined to the edge of species ranges, as has been suggested (Sutherst, Maywald & Skarratt 1995), and realistic assessments of range and abundance changes require consideration of the overall pattern of inter-relationships (Cammell & Knight 1992).

Because distribution and abundance are affected by dispersal and species interactions, predictions based on climate mapping must be seen, at best, as simply a 'null model' of expected species displacement with climate change. In practice, this 'null model' is likely to be in error to an unknown degree because it ignores the biotic effects of distribution and abundance.

In the study reported here, a simple laboratory system was used to demonstrate a possible general paradigm for the response of species assemblages to climate change. Dispersal, competition and enemy-victim interactions are shown to have important effects on distribution and abundance and, in systems where these factors are important, the effects of global warming are demonstrated not to be the simple consequences of individual species temperature responses. Species ranges and abundance in systems including dispersal and species interactions along experimental temperature clines are shown to be substantially different from those suggested by the physiology of single species and, consequently, range and abundance in assemblages cannot be predicted from those recorded for single species. The study demonstrated that the responses of simple assemblages to simulated global warming were not predictable from the species' distribution and abundance on the clines before warming.

Methods

EXPERIMENTAL ORGANISMS

Three *Drosophila* species were used: *D. melanogaster* Meigen, *D. simulans* Sturtevant and *D. subobscura* Collin, and a parasitoid wasp *Leptopilina boulardi* (Barbotin, Carton & Kelner-Pillaut). The responses of this grouping are likely to be paradigmatic of many animal assemblages, as the three *Drosophila* species do not have specialized life histories or larval diets. Furthermore, the four species are an element of a naturally occurring species assemblage. *Drosophila melanogaster* and *D. simulans* occur from the tropics to, in Europe, about latitude 54°N. *Drosophila subobscura* occurs from North Africa to the Arctic but does not occur in the tropics (Wheeler 1981). The parasitoid is warm-adapted, occurring in the tropics and subtropics (Nordlander 1980), extending as far as latitude 48°N in Europe (Carton *et al.* 1991) but absent further north (Davis *et al.* 1996). It therefore co-occurs with the three *Drosophila* species in southern and central Europe and the Mediterranean basin. The parasitoid preferentially oviposits in *D. melanogaster*, in which it suffers little mortality, but will also attack and cause

Table 1. Summary of the terms used for the different experimental systems

Term	System
Series	Set of eight cages connected together across four incubators at the same temperature
Cline	Set of eight cages connected together (two/cage) across four incubators at four different consecutive temperatures
Cold cline	Cline with incubators at 10°, 15°, 20° and 25°C
Hot cline	Cline with incubators at 15°, 20°, 25° and 30°C
Closed cline	Cline in which the tubes connecting cages between incubators are blocked with foam bungs
Open cline	Cline in which the tubes are not blocked and flies can disperse
Single species series (or cline)	Series or cline initiated with a single species either <i>D. melanogaster</i> , <i>D. simulans</i> or <i>D. subobscura</i>
Two species cline	Cline initiated with the two species <i>D. simulans</i> and <i>D. subobscura</i>
Three species cline	Cline initiated with the three species <i>D. melanogaster</i> , <i>D. simulans</i> and <i>D. subobscura</i>
Four species cline	Cline initiated with the three <i>Drosophila</i> species and the parasitoid <i>Leptopilina boulandi</i>

high host mortality in *D. simulans* and *D. subobscura*, even though the wasp larva rarely survives in these species (Carton *et al.* 1986; Kraaijeveld & van Alphen 1995).

The *Drosophila* species were all collected from Pontefract Lane fruit market, Leeds, UK, and had been maintained in laboratory mass culture for 2 years before being used in the experiments. The same strains were used in all the experiments. The parasitoid was originally collected in Tasagil, Turkey, and was maintained throughout on *D. melanogaster*.

EXPERIMENTAL ECOSYSTEMS

Experimental systems consisted of eight Perspex cages (each 100 × 150 × 300 mm) linked in series (see Table 1 for terminology). The eight cages were connected together in pairs and each pair housed in a different incubator. The tubing connecting the cages was 30 mm in diameter because this size restricted dispersal. Up to five replicate systems were accommodated in each group of four incubators (Fig. 1) and there were two such groups. The incubators in a group were initially all set to a nominal 20 °C and temperature clines later created by setting the incubators

sequentially to 10, 15, 20 and 25 °C ('cold' clines) representing the current spread of mean summer temperatures from southern Spain to northern England. To simulate global warming the overall temperature of the clines was raised by 5 °C (Bennetts 1995) to 15, 20, 25 and 30 °C ('hot' clines). Temperatures measured by probes inside the cages did not deviate significantly from the incubator setting (mean deviation = 0.28 SD = 0.445 *t* = 0.626, d.f. = 77, *P* > 0.05). The overall gross variability of these temperatures, including incubator faults and very occasional power failures, was about 2 °C (95% confidence interval (CI) = 1.78 °C) with most of the variability concentrated in the lowest temperature incubators (95% CI = 4.50 °C). In normal running, however, temperatures were less variable (95% CI = 0.88 °C).

Each of the cages contained six food tubes which were replaced sequentially with a fresh tube containing 50 mL standard, cereal-based *Drosophila* medium (Shorrocks 1972). The cages were reprovisioned at the rate of one tube every half generation, thus, because generation time is inversely related to temperature, hotter cages were reprovisioned more often but *Drosophila* at the four different temperatures received the same amount of food per generation. In

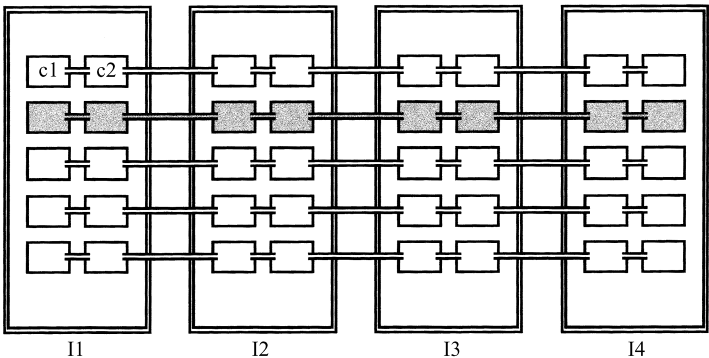


Fig. 1. The arrangement of Perspex cages (100 × 150 × 300 mm) in one set of four incubators (I1–I4) showing, shaded, an experimental series of eight cages linked together by tubing. Each pair of cages (e.g. c1–c2) experiences the same temperature.

four-species clines honey was provided as food for adult *L. boulandi*.

POPULATION MEASUREMENT

Experimental populations were assessed by weekly counts of the adult *Drosophila* on a standard 80 × 80 mm grid fixed on the rear wall of each cage. Because *D. melanogaster* and *D. simulans* are morphologically very similar (e.g. Patterson 1943; Moore 1952) and cannot be distinguished without detailed examination, the standard counts were adjusted by the proportions of these two species present in weekly samples of 100–150 flies drawn from each cage. Estimates of the real populations in each cage were then made by applying a series of calibration curves to the count data. These curves were produced by releasing known numbers of flies (between 50 and 1000 for each species and each temperature) into experimental cages and counting the numbers on the standard grid. This partial standard count was closely correlated with the real number of adult flies but the linear relationship overestimated numbers at both the lowest and highest densities. Biologically more realistic sigmoid curves [with general form $y = k/(1 + e^{a-bN})$], which reflected the spatial behaviour of the flies were therefore fitted separately to the counts for each species and temperature (Table 2). In two of the 15 calibrations, for *D. simulans* and *D. subobscura* at 30 °C, the sigmoid curve provided no better fit between real numbers and counts than did the overall mean number of adult flies. Consequently, experimental populations of *D. simulans* at 30 °C were estimated as the overall mean but this was unnecessary for *D. subobscura*, which did not occur at 30 °C. To avoid the initial phases of population increase and to standardize the time period considered for each treatment the analyses here are confined to counts made between weeks 5 and 25.

CAGE SERIES AND CLINES

The distribution and abundance of each species of *Drosophila* was first assessed when dispersal was possible between incubators but in the absence of temperature differences between incubators and without interspecific interactions. Nine one-species series,

three replicates for each species, were initiated by adding 25 male and 25 female flies to all eight cages in a series (a total of 400 flies per series). The start-up dates of these replicates, and for those in all other treatments, were staggered to avoid alterations in external conditions causing correlated changes across replicates. To determine the effect of a temperature cline on single species without interactions, the distribution and abundance of the three species in one-species cold clines were then remeasured. The cage series were converted to clines by resetting the incubators to the specified cold-cline temperatures.

DISPERSAL

A feature of this study is the explicit inclusion of dispersal in the experimental system. However, it proved impossible to assess dispersal rates in the clines accurately by directly monitoring flies moving between temperatures because numerous flies circulated in the connecting tubes without entering the cages at either end. Tests were therefore carried out to discover whether dispersal had a major effect on the distribution and abundance of individual species in the system by preventing dispersal altogether in one-species clines. Nine closed clines, three replicates for each species, were created by blocking the tubes between incubators in established cold one-species open clines.

INTERACTIONS

The effects of two kinds of interspecific interactions were examined; those between *Drosophila* species and those involving enemy–victim interactions between *Drosophila* and the parasitoid *L. boulandi*.

Interactions between *Drosophila* species were assessed in two ways. First, to determine the outcome of interactions between pairs of *Drosophila* species when dispersal between temperatures was not possible three replicates of each pair-wise combination of species were established in single, unconnected cages at all five cline temperatures (10, 15, 20, 25 and 30 °C). The cages were sampled weekly until one species was absent from three consecutive samples. Second, the effect of interactions was determined in a system,

Table 2. Coefficients (and *P* values) for the correlations between real numbers of adult flies and those predicted by sigmoid relationships of the form $y = k/(1 + e^{a-bN})$

	10°C	15°C	20°C	25°C	30°C
<i>D. melanogaster</i>	0.3244 (0.026)	0.1608 (0.297)	0.3042 (0.056)	0.5580 (0.001)	0.5211 (0.006)
<i>D. simulans</i>	0.4919 (0.001)	0.4422 (0.002)	0.6646 (0.001)	0.5386 (0.001)	No fit
<i>D. subobscura</i>	0.3044 (0.023)	0.4208 (0.003)	0.4809 (0.001)	0.3635 (0.021)	No fit

which was both clinal and allowed dispersal, by assessing the distribution and abundance of *Drosophila* species in combination. Three two-species clines were initiated by adding 50 *D. simulans* and 50 *D. subobscura* (equal sex ratios in both species) to every cage in each cline. In addition, to ensure that the outcomes of interactions in clines were not greatly influenced by the proportion of flies used to initiate them, six additional two-species clines were set up using different starting proportions of the two species. Three were started by adding *D. subobscura* to existing *D. simulans* clines at the rate of 10% *D. subobscura* to *D. simulans* and three more by adding *D. simulans* to existing *D. subobscura* clines at the same rate. Although these clines started with different proportions of the two species there was ultimately no significant difference between them [repeated-measure ANOVA (RMA) $F_{2,132} = 0.64$, $P = 0.528$]. The data from all three methods of establishment were therefore combined in subsequent analyses.

Three-species clines were initiated with equal proportions of each species as different starting frequencies did not influence the eventual outcome in two-species clines. The four replicates were therefore all started by adding 50 flies of all three species to every cage in a cline (400 flies of each species per cline).

Enemy–victim interactions were examined using the parasitoid *L. bouleardi*. Five four-species clines were created by adding adult wasps (sex ratio 1 : 1) to cold three-species clines at the rate of 10% of the pre-existing *Drosophila* adults in each cage irrespective of species. The additions were made 4 weeks after the three-species clines had been established. The data from these clines were also used to calculate temperature-specific diversities of the victim assemblage, the three *Drosophila* species.

SIMULATED GLOBAL WARMING

The effect of global warming on species assemblages in systems with both species interactions and dispersal between temperatures was examined by increasing the overall cline temperature. Hot clines were created from the nine existing two-species and the five three-species cold clines (containing just *Drosophila* species without parasitoids), by setting the incubators to the specified hot-cline temperatures.

DATA ANALYSIS

Data from cage series and clines were analysed as longitudinal studies of individual types of experimental systems using a multivariate RMA design (Crowder & Hand 1990) with polynomial contrasts and unique sums of squares. The weekly population estimates were used as within-subject factors and system type (e.g. series vs. clines or one-species clines vs. two- and three-species clines) and temperature as a between-subject factor. Occasional missing values

were interpolated using the mean of the two counts before and the two after the missing value (Norusis 1994).

Parasitoids may affect the diversity of the assemblages to which their hosts belong (LaSalle 1993), so the diversity of the *Drosophila* assemblage was calculated for each temperature from the weekly populations of the three *Drosophila* species in four-species clines. Simpson's index was used as the measure of *Drosophila* diversity in cold three-species clines (without parasitoids) and four-species clines (with parasitoids) because it is sensitive to the difference in abundance between species rather than to the number of species present (species richness) (Magurran 1988). Sensitivity to species richness was not required as richness was close to two at all temperatures in both cline types. Simpson's index also has low sensitivity to sample size while retaining the ability to distinguish differences in species composition. Assemblage diversity was determined as the mean diversity over weeks 20–25 and separate determinations were made at all four cold cline temperatures.

Results

CAGE SERIES AND CLINES

In cage series *D. melanogaster* appeared most abundant, with *D. subobscura* least abundant and *D. simulans* in an intermediate position (Fig. 2). However, a two-way ANOVA revealed that there were no sig-

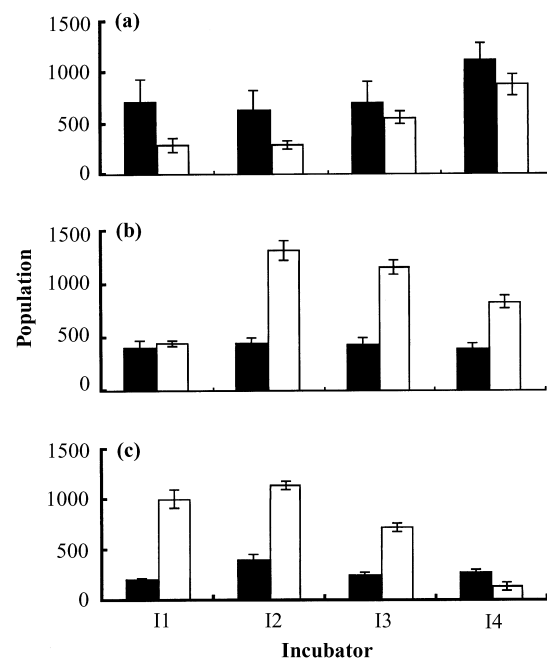


Fig. 2. Populations of *Drosophila melanogaster* (a), *D. simulans* (b) and *D. subobscura* (c) in one-species series (■) where all four incubators are at 20 °C and in one-species clines (□) where the incubators are at 10, 15, 20 and 25 °C. Error bars ± 1 SE based on means of all measures.

nificant differences between species ($F_{2,24} = 2.77$, $P = 0.082$) nor, emphatically, between incubators ($F_{3,24} = 0.182$, $P = 0.908$). There was also no significant interaction between species and incubator ($F_{6,24} = 0.301$, $P = 0.930$). Thus, in series, none of the three species showed any trend across incubators.

In contrast, in open one-species clines, where there was a temperature gradient, the populations were significantly different from those in series where there was no temperature gradient between incubators (RMA $F_{1,104} = 31.59$, $P < 0.001$) after accounting for the variance caused by species and temperature. In addition, the populations reached by each species in each incubator along a series were not correlated with the populations in the same incubators when these were part of a cline (*D. melanogaster* $r_{12} = 0.37$, $P = 0.23$; *D. simulans* $r_{12} = 0.18$, $P = 0.57$; *D. subobscura* $r_{12} = 0.30$, $P = 0.46$). Significant correlation would be expected if the temperature gradient in clines had no effect on single species populations. Within clines all three species are present throughout the available temperature range (Fig. 2). However, the species populations were significantly different at all temperatures except 10 °C (two-tailed *t*-test, all $d > 1.96$, $P < 0.05$) and each species reached its highest population density at a different temperature (Fig. 2). The temperature optima (calculated as the mean of temperature weighted by the number of flies at each temperature) were 20.92 °C (SD = 0.74) for *D. melanogaster* and 19.0 °C (0.39) and 16.2 °C (0.65) for *D. simulans* and *D. subobscura*, respectively.

DISPERSAL

Dispersal in clines, whatever its absolute value, markedly altered the populations achieved, as there were significant differences between open and blocked cold one-species clines independent of temperature and weekly variation for *D. melanogaster* and *D. subobscura* (RMA, respectively, $F_{1,40} = 7.90$, $P = 0.008$; $F_{1,40} = 15.69$, $P < 0.001$). The difference was not significant for *D. simulans* ($F_{1,48} = 3.58$, $P = 0.064$). In open clines, where dispersal was possible, all three species occurred and reproduced throughout the cline, occupying parts of the climatic range where, without dispersal, they died out or became very rare. Without dispersal *D. melanogaster* became very rare, and ultimately died out at 10 °C, as did *D. simulans*. *Drosophila subobscura* did not die out at 10 °C but became extinct at 25 °C, the highest temperature, in closed clines (Fig. 3).

Preventing dispersal changed species abundance within particular temperatures as well as changing species distributions. In closed clines *D. melanogaster* was more abundant at 20 °C and *D. simulans* at 25 °C than they were in open clines (one-tailed *t*-test, corrected for unequal variances, $t = 4.22$, d.f. = 178, $P < 0.005$; $t = 3.67$, d.f. = 178, $P < 0.005$, respectively). They were both less abundant, however, at 15 °C ($t =$

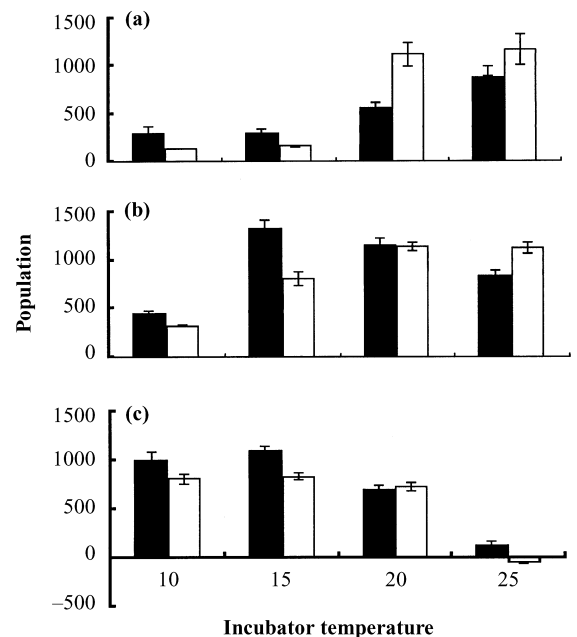


Fig. 3. Comparison of *Drosophila melanogaster* (a), *D. simulans* (b) and *D. subobscura* (c) populations in open one-species clines (■) and closed one-species clines (□). The apparently negative population for *D. subobscura* at 25 °C is caused by a minor bias in the population estimator at this temperature for very low real populations. Error bars ± 1 SE based on means of all measures.

3.20, d.f. = 178, $P < 0.005$ and $t = 4.31$, d.f. = 178, $P < 0.005$) as was *D. simulans* at 10 °C ($t = 4.56$, d.f. = 178, $P < 0.005$). In contrast, *D. subobscura* populations were significantly reduced at 25 °C ($t = 4.01$, d.f. = 152, $P < 0.005$), and increased at 15 °C ($t = 4.84$, d.f. = 178, $P < 0.005$). In general, preventing dispersal raised species populations at or near to their optimum temperature and reduced them at non-optimum temperatures compared to open clines.

INTERACTIONS

The eventual outcomes of pair-wise competition in single cages is clearly temperature dependent (Table 3). *Drosophila melanogaster* eliminated *D. subobscura* above 15 °C but was out-competed by this species at lower temperatures. In the absence of *D. melanogaster*, *D. simulans* ousted *D. subobscura* at high temperatures but *D. subobscura* dominated at lower temperatures. However, *D. melanogaster* out-competed *D. simulans* at all temperatures.

Competition in clines changes the distribution and the abundance of the three species (Fig. 4). There were significant differences between the populations of all three species on their own in one-species clines and the populations they reached with two competitors in three-species clines (RMA $F_{1,176} = 220.26$, $P < 0.001$). Similarly populations of *D. simulans* and *D. subobscura* on their own differed significantly from those of these species with either one or two competitors (RMA

Table 3. The outcome of competition between pairs of *Drosophila* species in single cages at five different temperatures. The winning member of the pair is indicated by its abbreviated name (mel = *D. melanogaster*, sim = *D. simulans*, sub = *D. subobscura*)

Competing <i>Drosophila</i>	Temperature (°C)				
	10	15	20	25	30
<i>D. melanogaster</i> – <i>D. simulans</i>	mel	mel	mel	mel	mel
<i>D. melanogaster</i> – <i>D. subobscura</i>	sub	sub	mel	mel	mel
<i>D. simulans</i> – <i>D. subobscura</i>	sub	sub	sim	sim	sim

$F_{2,152} = 475.62$, $P < 0.001$). The effects differed between species, with significant interactions of species with number of competitors in both the three-species and two-species comparisons (RMA $F_{2,176} = 20.62$, $P < 0.0001$ and $F_{2,152} = 103.01$, $P < 0.001$, respectively).

More specifically, the range of *D. melanogaster* is largely unaffected by interspecific competition but the species is driven to low numbers at 10 °C where the cold-adapted *D. subobscura* competes with it in three-species clines but is significantly more abundant at 20 °C ($t = 6.09$, d.f. = 340, $P \ll 0.005$) (Fig. 4a). Populations of *D. simulans* in two-species clines with *D. subobscura* were only significantly lower than in one-species clines at 15 °C ($t = 7.03$, d.f. = 214, $P < 0.005$) where it is influenced by *D. subobscura*. At

25 °C though *D. simulans* populations were significantly greater in two-species than in one-species clines ($t = 5.08$, d.f. = 212, $P < 0.005$). These two changes shifted the optimum for *D. simulans* towards 25 °C. In three-species clines, however, *D. simulans* suffered competition from both the other species and its abundance was very significantly reduced across the entire cline ($t > 6.0$, d.f. = 340, $P < 0.005$ for 15–25 °C) (Fig. 4b). Interactions also reduced the range of *D. subobscura* because it died out at 25 °C in both two- and three-species clines (Fig. 4c). Its abundance in two- and three-species clines was also significantly reduced compared to one-species clines throughout the remaining temperature range (all $t > 3.00$, d.f. = 214 or 376, $P < 0.005$) (Fig. 4c). The proportional reduction was greater at 15 °C than at 10 °C with the result that the highest populations occurred at 10 °C instead of at 15 °C as was the case in one-species clines. Species interactions thus shifted the apparent optimum of *D. subobscura* towards 10 °C.

The presence of *L. boulandi* significantly changed *D. simulans* and *D. subobscura* populations (RMA, respectively, $F_{1,78} = 18.02$, $P < 0.001$; $F_{1,80} = 10.36$, $P = 0.002$) but *D. melanogaster* was largely unaffected (Fig. 5a). *Drosophila simulans* populations, already very small in three-species clines without parasitoids, were reduced even further at 20 °C ($t = 5.15$, d.f. = 460, $P \ll 0.005$) (Fig. 5b). In contrast, *D. subobscura* showed no significant change at 20 and 25 °C but reached very significantly higher populations at 15 °C ($t = 5.12$, d.f. = 460, $P < 0.005$) and at 10 °C ($t = 7.29$, d.f. = 460, $P < 0.005$) when wasps were present than when they were not (Fig. 5c). These populations were close to those reached by *D. subobscura* when it was on its own (Fig. 2c).

As a consequence of these changes to *Drosophila* range and abundance, the presence of the parasitoid also increased fly diversity because Simpson's D was significantly reduced at 10 and 15 °C (respectively, $t = 6.07$, d.f. = 4, $P < 0.05$; $t = 3.42$, d.f. = 4, $P < 0.05$) (Fig. 6). This increase in diversity is also reflected in the long-term coexistence of *D. subobscura* and *D. melanogaster* at 15 °C in four-species clines, when wasps are present, whereas *D. subobscura* is eventually excluded by *D. melanogaster* at the same temperature in three-species clines (Fig. 7).

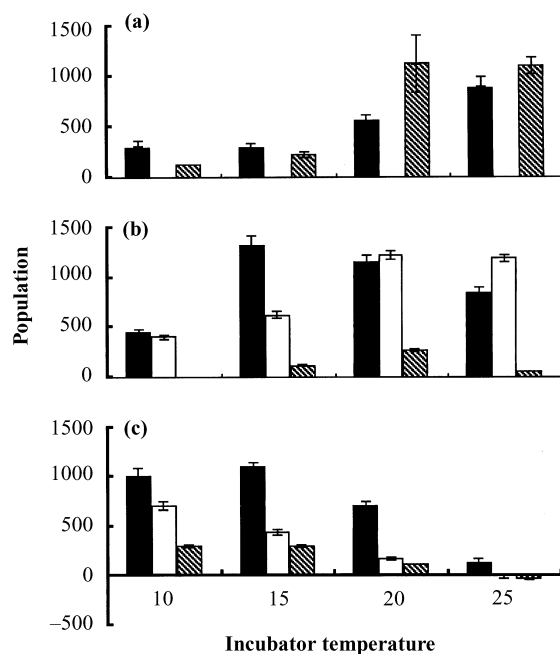


Fig. 4. Comparison of *Drosophila melanogaster* (a), *D. simulans* (b) and *D. subobscura* (c) populations in one-species (■), two-species (□) and three-species clines (▨). The apparently negative population for *D. subobscura* at 25 °C is due to a minor bias in the population estimator at this temperature for very low real populations. Error bars ± 1 SE based on means of all measures.

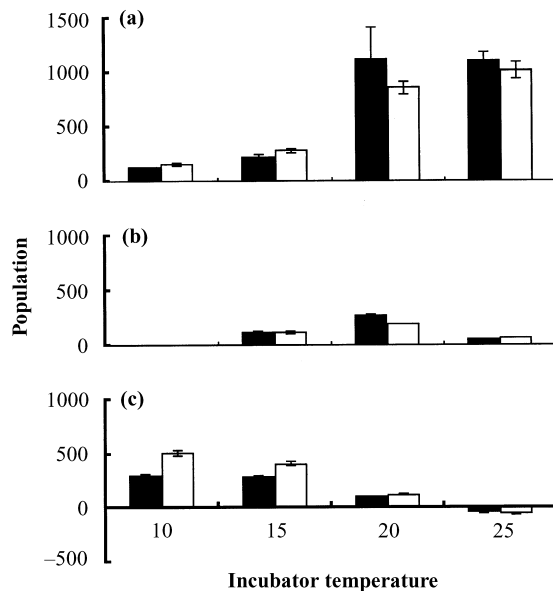


Fig. 5. Comparison of *Drosophila melanogaster* (a), *D. simulans* (b) and *D. subobscura* (c) populations in three-species cines, without the parasitoid *Leptopilina boulardi* (■), and in four-species cines, with the parasitoid (□). The apparently negative population for *D. subobscura* at 25 °C is due to a minor bias in the population estimator at this temperature for very low real populations. Error bars ± 1 SE based on means of all measures.

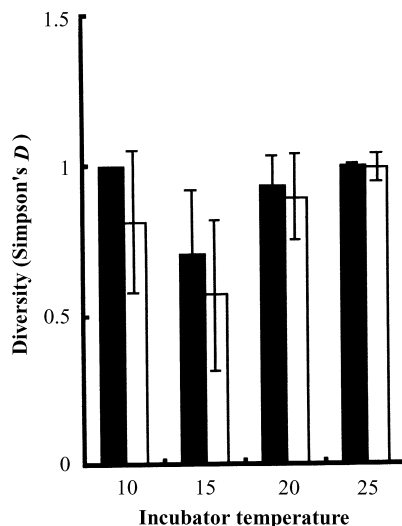


Fig. 6. Diversity (Simpson's D) of the *Drosophila* assemblage at all four incubator temperatures in three-species cines (■), without the parasitoid *Leptopilina boulardi*, and in four-species cines (□), with the parasitoid. Error bars ± 1 SD.

SIMULATED GLOBAL WARMING

When global warming was simulated by raising the overall cline temperatures by 5 °C to create hot cines, distribution and abundance were both changed (Fig. 8). There was a significant difference between populations of *D. melanogaster* in hot and in cold three-species cines (RMA, $F_{1,54} = 9.79$, $P = 0.003$) as

there also was for *D. simulans* (RMA $F_{1,54} = 33.27$, $P < 0.001$). However, simulated warming of two-species cines, where *D. melanogaster* was absent, did not significantly alter *D. simulans* populations (RMA $F_{1,30} = 0.44$, $P = 0.513$). In two-species cines *D. simulans* maintained a population at 30 °C but failed to do so in three-species cines. *Drosophila subobscura* populations were significantly altered in both two-species and three-species hot cines compared with its populations in cold cines (RMA $F_{1,30} = 9.55$, $P = 0.004$; $F_{1,54} = 5.18$, $P = 0.027$, respectively). In addition, as well as failing to establish populations at 30 °C in either two- or three-species hot cines *D. subobscura* was driven to negligible levels at 25 °C. Most markedly, however, *D. subobscura* abundance was significantly higher at 15 °C under simulated global warming than in cold cines at the same temperature, whether in two-species or three-species cines ($t = 6.50$, d.f. = 250, $P < 0.005$; $t = 6.17$, d.f. = 418, $P < 0.005$) (Fig. 8). Populations of *D. simulans* in hot and in cold two-species cines at 15 °C were not, however, significantly different ($t = 0.68$, d.f. = 250, $P > 0.05$) and *D. melanogaster* and *D. simulans* populations in hot three-species cines were significantly lower than those in similar cold cines ($t = 2.86$, d.f. = 418, $P < 0.005$; $t = 3.08$, d.f. = 418, $P < 0.005$; Fig. 8). At 15 °C, therefore, simulated global warming increased *D. subobscura* populations whilst reducing those of its potential competitors. This differential effect of global warming inverted the relative abundance of the species at 15 °C with *D. subobscura* becoming dominant over allospecifics in hot cines, whereas in cold cines it was least abundant at this temperature.

Discussion

This study demonstrates that dispersal and interactions between species can modify and disrupt links between temperature and species' local presence or local abundance. These factors will thus distort predictions of range shifts under global warming as it is axiomatic in ecology that species exist not on their own but in dynamic equilibrium with others, either horizontally (competition) or vertically (enemy–victim interactions) and that local presence and absence are strongly influenced by dispersal between populations (Hanski & Gilpin 1997).

Climate, particularly temperature, has long been accepted as a dominant influence on the distribution and abundance of species (Messenger 1959; Coope 1977), an influence exerted through effects on fecundity and mortality. Temperature is clearly important in this study as there is no correlation between *Drosophila* species abundance in single species series and in cline populations. Temperature affects the three species differently because they differ in their temperature optima. *Drosophila subobscura*, whose recorded temperature optima of 16.5 °C (Moreteau *et al.*

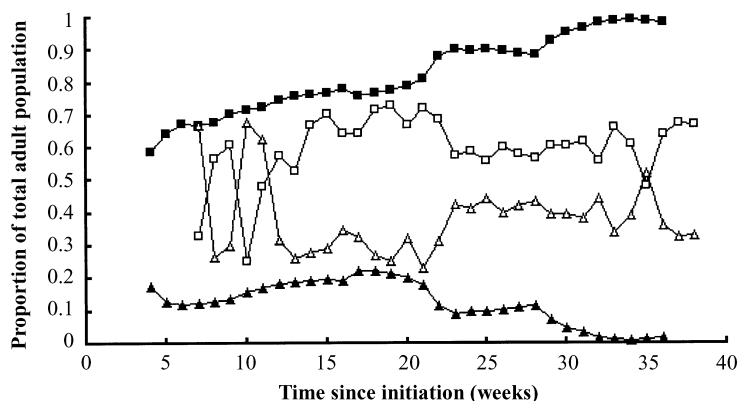


Fig. 7. Comparison of the smoothed weekly proportions of adult *Drosophila melanogaster* (■) and *D. subobscura* (▲) in three-species clines, without *Leptopilina boulardi* parasitoids (closed symbols), and in four-species clines, with *L. boulardi* parasitoids (open symbols). Both *Drosophila* species persist in the presence of the parasitoid but, in its absence, *D. melanogaster* ultimately excludes *D. subobscura*. (For clarity, data for the third member of the assemblage, *D. simulans*, is omitted.)

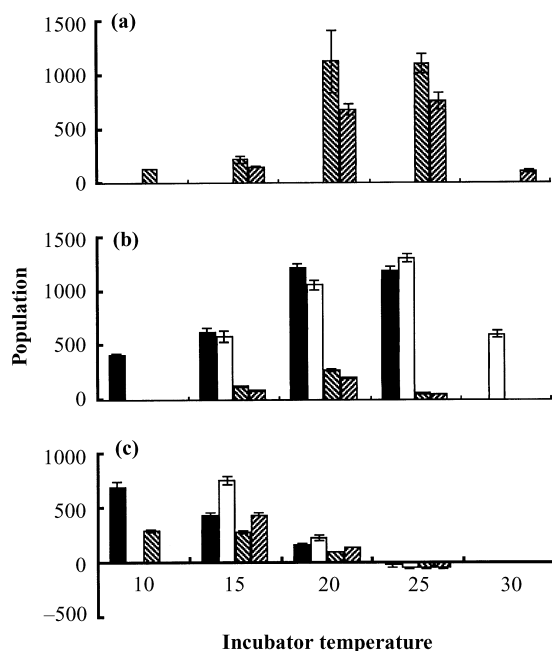


Fig. 8. Comparison of *Drosophila melanogaster* (a), *D. simulans* (b) and *D. subobscura* (c) populations in cold (■), and in hot (□) two-species clines; and in cold (▨) and in hot (▩) three-species clines. The apparently negative population for *D. subobscura* at 25 °C is due to a minor bias in the population estimator at this temperature for very low real populations. Error bars ± 1 SE based on means of all measures.

1997) or 19 °C (Krimbas 1993) accord with the single-species cline optimum of near 15 °C, is evidently cool-adapted compared to *D. melanogaster*, temperate strains of which have optima near that found in the single species clines in this study (cf. David *et al.* 1983; Delpuech *et al.* 1995). As in the single species clines in this study, *D. simulans* has an intermediate optimum (Cohet, Vouidibio & David 1980). If individual physiology was indeed the key determinant of species ranges, unaffected by either competition or dispersal,

it would be expected that these three species would order themselves along the temperature clines in the order of their temperature optima, occurring at less abundance in neighbouring parts of the clines. This was not the case in the present study.

Dispersal substantially modifies the picture and allows species, in the absence of interactions with other species, to occupy larger ranges than physiology or the ranges in blocked clines would suggest. The 'fundamental' niche (Hutchinson 1958) in the single dimension of temperature of each of the *Drosophila* species is therefore smaller than the realized niche when dispersal is possible; that is, the *Drosophila* form sink populations (Pulliam 1988) in parts of the cline. An analogous situation occurred for plants on sand dunes (Watkinson 1985) and is a feature of source-sink population dynamics. The dispersal rates between temperature zones in clines in the present study are higher than they are likely to be for many organisms in nature, even though individual *Drosophila* can disperse over large distances of 5–500 km (Gressitt & Nakata 1964; Jones *et al.* 1981; Coyne *et al.* 1982). Nevertheless, this system demonstrates the potential effect of long-distance dispersal such as occurs in, for example, the pest insects *Nilaparvata lugens* and *Heliothis virescens*. Because dispersal can evidently be very important, should species' ranges shift as a result of climate change, thus changing the spatial pattern of source-sink dynamics, species abundance and patterns of occurrence will also change. Under these circumstances, 'null model', simple climatic extrapolations, will not accurately predict new ranges and abundance. The degree of inaccuracy is unknown but would be greatest in species with substantial sink populations in parts of their current distribution.

The results of single-cage pair-wise interactions indicate that temperature strongly influences the outcome of competition. The data conform to the general pattern that cool-adapted species are competitively

dominant at low temperatures and warm-adapted species at high temperatures, although they did not show the commonly observed elimination of *D. melanogaster* by *D. simulans* at low temperatures (Moore 1952; Tantawy & Soliman 1967). On temperature clines, therefore, species with different temperature preferences should replace each other with little overlap. However, in two-species and in three-species clines this did not happen, because there is considerable species overlap maintained by dispersal, which opposes competitive exclusion. Nevertheless, in the experimental system in this study the introduction of competitors changes range and abundance as competitors are well known to do in nature (Connell 1961; Lawton & Hassell 1984). The effects differed between species, with *D. subobscura* abundance being reduced more than that of *D. simulans* in two-species clines, and *D. simulans* suffering more than either of the other species in three-species clines.

Theory shows that synergisms between dispersal and interspecific interactions have the power to induce spatial patterning in insect populations (Kareiva 1990; Holmes *et al.* 1994) and there is evidence that the spatial distribution of the western tussock moth, *Orgyia vetusa*, is restricted by parasitism (Brodmann, Wilcox & Harrison 1997). It is extremely unlikely that all the species involved in phenomena of these kinds will be affected in the same way by climate change, and existing species assemblages are thus bound to be disrupted. The degree of disruption will depend on the intensity and the scale of these effects.

Thus range and abundance are strongly influenced both by the identity and the number of competing species, and individual species can be differently affected, depending on the identity of other competitors in the assemblage. Consequently, if each species responds to climate change in a different way, as the widespread occurrence of non-analogue communities suggests is very likely for organisms as different as insects (Coope 1978, 1995), mammals (Graham & Lundelius 1984; Graham *et al.* 1996) and plants (Davis 1986; Davis & Zabinski 1992), it must be expected that existing combinations of species will break up and new combinations with different relative abundance will form as species respond and migrate differentially. Inevitably therefore the identity and number of competitors are likely to change. The multiple nature of range constraints is also evident in data from a quite different source. British macrolepidoptera occupy, on average, only 0.37% of the geographical range of their larval food plants and in many cases much less than this (Quinn, Gaston & Roy 1997). The precise reasons for this discrepancy are unclear but moths evidently require more than just their larval food plant and have other, sometimes severe, constraints on their distribution. Under these circumstances it is extremely unlikely that changes in food plant and moth distributions will be closely coupled. Moths cannot occur without their food

plants but this tells us next to nothing about a moth's actual distribution within the range of its food plant, either now or under global warming.

Given the importance of these competitive phenomena, it is extremely unlikely that changes in range and abundance will be accurately predicted by climate mapping or single-species response norms alone. Again, the magnitude of the discrepancy is unknown; it will depend on the number of competitors, the intensity of competition and the extent to which potential competitors show differential range changes as climate changes (Graham 1992; Valentine & Jablonski 1993; Coope 1995; Brubaker & McLachlan 1996).

The introduction of a natural enemy in the form of *L. boucardi* also has marked effects on the three *Drosophila* species. The increase in *D. subobscura* at 10 °C is intriguing, as *L. boucardi* itself does not occur at 10 °C. The fly must therefore be responding to the parasitoid's suppression of *Drosophila* elsewhere in the cline and thus a reduction in the numbers of competitors dispersing into the 10 °C cages. The parasitoid thus favours *D. subobscura* at lower temperatures by reducing the competition it experiences from the other two species. At high temperatures *D. melanogaster* is favoured because, although the parasitoid oviposits in *D. melanogaster*, members of the other two species that it attacks are also killed. As a consequence of the wasp's local effects on *D. melanogaster* and its indirect effects on *D. subobscura*, presence of the wasp promotes coexistence at 15 °C. The presence of *D. subobscura* at 15 °C in a system where it interacts with two other species is thus determined by its interaction with a natural enemy and not merely by its individual physiology. These findings indicate that the wasp and the *Drosophila* species are involved in complex indirect interactions (Holt & Lawton 1994). Similar complex interactions are imputed for two grapevine-feeding leafhoppers and a shared parasitoid (Settle & Wilson 1990) and are demonstrated between two aphid species and their natural enemies (Müller & Godfray 1997).

Because all species are enmeshed in a web of natural enemies in the form of predators, parasites or pathogens, such dynamics are likely to be frequent. It is very unlikely that all the interacting organisms will respond in precisely the same way to climate change and thus, in direct consequence, existing enemy-victim interactions will become uncoupled and new ones established. This uncoupling or coupling of interactions by global climate change may have major impacts on species ranges and abundance. It is once again evident that such impacts would override, or greatly modify, changes arising directly from species' individual responses to climate change.

This study has shown that dispersal, horizontal and vertical interactions have major effects on the ranges and abundance of the species making up an assemblage. They modify or disrupt the links between climate and species' local presence or local abundance

and will thus distort predictions of range shifts under global warming (Pacala & Hurtt 1993). Dispersal allows species to maintain populations away from their physiological optima and to interact with species with different climatic preferences. Interspecific competition tends to reduce species' abundance but its effects are temperature- and species-specific so that a species may be reduced in part of its range but not in others. Interspecific competition may also shift species' optima and reduce species ranges. Natural enemies produce more complicated effects because they can reduce abundance in some parts of a species' range and yet increase it in others through indirect interactions with competitors. In consequence, a system including species interactions and dispersal can produce substantial unexpected and counter-intuitive effects even in a simple laboratory system involving no more than four interacting species. There is no reason to believe that similar 'unexpected' changes in range and abundance will not occur in natural populations, providing only that current distributions are maintained and modified by a combination of climate, dispersal (source-sink) dynamics and interactions with other species, and that species respond idiosyncratically to climate change.

In attempting to determine the likely effects of changes in climate, or indeed of climatically varying factors in general, on species ranges and distributions, we must start asking how important dispersal and species interactions are in natural and agricultural ecosystems, how intense they are and on what scales they operate. Although it is likely that the pole-ward movement of species ranges, frequently posited as the key prediction of global warming (Peters & Darling 1985; Davis & Zabiniski 1992; Woodward 1992; Parmesan 1996), will remain broadly correct, the detailed effects on species, including pests, disease vectors and species of conservation concern, will be problematic and some of these problems may be expensive. Models incorporating dispersal and species interactions will be required for adequate predictions of the potentially serious applied consequences of global warming.

Acknowledgements

We thank P. Nicholson for statistical advice and M. Wilbraham for editorial assistance. The research was supported by BBSRC grant 24/GER00620 to Professors J.H. Lawton & B. Shorrocks and is part of the BBSRC Biological Adaptations to Global Environmental Change programme.

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Received 11 July 1997; revision received 24 October 1997