

in other granulite-facies terrains, too. This is supported by the occurrence of Cl-enriched minerals in many granulite terrains worldwide^{16,27,28}. It is likely that salt will also be found in these granulites. Salt inclusions in mangeritic²⁹ and pantelleritic³⁰ rocks suggest that a salt melt or a highly saline brine may be involved in the generation and the crystallization history of water-undersaturated magmas typical for granulites, by lowering the melting temperature and decreasing the water activity at the same time. On the other hand, the short-lived, episodic occurrence of saline fluids in the lower crust as shown here precludes their general importance for processes that lead to the formation of granulites or melts of low water activities.

Minerals as rich in chloride as those reported here seem to be confined to rocks in which a granulite-facies mineralogy reacted with an aqueous fluid^{19,27,28}. Two exceptions are active hydrothermal systems^{31,32} and metamorphosed evaporite sequences³³. The only occurrence of salt (NaCl–KCl solid solution) in regionally metamorphosed rocks apart from the Lofoten rocks was reported¹⁵ from amphibolite-facies marbles from the Alps, which was attributed to fluid immiscibility. However, the involvement of evaporites in primary chloride enrichment is possible in this case as well.

Cl-rich amphiboles and biotites are found on all Lofoten Islands. Even though salt saturation was demonstrated for only three samples, the Cl-bearing hydrosilicates provide evidence for the desiccation process in the whole Lofoten crustal segment. Consequently, in these lower crustal rocks fluid was not stable and not present during a period as long as 1.4 Gyr apart from very short periods of infiltration. During these periods, the infiltrating fluid was totally consumed as long as the buffer capacity of the granulite-facies assemblages was sufficient. Therefore, fluids are not likely to be present for geologically long periods, particularly in tectonically stable, cratonic areas³⁴. If fluids are present, they would be expected to be in equilibrium with a salt, which can be tested by investigating lower crustal rocks using the technique we describe here. Our discovery of metamorphic salt in partially retrogressed granulites may not be related to its scarcity, but to preparational difficulties with the water-soluble salt. □

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Making mistakes when predicting shifts in species range in response to global warming

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Many attempts to predict the biotic responses to climate change rely on the ‘climate envelope’ approach^{1–3}, in which the current distribution of a species is mapped in climate-space and then, if the position of that climate-space changes, the distribution of the species is predicted to shift accordingly^{4–6}. The flaw in this approach is that distributions of species also reflect the influence of interactions with other species^{7–10}, so predictions based on climate envelopes may be very misleading if the interactions between species are altered by climate change¹¹. An additional problem is that current distributions may be the result of sources and sinks¹², in which species appear to thrive in places where they really persist only because individuals disperse into them from elsewhere^{13,14}. Here we use microcosm experiments on simple but realistic assemblages to show how misleading the climate envelope approach can be. We show that dispersal and interactions, which are important elements of population dynamics¹⁵, must be included in predictions of biotic responses to climate change.

We designed experiments in which the distribution of species

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along temperature gradients was first observed in the absence of dispersal and interactions between species. The outcome of these experiments represents the real climate envelope for the species on their own. We then determined how interactions and dispersal distort these envelope distributions by contrasting them with the distributions in clines where both factors acted, and also with those in clines where dispersal, but not interaction, was possible. The interactions studied were between two, three or four species. Finally, we examined the impact of global warming on distributions and abundances in clines subject to both dispersal and interactions.

Our model assemblage contained combinations of three fruitfly species, *Drosophila melanogaster* Meigen, *D. simulans* Sturtevant and *D. subobscura* Collin, and a parasitoid wasp *Leptopilina boulardi* (Barbotin, Carton & Kelner-Pillaut). These species overlap in southern Europe and the Mediterranean basin^{16,17}, and are thus an element of a naturally occurring assemblage. The parasitoid pre-

ferentially oviposits in *D. melanogaster*, in which it suffers little mortality, but it also attacks *D. simulans* and *D. subobscura*, causing high mortality even though the wasp larva rarely survives¹⁸.

We established experimental clines by linking eight cages in series and housing each pair of cages in separate incubators at different temperatures. Each group of four incubators accommodated up to five replicates (Fig. 1), and we set up two such groups. The incubators in a group were sequentially set to 10, 15, 20 and 25 °C ('cold' clines) or, simulating global warming¹⁹, to 15, 20, 25 and 30 °C ('hot' clines).

Competitive interactions in our clines markedly altered the distributions and abundances of all three species from those found in single-species clines (*D. simulans* and *D. subobscura* with one or two competitors; repeated measure analysis of variance (RMA), $F_{1,176} = 177.40$, $P < 0.0001$; *D. melanogaster*, *D. simulans* and *D. subobscura* with two competitors; RMA $F_{2,168} = 237.78$, $P < 0.0001$) (Fig. 2). The species responded differently, with significant interactions of species with number of competitors (two-species interactions RMA, $F_{2,168} = 68.7$, $P < 0.0001$; three-species interactions, $F_{2,168} = 27.32$, $P < 0.0001$). Competitive effects in two-species clines were unbalanced as *D. subobscura* reduced *D. simulans* abundances at only 10 and 15 °C (one-tailed $t = 2.944$, d.f. = 660, $P < 0.01$; $t = 5.33$, d.f. = 665, $P \ll 0.001$, respectively) but *D. simulans* significantly reduced *D. subobscura* abundances at 15 and 20 °C (one-tailed $t = 5.72$, d.f. = 636, $P < 0.001$; $t = 8.45$, d.f. = 636, $P \ll 0.001$, respectively) and also throughout the temperature range (Fig. 2). The proportionately greater reduction in *D. subobscura* at 15 than at 10 °C in this two-species interaction shifted the apparent optimum temperature for *D. subobscura* to 10 °C, away from 15 °C where it had been when *D. subobscura* was on its own. Competition in three-species clines reduced the range of *D. simulans*, which was driven extinct at 10 °C, and of *D. subobscura*, which was driven extinct at 25 °C (Fig. 2). Competition also significantly reduced the abundance of *D. simulans* at all other temperatures (in all cases, one-tailed $t > 9.0$, d.f. = 210, $P \ll 0.001$) (Fig. 2). Our clines show the same strong influence of both the identity and number of competing species that is known in nature^{7,9}. The importance of interactions is that if species respond idiosyncratically to climate change, as the available evidence overwhelmingly suggests^{20–23}, the identity and number of

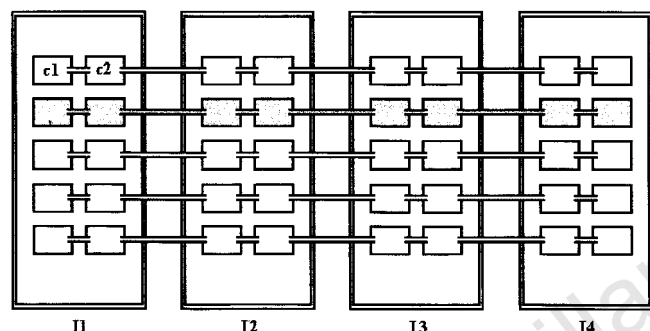


Figure 1 Experimental arrangement. The arrangement of perspex cages (100 × 150 × 300 mm) in one set of four incubators (I1–I4) showing an experimental series of eight cages linked together by tubing (shaded). Each pair of cages (for example, c1–c2) experiences the same temperature.

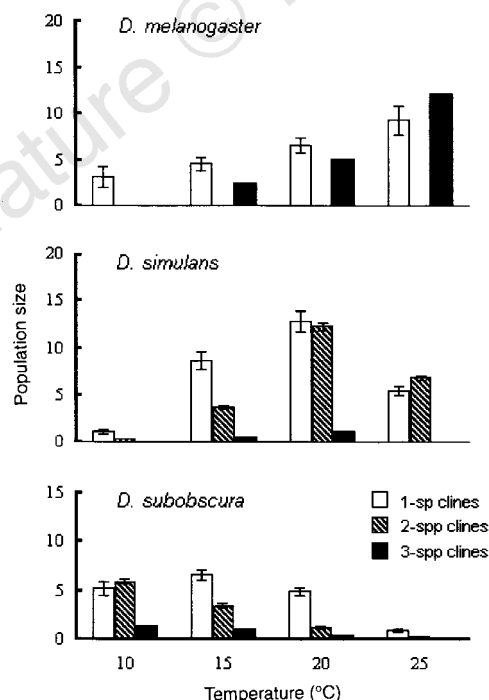


Figure 2 Comparison of *Drosophila* populations in single-species clines, two-species clines, and three-species clines. Two-species clines contained both *D. simulans* and *D. subobscura*, and three-species clines these two species as well as *D. melanogaster*. Error bars, ± 1 s.e. based on means of all measures.

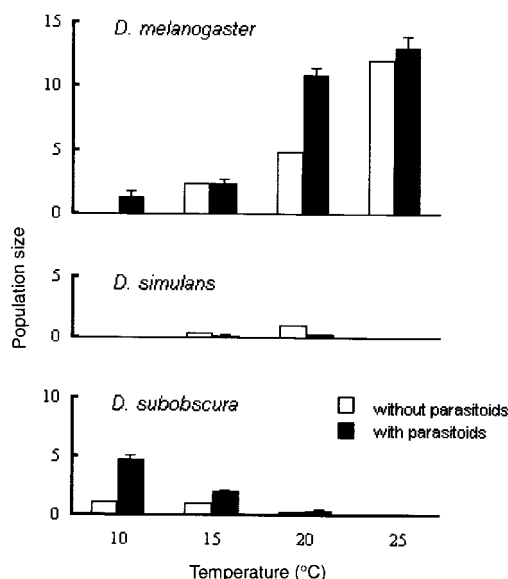


Figure 3 Comparison of *Drosophila* populations in cold three-species clines with or without *L. boulardi* parasitoids. Error bars, ± 1 s.e. based on means of all measures.

competitors will change, and competitive interactions will become uncoupled. Consequently, by ignoring these effects, the climate envelope approach risks making erroneous predictions of range and abundances after climate change.

Adding *L. boulandi* to our three-species clines significantly changed *D. subobscura* populations ($F_{1,180} = 12.40$, $P = 0.003$) and differentially affected the three *Drosophila* species (species and parasitoid interaction RMA $F_{2,216} = 6.09$, $P = 0.003$) (Fig. 3). At 20°C, apparent competition through the parasitoid²⁴ raised the abundance of *D. melanogaster* (one-tailed $t = 7.91$, d.f. = 411, $P \ll 0.001$) (Fig. 3) by decreasing the numbers of the other two *Drosophila*. In contrast, *D. simulans* became vanishingly rare throughout its range (Fig. 3). The wasp increased the abundances of *D. subobscura* at 10°C (Fig. 4) to values close to those reached by *D. subobscura* alone (Fig. 2). *L. boulandi* does not occur at 10°C, so this increase in *D. subobscura* must involve the parasitoid's suppression of competing *Drosophila* elsewhere in the cline, so favouring *D. subobscura* by reducing the numbers of competitors dispersing into the 10°C cages. These findings indicate that the wasp and the *Drosophila* species are involved in complex direct and indirect interactions like those between enemies and victims in natural situations^{8,10,24}. Uncoupling these interactions through divergent species responses to climate change¹¹ will greatly affect the ranges and abundances of species. It is once again evident that interactions will distort, or greatly modify, changes arising directly from climatic change.

In our clines, dispersal significantly altered distributions and abundances from the climate envelope distributions found in its absence (RMA $F_{1,126} = 6.15$, $P = 0.014$) (Fig. 4). Without dispersal, populations at extreme temperatures died out, *D. simulans* and *D. melanogaster* at 10°C and *D. subobscura* at 25°C, temperatures at which populations persisted in open clines. These temperatures are thus outside the physiological climate envelopes of the three species and must be classical sinks¹¹. Dispersal also altered abundances within distributions, lowering *D. melanogaster* and *D. simulans* populations at 20°C (one-tailed $t = 1.89$, d.f. = 216, $P < 0.05$; $t = 3.79$, d.f. = 184, $P \ll 0.001$, respectively) and 25°C (one-tailed $t = 3.34$, d.f. = 242, $P < 0.001$; $t = 1.03$, d.f. = 178, $P < 0.05$, respectively) and *D. subobscura* at 20°C (one-tailed

$t = 3.23$, d.f. = 222, $P < 0.001$). These results demonstrate that dispersal was an important determinant of both distributions and abundances in our model system, just as it is in nature^{14,15}, and markedly modified the simple climate envelope distributions. Dispersal frees local populations from direct dependence on local climate and allows populations to influence each other in metapopulation²⁵ and central-marginal²⁶ networks. Furthermore, as the spatial distribution of interdependent populations changes under global warming²⁷, the pattern and intensity of dispersal will also change. Thus simple climatic extrapolation¹⁻³ will not accurately predict the new ranges and abundances produced by climate change.

We tested the effects of global warming on clines containing interspecific competition and dispersal. Creating hot clines by raising overall cline temperatures by 5°C significantly altered the distribution and abundances of *D. subobscura* in both two-species and three-species clines (RMA $F_{1,30} = 10.44$, $P = 0.003$; $F_{1,54} = 9.49$, $P = 0.003$, respectively) (Fig. 5). Although *D. subobscura* maintained a small population at 25°C in cold clines, its range was reduced in hot clines because it was eliminated at 25°C (Fig. 5) by *D. simulans* or *D. melanogaster* dispersing into the lower temperature from the 30°C zone created in hot clines. Global warming thus drove *D. subobscura* out of the warm, low-latitude, part of its range in which its presence would be predicted from its range when alone. Furthermore, *D. subobscura* abundances within its reduced range also changed markedly under simulated global warming, with higher populations at 15°C in hot clines than at the same temperature in both two-species and three-species cold clines (one-tailed $t = 1.28$, d.f. = 244, $P < 0.05$; one-tailed $t = 5.75$, d.f. = 209, $P < 0.001$) (Fig. 5). This differential change inverted the relative abundances of the species at 15°C, with *D. subobscura* dominating allospecifics in hot clines. If pests were to behave in the same way, a currently unimportant population at 15°C might become economically important at the same temperature under global warming.

These results indicate that global warming can produce 'unexpected' changes of range and abundance in systems incorporating dispersal and species interactions. In the real world, interactions and feedbacks are likely to be even more complex than in our model

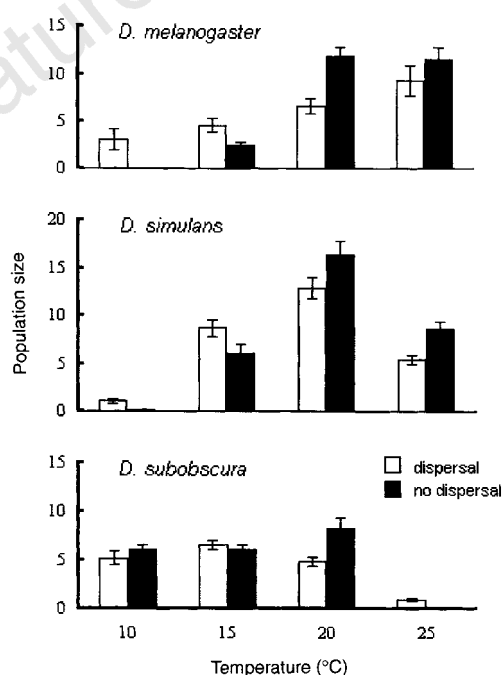


Figure 4 Comparison of *Drosophila* populations on their own, with and without dispersal. Error bars, ± 1 s.e. based on means of all measures.

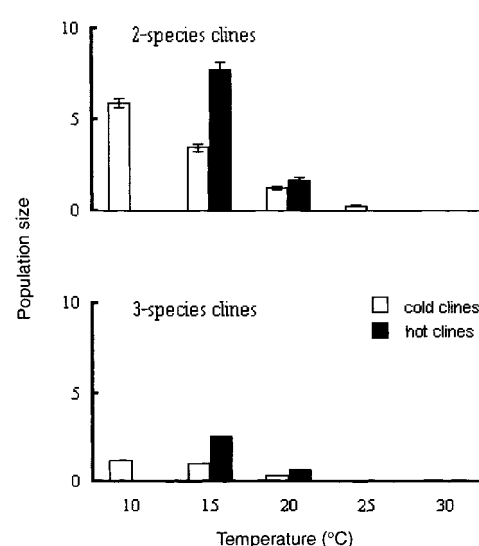


Figure 5 Comparison of *Drosophila subobscura* populations in cold and hot clines, either in two-species clines or three-species clines. Two-species clines include *D. simulans*; three-species clines also include *D. melanogaster*. The populations of *D. subobscura* at 15°C in hot clines are higher than in cold clines (the other species were unaffected). Error bars, ± 1 s.e. based on means of all measures.

system; hence, wherever dispersal and interactions operate in natural populations, we believe that global warming will provoke similar phenomena.

Our model system illustrates that horizontal (competition) and vertical (enemy–victim) interactions and dispersal markedly affect the distributions and abundances of species. Because these factors are omnipresent in nature, predicting changes in distribution and abundance under global warming by extrapolation of the climate envelope may lead to serious errors. Prediction using climate envelopes might be seen as a ‘null model’, but we predict that it will be frequently rejected given the accelerating changes initiated by global warming. Models incorporating dispersal and species interactions will be required for adequate predictions of the potentially serious applied consequences of global warming on conservation and medical and agricultural pest control. □

Methods

Cline construction and maintenance. The eight Perspex cages (each 100 × 150 × 300 mm) of a single cline were connected together, and to the pair in the neighbouring incubators, by tubing of 30 mm diameter which restricted adult dispersal between temperature zones to approximately 6% per day. Each cage held six tubes containing 50 ml standard cereal-based *Drosophila* medium which were replaced sequentially with fresh tubes. The reprovisioning frequency increased with temperature so the *Drosophila* at the four different temperatures received the same amount of food per generation. Honey was provided as food for adult *L. bouhardi* parasitoids. Nine single-species clines, three replicates for each species, were initiated by adding 25 male and 25 female flies to all eight cages of a cline, and three two-species clines were started similarly by adding 50 *D. simulans* and 50 *D. subobscura* to every cage. Five three-species clines were started with 50 flies of each of the three species in every cage, and four-species clines were started by adding wasps to five additional, four-week-old, three-species clines at the rate of 10% of the pre-existing *Drosophila* adults in each cage irrespective of species. Closed clines were created from established two-species clines by blocking the tubes between incubators with porous foam bungs, and hot clines were created by raising by 5 °C the temperatures of existing cold clines.

Estimating populations. The populations of adult *Drosophila* were assessed by weekly standardized partial counts of each cage. These counts and the real number of adult flies, irrespective of species, are closely related (no. of adults = $320 + (9.88 \times \text{count})$; $r = 0.814$, $P < 0.001$). Because *D. melanogaster* and *D. simulans* 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 withdrawn from each cage. 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.

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Automatic alerting does not speed late motoric processes in a reaction-time task

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When an irrelevant ‘accessory’ stimulus is presented at about the same time as the imperative signal in a choice reaction time-task, the latency of the voluntary response is markedly reduced¹. The most prominent cognitive theories agree that this effect is attributable to a brief surge in arousal (‘automatic alerting’), but they disagree over whether the facilitation is localized to a late, low-level motoric process² or to an earlier stage, the process of orienting to and then perceptually categorizing the reaction stimulus^{3,4}. To test these alternative hypotheses, we used the onset of the lateralized readiness potential (a movement-related brain potential) as a temporal landmark to partition mean reaction time into two time segments. The first segment included the time required to perceive the visual stimulus and decide which hand to react with; the second included only motoric processes. Presentation of an irrelevant acoustic stimulus shortened the first interval but had no effect on the second. We therefore rejected the motoric hypothesis.

The evidence that led Sanders² to propose a late motoric locus for the speeding of reaction time by automatic alerting was based on Sternberg’s⁵ additive factors method. These studies showed that the effects of task-irrelevant accessory stimuli do not interact with the effects of variables assumed to influence perceptual or decision processes, but they do interact with effects involving low-level motoric processes, such as tonic muscle tension. The additive factors method involves many assumptions that are difficult to verify, but the motoric hypothesis has also been supported by neurophysiological research. These experiments showed that the motoric processes underlying certain reflexes can be facilitated by accessory stimulation^{6,7}. However, more recent research⁸ indicates that the pattern of facilitation is quite different for voluntary and