Climate and species' range

SIR — Though physical evidence of global warming continues to accumulate[1–3], it is less clear whether the predicted biological consequences are occurring. The key prediction is that species' ranges should move both polewards in latitude and upwards in elevation[4–7]. To date, published claims of species' range shifts have extrapolated regional patterns from observations on a small part of a species' range. These studies all assume that changes in population density at a point[8–11] or movement of a boundary at one latitudinal end of a range[12,13] can be unambiguously interpreted as range shifts, rather than as merely local density changes, range expansions or contractions. Reliable evidence for range shifts must include examination of a species' entire range. I report here the first study to provide evidence of the predicted range shifts.

I censused populations of Edith's checkerspot butterfly (*Euphydryas editha*) throughout its range, and found significant latitudinal and altitudinal clines in population extinctions at sites undegraded by human activities, producing a northwards and upwards shift in the species' range. I documented extinction and persistence in 151 previously recorded populations of this butterfly, and excluded from the data set all sites where butterfly habitat was degraded and no longer usable by this species, including sites altered by human activities such as land-clearing, construction, overgrazing and introduction of exotic plants. Dense populations of this butterfly have persisted even in moderately disturbed (grazed or logged) sites, if enough suitable host plants remain.

Edith's checkerspot occurs as a mosaic of sedentary, discrete populations with intermittent colonizations, extinctions and re-colonizations[14–17]. At equilibrium, the rate of extinction should be constant and equal to the rate of colonization and recolonization. Climate warming should cause net extinctions to increase in the south and at low elevations and to decrease in the north and at high elevations. It is the net extinction rate that is of interest in the context of global warming .

I found a striking latitudinal cline in net extinction rates (Figs 1, 2*a*; $P = 0.009$). Sites where previously recorded populations still existed were on average 2° further north than sites where populations were extinct. Populations in Mexico were four times more likely to be extinct than those in Canada. Net extinctions also significantly decreased with altitude (Figs 1, 2*b*, $P = 0.04$). Populations above 2,400 m were significantly more persistent than those at all lower elevations ($P = 0.016$). Although a predicted result of climate warming is an increased extinction rate at the very lowest elevations, no such trend appears in the data.

Any factor affecting recolonization might vary systematically and produce the observed clines in net extinctions. However, recolonization was rare over long time periods and over a large portion of the range. Among 31 populations that were repeatedly visited after a recorded extinction, a maximum of 13 % were recolonized over a 30-year period. Further, the degree of isolation of populations (which would directly affect recolonizations) was historically similar at the extremes of the range. Over the past century, records documented 0.32 populations per 1,000 km^2 in mainland Canada and 0.87 populations per 1,000 km^2 in Mexico (density estimates restricted to the species range in each area). Recent human destruction of butterfly habitat and extirpation of populations could, by increasing isolation, reduce recolonization rates and inflate net extinction rates even in undegraded habitats. However, habitat degradation was latitudi-

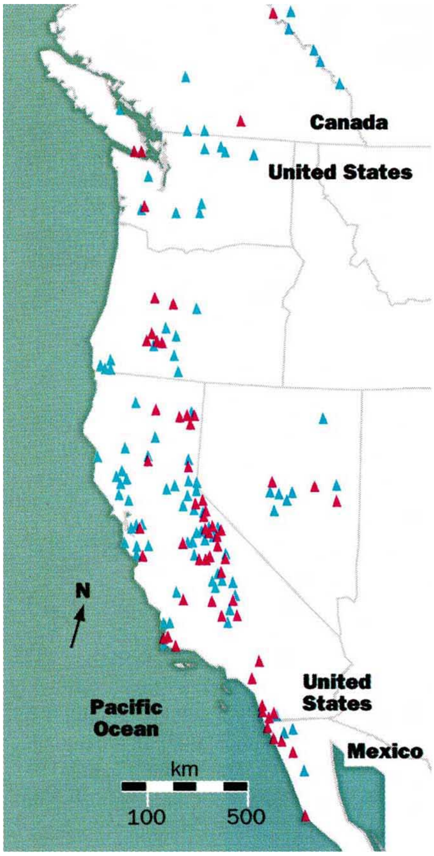

FIG. 1 Map of censused sites. Extinct populations are shown by red triangles, present populations by blue triangles. Because of space limitations, three censused populations in Colorado are not shown but are available from the author on request. I compiled historical population records from museum specimens, private collections and researchers' field notes. Between 1992 and 1996, I censused 115 sites with historical records to classify their current status as extinct or intact, and for 36 additional sites determined current status using information provided by K. Agnew, G. Austin, D. Bauer, D. A. Boughton, J. Brown, P. Chai, P. R. Ehrlich, J. Emmel, G. Gilchrist, C. Guppy, S. P. Harrison, D. Kinsinger, N. Kondla, A. Launer, S. O. Mattoon, A. R. Moldenke, D. D. Murphy, O. Shields, J. Shepherd, M. C. Singer, W. L. Swisher, C. D. Thomas, D. Vasco and R. R. White. I controlled for time elapsed since the initial record by sampling sites within each geographic region that represented the range of historically recorded dates. I did not census sites that: (1) could not be unambiguously located from the records; or (2) were degraded by loss of usable host plants. I censused all butterfly life stages at each included site, and considered sites less than 5 km apart to be part of the same population[17]. I visited sites during the flight season and searched for adults in suitable habitat within the general vicinity of the historical record (resulting in areas of 0.25 km^2 to 24 km^2 searched). If I found no adults, I searched potential host plants for egg clusters and larval webs, checking 100% of the host plants if the habitat was small. In larger habitats, I searched approximately 500 host plants or 50% of the plants present, whichever was smaller. More than 50% of the time that I found populations, I discovered an egg mass or larval web within the first 30 plants.

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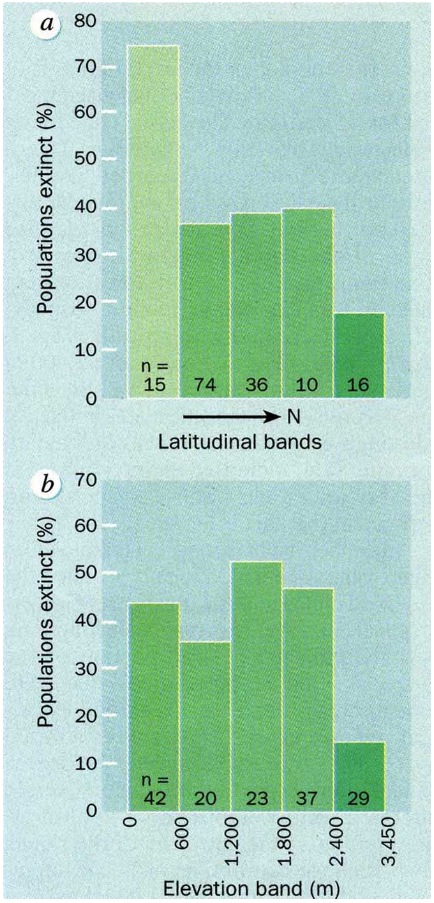

FIG. 2 Proportions of extinct populations in five latitudinal (*a*) and elevational (*b*) bands. a, Analysis with latitude as a continuous variable: Mann–Whitney rank test comparing latitudes of the two state groups, extinct and persistent (mean extinct group = 38.5°N, mean present group = 40.6°N, tied Z-value = −2.60, n=151, P = 0.009). Analysis with latitude as a categorical variable: to test for significant break points, I analysed extinctions by latitudinal bands with a 5 × 2 contingency table (5 levels of latitude evenly divided from 30° N to 53° N; 2 levels of status, extinct or present) using a log-likelihood ratio test: G = 15.75, d.f. = 4, P = 0.003. I performed post-hoc sub-divided analyses to test for significant differences among adjacent bands. Latitudinal bands of different shades of green are significantly different from each other at $P \leqslant 0.05$. *b*, Analysis with altitude as a continuous variable: Mann–Whitney rank test on altitude between the two state groups, extinct and persistent (mean extinct group = 1,280 m, mean present group = 1,585 m, tied Z-value = −2.05, n=151, P = 0.04). To test the significance of an apparent break point at 2,400 m, I analysed extinctions by elevational bands with a 5 × 2 contingency table (5 levels of elevation; 2 levels of status, extinct or present) using a log-likelihood ratio test: G = 12.16, d.f. = 4, P = 0.016. I performed post-hoc sub-divided analyses to test for significant differences among subsets of the elevational bands. Elevational bands of different shades of green are significantly different from each other at $P \leqslant 0.05$.

nally symmetrical: low at the extremes of the range, with about 20 % of previously recorded sites degraded in Mexico (n = 10) and 17 % in mainland Canada (n = 24), and higher for all other latitudes.

Thus, it is unlikely that the observed latitudinal cline in net extinctions was caused by differences in initial population isolation or subsequent land-use changes. This result, in conjunction with earlier detailed studies of climate-caused population extinctions in this butterfly[14,18–21], suggests climate change as the cause of the observed range shift. However, conclusive evidence for or against the existence of the predicted biological effects of climate change will come, not from attempts to analyse all possible confounding variables in single studies such as this one, but from replication of this type of study with additional taxa in other regions. Until this has been done, the evidence presented here provides the clearest indication to date that global climate warming is already influencing species' distributions.

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Base-rate errors and rain forecasts

SIR — The nature of the base-rate error - the neglect of prior probabilities in judging the probability of events — has recently been discussed[1]. Yet despite its potentially serious implications for many real-life issues, the base-rate error has yet to achieve wider recognition. I would therefore like to draw to readers' attention the effect of the base-rate error on a familiar (indeed, notorious) dilemma — that of how to respond to weather forecasts.

It seems obvious that decisions affected by the weather (going for a walk, for example) are best made by putting one's faith in the most accurate forecast available. Surprisingly, however, the base-rate effect can make this a sub-optimal approach.

The UK Meteorological Office's 24-hour forecasts of rain currently achieve around 83 per cent accuracy, while the probability of rain on the hourly timescale relevant to walks is around 0.08. The table reveals the impact of the base-rate error in the interpretation of forecasts of rain. With forecast accuracies of 83 per cent, one might expect that a forecast of rain during the one hour walk would be correct 83 per cent of the time. However, the hourly base-rate of rain in the United Kingdom is so low that forecasts of rain are more than twice as likely to be wrong as right: from the table, the probability of rain, given a forecast of rain — that is, $P(\text{rain}|\text{forecast of rain})$ — is 66/222=0.30, whereas $P(\text{no rain}|\text{forecast})$=156/222 =0.70

THE VARIOUS OUTCOMES OF FORECAST AND WEATHER OVER 1,000 1-HOUR WALKS

	Rain	No rain	Sum
Forecast of rain	66	156	222
Forecast of no rain	14	764	778
Sum	80	920	1,000

This result suggests that those who ignore Meteorological Office forecasts may fare better than those who abide by them. A decision-theoretic analysis shows that this is indeed the case. Let R, F and W represent the events of rain falling during the walk, rain being forecast, and going on the walk, respectively. Then

$$P(\mathrm{R}\&\mathrm{W})=P(\mathrm{R})[P(\mathrm{F}|\mathrm{R}).P(\mathrm{W}|\mathrm{F})+P(\sim\mathrm{F}|\mathrm{R}).P(\mathrm{W}|\sim\mathrm{F})] \tag{1}$$

with similar expressions for the three other permutations of R, W and negations ~R, ~W. The forecasting accuracy is captured by $P(\mathrm{F}|\mathrm{R}) = A$ and $P(\mathrm{F}|\sim\mathrm{R}) = B$, while the responses to the forecasts are represented by $P(\mathrm{W}|\mathrm{F}) = m$ and $P(\mathrm{W}|\sim\mathrm{F}) = n$; (1) then becomes

$$P(\mathrm{R}\ \&\ \mathrm{W}) = P(\mathrm{R})[Am + (1-A)n] \text{ etc} \tag{2}$$

Let L_{tot} represent the loss function, comprising the losses resulting from the outcomes of the various decisions:

$$L_{\text{tot}}=L_{00}P(\mathrm{R}\&\mathrm{W})+L_{11}P(\sim\mathrm{R}\&\sim\mathrm{W})+L_{10}P(\sim\mathrm{R}\&\mathrm{W})+L_{01}P(\mathrm{R}\ \&\sim\mathrm{W}) \tag{3}$$

Optimal strategies minimize L_{tot}. Substituting from equation (2), and keeping only terms in m and n,

$$L_{\text{tot}}\sim m\{P(\mathrm{R})AK-P(\sim\mathrm{R})B\}+n\{P(\mathrm{R})(1-A)K-P(\sim\mathrm{R})(1-B)\} \tag{4}$$

$$\text{where } K = (L_{00}-L_{01})/(L_{11}-L_{10}) \tag{5}$$

represents the relative losses resulting from the outcomes in equation (3). With $A = 0.83$, $B = 0.17$, $P(\mathrm{R}) = 0.08$, we find that basing our decision on Meteorological Office forecasts (m=0, n=1) gives $L_{\text{tot}}\sim (K-56)/74$, whereas ignoring forecasts of rain ($m = n = 1$) gives $L_{\text{tot}} \sim (K-12)/13$. Thus unless one is particularly concerned about getting wet ($K > 2$), the base-rate effect makes disregard of forecasts of rain the optimal strategy.

Similar reasoning also reveals that, contrary to popular belief, always carrying an umbrella is a sub-optimal strategy unless one is morbidly afraid of getting wet ($K > 56$). Indeed, unless $K > 12$, the base-rate effect makes even insouciant optimism a better strategy.

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